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The importance of pattern similarity between Müllerian mimics in predator avoidance learning

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Müllerian mimicry, where unpalatable prey share common warning patterns, has long fascinated evolutionary biologists. It is commonly assumed that Müllerian mimics benefit by sharing the costs of predator education, thus reducing *per capita* mortality, although there has been no direct test of this assumption. Here, we specifically measure the selection pressure exerted by avian predators on unpalatable prey with different degrees of visual similarity in their warning patterns. Using wild-caught birds foraging on novel patterned prey in the laboratory, we unexpectedly found that pattern similarity did not increase the speed of avoidance learning, and even dissimilar mimics shared the education of naive predators. This was a consistent finding across two different densities of unpalatable prey, although mortalities were lower at the higher density as expected. Interestingly, the mortalities of Müllerian mimics were affected by pattern similarity in the predicted way by the end of our experiment, although the result was not quite significant. This suggests that the benefits to Müllerian mimics may emerge only later in the learning process, and that predator experience of the patterns may affect the degree to which pattern similarity is important. This highlights the need to measure the behaviour of real predators if we are to understand fully the evolution of mimicry systems.

Keywords: *Parus major*; evolution; mimicry; aposematism; discrimination learning; receiver psychology

1. INTRODUCTION

Unpalatable animals across a wide taxonomic distribution signal their distastefulness to visually hunting predators using striking aposematic patterns (Poulton 1890; Cott 1940; Edmunds 1974). At a very general level, these warning patterns share common attributes such as being extremely conspicuous or containing the colours red or yellow, but the similarities between the patterns of some sympatric species render them almost indistinguishable (e.g. Heliconid butterflies (Kapan 2001), Peruvian poison frogs (Symula *et al.* 2001) and New Guinea pitohuis (Dumbacher & Fleischer 2001)). The adaptive advantage to having such similar patterns is assumed to be that individuals of both species benefit through sharing local predator education. According to the original mathematical model of Müller (1879), if a predator attacks a fixed number of prey before learning to associate a colour pattern with unpalatability, then prey species would benefit from having the same colour pattern since this number would then be shared between them. Therefore, there should be selection for colour monomorphism among species, and an increasing degree of mimicry between species should increase their *per capita* survival chances.

Although Müller's original idea dates back over a hundred years, his assumption that it takes predators longer to learn to avoid two aposematic patterns than a single pattern has not been experimentally tested in a Müllerian complex. This is surprising since mathematical simulations of Müllerian mimicry have shown that predator learning rules may be crucial in determining the evolutionary trajectories of mimicry systems (Speed 1993; Turner & Speed 1996; MacDougall & Dawkins 1998; Speed & Turner 1999).

These simulations use rules based on how animals learn to associate negative reinforcement with a single stimulus (Rescorla & Wagner 1972) and assume, like Müller, that predators learn each prey pattern separately when they are different. There are no experimental data to support or dispute the applicability of these learning rules to Müllerian mimicry, although predators taught to avoid a particular aposematic species will subsequently avoid its mimics (Brower 1958; Brower *et al.* 1963; Platz *et al.* 1971). Evidence for pattern convergence is striking in natural history observations (Cott 1940; Wickler 1968; Edmunds 1974), but there have been few experimental field studies (Mallet & Barton 1989; Speed *et al.* 2000; Kapan 2001). Perhaps the best experimental evidence for selection for pattern convergence by predators comes from a translocation study with Heliconid butterflies, where unpalatable individuals (either yellow or white in appearance) were moved to areas where they matched or contrasted with the locally abundant monomorphic model species (Kapan 2001). Survival rates for translocated butterflies were lower when they were a different colour from the dominant model in the area than when they were the same colour (especially when released at low densities). This suggests that visually hunting predators that had already learned to avoid the unpalatable butterfly local to the area generalized their avoidance to butterflies with similar patterns, although there were no direct observations of predation. Therefore, like the earlier studies with captive birds (Brower 1958; Brower *et al.* 1963; Platz *et al.* 1971; Alatalo & Mappes 1996), this shows the benefits to mimics of generalization by educated predators, but does not test Müller's idea that one pattern is easier to learn to avoid than two.

Here, we test specifically the main assumption of Müllerian mimicry that *per capita* survival rates of mimetic species will increase with increasing similarity between their patterns owing to them sharing predator education.

