

Eira Ihalainen

Experiments on Defensive Mimicry

Linkages between Predator Behaviour
and Qualities of the Prey







“It’s not about big ideas. It’s... It’s work. You’ve got to chip away at a problem.”

-from the movie Proof

ABSTRACT

Ihalainen, Eira

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Defensive mimicry is divided into Batesian mimicry, where an edible prey species mimics a warning signal of an aposematic (unprofitable) model species to avoid predation, and Müllerian mimicry, where aposematic species share a warning signal. Müllerian co-mimic species are assumed to have a mutualistic relationship because they share the mortality due to sampling by predators which are learning to avoid their signal. Batesian mimics are assumed to increase model mortality. Consequently, Batesian and Müllerian mimicry systems are expected to have different evolutionary trends but some of their characteristics can overlap in nature. Theoretical work suggests that because unprofitability or profitability of prey is not absolute, this could result in intermediate forms of mimicry between mutualistic and parasitic systems. In this thesis I focus on the relationship between mimetic prey with varying defences. Great tits (*Parus major*) foraged on artificial prey items in laboratory experiments which tested how the different qualities of mimetic prey such as warning signals, levels of chemical defence and abundance affect the mortality of the prey via avoidance learning, memory and generalisation of the predators. The results show that variation in the level of defence can interact with signals but it does not affect the co-mimic relationship; abundance of the mimetic prey can even offset the parasitic effect of fully edible Batesian mimics. Simple facilitation of predator learning did not seem to select for signal similarity in Müllerian mimicry but generalisation by experienced predators was important. Because predator behaviour in relatively simple experiments produced complex mimicry dynamics, defensive mimicry may be more diverse a phenomenon than currently understood.

Keywords: aposematism; Batesian mimicry; discrimination; learning; Müllerian mimicry; memory; predator psychology; quasi-Batesian mimicry; warning colours

Eira Ihalainen, University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, FI-40014 University of Jyväskylä, Finland

Author's address Eira Ihalainen
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland
E-mail eiraihal@jyu.fi

Supervisors Professor Johanna Mappes
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland

Docent Leena Lindström
Department of Biological and Environmental Science
P.O. Box 35
FI-40014 University of Jyväskylä
Finland

Reviewers Dr. Candy Rowe
University of Newcastle
Henry Wellcome Building for Neuroecology
Framlington Place
Newcastle upon Tyne
NE2 4HH
U.K.

Professor Graeme D. Ruxton
Graham Kerr Building
University of Glasgow
G12 8QQ
UK

Opponent Professor Thomas N. Sherratt
Department of Biology
Carleton University
1125 Colonel By Drive
Ottawa
ON K1S 5B6
Canada

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on five original articles, which will be referred to by their Roman numerals I-V in the text. I am the first author of articles II, IV and V and have contributed significantly to planning, data collection and analyses as well as writing of each article. Authors after the first author are in alphabetical order.

- I Ham, A. D., Ihalainen, E., Lindström, L. & Mappes, J. 2006. Does colour matter? The importance of colour in avoidance learning, memorability and generalisation. *Behavioral Ecology and Sociobiology* 60: 482-491.
- II Ihalainen, E., Lindström, L. & Mappes, J. 2006. Investigating Müllerian mimicry: predator learning and variation in prey defences. *Journal of Evolutionary Biology*: In press. doi:10.1111/j.1420-9101.2006.01234.x.
- III Rowland, H. M., Ihalainen, E., Lindström, L., Mappes, J & Speed, M.P. Mutualism rules the mimicry world? (Manuscript)
- IV Ihalainen, E., Lindström, L., Mappes, J. & Puolakkainen, S. Butterfly effects in mimicry? Unpredictable relationship between Müllerian co-mimics. (Submitted)
- V Ihalainen, E., Lindström, L., Mappes, J. & Puolakkainen, S. Can experienced birds select for Müllerian mimicry? (Manuscript)

1 INTRODUCTION

Avoiding predation is essential to an individual's survival and fitness, and animals have evolved a variety of behavioural and morphological anti-predator strategies (see Ruxton et al. 2004, Caro 2005 for recent reviews). Aposematism and defensive mimicry are mainly studied as morphological defences against predation although behaviour can be a part of these strategies as well (see Howarth et al. 2001, Srygley 2004).

1.1 Aposematism

Aposematic species are toxic, distasteful or otherwise unprofitable as prey and they advertise this unprofitability (i.e. secondary defence) to potential predators via warning signals. Warning signals can be sounds or odours but the best known examples are conspicuous visual signals i.e. bright warning colours (see e.g. Mallet et al. 1996, Summers & Clough 2001, Mappes et al. 2005 for colourful examples). The main body of warning signal research has sought to understand why aposematic animals are conspicuous rather than cryptic (camouflaged) and how such signals evolve given their higher detectability to predators. Because warning signals are aimed at predators, several benefits of signalling have been found by studying the reactions of predators towards aposematic prey.

Avian predators have been shown to possess unlearned aversions to typical warning colours e.g. black combined with red and yellow (see review by Schuler & Roper 1992, Mastorta & Mench 1995, Lindström et al. 1999). Such avoidance might also be a result of novelty effects, such as neophobia (Schlenoff 1984) or dietary conservatism (Marples et al. 1998, Thomas et al. 2003). Higher visibility of conspicuous signals compared to cryptic appearance can also be compensated for by faster avoidance learning of predators (Sillén-Tullberg 1985a, Roper & Wistow 1986, Roper & Redston 1987) and better memorability (Roper & Redston 1987, Roper 1994). There is also evidence that typical warning colours are superior in promoting avoidance of unpalatable prey (Mappes &

Alatalo 1997b) even irrespective of whether they are conspicuous against their viewing background or not (Sillén-Tullberg 1985b).

It has also been suggested (Wallace 1867, Fisher 1958) that aposematic prey species benefit from bright coloration simply because it makes them most distinguishable from edible prey that are typically camouflaged (Sherratt & Beatty 2003, see also Jansson & Enquist 2003). Experimental studies on this possibility are scarce since in experiments where predators had to discriminate distasteful prey from edible prey, unpalatability has been signalled by typical warning colours without the inverse situation (see Gagliardo & Guilford 1993, Rowe & Guilford 1996) (e.g. yellow signals palatability and green signals unpalatability), or with colours (e.g. green and blue) that are not typical warning colours (e.g. Gittleman & Harvey 1980).

