

Investigating Müllerian mimicry: predator learning and variation in prey defences

E. IHALAINEN, L. LINDSTRÖM & J. MAPPES

Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland

Keywords:

aposematism;
memory;
palatability spectrum;
quasi-Batesian mimicry.

Abstract

Inexperienced predators are assumed to select for similarity of warning signals in aposematic species (Müllerian mimicry) when learning to avoid them. Recent theoretical work predicts that if co-mimic species have unequal defences, predators attack them according to their average unpalatability and mimicry may not be beneficial for the better defended co-mimic. In this study, we tested in a laboratory environment whether a uniform warning signal is superior to a variable one in promoting predator learning, and simultaneously whether co-mimics are preyed upon according to their average unpalatability. There was an interaction of signal variation and unpalatability but inexperienced birds did not select for signal similarity in artificial prey; when the prey was moderately defended a variable signal was even learnt faster than a uniform one. Due to slow avoidance learning, moderately defended prey had higher mortality than highly defended prey (although this was not straightforward), but mixing high and moderate unpalatability did not increase predation compared with high unpalatability. This does not support the view that predators are sensitive to varying unpalatability. The results suggest that inexperienced predators may neither strongly select for accurate Müllerian mimicry nor affect the benefits of mimicry when the co-mimics are unequally defended.

Introduction

Aposematic species that are, for example, chemically defended (toxic, distasteful), communicate to predators their unprofitability as food via warning signals, such as conspicuous colouration (Poulton, 1890). Predators sometimes avoid attacking signalling prey innately (e.g. Smith, 1975, 1977; Schuler & Hesse, 1985; Rowe & Guilford, 1996) or perhaps as a result of conservative behaviour (Marples & Kelly, 1999; Thomas *et al.*, 2003). Considerable effort has been put into understanding a predator-prey relationship where the predators must learn to avoid aposematic species (for a recent review see Ruxton *et al.*, 2004 pp. 94–103). Predator learning is also at the core of the theory that first attempted to explain

why some aposematic species resemble each other with sometimes striking accuracy. Müller (1879) assumed that inexperienced predators need to learn about different warning signals separately, and that they need a fixed amount of trials and errors to learn to avoid a certain signal. He proposed that if prey species share a warning signal, they share the costs of predator education (i.e. lower their per capita mortality that is due to sampling by naïve predators). This provides a possible explanation as to why similarity in appearance might be selected for in aposematic species.

Müllerian mimicry (close resemblance between aposematic species) and the relationship of the co-mimic species have attracted theoretical interest. The dynamics of the system and possible evolutionary routes to a shared signal have been considered (e.g. Fisher, 1927; Turner, 1977, 1987; Sheppard *et al.*, 1985; Turner & Mallet, 1996; Mallet, 1999; Balogh & Leimar, 2005). Mutualism and tendency towards monomorphism in the warning signal have been attributed to classical

Correspondence: Eira Ihalainen, Department of Biological and Environmental Science, PO Box 35, FI-40014 Jyväskylä, University of Jyväskylä, Finland.
Tel.: +358 14 2602244; fax: +358 14 2602321; e-mail: eiraihal@cc.jyu.fi

Müllerian mimicry (see e.g. Turner, 1987; Mallet, 2001), since it is essentially a 'strength in numbers' scenario where an increase in the density of any co-mimic species should benefit all (Müller, 1879). Mark-recapture studies with aposematic butterflies have demonstrated the benefits of mimicry in the field by showing that it is disadvantageous for the prey to deviate from the common warning signal (Mallet & Barton, 1989; Kapan, 2001). However, the predators in the wild were not necessarily naïve; therefore, the experiments are likely to reflect the role of generalization from familiar signals to unfamiliar ones (which can also be an important factor in the evolution of mimicry) rather than the role of initial avoidance learning. Signal generalization has also been studied in some laboratory experiments that touch upon Müllerian mimicry (Brower, 1958; Alatalo & Mappes, 1996). In a laboratory study that concentrated on avoidance learning of bird predators similarity of warning signals did not clearly benefit artificial co-mimics (Rowe *et al.*, 2004), which does not support the fundamental assumption of the classical theory. Despite the general expectation of monomorphism, there is also a theoretical reason to expect some variation in the warning signals of Müllerian co-mimics (Fisher, 1958): since the co-mimic species are unpalatable, it is to the predators' 'benefit to recognize similar patterns as signalling unpalatability' (Huheey, 1988) and even imperfect mimicry could be 'tolerated'.

The original Müllerian mimicry theory has also been under discussion because it does not consider possible differences in the strength of the secondary defences (like chemicals) of the co-mimic species. What at least tentatively separates Müllerian and Batesian mimicry is the inedibility/edibility of the mimics. In Batesian mimicry, an edible mimic gains protection from predators by resembling an aposematic model. The predators learn to avoid their signal because of the unpalatability of the model species. The edible mimic 'parasitises' on this learnt avoidance since the predators may mistake the mimic for the model (Bates, 1862). The model-mimic dynamics in Batesian mimicry are expected to differ from Müllerian mimicry (see e.g. Turner, 1987; Joron & Mallet, 1998). The edible mimics are at an advantage when rare, and increasing frequency of Batesian mimics harms the model since edible look-alikes encourage the predators to attack the models as well (Pilecki & O'Donald, 1971; Huheey, 1980; Lindström *et al.*, 1997). The idea that there might be intermediate forms of mimicry between 'pure' Müllerian and Batesian mimicry was first proposed in the early 1900s (see Marshall, 1908) but the theoretical work examining this possibility in more detail is more recent.

It has been shown that chemically defended species differ in their levels of defence both within (e.g. Brower *et al.*, 1968; Eggenberger & Rowell-Rahier, 1992) and between species (e.g. Brower, 1958; Brower *et al.*, 1963; Bowers & Farley, 1990). This observation is behind the

studies that challenge the original Müllerian mimicry theory. If Müllerian co-mimics are not equally unpalatable, predators might react to this and cause co-mimic relationships that are not mutualistic but resemble Batesian mimicry, hence the name quasi-Batesian mimicry (Speed, 1993). This could occur if the presence of a less defended species, which provides less severe punishment, would cause slower avoidance learning of the co-mimics or otherwise encourage attacks on them. Some mathematical models consider the effects a moderately defended co-mimic could have on mimicry dynamics due to learning and forgetting by predators (Huheey, 1976; Owen & Owen, 1984; Turner *et al.*, 1984; Speed, 1993; Turner & Speed, 1996; Mallet, 1999; Speed & Turner, 1999 see also MacDougall & Dawkins, 1998; Speed, 1999a), whereas others concentrate on state-dependent foraging (Kokko *et al.*, 2003; Sherratt *et al.*, 2004). In the predator psychology based models different learning and forgetting rules can produce a situation where a 'virtual 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 dependent model (Speed, 1999a).

Experimental work focusing on the unpalatability levels of Müllerian co-mimics is only just starting to catch up with the theoretical work. Speed *et al.* (2000) found support for the prediction that differences in unpalatability affect the co-mimic relationship, because the less defended co-mimic diluted the protection of the better defended co-mimic. The experiment of Speed *et al.* (2000) did not strictly concentrate on the predator learning process. Lindström *et al.* (2006) manipulated both the similarity of warning signals and the unpalatability level of the prey in an experiment where inexperienced, wild Great tits (*Parus major*) learned to avoid artificial aposematic prey in a 'novel world' laboratory environment. They found that variation in these traits need not affect mimetic dynamics. However, the patterns used to create warning signal variation were treated unequally by the birds (i.e. the birds learned about one signal faster than the other), which may interfere with interpreting the effect of variation *per se* from the predator learning point of view.