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We manipulated the degree of visual similarity between pairs of Müllerian mimics and looked at how this affected the speed with which avian predators learned to avoid unpalatable prey. The study was carried out in a 'novel world' (Alatalo & Mappes 1996; Lindström *et al.* 2001), where wild-caught great tits (*Parus major*) foraged on the floor of a laboratory for food packaged in small paper packets. The advantage of using this system is that these paper packets can be printed with novel monochromatic symbols towards which the birds are unlikely to have any pre-existing biases.

However, before we could test the learning in Müllerian mimicry, we had to create appropriate patterns for our mimics. The results from three initial experiments confirmed that the patterns we selected did not elicit initial biases (preference test), were more conspicuous than cryptic palatable prey (visibility test) and had different levels of similarity (discrimination test) when given to our predators. After these initial experiments we tested Müller's original predictions that

(i) predator avoidance learning should be faster when mimics are more similar; and
(ii) *per capita* survival rates of mimics should be enhanced when they appear more similar to each other.

2. MATERIAL AND METHODS

(a) *Predators*

We used wild-caught great tits (*P. major*) in a series of experiments in an artificial laboratory environment that has been called the 'novel world' (for further details see Alatalo & Mappes (1996) and Lindström *et al.* (1999*a*, 2001)). Wild great tits were caught around Konnevesi Research Station between January and April 2001 and in December 2002. Birds were caught and held under licences from the Central Finland Regional Environment Centre (nos. LS-2 and LS-12, Dnro 0900L0872/254; LS-46/01, Dnro 0901L0448/254) with permission from the Ethical Committee of the University of Jyväskylä (permission nos 29/14.11.2000 and 19/5.6.2001). Birds were housed individually in illuminated plywood cages (65 cm × 80 cm × 65 cm) where they had free access to sunflower seeds and water, except during training periods when only artificial prey were present. After the experiment, all birds were released in the area from which they were taken.

(b) *Artificial prey*

We used artificial prey consisting of small slices of almond (*ca.* 80 mg) glued between two 10 mm × 10 mm pieces of white paper. Birds were initially trained to open these paper packages in their cages and eat the food inside. The artificial prey that we used in the experiments were similar to these training prey except that they had monochromatic symbols printed on them. We had one prey type that always contained palatable pieces of almond and was printed with a cross (✕); this symbol was cryptic when presented in the experimental set-up (see § 2*d*). We also had three prey types containing unpalatable pieces of almond that had been soaked in 67 g l⁻¹ of chloroquinine phosphate solution for 1 h. Three symbols were used to signal unpalatability, which were deliberately chosen to be more conspicuous than the palatable cryptic prey so that they were truly aposematic. In previous experiments, great tits learned to discriminate between palatable and unpalatable prey using

crosses and crossed squares (▧) (Lindström *et al.* 1999*b*; Riipi *et al.* 2001), and therefore we decided to use the crossed square as our focal model aposematic prey pattern. We then chose two further signals that were not only conspicuous but also visually distinguishable from the model to different degrees. One was a simple square (■), which we considered to be more similar to the model than our second symbol, a star (✳). We checked our subjective interpretation of the degree of similarity by measuring the degree of coincidence between black and white areas of the patterns: the model and the square showed 95% coincidence in the black and white areas of their patterns, while the model and the star shared only 80% of their black and white patterns. We also conducted a discriminability test, which showed that birds perceived the model to be more akin to the square than to the star (see § 2*e*). As a consequence we refer to the squares as 'similar mimics' and to the stars as 'dissimilar mimics' in relation to the model in our experiments.

(c) *Preference test*

We first looked to see whether birds showed any innate bias towards any of our aposematic symbols. Subjects were randomly assigned to one of two groups, which received 12 sequential presentations of two prey items, which were a pair of either similar mimics (i.e. a model and a square, *n* = 13) or dissimilar mimics (i.e. a model and a star, *n* = 15). Subjects were tested individually in a white-floored cage (30 cm × 24 cm × 40 cm) and offered two palatable prey items on a tray that was placed on the floor *ca.* 10 cm from a perch (see details in Lindström *et al.* (1999*a*)). The pieces of almond in each prey package weighed 85–100 mg to ensure that birds could not bias their choices according to reward size. After birds had taken and eaten one of the prey items, the rejected prey was removed and, after a short delay, a new pair of prey was offered. The positions of the two prey types were swapped between each trial to control for side biases. The experiment was conducted in two series of six trials with a break between the series, and the number of each prey type that each bird took was recorded.