1.2 Defensive mimicry

Defensive mimicry where two or more species' warning signals resemble each other is a long known phenomenon. Henry Bates described mimetic systems where edible species mimic aposematic species and suggested that this could be a way for the edible species to avoid predation (Bates 1862). Fritz Müller was the first to suggest why aposematic species could benefit from resembling each other (Müller 1879).

1.2.1 Batesian mimicry

In Batesian mimicry (Bates 1862) a palatable mimic species and an unpalatable model species are protected because predators learn to avoid their signal due to the unprofitability of the model. The mimic 'parasitises' this avoidance: the predators may mistake the mimic for the model and reject it by sight (Brower 1958b, Brower et al. 1960, Boyden 1976) but the mimics (being edible) do not contribute to predators' avoidance learning. Therefore, Batesian mimics should only occur sympatric to their models (Bates 1862, Pfenning et al. 2001). It is also assumed that mimics should be rare compared to their models (Bates 1862, Fisher 1958, Sheppard 1959, but see Brower 1960, Nonacs 1985). This is because the edible mimics weaken the predators' association between the warning signal and unpalatability slowing down avoidance learning or otherwise encouraging attacks on the signalling prey. The models thus suffer highest mortality when the mimics are common but so do the mimics themselves (Lindström et al. 1997). Because the mimic is an edible 'cheat' it is assumed that predators should discriminate carefully between models and mimics since by rejecting the mimic they lose a potential prey species. Therefore, the mimics would be under strong selection to evolve accurate resemblance of the models (e.g. Fisher 1958, Huheey 1988, Mappes & Alatalo 1997a, but see e.g. Edmunds 2000). Also, since the mimics are best protected when rare compared to their model species, Batesian mimics could have an evolutionary tendency towards

signal polymorphism whereby the mimic species has several signal morphs resembling different models (see e.g. Huheey 1988, Ruxton et al. 2004 pp. 151-152) but such polymorphisms need not to be a general rule for Batesian mimics (as noted by e.g. Carpenter & Ford 1933, Joron & Mallet 1998).

1.2.2 Müllerian mimicry

In Müllerian mimicry, both (or all) co-mimics are unpalatable, and according to the original theory they benefit from their common warning signal by sharing the costs of 'predator education'. Müller (1879) assumed that inexperienced predators need to learn about different warning signals separately, and that they kill a certain amount individuals to learn to avoid a certain signal. He proposed that if prey species share a warning signal they decrease their per capita mortality that is due to sampling by naïve predators. The relationship of the co-mimic species is expected to be mutualistic (e.g. Fisher 1958); although the benefits of mimicry may not be equal to the mimetic counterparts, increasing abundance of any of the co-mimics is still beneficial to all (Müller 1879, Mallet 1999). Therefore, a tendency towards monomorphism in the warning signal has been attributed to classical Müllerian mimicry (see e.g. Turner 1987, Huheey 1988, Joron & Mallet 1998). On the other hand, because it is in the predators' interest to avoid aposematic species, it has been suggested (e.g. Fisher 1958) that Müllerian co-mimics would not be strongly selected for precise resemblance and some inaccuracy in the signals would be 'tolerated' (Huheey 1988).

1.2.3 The question of intermediate mimicry

Inedibility or edibility of the mimetic counterparts it thought to cause very different dynamics between the mimetic species in Batesian and Müllerian mimicry (parasitism vs. mutualism) and consequently also different evolutionary trends i.e. signal polymorphism vs. monomorphism (see Turner 1987, Mallet 1999 for discussions about advergence vs. convergence). However, it has long been acknowledged that inedibility or edibility are not absolute qualities (due to e.g. hunger of the predators) and knowing whether a mimetic system is Batesian or Müllerian could therefore be difficult, or that there could be a continuum of intermediate forms of mimicry between 'pure' Müllerian and Batesian extremes (see Marshall 1908).

The theoretical work examining the possibility of intermediate mimicry in detail is more recent and its foundations are based on the observation that chemically defended (toxic or distasteful) species differ in their levels of defence both within (e.g. Brower et al. 1968, de Jong et al. 1991, Eggenberger & Rowell-Rahier 1992) and between species (e.g. Brower 1958a, Brower et al. 1963, Bowers & Farley 1990). The question of intermediate mimicry is partly semantic and depends on how mimetic systems are classified (see Benson 1977, Owen & Owen 1984). Still, if Müllerian co-mimics are not equally defended it is relevant to ask whether the difference could affect predator behaviour and the dynamics

of mimicry. This question challenges the current understanding of mimetic systems and has been studied mostly by means of mathematical modelling.

Some computer simulations consider the effects a moderately defended co-mimic could have on mimetic relationships due to learning and forgetting by predators (Huheey 1976, Owen & Owen 1984, Turner et al. 1984, Speed 1993, Turner & Speed 1996, see also MacDougall & Dawkins 1998, Mallet 1999, Speed 1999a, Speed & Turner 1999) whereas others concentrate on state-dependent and optimal foraging (Kokko et al. 2003, Sherratt et al. 2004). Different learning and forgetting rules can produce a situation where a simulated predator attacks a mixture of highly and moderately defended co-mimics more often than highly defended prey alone (see Speed & Turner 1999) and this is also directly assumed in a simple number based model (Speed 1999a). Such a situation resembles Batesian mimicry; increasing the abundance of the less defended co-mimic increases the mortality of the other (but see Owen & Owen 1984, Speed 1999b), hence the name quasi-Batesian mimicry (Speed 1993). However, as discussed by Turner & Speed (1996), how predators actually learn when the same signal indicates different prey qualities is poorly understood (see also Joron & Mallet 1998 and references therein).

Since unpalatability is a 'Müllerian trait', variation in it has been seen as a problem of Müllerian theory and accordingly the question of intermediate mimetic systems has been approached from the Müllerian end. The frameworks of thought for Batesian and Müllerian mimicry also differ in aspects other than edibility or inedibility of the mimics. Current understanding of Batesian mimicry emphasises the importance of the model-mimic ratio (e.g. Brower 1960, Huheey 1980, Nonacs 1985, Lindström et al. 1997) whereas the total abundances of models and mimics have received only some theoretical attention (Owen & Owen 1984, Speed 1999a, Speed & Turner 1999). In contrast, Müllerian mimicry is easily understood as a 'strength in numbers' scenario where the absolute numbers or total density of the co-mimics produce the mimetic benefit (Müller 1879). These two frameworks need not to be radically different (see Results and discussion) but the different emphasis for the two systems does complicate the approach to possible intermediate dynamics.