In the current study, we combine the hypothesis that signal monomorphism in aposematic prey aids predator learning with the predator psychology view which predicts that predators adjust their attack rates according to the average unpalatability of the co-mimics when they differ in their level of defence. We apply these ideas to inexperienced predators and ask whether variation in both the warning signal and the unpalatability level of aposematic prey affects avoidance learning. We used the same laboratory environment as in Lindström *et al.* (2006), but with warning signals that were equal (i.e. the birds learnt to avoid them at the same rate). By using these signals we were able study

the effect of unbiased variation on learning. Great tits foraged on black and white artificial prey items presented on a black and white background in an aviary. In an artificial environment like this, wild birds are inexperienced predators. The birds search for the prey whose abundance, unpalatability and signals are relatively easy to manipulate. Once the birds were familiarized with the laboratory system, a learning experiment was conducted where they had to learn to discriminate aposematic prey from edible, cryptic prey. The aposematic prey had either invariable or variable signal and was moderately or highly distasteful or a mixture of both. Subsequently the birds also completed a 'memory test'. Following Müller's classical theory, learning should be faster when the warning signal is uniform rather than variable. Parallel to this, the predator psychology view predicts that learning should be faster for highly distasteful prey than for moderately distasteful prey or a mixture of these.

Material and methods

Wild Great tits were trapped at feeding sites and subsequently ringed for identification. Each bird was kept individually in a plywood cage indoors with a daily light period of 11.5 h. Sunflower seeds, tallow and fresh water were available *ad libitum* except before the experimental trials when the birds were food deprived to ensure motivation to search for the artificial prey. The experiment was run from October 2003 to February 2004 and February 2005 to March 2005 at Konnevesi Research Station in central Finland by the permissions from the Central Finland Regional Environment Center (permission numbers KSU-2003-L-327/254 and KSU-2004-L-238/254) and the Experimental Animal Committee of the University of Jyväskylä (permission numbers 43/08.09.2003 and 29/31.05.2004). After the experiment, the birds were released at the site of their capture. A total of 110 birds were used for the study. The data were

analysed with SPSS 11.5 for Windows statistical package. All tests are two-tailed and nonparametric tests are used where the data did not meet the requirements of parametric tests.

Artificial prey

The prey items were small pieces (approximately 0.1 g in weight) of almond glued (with nontoxic glue UHU Stic) between two 8 mm × 8 mm pieces of paper. One black-and-white signal was printed on both sides of the paper shell of the prey items. A cross symbol that was also printed on the background on aviary floors created cryptic prey items (see Aviaries). The two different warning signals were a square and a diamond (see Fig. 1). Almond for aposematic prey was made either highly unpalatable by soaking it as slices for an hour in a solution of 30 ml of water and 2 g of chloroquine phosphate (malaria drug Heliopar, henceforth 'quinine'), or mildly unpalatable by soaking in a solution containing only 0.25 g of quinine. The birds experience the difference in quinine concentration as a difference in distastefulness (Lindström *et al.*, 2006). After soaking, the almond slices were dried at room temperature and cut into pieces. The cryptic palatable prey items contained untreated almond.

Aviaries

The experiments were conducted in three aviaries. The large aviary was 3.5 m high with a floor area of 57 m². The floor was covered with white A3 size paper sheets, which were glued together and covered with adhesive plastic. There were 70 printed crosses and 10 fake cryptic prey items in random positions on each sheet. The fake prey items (8 mm × 8 mm pieces of cardboard with printed crosses glued on the top) were glued to the sheets to make the background three-dimensional in order to make the cryptic prey better camouflaged. The

Unpalatability / signal	Invariable (one signal)		Variable (both signals)	
Moderate	Treatment 1 100 mo + 100 cr ■ ×		Treatment 4 50 mo + 50 mo + 100 cr ■ ◆ ×	
	100 mo + 100 cr ◆ ×		50 mo + 50 mo + 100 cr ◆ ×	
Mixed (moderate and high)	Treatment 2 50 hi + 50 mo + 100 cr ■ ■ ×		Treatment 5 25 hi + 25 mo + 25 hi + 25 mo + 100 cr ■ ■ ◆ ◆ ×	
	50 hi + 50 mo + 100 cr ◆ ◆ ×		25 hi + 25 mo + 25 hi + 25 mo + 100 cr ◆ ◆ ×	
High	Treatment 3 100 hi + 100 cr ■ ×		Treatment 6 50 hi + 50 hi + 100 cr ■ ◆ ×	
	100 hi + 100 cr ◆ ×		50 hi + 50 hi + 100 cr ◆ ×	

Fig. 1 Experimental design of the learning trial, and the signals of the prey. There was a total of 100 aposematic prey items presented in every treatment. When the signal was invariable, all aposematic prey had the square or the diamond signal. In variable signal treatments half of the 100 aposematic prey showed the square signal and the other half showed the diamond signal. On unpalatability levels, 'moderate' and 'high' all aposematic prey were moderately (mo) or highly (hi) distasteful, respectively. In case of mixed unpalatability, half of the aposematic prey items were highly distasteful and the other half only moderately distasteful. In all treatments, there were also 100 cryptic, edible prey items (cr) presented. The cross pattern matched the background.

paper sheets formed a grid with 15 rows and 22 columns on the floor. There were wooden dividers (c. 6 cm wide boards) placed between rows, with the purpose of making prey handling and movement of the birds more easy. In the large aviary, there were eight perches at the height of 0.5 m for prey handling. The small aviaries were both 2.4 m high with a floor area of 13.5 m². The floors of these two aviaries were covered similarly to the large aviary, but there were eight rows of 10 paper sheets. These aviaries had two perches.

In the experimental setup, only one prey item occupied a sheet, so as to be able to identify the attacked items by their coordinates. During the experiments, the birds were observed through a one-way window. Fresh water was always available in the aviaries.

Training of the birds

All birds were trained to handle the artificial prey in their home cages in four steps by offering them (i) small almond slices; (ii) five one-sided prey items, a piece of almond glued onto white piece of paper, sized 8 mm × 8 mm; (iii) five prey items with the almond sticking out from the paper shell and finally; (iv) five prey items with the almond completely hidden inside the paper shell. The bird had to eat all items before the training progressed to the next phase.

The birds were also trained to forage from the cross symbol background, and familiarized with the aviaries to ensure that they could utilize the perches, and would readily search for the artificial prey in the experiments. 'Background training' was conducted in the small aviaries. We placed three cryptic prey items and 12 completely white prey items on the floor so that they were in groups of three (one cryptic group and four white groups). One prey item in the group was always on the divider, so that it was clearly visible. The second item was close to the board and the third was in the middle of the sheet. Each bird had to find and eat all prey items. The three cryptic prey items were used, since it is realistic to assume that predators would have some experience of the cryptic prey before they first encounter aposematic prey. To familiarize the birds with the large aviary, several birds at a time were allowed to feed and stay overnight inside. During the familiarization period, the cross-symbol background was replaced by transparent plastic with peanuts, mealworms and sunflower seeds available on the floor.