(d) *Visibility test*

As in the natural world, we wanted our unpalatable prey to be more conspicuous than the palatable cryptic prey. To test this, we conducted a visibility test in two identical aviaries (3.4 m × 3.9 m × 2.5 m) where the floors were covered with eight rows and 10 columns of A3 size (42 cm × 29.6 cm) white paper sheets (80 in total) covered with transparent self-adhesive book-covering film (Pelloplast). Each sheet had 70 crosses irregularly printed on it, and 10 fake cryptic prey items (a cryptic cross glued onto paperboard) were glued to each sheet. Thus, the sheets were three-dimensional, which made it more difficult for the birds to detect the prey, encouraging them to pay attention to the symbols to find food. Between each row there was a wooden plank along which the birds could move and handle the prey. There were two handling perches, one on each side of the room, and water was provided at all times. Aviaries were illuminated with four 75 W bulbs. We used 14 subjects from the preference test, taking seven birds from each treatment (i.e. seven birds had been given similar mimic pairs and the other seven had received dissimilar mimic pairs). Birds in this experiment were given the same symbols as they had received in their preference test to ensure that they were equally familiar with both conspicuous symbols. To equalize any potential bias against cryptic prey, they were given five of each prey type (the cryptic and both conspicuous prey) in their cages prior to testing. In the experiment, birds were given 15 cryptic

Table 1. Configurations of unpalatable prey types experienced by each experimental group in the Müllerian mimicry experiment ($n = 10$ for all groups).

group number	unpalatable prey present	symbols	mimic density[a]	mimicry (%)[b]
1	dissimilar mimic only	✳	20	100
2	similar mimic only	■	20	100
3	model only	▉	20	100
4	model/similar mimic	▉/■	20 (10/10)	95
5	model/dissimilar mimic	▉/✳	20 (10/10)	80
6	model only	▉	40	100
7	model/similar mimic	▉/■	40 (20/20)	95
8	model/dissimilar mimic	▉/✳	40 (20/20)	80

[a] Figures in parentheses refer to the numbers of each prey type when there is more than one.
[b] Mimicry refers to the degree of coincidence between patterns of the two halves of the mimicry complex; situations where there is only one symbol type can be considered as two species with identical patterns (100% mimicry).

prey, 15 models and either 15 similar mimics (the squares) or 15 dissimilar mimics (the stars), all palatable, placed randomly on the background sheets. Birds were allowed to attack (touch or eat) 21 prey in each of two trials on consecutive days, and the order of their attacks was recorded.

(e) *Discrimination test*

To ensure that the unpalatable prey patterns were visually distinct to birds, we gave two new groups of birds a series of trials where they had to learn to discriminate between 20 models and either 20 squares ($n = 6$) or 20 stars ($n = 5$). One of the prey types contained unpalatable pieces of almond (the model was unpalatable for three birds in each treatment). These trials were carried out in the experimental aviaries, but the sheets were plain white to ensure that all prey were highly visible. Prey were randomly arranged on the sheets. Birds were given a single trial a day on consecutive days, and were allowed to attack (touch or eat) 15 prey in each trial. The number of trials that a bird was given depended upon the discrimination task: there were four trials for the birds given the easier (model versus star) discrimination, and five trials for those with the harder (model versus square) discrimination. The number of palatable and unpalatable prey attacked was recorded.

(f) *Müllerian mimicry experiment*

We tested 80 new birds over a seven week period in a learning experiment where each bird received a series of five trials and trials were run on consecutive days. Subjects were randomly assigned to one of eight experimental treatments that were run in parallel throughout this period (groups were balanced for gender). In each trial, all groups were given 20 cryptic palatable prey (crosses) but the type and number of unpalatable prey varied according to experimental group (see table 1 for details). To test whether there were any differences in the speed of learned avoidance of our three unpalatable prey patterns, three groups were given 20 unpalatable prey that were either all models, all squares or all stars (groups 1–3 in table 1). To look for the selection pressure necessary for Müllerian mimicry, we gave two further groups of birds 20 unpalatable prey that were either equal numbers of models and squares or equal numbers of models and stars (groups 4 and 5 in table 1). Comparing the numbers of unpalatable prey attacked in groups 4 and 5 with those in groups where there was only one prey pattern (groups 1–3) allowed us to test the importance of increasing visual similarity. This is because these five groups can be thought of as being