Furthermore, the importance of relative and absolute abundances of different prey types to the evolution of mimicry can be confused because terms like 'frequency dependent' and 'density dependent' can be used to describe within-population processes but also between-species phenomena. For example, the spread of a warning coloured morph within a species can be 'frequency dependent' (see e.g. Mallet & Singer 1987) but the effect of the model-mimic ratio in Batesian mimicry can also be called a 'frequency dependent' relationship between species (Pfenning et al. 2001, but see Turner 1987).

1.3 Aims of the study

In this thesis I study aposematism and defensive mimicry with laboratory experiments that concentrate on the learning, memory and generalisation of avian predators. Paper I begins with testing whether typical warning colours aid the predators' discrimination of unpalatable and palatable prey when they signal distastefulness rather than edibility, or whether it is sufficient that defended prey have a distinct appearance. I have been especially interested in the benefits of warning signal mimicry and whether varying defences of the mimetic prey could affect mimetic relationships and result in intermediate types of mimicry.

To study the mechanisms behind Müllerian mimicry, the experiments in papers I and II test whether predators' avoidance learning is faster for uniform than for variable signals. In paper II I also test whether variation in the level of defence of the mimetic prey affects predator learning in comparison to uniformly high or low levels of defence (i.e. distastefulness). Paper III examines the effect of total numbers of mimetic prey in both Müllerian and Batesian mimicry. Papers I, II, IV and V also touch upon predator memory and its effects on the survival of defended prey. Signal generalisation is discussed in all the sub-studies, particularly in papers I and V where the predators have been trained to avoid certain warning signals before they are presented with somewhat different looking prey. Paper IV is tied back to the general question of the warning signal design of aposematic prey by showing that signal design of the prey species can affect mimetic relationships. Paper V asks whether experienced predators could select for Müllerian mimicry. By addressing these topics I seek to shed light on the dynamic nature of mimetic systems that are based on aposematism. I hope to provide empirical data that will help in understanding the interplay of predator psychology, mortality of defended prey and the evolution of defensive mimicry.

2 MATERIAL AND METHODS

All experiments were conducted at the Konnevesi Research Station in central Finland in the autumn and winter (between September and April) during years 2001-2005. In all the experiments, wild Great tits (*Parus major*) were used as predators of artificial prey in a laboratory.

2.1 Predators

Great tits are suitable predators for laboratory studies of this kind as they are visual hunters and common in central Finland in the winter time outside their breeding season. Great tits are also easy to capture from gardens, and are generalist predators with a varied diet (see Royama 1970) which is a likely reason why they are easy to train to handle artificial prey. Great tits also seem to behave naturally in laboratory conditions. The birds were trapped from feeding sites using a simple trap containing peanuts as bait. They were ringed for identification and released back into the wild at the site of their capture after the experiments. Each bird was kept individually in a plywood cage indoors. Food and fresh water was available *ad libitum* except prior to the experimental trials when the birds were food deprived to ensure motivation to forage on the artificial prey. The birds were captured and used in the experiments by permissions from Central Finland Regional Environment Center and Experimental Animal Committee of the University of Jyväskylä.

2.2 Prey

Many characteristics of prey that are of interest in mimicry studies such as their warning signals, taste and abundance are easy to manipulate by using artificial prey items. Since wild-caught predators do not have prior experience on artificial prey items, it is possible to use adult birds in experiments that focus on

predator learning and on how the characteristics of the prey affect it. Some effects of co-evolution between predators and prey can also be excluded by using artificial prey (Lindström 1999). Edible alternative prey were presented in all experiments that included a realistic discrimination task whereby the birds had to learn to avoid aposematic prey and forage on the edible prey.

Experiment I concentrated on discrimination of unpalatable and palatable prey that had either typical warning colours (red yellow and orange) or typically cryptic grey appearance. The prey items were pieces of peanut glued under squares of paper (1 cm × 1 cm). The peanuts of the unpalatable prey were soaked in a solution of water and chloroquine phosphate (malaria drug Heliopar, henceforth chloroquine), which gave them a bitter taste aversive to the birds. The prey was presented to the birds on a white plywood tray with small evenly spaced wells drilled into it. The paper prey items were placed on the tray so that the peanut glued on the underside was hidden inside the wells (Figure 1). The trays with the prey were presented to the birds in an experimental box made of plywood and sized 50 cm × 50 cm × 70 cm.

In the remaining papers II-V, which concentrate on the dynamics of mimicry, black-and-white prey were used. These prey items were small pieces of almond glued between two 8 mm × 8 mm pieces of white paper. One black symbol was printed on both sides of the paper shell of the almond. The symbols that acted as warning signals of mimetic prey were conspicuous (see below and Figure 2). Aposematic prey was made either highly or moderately unpalatable by soaking the almond in a solution of water and of chloroquine; a high concentration of chloroquine resulted in high unpalatability and a lower concentration in moderate unpalatability. Edible prey items contained untreated almond. The pieces of almond were completely hidden inside the paper shell and the birds could not discern the taste of the almond without tasting it. The black-and-white prey was presented to the birds on the floors of indoor aviaries (Figure 3). The floors were covered with white paper sheets with black cross symbols printed on them. Cryptic prey items were edible and considerably less visible than the mimetic prey; their black cross symbol matched that of the viewing background (Figure 2).

Prior to the experiments the birds were trained in a stepwise manner to handle the artificial prey and familiarised with the boxes (I) or aviaries (II-V) so that they would readily start foraging in the actual trials. Blank white prey was used in training (with the exception of three additional cryptic prey items per individual in sub-studies II-V).

2.3 Testing 'predator psychology' and prey mortality

In all the experiments the general outline was to present the great tits with assemblages of prey with different qualities and observe predator behaviour, particularly learning, memory and generalisation which sought to address how the qualities of the prey affected their mortality.