The birds were always trained to handle the prey items before the background training, but for practical reasons they were familiarized with the large aviary at varied stages of their training.

Testing the signals

The two warning signals (see Fig. 1) had an equal area of black on white background but were still tested for

visibility and relative acceptability. Ten birds that had completed handling training were used for a preference test and subsequently for a visibility test.

Before the preference test, the birds were familiarized with an experimental cage (plywood, sized 50 cm × 50 cm × 70 cm) for at least an hour and during that time five plain white edible prey items were offered on a Petri dish with brown paper on the bottom. The cages contained a perch and a water bowl with the floor covered by brown paper. In the actual preference test prey items were offered in pairs through a hatch, so that the square and the diamond signals were in turn on the left and on the right side of the Petri dish. The untreated almond pieces inside were weighed (0.085–0.100 g) to make the birds choose by signal rather than the amount of food. Five pairs were offered and the birds were allowed to eat both prey items. Observations were made through a small net covered window on the cage. The birds did not show any relative preferences for the warning signals. Over all the five pairs of prey offered in the preference test, both signals were chosen first 25 times (ten birds which five pairs were offered to). From the very first pair offered, both signals were chosen first five times.

Before the visibility test, the birds had to eat two prey items with each of the warning signals and seven prey items with the cross-signal in their home cages. This was to encourage them to attack all signals (as they were not trained to forage from the cross-symbol background) and to give them comparable experience on the cryptic cross that was not included in the preference test. In the visibility test, 20 prey items of each signal (square, diamond and cross) were randomly distributed on the cross-background in a small aviary. Each bird was allowed to find (peck or eat) 20 prey items. The numbers of each signal found were recorded. There was no difference in the numbers of squares and diamonds found by the birds in the visibility test (paired samples test $t_9 = 0.466$ $P = 0.653$) but less cryptic prey items were found (paired samples test $t_9 = 5.571$ $P < 0.001$ and $t_9 = 6.943$ $P < 0.001$ comparing numbers of cryptic prey found to squares and diamonds, respectively). A signalling prey item was four times as visible to the birds as a cryptic prey item; on average 8.9 of both signalling items were found compared with 2.2 cryptic items.

We used four additional birds to confirm they were able to see the difference between squares and diamonds to ensure they would experience the intended signal variation as variation. After handling training, two birds were given five edible squares that they had to eat in their home cages. Subsequently, 40 edible squares and 40 unpalatable diamonds were randomly distributed in a small aviary. The birds were allowed to kill (open the paper shell and taste or eat the almond inside) 40 prey items in a trial, each trial was repeated three times, once a day. The two remaining birds were tested similarly but with diamonds as edible prey and squares as unpalatable

prey. The birds learned to avoid the unpalatable signal and choose the palatable one; when the number of unpalatable prey killed was compared across the 3 days, the numbers decreased (Friedman test $\chi^2 = 7.249$, $P < 0.05$) and were also lower than random expectation on the third day (one-sample t -test $t_3 = -4.893$, $P < 0.05$). Simultaneously, the numbers of palatable prey killed increased as the squares and diamonds were the only prey types presented in this test. This confirms that the birds could perceive the difference in the signals.

Variation experiment

For the variation experiment, we used 96 birds that had completed full training and thus had limited experience of the cryptic prey and no experience of the aposematic prey.

Learning

The learning part of the experiment was run in the large aviary where 100 palatable cryptic prey items and 100 aposematic prey items were randomly distributed. The learning trial was essentially a discrimination task where the birds had to learn to avoid the aposematic prey and prey on the cryptic prey, which kept the birds motivated to forage. Each bird had to kill 50 prey items before the trial was terminated. The total number of each prey type killed was recorded. We introduced variation to both signal and unpalatability of the aposematic prey using a two by three design (Fig. 1). Signal was either invariable (aposematic prey items showed only the square or the diamond signal) or variable (half of the aposematic prey had the square and the other half the diamond signal). It is important to note that the birds treated the two conspicuous signals in a similar manner in the learning phase, since the numbers of squares and diamonds killed did not differ in any within-treatment comparisons (all $P > 0.212$). Consequently, 'square or diamond alone' could safely be merged into 'invariable signal' factor, and possible effects of signal variation on learning were not confounded by differences in the 'educational efficacy' of the two patterns.

The level of unpalatability was moderate, high or mixed. In the case of mixed unpalatability, half of the prey items were highly unpalatable and the other half only moderately so. In the treatment where there was variation in both signal and unpalatability (treatment 5) there were four different types of aposematic prey presented (squares and diamonds both as highly and moderately unpalatable), 25 of each (Fig. 1).

Memory

A week after the learning trial the birds participated a memory test that was run in the small aviaries. Two of the 96 birds died before the memory test, and one totally refused to forage and was excluded from the test.

We presented the birds with 30 cryptic prey items and 30 signalling prey items that were all squares, all diamonds (invariable signal) or 15 squares and 15 diamonds (variable signal) according to the signal treatment from the individual's preceding learning trial. Each bird was required to kill 15 prey items, and the number of each prey type killed was recorded. All prey items were palatable in this test. There are two consequences of offering edible signalling prey in the memory test. It ensures that the birds cannot improve their discrimination between distasteful and edible prey (i.e. continue learning in this test) though they can potentially start to re-learn and accept previously aposematic prey. However, we assume that their readiness to sample and accept signalling prey reflects the strength of their learnt signal-taste association. By this simple experiment, we are not studying any details of memory; the test could be seen as a long-term 'double check' of the level of learning.

Results

In the learning trial, we introduced variation both in signal and unpalatability to the aposematic prey population to study how variation affects learning of inexperienced predators. We compared the total numbers of aposematic prey the birds killed in each treatment to assess the effects of variation on learning. We examined how learning progressed in the different treatments by comparing more detailed learning curves. The strength of avoidance the birds acquired during the learning trial was then measured by total numbers of signalling prey killed in a memory test.

Learning

The total numbers of killed aposematic prey showed an interaction between the signal treatment (invariable/variable) and the level of unpalatability (moderate, mixed or high) (ANOVA $F_{2,90} = 3.507$, $P \leq 0.05$), i.e. the effect of unpalatability level depended on the signal treatment and vice versa (Fig. 2). Therefore, we looked at the effect of signal variation within each unpalatability treatment separately, and also the effect of unpalatability level within each signal treatment by using tests of simple effects.