Müllerian mimicry pairings where there is 80%, 95% or 100% pattern similarity (see table 1). We also looked for an effect of prey density on learning rates by increasing the number of unpalatable prey presented from 20 to 40 in three final groups (groups 6–8 in table 1). At this density we used only the models on their own (100% or perfect mimicry) and two further groups that had 20 models and 20 similar mimics (95% mimicry) or 20 models and 20 dissimilar mimics (80% mimicry). Birds were allowed to open 15 prey in each of five trials conducted on consecutive days. The number of each prey type eaten was recorded.

3. RESULTS

(a) *Preference test*

For each pair of prey that was presented, either the model and the similar mimic (the square) or the model and the dissimilar mimic (the star), we recorded both the type of prey that a bird first attacked, as our measure of preference, and the type that it finally took to the perch to eat since this differed in some cases. We looked for a bias in the first six trials and all 12 together, for similar and dissimilar mimics separately, in each case using a one-sample t-test against the random expectation. As we performed multiple tests of the same hypothesis, the significance thresholds were Bonferroni corrected. Analysing which prey type the birds touched first did not reveal any biases, either in the first six trials (one-sample t-test on the number of models attacked, random expectation = 3: with similar mimics, mean $\pm$ s.e. = 3.1 ± 0.26, $t = 0.291$, $p > 0.1$, d.f. = 12; with dissimilar mimics, mean $\pm$ s.e. = 3.1 ± 0.35, $t = 0.381$, $p > 0.1$, d.f. = 14) or across all 12 trials (one-sample t-test on the number of models attacked, random expectation = 6: with similar mimics, mean $\pm$ s.e. = 5.8 ± 0.44, $t = 0.353$, $p > 0.1$, d.f. = 12; with dissimilar mimics, mean $\pm$ s.e. = 6.7 ± 0.59, $t = 1.361$, $p > 0.1$, d.f. = 14). The results for the numbers eaten at the perch similarly showed no significant biases.

(b) *Visibility test*

We calculated the visibility scores of each prey type by attributing a value of 21 to the first prey attacked, 20 to the second one, and so on, with the last prey eaten being given a value of 1. We then summed these scores for each prey type to give the relative risk of being detected by a predator. These scores are non-independent within each

Table 2. Mean (± s.e.) visibility scores (see § 2b for details of how the scores were calculated) for all prey types used in the visibility test.
(Relatively low scores indicate that the birds were slow to find these prey, whereas high scores indicate that these prey were detected more readily. Bonferroni corrected threshold for significance is 0.017.)

treatment	prey type	visibility score	paired *t*-test, with co-mimic ■/✳	paired *t*-test, with cryptic prey ✕
similar, *n* = 7	▐	105.14 (± 6.35)	$t = 0.36, p = 0.73$	$t = 8.07, p = 0.0002$
	■	101.14 (± 5.69)		$t = 8.94, p = 0.0001$
	✕	24.43 (± 5.01)		
dissimilar, *n* = 7	▐	112.43 (± 4.83)	$t = 3.03, p = 0.023$	$t = 8.80, p = 0.0001$
	✳	85.93 (± 5.63)		$t = 5.14, p = 0.002$
	✕	32.64 (± 5.81)		

trial but a rough guide to their differences was gauged by paired *t*-tests (Bonferroni corrected by dividing the significance thresholds by the number of tests, i.e. three). Table 2 shows the visibility scores for each prey type in each experimental group, with higher values indicating consumption earlier in the trials. The visibility scores for our three aposematic patterns were significantly higher than those for the cryptic prey, confirming that they were more conspicuous. However, although the visibility scores of the models and the similar mimics were the same, when the birds were given models and dissimilar mimics, there may have been a tendency for them to attack more of the models (see table 2).