2.3.1 Specific colours as warning signals

To test whether typical warning colours enhance avoidance learning only when associated with unpalatability, great tits in sub-study I were trained individually to discriminate edible and distasteful prey when unpalatability was signalled by red, yellow or both red and yellow (i.e. variable signal) and palatable prey was grey. In the inverse situation unpalatability was signalled by grey, and palatable prey was yellow or both red and yellow simultaneously. Twenty trays containing four prey items (colours according to the treatment) were presented in succession to teach the birds the discrimination task. The prey items on each tray were given a score that marked the order in which they were attacked. Mean scores of the unpalatable prey at the end of training were used to assess the 'level of learning' of the birds in the different treatments.

2.3.2 Benefits of mimicry and effects of unpalatability levels

To assess the benefits of a shared signal in the experiment with colours (I) we compared the bird's learning scores in treatments where both yellow and red were used in training to the treatments where only one of these colours was used. Furthermore, the extent to which the birds generalised their learned avoidance or preference of the training colours to orange was assessed in a subsequent memory / generalisation test.

In sub-studies II-V the aim was to test how signals and different levels of unpalatability affect the benefits of mimicry. The great tits foraged individually on the black-and-white prey in the aviaries. The general procedure was to present each bird with a setup of defended signalling prey and cryptic edible prey arranged randomly on the aviary background. The signals, unpalatability levels and numbers of the defended prey varied according to the experiment and treatments. The birds were allowed to kill (eat or taste) a certain number of prey items to learn to avoid the defended prey and to forage on the cryptic prey. The birds were observed from behind a window and numbers of each prey type killed were recorded. To analyse the importance of signal similarity and signal design as well as the effects of unpalatability levels of the prey, learning rates of the birds and mortalities / predation risks of the prey types were calculated from the numbers of each prey type the birds killed. Learning trials in sub-studies II, IV and V were also paired with subsequent 'memory tests' where the birds were presented with the same signals as in the learning trials but the prey items were edible so that the birds could not improve their discrimination of the prey types. This was to assess the level of learning or the birds' willingness to attack the prey type again after the different experimental treatments and to assess the long term predation risks of the different prey types by asking 'what would happen next time the predators meet the prey'.

The experiment in paper II was designed to test whether a shared warning signal aids predator learning compared to variable signals and also whether the birds avoid prey with mixed unpalatability less than prey which is highly distasteful. The defended prey used either a uniform signal (a black square or a

diamond shape) or two different signals (both the square and the diamond) (Figure 2) and they were either all highly distasteful, all moderately distasteful or a mixture of the two unpalatability levels. The total amount of defended prey was the same in all treatments.

In the next experiment (III) I studied the effect of dilution by density which is part of the mutualistic co-mimic relationship in Müllerian mimicry by applying the scenario of increasing numbers of mimetic prey to unequally defended co-mimics as well as edible Batesian mimics. The number of highly unpalatable 'model' prey was kept constant. In the different treatments the numbers of moderately unpalatable 'mimics', which had either visually perfect or imperfect resemblance to the models, was increased. There were also treatments in which the number of visually perfect edible mimics was increased. The warning signals were the same square and the diamond symbols as above (Figure 2).

In the fourth experiment the relationship of unequally defended prey was tested with a square and an asymmetrical star symbol as warning signals of the prey (Figure 2). Similarly to sub-study II the combined number of aposematic prey was kept constant and the proportions of highly and moderately defended prey was altered. Unlike in sub-study II however, the two warning signals were reliable cues of the unpalatability levels of the defended prey. There were treatments where the proportion of the visually imperfect moderately defended 'mimics' was either very low or equal to that of the highly defended 'models'.

Finally, in paper V the focus shifted from the learning process of the predators to whether experienced hunters could affect the evolution of Müllerian mimicry. Great tits were first trained to avoid a highly unpalatable model in a learning trial similar to those described above. On the following day, a moderately unpalatable imperfect mimic was introduced. The mimics were presented alongside the familiar models in different frequencies to test the reactions of experienced predators on familiar prey (that could be seen as perfect mimics to the models they were trained with) and new imperfect mimics. The square and star signals (Figure 2) were used in this experiment.

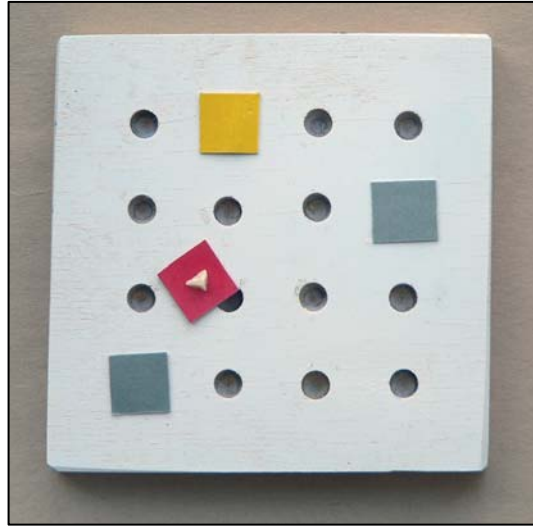


FIGURE 1 The artificial prey items and the board on which they were presented to the birds in sub-study I.