When the unpalatability levels were analysed for simple effects of signal variation, the numbers of aposematic prey killed differed between the signal treatments only in the case of moderately unpalatable prey (treatments 1 and 4; univariate tests $F_{1,90} = 5.614$, $P < 0.05$). Perhaps unexpectedly, the birds killed less moderately defended prey when their signal was variable rather than invariable (Fig. 2). Variation in the signal did not seem to affect learning when the level of unpalatability was high (treatments 2 and 5; $F_{1,90} = 0.512$, $P = 0.476$) or mixed (treatments 3 and 6; $F_{1,90} = 1.027$, $P = 0.314$). This

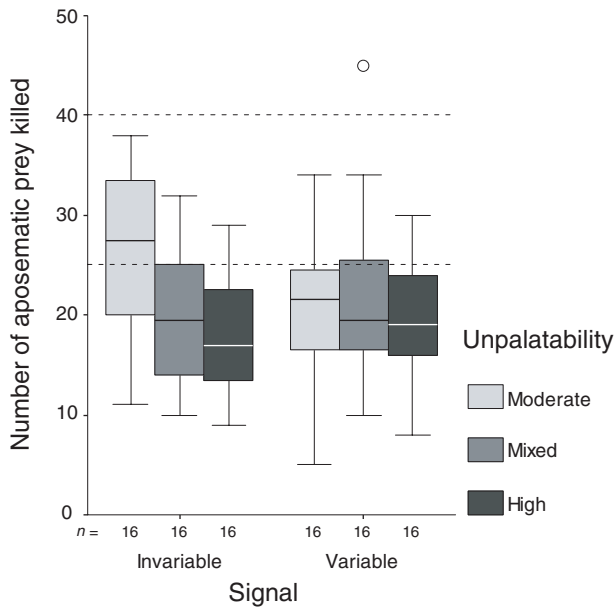


Fig. 2 Total numbers of aposematic prey killed in the learning trial. Reference lines show different expected numbers: random predation would have resulted in 25 killed aposematic prey. If the prey items had been killed according to their visibilities, 40 aposematic items would have been taken. This is an estimate based on the visibility test in this study. Boxplots show minimum, maximum and the upper and lower quartiles around the median. Open circles denote outliers.

shows that variation in the warning signal did not have negative effects on learning.

When the signal treatments were analysed separately, unpalatability affected learning in the case of invariable warning signal, as birds killed different amounts of aposematic prey in the unpalatability treatments 1, 2 and 3 (univariate tests $F_{2,90} = 6.022$ $P < 0.01$). Pairwise comparisons showed that the birds who experienced only moderately unpalatable prey killed more aposematic individuals than birds in the other treatments (LSD = 6.625, $P = 0.010$ and LSD = 8.312, $P = 0.001$ compared with mixed and high unpalatability respectively). However, there was no difference in the numbers of aposematic prey killed between the high and mixed unpalatability treatments (LSD = 1.687, $P = 0.507$) (Fig. 2). When the signal was variable (treatments 4–6), the numbers of aposematic prey killed did not differ between the unpalatability treatments ($F_{2,90} = 0.517$ $P = 0.598$) (Fig. 2). These results indicate that the two concentrations of quinine did create different levels of punishment, but the moderate, mixed and high unpalatability levels did not translate to corresponding learning rates in a straightforward way.

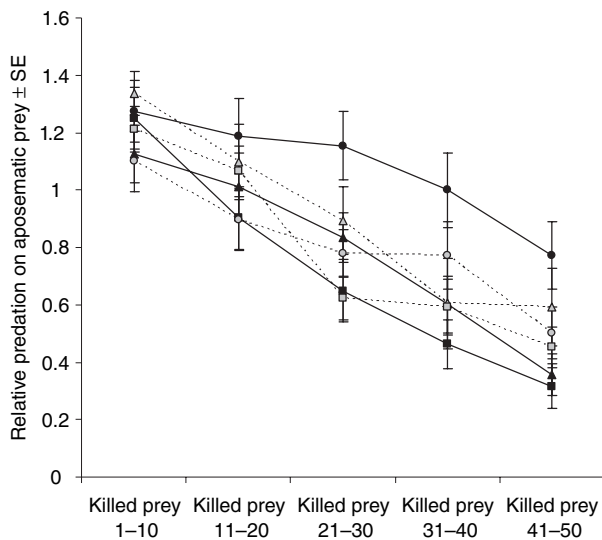
Overall, the total numbers of aposematic prey killed were thus similar for all treatments except treatment 1 where all aposematic prey was moderate and had an

invariable signal. In that case, the birds killed more defended prey than in the other treatments. This pattern is especially clear if one outlier bird that killed 45 aposematic prey items in the treatment 4 (variation both in signal and unpalatability) is excluded (Fig. 2).

We produced learning curves by dividing the 50 prey items the birds were allowed to kill into five steps of 10 prey items. For each step and each bird separately, we counted the numbers of aposematic prey that were killed within the step and divided the observed number with the expected number. The expected numbers were also calculated for each step and each bird separately based on what was left for the bird to kill in the setup. This way we got a measure of relative predation that takes into account the random probability that an aposematic prey item will be taken from the setup. The learning curves were thus standardized such that values above one indicate higher than random predation and those below one indicate lower than random predation (Fig. 3). However, controlling for the random probability did not change the shape of the curves noticeably when compared with curves drawn from absolute numbers of killed prey.

The learning curves showed the same pattern as the total numbers of killed aposematic prey. There was an interaction of the signal and unpalatability treatments (repeated measures ANOVA $F_{2,90} = 3.571$, $P < 0.05$). The unpalatability treatments were then analysed separately to examine the effect of signal variation. When unpalatability was moderate (treatments 1 and 4), there was, again, a difference in the learning rates of birds who experienced invariable and variable signals (repeated measures ANOVA $F_{1,30} = 4.650$, $P < 0.05$) and the difference was as already observed, that learning was faster when there was variation in the warning signal. For the other two unpalatability levels there were no differences in learning between the signal treatments ($F_{1,30} = 0.963$, $P = 0.334$ for mixed and $F_{1,30} = 0.724$, $P = 0.402$ for the high unpalatability treatment) (Fig. 3). In all unpalatability levels, the learning trend was significant (within-subjects effects all $P < 0.001$) and the trend was of similar direction for signal treatments as there were no interactions between the learning factor and signal treatment (all $P > 0.522$) which also means that the birds did learn even in treatment 1 (moderate unpalatability, invariable signal) (Fig. 3).

The invariable and variable signal treatments were also analysed separately; unpalatability level affected learning in the case of invariable warning signal (treatments 1, 2 and 3; $F_{2,45} = 6.196$, $P < 0.01$). Avoidance learning was slower for moderate unpalatability (treatment 1) than for mixed (LSD = 0.292, $P = 0.010$) or high unpalatability (LSD = 0.362, $P < 0.01$) but there was no difference in learning between mixed and high unpalatability (treatments 2 and 3; LSD = 0.070, $P = 0.524$). In case of variable signal (treatments 3–6), however, the birds' learning curves did not differ between the unpalatability



- 1 (mod. & inv.)
- ▲ 2 (mix. & inv.)
- 3 (high & inv.)
- 4 (mod. & var.)
- △ 5 (mix. & var.)
- 6 (high & var.)

Fig. 3 Learning measured as relative predation pressure on the aposematic prey during the learning trial. Predation pressure is in shown relation to the random probability that an aposematic prey item will be taken from the experimental setup. Thus, values above one indicate higher than random predation and those below one indicate lower than random predation. Labels show treatment numbers and the corresponding signal and unpalatability treatments respectively. Mod. denotes moderate unpalatability; mix., mixed unpalatability; high, high unpalatability; inv., invariable signal; var., variable signal. Bars show standard errors.

treatments (repeated measures ANOVA $F_{2,35} = 0.581$, $P = 0.564$) (Fig. 3).