(c) Discrimination test

In the first trial, birds attacked prey types equally and at random (see figure 1). We tested for discrimination in every trial by comparing the scores with random expectation using one-sample *t*-tests (Bonferroni corrected for the number of tests, i.e. the significance threshold was 0.0125 for the test with the dissimilar mimics and 0.01 for that with the similar mimics). When birds had to discriminate between models and dissimilar mimics, there was a significant avoidance of unpalatable prey from trial 3 onwards, with the number of unpalatable prey eaten being lower than that expected by chance (one-sample *t*-test, test value = 7.5: trial 3, $t = 7.01, p < 0.01$, d.f. = 5; trial 4, $t = 5.09, p < 0.01$, d.f. = 5). Discrimination between the model and the similar mimic apparently took longer to learn: there may have been a slight tendency for birds to avoid unpalatable prey in trial 4 (one-sample *t*-test: $t = 2.25, p = 0.088$, d.f. = 4), but a significant reduction in the number of unpalatable prey eaten was seen only in trial 5 (one-sample *t*-test: $t = 6.50$, $p < 0.01$, d.f. = 4). Comparing individual bird's regression slopes of the number of unpalatable prey eaten plotted against trial number confirmed that learning was faster when the mimic was dissimilar compared with when it was similar (*t*-test: $t = 2.64, p < 0.05$, d.f. = 9). Birds therefore perceive the difference between the model and the mimics, and find the square more similar to the model than to the star as seen in the differences in the learning rates between the two discriminations.

(d) Müllerian mimicry experiment

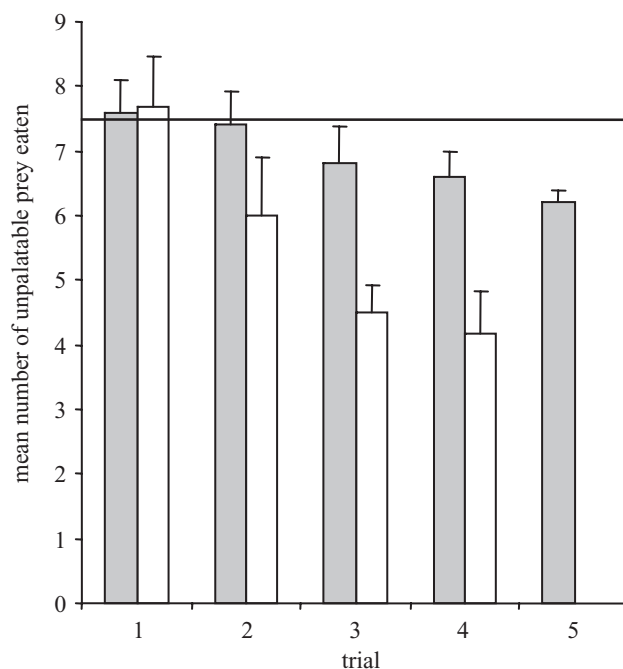All three of our aposematic patterns were effective signals, with birds learning to avoid the unpalatable prey

Figure 1. The mean number (+ s.e.) of unpalatable prey eaten in each trial of the discrimination learning test. Shaded bars represent trials where the model and mimic were similar (■, 95% pattern coincidence), whereas unshaded bars represent trials where the model and mimic were dissimilar (✳, 80% pattern coincidence). The line at 7.5 indicates random choice, with scores less than 7.5 showing that subjects discriminated against unpalatable prey.

during the experiment. We first looked to see whether there were any differences in the ways that birds learned about each of our three conspicuous signals by comparing the results from the three groups that had received 20 unpalatable prey of only a single prey type (groups 1–3 in table 1). We analysed both the total number of unpalatable prey eaten and how quickly birds learned to avoid the unpalatable prey. There were no significant differences in the total number of unpalatable prey eaten between the three signals (one-way ANOVA: $F_{2,27} = 0.18, p > 0.1$). To test for any more subtle differences in the speed of learning between the three different aposematic signals, we compared the mortalities of the unpalatable prey type across all trials. Mortality was calculated as the number

of that prey type eaten divided by the total number of that type that were available, and these proportional data were then arcsine square-root transformed to be used in the ANOVA. All groups showed significant learning in the discrimination task with mortality decreasing across trials (repeated-measures ANOVA: $F_{4,108} = 39.24$, $p < 0.001$), but there was no interaction between learning and the prey type ($F_{8,108} = 0.766$, $p > 0.1$) showing that there were no differences in the rates of learning between our three conspicuous symbols. As there were no apparent differences in the numbers eaten or the learning rates among our three aposematic symbols, we pooled the results from these three groups in the following analyses.