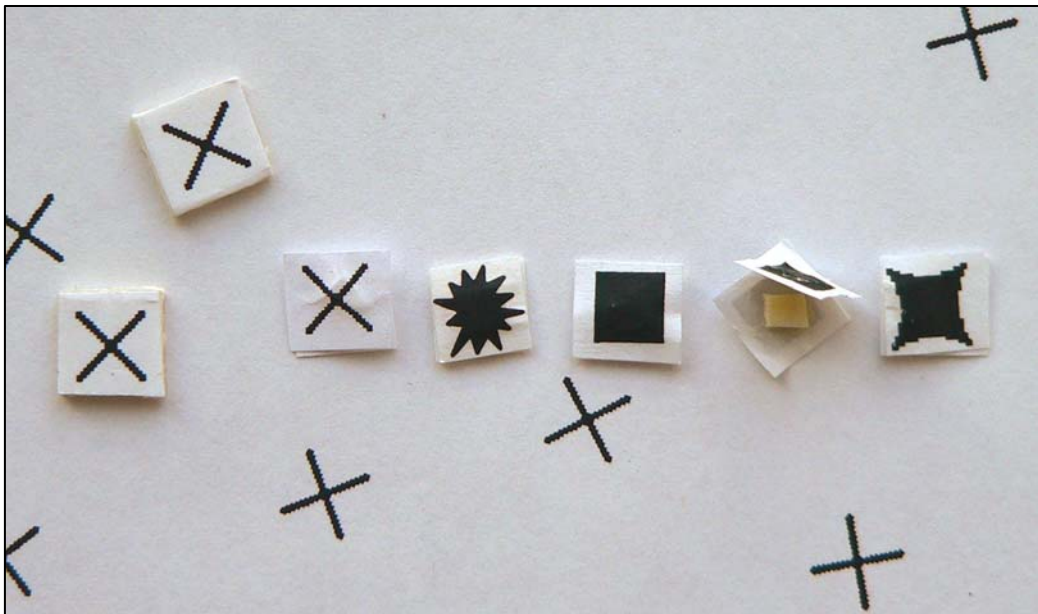


FIGURE 2 The artificial prey items used in sub-studies II-V presented on the black-and-white aviary background. Items from the left are 1) two 'fake prey items', 2) a cryptic cross (II-V), 3) an asymmetrical star (IV & V), 4) a square (II-V), 5) an opened square prey item and 6) a prey item with a diamond shaped signal (II & III).



FIGURE 3 The experimental aviary used in the main experiments of sub-studies II-V. The black-and-white background on which the prey items were presented covers the aviary floor.

3 RESULTS AND DISCUSSION

In these experiments I have manipulated different qualities of aposematic and mimetic prey and observed how they affect the predation risk of the prey via predator behaviour.

3.1 Learning about variable prey defences

The theory of aposematism suggests that predator psychology is a key to explaining why defended prey use colourful and conspicuous warning signals instead of camouflage as an antipredator strategy (see Ruxton et al. 2004 and also Rowe & Skelhorn 2004 for a review). Predators learn efficiently to avoid signals that contrast strongly with their viewing background (Gittleman & Harvey 1980, Roper & Redston 1987) and also certain typical warning colours per se have been shown to facilitate avoidance learning (Sillén-Tullberg 1985b, Gamberale-Stille & Guilford 2003). A third but less tested possibility is the question of reliable signalling (Wallace 1867, Fisher 1958): since many edible species rely on crypsis, conspicuousness that is achieved by using typical warning colours could efficiently distinguish unprofitable prey from edible prey (Sherratt & Beatty 2003, see also Jansson & Enquist 2003). Experiment I lends support to the third hypothesis: the birds learnt the discrimination task between edible and distasteful prey equally well, irrespective of whether unpalatability was signalled by typical warning colours (red, yellow) or grey. This suggests that there need not to be a 'special alliance' between secondary defences and typical warning colours but it may be sufficient that signals with opposing messages are distinguishable. However, if contrast is more important a feature than colour of the signals per se (but see Sillén-Tullberg 1985b, Gamberale-Stille & Guilford 2003) the finding could also be explained by the fact that grey was also relatively visible in this experiment.

Aposematic prey could also gain protection from predation by resembling each other: Müllerian mimicry theory predicts that a common shared signal is a better strategy against inexperienced predators than different signals (Müller

1879). In sub-study II, prey with a uniform signal did not have such a benefit of lower predation risk compared to prey with two signals when great tits were learning to avoid them. The same result has also been found in previous similar experiments (Rowe et al. 2004, Lindström et al. 2006). The birds in sub-study II thus readily generalised the square and the diamond signal (Figure 2). Considering the theoretical expectation of wide generalisation in Müllerian mimicry (Fisher 1958, Huheey 1988), the benefits of a shared signal could only show with more distinct warning signals. In the experiment with colours (I) there was also no evidence that a single warning signal was easier for the birds to learn than two signals even though yellow and red are two clearly different colours. Moreover, signal variation had a curious effect in sub-study II: when the aposematic prey was moderately defended, the birds learned better to avoid two signals than only one signal, which opposes the Müllerian prediction. This benefit of faster learning of two signals did not seem to have long term effects on the mortality of the mimetic prey however, because the result was not the same in the memory test. It may be that mimetic benefits only show when learning is measured in complex environments where predators have to identify numerous types of prey, or that the benefits are only obvious when one mimetic counterpart is rare compared to the other (Beatty et al. 2004). To date, laboratory experiments with wild predators have not supported the fundamental assumption that signal monomorphism protects Müllerian co-mimics simply because one signal is easier for the predators to learn than two signals.

The variable levels of secondary defences of Müllerian co-mimics are potentially interesting because it has been suggested that unequal defences could alter the 'purely Müllerian' mutualistic mimetic relationship (e.g. Huheey 1976, Speed 1993). The methods of modelling the dynamics of unequally defended co-mimics have been criticised (e.g. Mallet & Joron 1999) and experiments can hardly mirror any theoretical simulations accurately. Instead, sub-studies II-IV ask how predators learn about variable prey defences in different situations. The way unpalatability levels affected the predation pressure on the prey via predator learning (and memory) was not straightforward. Unpalatability interacted with the signals of the defended prey. In paper II, moderately distasteful prey were attacked more often than highly distasteful prey when their signal was uniform but not when the signal was variable. The effect of unpalatability also depended on the efficacy of the warning signal (IV). Importantly, paper II shows that the numbers of defended prey that the birds attacked (i.e. learning rate) did not differ between treatments where unpalatability was high or a mixture of high and moderate distastefulness. This suggests that although avian predators can be affected by the severity of punishment from distasteful food, they may not simply react to the average unpalatability of mixtures of aposematic prey (see also Skelhorn & Rowe 2004), as could be predicted based on theoretical work on quasi-Batesian mimicry (Huheey 1976, Speed 1993, Speed 1999a, Speed & Turner 1999).

