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Relative importance of taste and visual appearance for predator education in Müllerian mimicry

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Müllerian mimicry, by definition, is the visual resemblance between two or more aposematic prey species. According to classical Müllerian mimicry theory, comimics draw mutual benefits from the resemblance because predators have to learn to avoid only one colour pattern. In contrast, the relatively untested quasi-Batesian mimicry theory suggests that, because of differences in unpalatablility, the less toxic mimic acts like a parasite on the more defended prey, decreasing its fitness. We tested predation pressures on artificial mimicry complexes in which comimics varied both in visual similarity and in taste. Both signal and taste were important for the survival of comimics. Predators learned to avoid two similarly conspicuous comimics differently when they were presented alone, suggesting that the signals were unequal. Despite the discrepancy in signal, imperfect visual mimicry did not increase the total number of comimics eaten, as suggested by the classical theory. Great tits, *Parus major*, learned to avoid highly unpalatable prey faster than mildly unpalatable prey. However, variation in palatability did not unequivocally increase the total mortality of models; instead, the effects depended on the signal of the prey. These results indicate that Müllerian mimicry dynamics may change depending on the configuration of mimicry complexes.

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Müllerian mimicry (Müller 1879) is a classic example of an antipredatory defence, where two or more aposematic species have sometimes strikingly similar warning patterns, such as the warning colours of the poison frogs of Peru (Symula et al. 2001). It also, however, includes imperfect mimicry such as the crude yellow and black colour pattern shared by several species (see references in Gilbert 2005). The benefit of this resemblance is that if predators learn to avoid the warningly coloured prey from a fixed experience (Cott 1940; Edmunds 1974; but see discussion by Sherratt 2002a; Sherratt & Beatty 2003), mimetic species (i.e. possessing adequate similarity) will have lower per capita mortality rates than dissimilar species for which predators have to learn each pattern separately (Müller 1879; but see Ihalainen & Suutari 2003; Rowe et al. 2004). On the basis of this premise, Müllerian mimicry is considered an example of mutualism where the cost of educating a predator is shared between similar prey types and the benefits of the resemblance can be calculated for each prey type by its frequency in a population (Müller 1879; Joron & Mallet 1998). Müllerian mimicry,

like aposematism, is a strategy that is more beneficial the more common it is (Greenwood et al. 1989; Lindström et al. 2001a; Kapan 2001). This positive frequency dependence creates selection against dissimilar patterns, further promoting monomorphism in a warning pattern (Benson 1972; Mallet & Barton 1989; Kapan 2001).

Surprisingly, although Müller's original idea on the shared learning costs of comimics dates back to the 19th century, the data supporting the theory are mainly indirect observations of predation in the field (Benson 1972; Mallet & Barton 1989; Kapan 2001). These mark–recapture studies show that dissimilar butterflies introduced to established mimicry rings are heavily predated compared to perfect mimics that share the common warning pattern, supporting Müller's idea. Similarly, predation experiments in the laboratory have concentrated on testing the value of the predator's ability to generalize (predator generalization), that is, if the predator is aware of the model, how it behaves against a similar mimic (e.g. Brower 1958; Alatalo & Mappes 1996). These results only confirm that predators are capable of generalizing an acquired avoidance to another species. The available data on predator learning patterns with respect to mimicry indicate, contrary to the theory, that dissimilarity does not always have negative effects on avoidance learning towards conspicuous prey (Ihalainen & Suutari 2003; Rowe et al.

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2004). Thus, the learning process might not promote similarity.

Furthermore, Müller's (1879) theory did not consider the degree of unprofitability of the two prey types but only the signal similarity (but see Turner 1984; Mallet 1999). It was later suggested that the resemblance between comimics might not be mutually beneficial but that the dynamics might depend on the difference in palatability between the comimics (Huheey 1976, 1984; Owen & Owen 1984; Speed 1993, 1999; Speed & Turner 1999). The basis for this assumption is that mimicry can be found between aposematic models and nonaposematic (perfectly edible) mimic species. This phenomenon is called Batesian mimicry (Bates 1862) where predators are deceived into avoiding conspicuous mimics along with the aposematic models. The dynamics of Batesian mimicry differ from those of Müllerian mimicry in that the resemblance benefits only the mimics. As the Batesian mimics are perfectly edible to predators, the protection achieved by resembling the aposematic models is eroded the more common the Batesian mimics are in the prey population (Fisher 1930; Nur 1970; Matthews 1977; Turner 1987). If mimics are too common, the predators do not learn to avoid the aposematic signal and this limits the population size of the mimics. Therefore, some Batesian mimics are polymorphic, resembling several models (e.g. the females of *Papilio dardanus*: Clarke & Sheppard 1960, 1962; Nijhout 2003). The dynamics of Batesian mimicry also depend on the degree of unprofitability of the model (Duncan & Sheppard 1965; Lindström et al. 1997), the accuracy of the mimicry (Goodale & Sneddon 1977; Mappes & Alatalo 1997) and the availability of alternative prey (Hetz & Slobodchikoff 1988; Kokko et al. 2003; Lindström et al. 2004). Highly toxic models can therefore maintain higher numbers of inaccurate Batesian mimics without costs (but see Sherratt 2002b). If there are palatability differences between Müllerian comimics, the dynamics of Müllerian mimicry might be more similar to those of Batesian mimicry than assumed by classical Müllerian mimicry theory.