A prediction arising from the original hypothesis of Müller (1879) is that increasing pattern similarity between unpalatable species should reduce the number of unpalatable prey eaten. We therefore looked at the effect of mimic similarity (100%, 95%, 80%) at both densities (20 or 40) on the total number of unpalatable prey eaten across all five trials. There was no interaction between mimic similarity and density (two-way ANOVA: $F_{2,74} = 1.453$, $p > 0.1$), but there was a main effect of density, with birds eating more unpalatable prey at higher the density ($F_{2,76} = 11.27$, $p < 0.01$). There was no effect of pattern similarity on the numbers eaten ($F_{2,76} = 0.89$, $p > 0.1$), which suggests that birds are not learning to avoid unpalatable prey more quickly when patterns are more similar.

However, analysing just the total numbers eaten in all trials could mask differences that are occurring in the learning process across the trials. We therefore analysed the total mortality of unpalatable prey using a two-way ANOVA with mimic density and pattern similarity as main factors, but also including trial number in a repeated-measures design (see figure 2). There was no three-way interaction between trial, mimic density and pattern similarity (repeated-measures ANOVA: $F_{8,296} = 0.74$, $p > 0.1$) and no two-way interaction between mimic density and trial ($F_{4,304} = 1.09$, $p > 0.1$), although there was a nearly significant interaction between pattern similarity and trial ($F_{4,304} = 1.76$, $p = 0.085$). There was a significant effect of learning as seen by a main effect of the trial ($F_{4,304} = 73.61$, $p < 0.001$), and also unpalatable prey had lower mortality at higher density ($F_{1,76} = 50.8$, $p < 0.001$; see figure 2). Therefore, birds seem to be learning to avoid unpalatable prey at similar rates regardless of the degree of mimicry, although the nearly significant interaction between trial number and pattern similarity suggests that there may be a weak effect of pattern similarity on learning rates.

Closer inspection of figure 2 suggests that in trial 5 the mortality is affected by pattern similarity in the way predicted by mimicry theory, i.e. at both unpalatable-prey densities, mortality of unpalatable prey decreases with increasing pattern similarity. We therefore analysed the mortality of unpalatable prey in just the fifth trial, where learning was most advanced. There was a significant effect of unpalatable prey density (two-way ANOVA: $F_{1,76} = 10.17$, $p < 0.01$) and a nearly significant effect of pattern similarity ($F_{2,76} = 2.41$, $p = 0.097$); there was no significant interaction ($F_{2,74} = 0.25$, $p > 0.1$). Again, this analysis suggests that the degree of similarity between unpalatable prey might be starting to become an important factor in the learning process by trial 5.
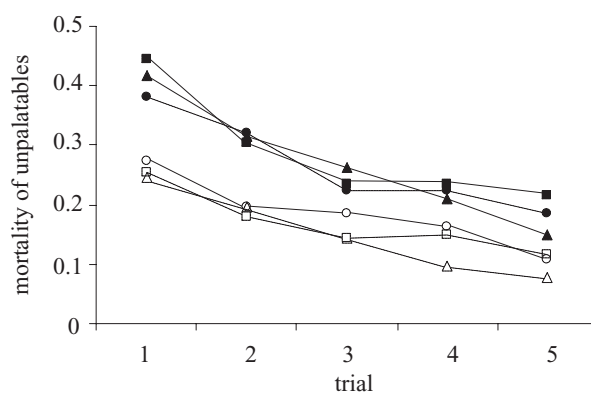
Figure 2. The mean mortality of unpalatable prey in each of the five learning trials, showing the effects of prey density and similarity (standard errors are not shown for clarity). Filled symbols represent the scores when there were 20 unpalatable prey, and open symbols represent the scores when there were 40 unpalatable prey presented. At each density, squares represent 80% mimicry (where stars and models were presented together), circles represent 95% mimicry (where squares and models were presented together) and triangles represent 100% mimicry (where the model or one of the mimics was presented alone).