3.2 Relative and absolute abundance

Paper II did not support the quasi-Batesian idea that moderately defended co-mimics could act as a Batesian-like parasitic mimics. In paper II (and IV) the total amount of defended prey (highly defended 'models' and moderately defended 'mimics' together) was kept constant and the relative frequencies of the unequally distasteful prey types was altered; this is a 'Batesian approach' in the sense that relative model-mimic frequencies are the base of Batesian dynamics (e.g. Brower 1960, Huheey 1980, Nonacs 1985, Lindström et al. 1997). It could be argued that because the benefit of mimetic resemblance in Müllerian mimicry comes from diluted per capita mortality (Müller 1879), the effect of moderately defended mimics should also be studied by increasing the total numbers of the less defended prey while keeping the amount of the better defended co-mimic constant. This would reflect for example a situation where a mimetic morph spreads within the less defended 'mimic' species and consequently from the point of view of the shared signal, the total numbers of prey with that signal would increase.

The relative frequency framework in Batesian mimicry and the total number framework in Müllerian mimicry are at least partly useful concepts as they help to intuitively understand the basis of why such mimetic systems could evolve and what the relationships of the mimetic species could be like. Such a division of frameworks is perhaps also unsound (and not a rule without exceptions, see Owen & Owen 1984, Speed 1999a). If the absolute abundance of one mimetic counterpart is increased, the relative frequencies of the species in the mimicry complex also change. If a mimicry complex has dynamics that depend strongly on the relative frequencies of the species it does not exclude the possibility that the total abundances of the species could affect their mortalities and relationship as well. Moreover, Müller's original theory could also be interpreted differently to the simple 'increasing numbers' -scenario. As an exercise of mind, one could imagine there is an aposematic species that uses say, a red warning signal and also a number of other species that use different warning signals (alternatively the other species could be cryptic). If a red mutation starts to spread in one or many of the other species turning them into co-mimics of the original red species then the total amount of red signals does increase, but the total amount of all prey available in the system does not have to change. From the point of view of simulations and experiments this is an important consideration as it broadens the perspective of mimicry to the whole prey community, and also to the predator community by raising the question of overall predation pressure (see below).

In experiment III the number of highly unpalatable models was kept constant in all treatments and the numbers of either moderately unpalatable or completely palatable mimics was increased. In this way, the total amount of prey available to the birds increased. The mortality of the highly and moderately unpalatable co-mimics decreased with increasing number of mild

mimics showing that the mild mimics were Müllerian rather than quasi-Batesian counterparts to the models. However, increasing the numbers of edible Batesian mimics did not increase model mortality either; Batesian mimics had no effect on model mortality. In absolute numbers the birds did kill more signalling prey (models and mimics together) when there were more Batesian mimics, showing that the edibility of the mimics encouraged attacks on the mimetic complex or interfered with avoidance learning. The effect of dilution due to increased amount of prey simply outweighed the effect the increase in absolute number of attacks had on the *per capita* mortality of the models (see Speed 1999a).

Mortality in this case was first calculated for each prey type as the proportion that was killed of the number that was presented to the birds. This does not take into account that the total amount of prey available changed (see also Sherratt et al. 2004). A relative predation risk was then calculated in a way that takes into account the random probability that each prey item is killed and that way the increase in the total amount of prey is accounted for. This relative predation risk of models did increase with increasing numbers of Batesian mimics. Note that when the total number of prey available is kept constant as in II, IV & V, mortalities and relative predation risks give the same results. Random predation *per se* may not be a realistic expectation in the learning trials because of the visibility difference of the mimetic and cryptic prey. Before learning takes place the birds typically start by attacking the visible prey. However, because the number of cryptic prey is always constant, the comparisons between the models within or between treatments are unaffected.

Calculating the predation risk in relation to random predation is essentially a control for predation effort / overall predation pressure. Predation effort could also be controlled by letting the predators eat more when there is more prey in the system or by keeping the total amount of prey constant (as in II), although the results might not be exactly the same. The case of Batesian mimics in paper III also illustrates that there is perhaps more to the dynamics of Batesian mimicry than the simple scenario of model-mimic ratio reveals.

Such a numerical exercise of mind is also biologically relevant because it raises questions such as: is it correct to assume that co-mimics have independent population dynamics so that one species could increase in numbers without affecting the population of another species? Prey species that share predators are at least not completely independent of each other. Or, if mimetic species can increase in numbers, how will the predator community respond; will there also be more predators eating the prey?

Comparing these experimental data directly to the results of computer simulations that address the relationship of unequally defended co-mimics is complicated for a number of reasons. These experiments concentrate on the learning process of predators when presented with a discrimination task between visible and cryptic prey whereas computer simulations can run for thousands of iterations (e.g. Turner & Speed 1996, Speed & Turner 1999) or focus on experienced predators (Kokko et al. 2003, Sherratt et al. 2004). Depending on the specific focus of theoretical work, some simulations

concentrate only on the co-mimics (again see e.g. Turner & Speed 1996, Speed & Turner 1999) whilst some include alternative prey (Sherratt et al. 2004) which can also be cryptic and hard to find (Kokko et al. 2003) as in these experiments. Sometimes the authors report combined percentage of a model-mimic pair killed when the attack probability is determined by learning and forgetting rules (Turner & Speed 1996, Speed & Turner 1999), and sometimes 'attack probability on encounter' (Sherratt et al. 2004).

Nevertheless, based on experiments II and III the basic idea that a moderately defended co-mimic could harm a highly defended co-mimic during learning does not seem likely. Interestingly, the learning trials and the subsequent memory tests did not always show the same pattern of prey mortalities (II, IV, see also the difference between the first and the second day in V). Computer simulations sometimes use rules where learning rate and the future 'attack asymptote' are related i.e. that moderate defences result in slower learning and higher asymptote (see Turner & Speed 1996). The discrepancies between learning and future attacks in the present study are (at least mostly) interactions of taste and signal but it would be interesting to test with long term studies whether learning rates and future attack rates (when learning is complete) could be decoupled.

In an experiment with garden birds quasi-Batesian dynamics have been found (Speed et al. 2000). The bird predators were of different species, the total density of artificial prey was lower, the predators had a different level of experience on the prey and the signals of the prey were different (e.g. colour and visibility) than in my studies and all these factors could have affected the result (see Exnerová et al. 2003 for reactions of bird species to aposematic prey).

3.3 Signal efficacy

In papers IV and V the square and the asymmetrical star were used as the signals of the defended prey (Figure 2). These signals differed in efficacy despite the fact that they were equally visible and the birds did not have any initial preferences or aversions to either of them when palatable (IV). The star was more effective a signal than the square; prey using the star signal were generally attacked less. The effect of unpalatability levels on predation depended strongly on signal efficacy and due to this interaction, the effect of changing co-mimic frequencies was not straightforward either.