Memory

Since all prey was edible in this test, the birds could have re-learned to accept the conspicuous prey as food if they sampled the signalling prey items. However, we did not observe a trend that the birds would gradually kill more and more signalling prey in the memory test: we divided the 15 prey items the birds were allowed to kill into three series of five items and compared the numbers of signalling prey killed in the first and the last series. None of the six treatments showed significant changes in the numbers of signalling prey killed in the beginning and the end of the memory test (Wilcoxon test, all $P > 0.171$). This was also true for relative predation of signalling prey that was calculated for the series of five items similarly to the learning curves above (Wilcoxon test, all $P > 0.138$). Relative predation takes into account that the birds could, for example, concentrate on the cryptic prey and thus increase their attacks on the signalling prey towards the end of the trial because the cryptic prey would become rare and more difficult to find. The total numbers of prey killed in the learning trial and in the memory test correlated positively in all treatments ($0.350 \leq r \leq 0.810$, over all treatments $r = 0.638$, $P < 0.001$) indicating that birds that killed more defended prey in the learning trial were also more willing to sample the signalling prey in the memory test. A negative correlation would have suggested that a higher level of punishment during learning results in stronger avoidance in the future.

For the total number of signalling prey killed in the memory test, there was a main effect of unpalatability level (ANOVA $F_{2,87} = 3.295$, $P < 0.05$). *Post-hoc* test revealed that birds from the moderate unpalatability

treatments (1 and 4) killed more signalling prey in the memory test than birds from the mixed (LSD = 2.040, $P < 0.05$) or high (LSD = 2.080, $P < 0.05$) unpalatability treatments but there was no difference in the numbers of signalling prey consumed when the mixed (2 and 5) and high unpalatability treatments (3 and 6) were compared (LSD = -0.040, $P = 0.963$) (Fig. 4). There was no main effect of signal treatment ($F_{1,87} = 0.053$, $P = 0.818$) and no two-way interaction between the unpalatability and signal treatments ($F_{2,87} = 0.318$, $P = 0.729$) which

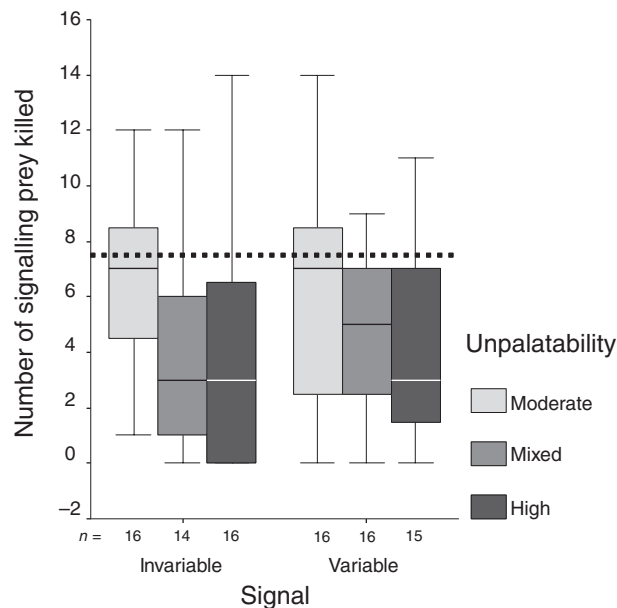


Fig. 4 Total numbers of signalling prey killed in the memory test. Reference line shows the random expectation for the number of signalling prey killed. Boxplots show minimum, maximum and the upper and lower quartiles around the median.

shows that the birds from the moderate unpalatability treatments killed more signalling prey irrespective of whether the signal was (and had been in the learning trial) invariable or variable (Fig. 4). This is in contrast to the learning trial where the mortality of the moderately defended prey depended on the signal treatment (compare Figs 2 and 4). It seems that this interaction disappeared in the memory test as the birds had ‘forgotten’ (see Discussion) about the inedibility of the signalling prey in the case of moderately defended prey with a variable signal (treatment 4). To measure ‘forgetting’ we compared the end of the learning trial and the beginning of the memory test; we subtracted the numbers of signalling prey killed within the last 10 prey items of the learning trial from the first 10 prey items of the memory test. This difference was significantly different from zero only in the case of treatment 4 (one-sample t -test $t_{15} = 2.611$, $P < 0.05$) (Fig. 5) indicating a change in the willingness to attack signalling prey.

Overall, the birds that had experience on either mixed or high unpalatability clearly avoided previously unpalatable prey (i.e. killed less signalling prey in the memory test than expected by their frequency alone) (one-sample

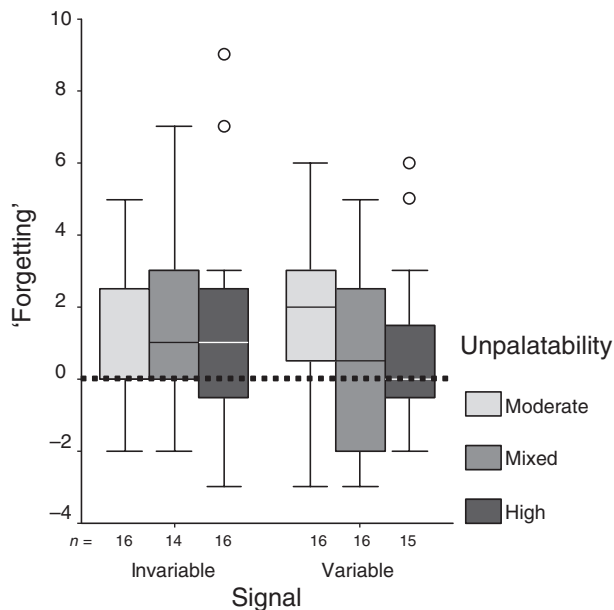


Fig. 5 ‘Forgetting’ measured as the difference in the numbers of signalling prey killed between the first 10 prey items of the memory test and the last 10 prey items of the learning trial. Values above the zero reference line indicate that the birds have been more willing to attack the signalling prey in the beginning of the memory test than in the end of the learning trial. Values below zero indicate that the birds have killed less signalling prey in the beginning of the memory test than in the end of the learning trial. Boxplots show minimum, maximum and the upper and lower quartiles around the median. Open circles denote outliers.

test $t_{29} = -5.258$, $P < 0.001$ for mixed and $t_{30} = -4.321$, $P < 0.001$ for high unpalatability, tested against random expectation of 7.5). The numbers of signalling prey killed by the birds from the moderate unpalatability treatments did not differ from random expectation ($t_{31} = -1.681$, $P = 0.103$). Thus, the memory test does not demonstrate a benefit of invariable vs. variable signal. It shows that high unpalatability has created stronger avoidance than moderate unpalatability but that the mixture of these produced a strong avoidance as well.

Discussion

The classical Müllerian mimicry theory assumes that signal monomorphism in aposematic prey aids avoidance learning of predators (Müller, 1879), and thus predicts that predators learn faster if a warning signal is uniform rather than variable. This theory does not take into account that the levels of unpalatability (or other secondary defences) of the co-mimics can vary in nature. Recent theoretical work predicts that differences in unpalatability among prey that share a warning signal can cause predators to attack a mixture of highly and moderately unpalatable prey more than highly unpalatable prey alone (Speed, 1993, 1999a; Speed & Turner, 1999). We did not find unambiguous support for these hypotheses in an experiment where inexperienced bird predators learned to avoid aposematic prey. Variation in unpalatability and signal of the aposematic prey did not have negative effects on predator learning (i.e. did not increase attacks on the defended prey) (Fig. 2). Instead, the signal type (variable/uniform) and unpalatability (moderate/mixed/high) had an interaction, and moderately defended prey gained greater benefit from signal variation than signal monomorphism (Fig. 2), which contradicts the classical assumption.