This finding led us to look more closely at the data from trial 5, and analyse the mortality of each unpalatable prey type separately in this final trial (see figure 3). For the models, at both densities the mortality is as predicted from Müllerian mimicry theory, with *per capita* mortality being higher when paired with the dissimilar mimic (stars), than when paired with the similar mimic (squares) and lowest of all when it is the only pattern (identical mimic; figure 3a). It is possible to see the same effect on mortality of the mimics, with mortality being lower when they are the only prey type present than when they are paired with the model (figure 3b). We can test this ordered prediction in these data using a non-parametric ANOVA (Meddis 1984). The prediction that increasing similarity decreases mortality was supported: mortality for unpalatable prey was lower when there was 100% mimicry than when there was 95% or 80% mimicry, in the predicted order (specific non-parametric ANOVA 100% > 95% > 80%: $Z = 1.68$, $p < 0.05$). However, this test is not a wholly balanced design since birds from the 80% and 95% mimicry groups at low density contribute two points to the model. Owing to the non-independence of the data, we repeated the test using just the results for the models where there is a balanced design (i.e. the data from figure 3a only). In this case, the prediction is not quite significant (specific non-parametric ANOVA 100% > 95% > 80%: $Z = 1.56$, $p = 0.06$).

4. DISCUSSION

The results of our experiment were surprising. Predator avoidance learning was not significantly faster when one pattern signalled unpalatability than when there were two different patterns, and increasing pattern similarity between the mimics did not improve their mortality over all trials (seen in figure 2). This is contrary to the traditional assumption of Müllerian mimicry that mimics share the cost of predator education because one pattern should be easier to learn than two (Müller 1879).
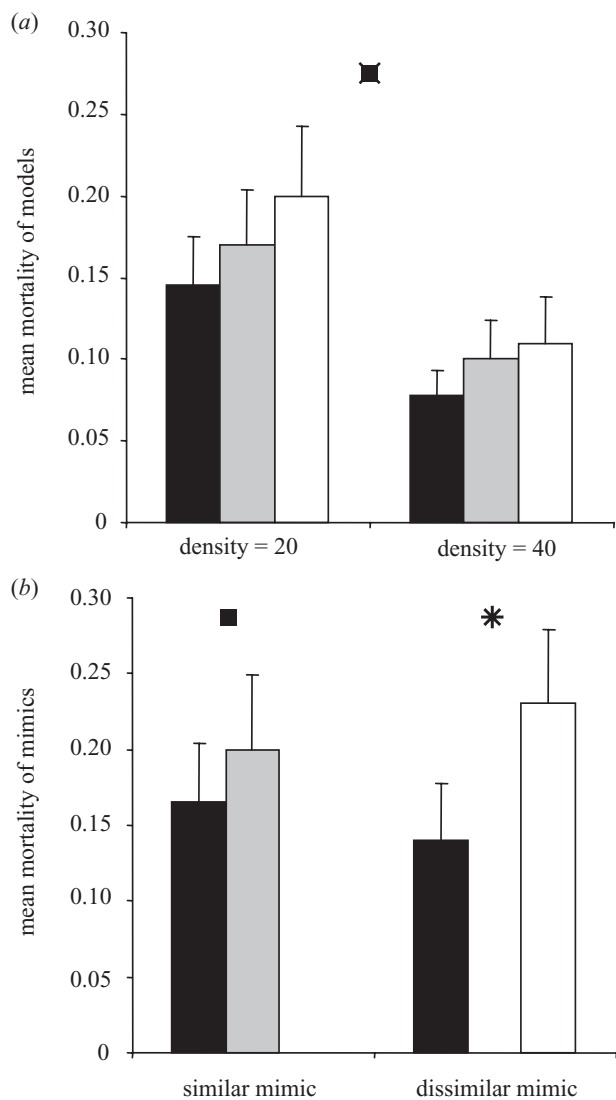
Figure 3. The mean mortality (+ s.e.) of each aposematic prey type in trial 5 of the Müllerian mimicry experiment. (a) The mortality of the models at both densities when they were presented alone (100% mimicry, black bars), with similar mimics (95% mimicry, grey bars) or with dissimilar mimics (80% mimicry, white bars). (b) Mean mortality for both the mimics, when presented alone (100% mimicry, black bars) or with the models (95% mimicry, grey bars for the similar models; 80% mimicry, white bars for the dissimilar mimics).

Although there were no detectable effects of pattern similarity on learning and mortality rates across our experiment, our data do suggest that benefits of pattern similarity may emerge at a later stage in the learning process (see figure 3). This was consistent at both unpalatable-prey densities that we used, although, as one might expect, the mortality rates were lower at the higher density (Lindström *et al.* 2001). These results show that the way in which predators learn to avoid Müllerian mimics is more complicated than previously thought (but see Turner & Speed 1996).