The design of effective warning signals in general has been studied rigorously (e.g. Gittleman & Harvey 1980, Sillén-Tullberg 1985b, Guilford & Dawkins 1991, Roper 1993, Gamberale & Tullberg 1996a, Osorio et al. 1999, Jetz et al. 2001, Rowe 2002, see also Ruxton et al. 2004 for a recent review) but relative signal efficacy has rarely been considered in studies of mimicry (but see Lindström et al. 2006). This is despite the general notion that Müllerian systems can have 'models' that attract other co-mimics to resemble them and there would be advergence in the evolution of signals rather than convergence (Mallet 1999), and

some traits that affect signal efficacy are included in the list of traits (Mallet 1999) that can make a species a model in a Müllerian system. Fairly mechanistic experiments such as these do not provide detailed understanding of such evolutionary trends, however.

3.4 Experience and generalisation

Wild birds in the field have selected against rare and unfamiliar warning signals and for locally common ones in experiments with transferred butterflies (Benson 1972, Mallet & Barton 1989, Kapan 2001). This is evidence for the general Müllerian principle that a common warning signal is a better protection against predators but not necessarily due to education effects. It is likely, that the birds in the field experiments have not been naïve but familiar with their local prey. Learning experiments with naïve birds have not given such support to the Müllerian theory (Rowe et al. 2004, I, II). Experiment V suggests that experience of the predators is an important difference between the field studies and learning studies. Experienced birds seem to select for Müllerian mimicry also in the laboratory because a common and familiar signal is a better protection against them (V). Rare mutations themselves are also interesting: it is likely that mimicry at least evolves through visually inaccurate stages (see Turner 1977, Balogh & Leimar 2005) and perfect interspecific mimicry is unlikely to evolve if visually imperfect mutations never survive. The predation risk of the rare and novel 'mimics' was higher than that of the common and familiar 'models' in experiment V suggesting that new imperfect mimics can initially have similar problems in establishing themselves than aposematic morphs in general (see Lindström et al. 2001 for antiapostatic selection). The magnitude of such problems is likely very context dependent, however. The new mimics benefited from some generalisation to the models; joining a mimicry ring may indeed be an easier way to aposematism than evolving a unique signal (Mallet & Joron 1999, see also Beatty et al. 2004). Therefore, the success of new morphs likely depends on how predators generalise signals, which depends on the degree of visual similarity but also other aspects (and of course the relative fitness of the new morph and the wild type within the new mimic species then plays the key role).

Birds can for example show peak shifts towards unfamiliar signals (Gamberale & Tullberg 1996b) or generalise asymmetrically between two different signals (Goodale & Sneddon 1977). It has been suggested that predators should generalise more broadly between Müllerian co-mimics than Batesian models and their mimics (Fisher 1958, Huheey 1988). Interestingly, paper I also indicates that birds may generalise from familiar to unfamiliar signals more readily after a negative experience than a positive experience. This seems to be in line with the observation that in case of edible Batesian mimics the severity of punishment from eating a model affects how broadly the

predator generalises to the signals of the mimics (Goodale & Sneddon 1977, Darst & Cummings 2006).

The present experiments give further examples of how generalisation is sensitive to context. The square and the diamond symbols (Figure 2) that were used to create variation in the warning signal were readily generalised in experiment II. However, they were treated differently by the birds when they were reliable signals of the level of unpalatability. In experiment III the diamonds were always moderately distasteful. In that case, the birds attacked the diamonds more than the highly defended squares. On the other hand, the birds overlooked reliable signalling in the case of square and star signals; prey with the more effective star signal were attacked less during learning regardless of their unpalatability level in experiment IV. Furthermore, in experiment V where one of these signals was presented first and the other introduced later, there was only slight generalisation between them. This was the case also in a study by Lindström et al. (2006). In contrast, when both squares and stars were presented simultaneously (IV), the birds treated them differently in training but did not differentiate between them in a memory test. This kind of sensitivity to the context of presentation and previous experience is at least important to keep in mind in studies of mimicry but it is also potentially interesting if the first experience the predators get has long term effects on their choice of prey (see Evans & Waldbauer 1982, Thomas et al. 2003).

Focus on experienced predators and rare, novel and imperfect mimics give a different perspective to the evolution of mimicry than studies of predator learning. It seems plausible that although a new co-mimic morph that resembles for example a more common species would benefit from diluted mortality that is due to predator education, generalisation by experienced predators will also be an important selection pressure for Müllerian mimicry. Despite the ongoing discussion (e.g. Mallet 1999, Sherratt et al. 2004) the relative importance of naïve and experienced predators as selective agents remains unsolved because there are no comprehensive data from the wild on how much experienced predators kill aposematic prey.

4 CONCLUSIONS

Aposematism and defensive mimicry are anti-predator strategies which provide a range of challenges for those interested in asking questions about the dynamics of the phenomena and mechanisms behind their evolution. Several benefits that defended species could draw from conspicuous signalling have been described and tested, and they are not mutually exclusive. This study suggests that colours that are typical to visual warning signals may simply clearly distinguish unprofitable prey from edible prey (I). In practice, this is often the same as contrasting with the viewing background because edible species commonly rely on camouflage, but the view emphasises the aspect of reliable signalling.

Predator learning and memory are often used to explain the function of warning signals and the dynamics of defensive mimicry, especially the benefits of a shared warning signal in Müllerian mimicry. The learning rates of predators in these experiments did not differ for uniform and variable warning signals indicating that the explanation for the evolution of Müllerian mimicry is not as simple as 'one thing is easier to learn than two' (I, II). The evolution of a shared warning signal becomes easier to understand even in a simple system of two signals when the problem is approached from the point view of rare and unfamiliar signal morphs (V).