Overall, the predation pressure was similar for the aposematic prey in all treatments except where all aposematic prey was moderately unpalatable and had a uniform signal (treatment 1). Thus, when there was no variation in the warning signal (treatments 1–3), the birds killed more aposematic prey when they were moderately defended rather than highly defended, indicating that when the punishment was less severe, they were slower to learn to avoid the aposematic prey and forage on the cryptic prey. This is in accordance with the general understanding of animal learning (see Pearce, 1997 pp. 56–59) and also in line with the learning rate rules used in computer simulations by Speed (1993) and Turner *et al.* (1984). Although slow, learning did take place in the case of moderately distasteful prey as well, since the relative amount of aposematic prey sampled declined during the trial (Fig. 3). Despite the elementary finding that moderate unpalatability was indeed moderate, presenting the birds with a mixture of both highly and moderately unpalatable prey did not change their rate of learning compared with the situation where all

prey was highly distasteful (Figs 2 and 3). 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, as could be predicted based on theoretical work on quasi-Batesian mimicry (Huheey, 1976; Speed, 1993, 1999a; Speed & Turner, 1999). However, computer simulations used in theoretical studies are typically run for thousands of iterations and learning and forgetting are seen as an ongoing alteration in attack probability, whereas in this experiment we apply the prediction to the period of the predator's first encounters with defended prey.

Variation in unpalatability level did not seem to hamper learning (see also Skelhorn & Rowe, 2004), which may be explained through the observation that the birds typically started the trial by attacking the visible aposematic prey. In the case of mixed unpalatability half of this prey was still highly unpalatable, and it could be that after the first bites the birds lost sensitivity to the quinine concentration and simply did not detect the difference in distastefulness. If they did detect the difference, the result may be due to risk-averse behaviour; the highly unpalatable prey items may be so distasteful to the birds that they were discouraged to attack the aposematic prey altogether. With equal probabilities of encountering highly and moderately defended aposematic prey, the risks of eating a defended item would outweigh the possible benefits of eating one. The birds' aversion to variable unpalatability could also be due to some effect of contrast in the rewards from the different prey types (see Alm Bergvall & Leimar, 2005).

Furthermore, when the warning signal was variable (treatments 3–6), the level of unpalatability did not affect the birds' learning rate, even when comparing highly and moderately unpalatable prey (Figs 2 and 3). Instead, when the signal was variable the birds killed approximately the same amount of aposematic prey as in treatments 2 and 3 (variably and highly defended with invariable signal, respectively) irrespective of the level of unpalatability. This further suggests that the predator's reactions to levels of defence are not straightforward and that variation in the signal did not hamper learning. In the case of moderately unpalatable prey, the birds preyed on them less when their signal was variable rather than uniform (Figs 3 and 4, treatments 1 and 4), which opposes the basic assumption of Müllerian mimicry theory (Müller, 1879).

Müllerian mimicry theory assumes that for aposematic prey a shared signal is better a strategy against inexperienced predators than different signals (Müller, 1879). Our results do not support this but they are in accordance with previous findings from similar experiments (Rowe *et al.*, 2004; Lindström *et al.*, 2006, see also Ham *et al.*, 2006). From the prey's perspective, it seems that having a variable signal was as good a strategy as having a monomorphic signal to advertize unprofitability. How-

ever, it is also assumed that some variation is allowed in the warning signal of Müllerian co-mimics, as it is in the predator's interest to generalize unpalatable prey and avoid them. Accurate resemblance is more likely in Batesian mimicry where a predator loses a potential prey item when mistaking a mimic for a model (e.g. Fisher, 1958; Huheey, 1988; Mappes & Alatalo, 1997; but see Goodale & Sneddon, 1977; Cuthill & Bennet, 1993; Dittrich *et al.*, 1993). Since the birds in the pilot test confirmed that Great tits can distinguish between the two conspicuous signals, it cannot be argued that the birds would not be able to see or would completely ignore variation in the warning signal. In the absence of colours, differences in pattern could become significant, but the signals seemed in retrospect to be readily generalized by the birds. Signal variation was not without its effects, however, in the case of moderately defended prey signal variation decreased predation. The data for moderately defended prey illustrates the possibility that instead of interfering with learning a variable signal could make inexperienced birds more careful in their approach to unfamiliar prey. One could speculate that if moderate defences in aposematic species (Srygley & Chai, 1990; Sargent, 1995) are common, such gain from dissimilar signals could help in explaining the variation in warning signals that is sometimes said to be paradoxical (Joron & Mallet, 1998).

However, the possible benefit of predator wariness seemed short-lived; in the memory test the birds were more willing to attack signalling prey when they had experienced moderately distasteful prey in the learning trial, and this was independent of the signal treatment. The change in killing rate of signalling prey between the end of the learning trial and the beginning of the memory test (forgetting) was clearest in treatment 4 (moderately defended, variable signal). So, despite the (hypothetical) hesitation to attack the variably signalling prey during learning the birds seemed to have learnt about the moderate defences and were more willing to sample such prey later. Alternatively, the combination of mild taste and variable signal was the most forgettable association.

The birds that had previously experienced mixed unpalatability were as reluctant to sample the signalling prey in the memory test as were the birds that had encountered highly defended prey (Fig. 4). This further indicates that predators may not simply react to average unpalatability of a prey mixture. The memory test did not show any benefits of having a monomorphic signal compared to having a variable signal.

The notion that variation in the warning signal and secondary defences seems to matter little should be generalized cautiously. For example, when both unpalatability and signal were variable (treatment 5), one bird killed 45 aposematic prey items and only five cryptic ones, which indicates that variation might confuse some individuals (Fig. 2). The experimental environment used

in the present study was relatively simple: predators in more complex environments may behave differently and thus create different selection pressures on aposematic prey (Beatty *et al.*, 2004). For instance, the birds always faced only one type of edible, cryptic prey so that 'the flip side of the coin' in the discrimination task remained the same despite the added variation in the aposematic prey (as noted by Ruxton *et al.*, 2004 p. 125). The birds might simply have concentrated on the edible prey. If it is natural behaviour for a naïve predator to first learn the coarse distinction between what to eat and what to avoid (see Wallace, 1867; Fisher, 1958, p. 165; Sherratt & Beatty, 2003) rather than to gain detailed knowledge of prey that is inedible, the result that signal/unpalatability variation in inedible prey matters little to inexperienced predators could hold in more species rich systems as well.

It should also be kept in mind that here we are studying the learning phase of predators (see also Rowe *et al.*, 2004 for discussion), following Müller's (1879) original idea. However, natural prey populations are also exposed to experienced hunters and different predator species. Field experiments with transferred aposematic butterflies have indeed demonstrated the benefits of similarity in appearance (Mallet & Barton, 1989; Kapan, 2001). In these experiments, the predator community was likely to have been more varied. Some Müllerian co-mimic species resemble each other with noticeable accuracy (see e.g. Symula *et al.*, 2001), which also suggests that there can be selection against signal variation but considering the present results and those of Rowe *et al.* (2004) and Lindström *et al.* (2006), inexperienced predators may not be the selective agent for accurate mimicry (see Langham, 2004, 2006 but see Beatty *et al.*, 2004). Long-term studies where the behaviour of predators could be observed when they gain more experience could prove fruitful. Furthermore, individual variation in the behaviour of the inexperienced predators and their learning abilities should not be overlooked. For example, even in the case of highly unpalatable prey, some individual Great tits consumed less than 10 aposematic prey items to learn to avoid them whilst others took more than 20 (Fig. 2). Similarly, in the memory test some birds ate 14 signalling prey items whilst some took none (Fig. 4), and some birds even seemed to increase their avoidance of the conspicuous prey compared with the end of the learning trial (Fig. 5).