Müllerian mimicry theory proposes that predator behaviour exerts strong selection on pattern monomorphism in unpalatable prey. Experiments with avian predators have indeed shown that once a bird is familiar with an aposematic pattern it will generalize to avoid other prey patterns that appear similar (Brower 1958; Brower *et al.* 1963; Platz *et al.* 1971; Alatalo & Mappes 1996). These studies support the idea that educated predators can select for pattern convergence, but they do not demonstrate any benefits of convergence through sharing the costs of educating naive predators as Müller (1879) suggested. What our data show is that a more general similarity, such as being conspicuous, may be sufficient for mimics to benefit in the initial education process. The lack of strong selection against pattern dissimilarity could explain imperfect mimicry and problematic polymorphisms in Müllerian mimicry complexes (Turner 1987; Joron & Mallet 1998; Mallet & Joron 1999). This finding is in some sense counter-intuitive since there are many examples of perfect mimicry between unpalatable species in a wide range of taxa (Kapan 2001; Symula *et al.* 2001; Dumbacher & Fleischer 2001), so is it that perfect mimicry is selected by educated rather than naive predators?

There is some evidence to support this idea in the later stages of our experiment. In the last two trials, mortality of unpalatable prey was consistent with the predictions of Müllerian mimicry, with increasing pattern similarity tending to reduce mortality. It could be that birds recognized the difference between the model and the mimic patterns from the start of the experiment, but that the differences in learning were so small that they were undetectable in the early trials. Alternatively, it could be that the birds responded to our conspicuous patterns as if they were identical because it takes them time to realize that there are differences between them. Our discrimination test showed that it took birds several days to learn to distinguish between our model and the dissimilar mimic, and slightly longer to distinguish between the model and the similar mimic. Therefore, perhaps it is not surprising that there is no evidence that birds are learning the patterns separately in the first few days of the mimicry experiment, since predators may become aware of the pattern differences only after several days. How predators perceive differences between symbols in the learning process may be a crucial factor in determining pattern similarity in natural mimicry systems; however, there are differences between our mimicry system in the laboratory and those in the wild that suggest that we should be cautious before we extrapolate these results to all natural predator–prey systems.

One potential difference between the selection pressures we measured in the laboratory and those that may occur in the wild is that we used a generalist predator, and perfect Müllerian mimicry may evolve in response to predation from more experienced specialists. Specialist butterfly predators, for instance, may pay more attention to subtle differences in wing patterns because they have a lot of experience with these prey, and selection may be even more intense when food is scarce. It may also be that the use of artificial symbols in our experiment masked birds' abilities to discriminate among symbols when the signal or context is more familiar (Osorio *et al.* 1999; see also Gamberale-Stille & Tullberg 2001). Secondly, we used equal frequencies of models and mimics in our mimicry complex, and different results might have been obtained if we had fewer mimics than models. If mimics were relatively rare, we might see stronger selection for pattern similarity since positive frequency-dependent selection could act against the mimic if it were too dissimilar (see, for example, Kapan

2001; Lindström *et al.* 2001). Finally, our results may be partly caused by the identical unpalatability of our model and mimic since this could reduce the need for the predator to pay attention to the patterns. If models and mimics differ in their unpalatability, as in cases of quasi-Batesian mimicry (Speed 1993), it may be beneficial to a predator to learn these prey separately, and therefore we might expect more pattern similarity between models and mimics.

Despite these potential constraints on the interpretation of our results, what our data do seem to show is that birds can learn to avoid unpalatable prey with relatively dissimilar patterns as readily as those that have identical patterns. Experimental evidence of predator behaviour is scarce, and this is the first investigation of how naive birds actually learn to avoid Müllerian mimics encountered simultaneously in their environment. There has been a proliferation of models of Müllerian dynamics that depend upon knowing predator learning rules and much debate on the accuracy of the outcome of these models (Speed 1993, 1999; Turner & Speed 1996; MacDougall & Dawkins 1998; Joron & Mallet 1998; Mallet & Joron 1999; Speed & Turner 1999; Mallet 1999). Our unexpected result can only highlight the need for more accurate assessment of predator behaviour to understand the evolution of Müllerian mimicry and mimicry systems in general.

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