The avian predators did not react in a straightforward way to unpalatability levels of Müllerian co-mimics; they did not treat a mixture of highly and moderately defended prey as 'average bad', which suggest that Müllerian and Batesian mimicry may not have overlapping features or intermediate, quasi-Batesian mimicry between them simply because unpalatability and palatability of the prey are varying traits (II). Moreover, even perfectly edible Batesian mimics can dilute the per capita mortality of their aposematic models despite the fact that in absolute numbers they induce attacks on the mimicry complex (III). This invites questions about the importance of relative and absolute abundance of the mimetic prey as well as the responses to those by the predator community as a whole. The study of aposematism is moving towards a broader view of signalling and chemical

defence taking into account other aspects of the ecology of the species (see Ojala 2006). Studies of mimicry are also taking steps towards a more elaborate understanding of life as a mimetic species (Srygley 2004) and a towards a broader community context (Beatty et al. 2004, Franks & Noble 2004).

Interestingly, this study demonstrates how very simple mimicry complexes where only a few characteristics of the prey are manipulated can show interactions between the different qualities of the prey and create a complex image of mimetic relationships (II, IV). A more extensive approach and a biologically more realistic study system could show defensive mimicry as far richer a phenomenon than is currently appreciated.

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YHTEENVETO (RÉSUMÉ IN FINNISH)

Varoitussignaalien jäljittely puolustusstrategiana: Kokeita peto-saalis-suhteista

Aposemaattiset lajit mainostavat syömäkelvottomuuttaan saalistajille näkyvin varoitussignaalein kuten värein. Tyypillisiä varoitussignaaleja esimerkiksi hyönteisillä ovat keltainen, punainen tai oranssi yhdistettynä mustaan. Saalistajien on tavallisesti opittava kokeilemalla välttämään aposemaattisia lajeja.

Varoitussignaaleja myös jäljitellään luonnossa. Batesin mimikria (myös 'mimikry') on ilmiö, jossa syömäkelpoinen matkijalaji huijaa saalistajia jäljittelemällä aposemaattisen mallilajin signaalia. Signaali suojaa matkijalajin yksilöitä saalistukselta, mutta matkijoiden oletetaan haittaavan mallilajia: koska matkijat ovat syömäkelpoisia ja saman näköisiä kuin myrkylliset tai pahanmakuiset mallit, saalistajat oppivat sitä hitaammin välttämään niiden signaalia, mitä enemmän matkijoita ne kohtaavat. Matkijoiden runsastuminen siis lisää mallien ja lopulta myös matkijoiden itsensä kuolleisuutta. Müllerin mimikriassa taas aposemaattiset lajit puolustautuvat käyttämällä samaa signaalia ja näiden 'näköislajien' uskotaan hyödyttävän toisiaan: mitä useampi syömäkelvoton yksilö lajista riippumatta käyttää samaa signaalia, sitä pienempi on yhden yksilön riski joutua kokemattoman pedon saaliiksi. Samalla tavoin signaloivien lajien suhde Batesin ja Müllerin mimikriassa on siis hyvin erilainen, ja siksi oletetaan, että myös mimikrian evoluutio on näissä systeemeissä erilaista.

Koska lajien syömäkelpoisuudessa tai -kelvottomuudessa on kuitenkin vaihtelua, on esitetty, että jos näköislajien pahanmakuisuudessa on eroja Müllerin mimikriassa, niiden välinen suhde voisi olla loisisa kuten Batesin mimikriassakin.

Tässä työssä tutkin kokeellisesti, onko aposemaattisille lajeille hyötyä varoitussignaalin yhdenmukaisuudesta ja vaikuttaako pahanmakuisuuden vaihtelu näköislajien suhteeseen. Keskityin erityisesti siihen, kuinka näköislajien puolustus vaikuttaa saalistajien oppimiseen ja muistiin ja sitä kautta saaliin kuolleisuuteen. Kokeissa käytin keinotekoisia saaliita, joita talitiaiset (*Parus major*) söivät laboratoriossa.

Yhdenmukainen varoitussignaali ei nopeuttanut talitiaisten välttämiso-
pimista verrattuna kahteen eri signaaliin eikä sinänsä hyödyttänyt näköislajeja. Toisaalta linnut, joilla oli jo kokemusta aposemaattisesta saaliista, välttivät ennestään tuttua ja runsasta varoitussignaalia enemmän kuin uutta ja harvinaista. Tämä osoittaa, että signaalin runsaus vähentää aposemaattisten lajien kuolleisuutta, mutta yleisen signaalin etu ei välttämättä johdu saalistajien oppimisprosessista, kuten Müllerin mimikrian teoria olettaa. Kokeneiden saalistajien suhtautumisella varoitussignaaleihin saattaa olla suuri merkitys.

Pahanmakuisuuden merkitys ei ollut yksiselitteinen. Linnut, jotka söivät pelkästään erittäin pahanmakuisia aposemaattisia saaliita, oppivat välttämään niitä nopeammin kuin linnut, jotka söivät pelkästään miedosti pahanmakuisia

saaliita. Vaihteleva pahanmakuisuus ei kuitenkaan haitannut lintujen oppimista ja muistia siten, että näköislajien suhde olisi muuttunut molempia hyödyttävästä loisivaksi. Lisäksi pahanmakuisuuden vaikutus saaliin kuolleisuuteen riippui osin varoitussignaalin tehosta (ja myös signaalin yhdenmukaisuudesta). Täysin syömäkelpoiset matkijat hidastivat runsastuessaan lintujen välttämisoppimista, ja syötyjen mallien absoluuttinen määrä kasvoi, kuten Batesin mimikrian teoria olettaa. Mallien suhteelliseen kuolleisuuteen tällä ei kuitenkaan ollut vaikutusta, koska matkijoiden runsastuessa kokonaissaalismäärän kasvu tasasi mallien saalistuspainetta. Tämä muuttaa osittain käsitystä Batesin mimikrian loisivasta luonteesta ja tuo esille sen, että malli- ja matkijalajien runsaussuhde mutta myös kokonaisyksilömäärä voi muuttaa niiden suhdetta luonnossa.

Tutkimukseni osoittaa, että yksinkertaisissakin mimikriasysteemeissä saalislajien ominaisuudet (kuten signaali ja maku) voivat vaikuttaa yksilöiden kuolleisuuteen yllättävällä tavalla. Toisaalta on selvää, että myös populaatioiden suhteellinen ja absoluuttinen runsaus voi vaikuttaa saalistuspaineeseen, joten toisiaan jäljitteleviä lajeja on tutkittava myös laajemmassa yhteydessä mimikrian evoluution ymmärtämiseksi.

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