Interestingly, Skelhorn & Rowe (2004) found that two different defence chemicals in artificial Müllerian co-mimics resulted in faster avoidance learning than one chemical. Two different chemicals is not necessarily the same thing as two levels of unpalatability but considering the variety of chemicals in aposematic prey (see Weller *et al.*, 1999; Nishida, 2002), the result is something to take into account when predicting predator behaviour towards defended prey. Note that in an experiment similar to the present study by Lindström *et al.* (2006) the

effect of unpalatability on prey mortality depended on the design and thus the strength of the signals in question. The present results are not confounded by differences in signal efficacy but the general observation of the inconsistent effect of unpalatability level still holds. This may seem discouraging from the point of view of the theoretical developments that try to close the gap between Müllerian and Batesian mimicry. Moreover, the concept of quasi-Batesian mimicry is not fully accepted on theoretical grounds (Mallet & Joron, 1999; Mallet, 1999). However, there are also data that lend support to the importance of varying unpalatability level (Speed *et al.*, 2000) and the data comes from an experiment very different to this present study. Therefore, to increase our understanding of Müllerian mimicry and the role of predator behaviour in it, and to produce more applicable building blocks for theoretical work, experiments that use different predator species, with different amounts of experience, and more complex prey communities, as well as studies where memory and forgetting can be observed over a long-term (see Speed, 1999b) will likely prove useful. In addition to studies of the underlying behavioural mechanisms, experiments with different total densities of prey will give useful insights to the evolution of mimicry.

Acknowledgments

We thank Helinä Nisu, Joonas Pekkanen, Hannah Rowland, the staff in Konnevesi Research Station and the resident Great tits in Konnevesi for proficient assistance. Thanks to Mike Speed and the journal club in our department for helpful comments on the manuscript and to Olof Leimar and Alexandra Balogh for hints about contrast effects. Two anonymous reviewers gave valuable comments on the manuscript. The study was financed by the Academy of Finland under the Finnish Centre of Excellence programme.

References

- Alatalo, R.V. & Mappes, J. 1996. Tracking the evolution of warning signals. *Nature*, **382**: 708–710.
- Alm Bergvall, U. & Leimar, O. 2005. Plant secondary compounds and the frequency of food types affect food choice by mammalian herbivores. *Ecology*, **86**: 2450–2460.
- Balogh, A.C.V. & Leimar, O. 2005. Müllerian mimicry: an examination of fisher's theory of gradual evolutionary change. *Proc. R. Soc. Lond. B*, **272**: 2269–2275.
- Bates, H.W. 1862. Contributions to an insect fauna of the amazon valley lepidoptera: Heliconidae. *Trans. Linn. Soc. Lond.* **23**: 495–556.
- Beatty, C.D., Beirincx, K. & Sherratt, T.N. 2004. The evolution of müllerian mimicry in multispecies communities. *Nature*, **431**: 63–67.
- Bowers, M.D. & Farley, S. 1990. The behaviour of grey jays, *perisoreus canadensis*, towards palatable and unpalatable lepidoptera. *Anim. Behav.* **39**: 699–705.

- Brower, J.v.Z. 1958. Experimental studies of mimicry in some north american butterflies part i the monarch, *Danaus plexippus*, and viceroy, *Limenitis archippus archippus*. *Evolution*. **12**: 32–47.
- Brower, L.P., Brower, J.v.Z. & Collins, C.T. 1963. Experimental studies of mimicry 7. Relative palatability and müllerian mimicry among neotropical butterflies of the subfamily heliconiinae. *Zool. N. Y. Zool. Soc.* **48**: 65–81.
- Brower, L.P., Ryerson, W.N., Coppinger, L.L. & Glazier, S.C. 1968. Ecological chemistry and the palatability spectrum. *Science*. **161**: 1349–1350.
- Cuthill, I.C. & Bennet, A.T.D. 1993. Mimicry and the eye of the beholder. *Proc. R. Soc. Lond. B.* **253**: 203–204.
- Dittrich, W., Gilbert, F., Green, P., McGregor, P. & Grewcock, D. 1993. Imperfect mimicry: a pigeon's perspective. *Proc. R. Soc. Lond. B.* **251**: 195–200.
- Eggenberger, F. & Rowell-Rahier, M. 1992. Genetic component of variation in chemical defence of *Oreina gloriosa* (coleoptera: Chrysomelidae). *J. Chem. Ecol.* **18**: 1375–1387.
- Fisher, R.A. 1927. On some objections to mimicry theory; statistical and genetic. *Trans. R. Entomol. Soc. Lond.* **75**: 269–278.
- Fisher, R.A. 1958. *The General Theory of Natural Selection*. Denver Publication, New York.
- Goodale, M.A. & Sneddon, I. 1977. The effect of distastefulness of the model on the predation of artificial batesian mimics. *Anim. Behav.* **25**: 660–665.
- Ham, A.D., Ihalainen, E., Lindström, L. & Mappes, J. 2006. Does colour matter? The importance of colour in avoidance learning, memorability and generalisation. *Behav. Ecol. Sociobiol.* **60**: 482–491.
- Huheey, J.E. 1976. Studies of warning coloration and mimicry. VII. Evolutionary consequences of batesian-müllerian spectrum: a model for müllerian mimicry. *Evolution*. **30**: 86–93.
- Huheey, J.E. 1980. Studies in warning coloration and mimicry vii. Further evidence for a frequency-dependent model of predation. *J. Herpetol.* **14**: 223–230.
- Huheey, J.E. 1988. Mathematical models of mimicry. *Am. Nat.* **131**: S22–S41.
- Joron, M. & Mallet, J.L.B. 1998. Diversity in mimicry: paradox or paradigm? *TREE*. **13**: 461–466.
- Kapan, D.D. 2001. Three-butterfly system provides a field test of müllerian mimicry. *Nature*. **409**: 338–340.
- Kokko, H., Mappes, J. & Lindström, L. 2003. Alternative prey can change model-mimic dynamics between parasitism and mutualism. *Ecol. Lett.* **6**: 1068–1076.
- Langham, G.M. 2004. Specialized avian predators repeatedly attack novel color morphs of *Heliconius* butterflies. *Evolution*. **58**: 2783–2787.
- Langham, G.M. 2006. Rufous-tailed jacamars and aposematic butterflies: do older birds attack novel prey? *Behav. Eco.* **17**: 285–290.
- Lindström, L., Alatalo, R.V. & Mappes, J. 1997. Imperfect batesian mimicry – the effects of the frequency and the distastefulness of the model. *Proc. R. Soc. Lond. B.* **264**: 149–153.
- Lindström, L., Lyytinen, A., Mappes, J. & Ojala, K. 2006. Relative importance of taste and visual appearance for predator education in müllerian mimicry. *Anim. Behav.* **72**: 323–333.
- MacDougall, A. & Dawkins, M.S. 1998. Predator discrimination error and the benefits of müllerian mimicry. *Anim. Behav.* **55**: 1281–1288.
- Mallet, J.L.B. 1999. Causes and consequences of a lack of coevolution in müllerian mimicry. *Evol. Ecol.* **13**: 777–806.
- Mallet, J.L.B. 2001. Mimicry: an interface between psychology and evolution. *PNAS*. **98**: 8928–8930.
- Mallet, J.L.B. & Barton, N.H. 1989. Strong natural selection in a warning-color hybrid zone. *Evolution*. **43**: 421–431.
- Mallet, J.L.B. & Joron, M. 1999. Evolution of diversity in warning color and mimicry: polymorphisms, shifting balance and speciation. *Annu. Rev. Ecol. Syst.* **30**: 201–233.
- Mappes, J. & Alatalo, R.V. 1997. Batesian mimicry and signal accuracy. *Evolution*. **51**: 2050–2053.
- Marples, N.M. & Kelly, D.J. 1999. Neophobia and dietary conservatism: two distinct processes?. *Evol. Ecol.* **13**: 641–653.
- Marshall, G.A.K. 1908. On diaposematism with reference to some limitations of the müllerian hypothesis of mimicry. *Proc. Entomol. Soc. Lond.* **1**: 93–142.
- Müller, F. 1879. Ituna and thyridia: a remarkable case of mimicry in butterflies. *Proc. Entomol. Soc. Lond.* XX–XXIX.
- Nishida, R. 2002. Sequestration of defensive substances from plants by lepidoptera. *Annu. Rev. Entomol.* **47**: 57–92.
- Owen, R.E. & Owen, A.R.G. 1984. Mathematical paradigm for mimicry: recurrent sampling. *J. Theor. Biol.* **109**: 217–247.
- Pearce, J.M. 1997. *Animal Learning and Cognition. An Introduction*. Psychology Press, Hove, UK.
- Pilecki, C. & O'Donald, P. 1971. The effects of predation on artificial mimetic polymorphisms with perfect and imperfect mimics at varying frequencies. *Evolution*. **25**: 365–370.
- Poulton, E.B. 1890. *The Colours of Animals Their Meaning and Use Especially Considered in the Case of Insects*. Kegan Paul, Trench, Trübner & Co. Ltd, London.
- Rowe, C. & Guilford, T. 1996. Hidden colour aversions in domestic chicks triggered by pyrazine odours of insect warning displays. *Nature*. **383**: 520–522.
- Rowe, C., Lindström, L. & Lyytinen, A. 2004. The importance of pattern similarity between müllerian mimics in predator avoidance learning. *Proc. R. Soc. Lond. B.* **271**: 407–413.
- Ruxton, G.D., Sherratt, T.N. & Speed, M.P. 2004. *Avoiding Attack – The Evolutionary Ecology of Crypsis, Warning Signals and Mimicry*. Oxford University Press, Oxford.
- Sargent, T.D. 1995. On the relative acceptabilities of local butterflies and moths to local birds. *J. Lepid. Soc.* **49**: 148–162.
- Schuler, W. & Hesse, E. 1985. On the function of warning coloration: a black and yellow pattern inhibits prey-attack by naive domestic chicks. *Behav. Ecol. Sociobiol.* **16**: 249–255.
- Sheppard, P.M., Turner, J.R.G., Brown, K.S.J., Benson, W.W. & Singer, M.C. 1985. Genetics and the evolution of müllerian mimicry in *Heliconius* butterflies. *Phil. Trans. R. Soc. Lond. B.* **308**: 433–613.
- Sherratt, T.N. & Beatty, C.D. 2003. The evolution of warning signals as reliable indicators of prey defence. *Am. Nat.* **162**: 377–389.
- Sherratt, T.N., Speed, M.P. & Ruxton, G.D. 2004. Natural selection on unpalatable species imposed by state-dependent foraging behaviour. *J. Theor. Biol.* **228**: 217–226.
- Skelhorn, J. & Rowe, C. 2004. Tasting the difference: do multiple defence chemicals interact in müllerian mimicry? *Proc. R. Soc. Lond. B.* **272**: 339–345.
- Smith, S.M. 1975. Innate recognition of coral snake pattern by a possible avian predator. *Science*. **187**: 759–760.
- Smith, S.M. 1977. Coral-snake pattern recognition and stimulus generalisation by naive great kiskadees (aves: Tyrannidae). *Nature*. **265**: 535–536.

- Speed, M.P. 1993. Müllerian mimicry and the psychology of predation. *Anim. Behav.* **45**: 571–580.
- Speed, M.P. 1999a. Batesian, quasi-batesian or müllerian mimicry? Theory and data in mimicry research. *Evol. Ecol.* **13**: 755–776.
- Speed, M.P. 1999b. Robot predators in virtual ecologies: the importance of memory in mimicry studies. *Anim. Behav.* **57**: 203–213.
- Speed, M.P. & Turner, J.R.G. 1999. Learning and memory in mimicry: II. Do we understand the mimicry spectrum? *Biol. J. Linn. Soc.* **67**: 281–312.
- Speed, M.P., Alderson, N.J., Hardman, C. & Ruxton, G.D. 2000. Testing müllerian mimicry: an experiment with wild birds. *Proc. R. Soc. Lond. B.* **267**: 725–731.
- Srygley, R.B. & Chai, P. 1990. Predation and the elevation of thoracic temperature in brightly colored neotropical butterflies. *Am. Nat.* **135**: 766–787.
- Symula, R., Schulte, R. & Summers, K. 2001. Molecular phylogenetic evidence for a mimetic radiation in peruvian poison frogs supports a müllerian mimicry hypothesis. *Proc. R. Soc. Lond. B.* **268**: 2415–2421.
- Thomas, R.J., Marples, N.M., Cuthill, I.C., Takahashi, M. & Gibson, E.A. 2003. Dietary conservatism may facilitate the initial evolution of aposematism. *Oikos*. **101**: 458–466.
- Turner, J.R.G. 1977. Butterfly mimicry: the genetical evolution of and adaptation. *Evol. Biol.* **10**: 163–206.
- Turner, J.R.G. 1987. The evolutionary dynamics of batesian and müllerian mimicry: Similarities and differences. *Ecol. Entomol.* **12**: 81–95.
- Turner, J.R.G. & Mallet, J.L.B. 1996. Did forest islands drive the diversity of warningly coloured butterflies? Biotic drift and the shifting balance. *Proc. R. Soc. Lond. B.* **351**: 835–845.
- Turner, J.R.G. & Speed, M.P. 1996. Learning and memory in mimicry. I. Simulations of laboratory experiments. *Phil. Trans. R. Soc. Lond. B.* **351**: 1157–1170.
- Turner, J.R.G., Kearney, E.P. & Exton, L.S. 1984. Mimicry and the monte carlo predator: the palatability spectrum and the origins of mimicry. *Biol. J. Linn. Soc.* **23**: 247–268.
- Wallace, A.R. 1867. Journal of proceedings of the entomological society of London. In: *In Transactions of the Entomological Society of London* vol. III.
- Weller, S.J., Jacobson, N.L. & Conner, W.E. 1999. The evolution of chemical defences and mating systems in tiger moths (lepidoptera: Arctiidae). *Biol. J. Linn. Soc.* **68**: 557–578.

Received 16 May 2006; revised 19 July 2006; accepted 31 July 2006