Several studies have drawn attention to Müller's original theory (Huheey 1976, 1984; Owen & Owen 1984; Speed 1993, 1999; Speed & Turner 1999; Speed et al. 2000) and, in particular, its failure to take into account the palatability differences between comimics (but see Turner et al. 1984; Mallet 1999; Mallet & Joron 1999; Turner & Speed 1999). There are two main reasons why differences in palatability need to be taken into account to understand the dynamics of mimicry complexes. First, there is enormous intraspecific variation in toxic compounds present in some prey species (e.g. in the most detailed aposematic species studied, the monarch butterfly, *Danaus plexippus*: Brower et al. 1968, 1972). Therefore, it is unlikely that unrelated species would be exactly or even similarly unpalatable. In fact, some studies have indicated that Müllerian mimics are indeed differently palatable to predators (Brower 1958; Brower et al. 1963; Ritland & Brower 1991). Second, predators learn to avoid highly unpalatable prey more quickly than moderately unpalatable prey (Duncan & Sheppard 1965; Lindström et al. 1997). Thus, it is logical to assume that variation in the levels of unpalatability of Müllerian comimics interferes with predators' avoidance learning.

If the less toxic mimic slows the avoidance learning of the predator, this should increase the number of mimetic aposematic prey that need to be eaten to produce avoidance by predators (Speed et al. 2000). Mathematical simulations (Speed 1993, 1999) and empirical data (Speed et al. 2000) suggest that it is the more toxic species that pays this increase in total number of aposematic prey eaten, as its mortality would increase compared to a situation without mimicry. If these were the case, then the less defended prey would benefit from the mimicry in the same way that Batesian mimics benefit. Thus, Speed (1993, 1999) suggested that mimicry between two unpalatable species resembling each other without mutual benefits should be termed quasi-Batesian mimicry. Despite the wide interest in the dynamics of Müllerian mimicry (e.g. Huheey 1976; Turner et al. 1984; Speed 1993; Turner & Speed 1996; Joron & Mallet 1998; Mallet 1999; Mallet & Joron 1999; Speed & Turner 1999), only a few experimental studies have tested how the palatability difference between Müllerian comimics affects the attack rates and the learning performance of wild predators (Speed et al. 2000; Ihalainen & Suutari 2003; but see the overview of psychological literature on learning, e.g. Mackintosh 1994).

In our first experiment we tested the predation pressures that naïve predators generate on an aposematism complex with two conspicuous prey types and one cryptic prey type. The density of cryptic palatable prey undoubtedly affects the number of models and mimics eaten (Kokko et al. 2003; Lindström et al. 2004). To overcome this problem we kept the total density of aposematic prey constant (model alone versus model + mimic) in our experiment. This allowed us to test directly whether the number of aposematic prey eaten increases as a result of the introduction of the mimic. We used both visually imperfect and perfect mimicry to assess the importance of the signal in mimicry systems. To produce imperfect mimicry, we used symbols that were slightly different, that is, predators could potentially separate the two unpalatable conspicuous prey types. However, even though our models and mimics were not classic mimics (i.e. indistinguishable), they were similar enough to produce a mimetic advantage. We were also interested in testing whether variation in level of unpalatability within perfect visual mimicry had similar effects. As we presented the comimics in equal frequencies (50:50), the fitness benefits for both prey types were assumed to be equal (Müller 1879; see also Marshall 1908). Any deviation, therefore, indicates that one type benefited more from the resemblance. In a second experiment we tested whether predators remembered unpalatable prey and generalized their avoidance to other prey types. These experiments allowed us to assess: (1) the importance of the signal of unpalatable prey for predation pressure; (2) the importance of taste for predation pressure; (3) whether variation in palatability within the mimicry complex increases the predation of 'models' and whether the presence of a mildly unpalatable 'mimic' introduces quasi-Batesian dynamics to the mimicry system; and (4) how experience, imperfect mimicry (difference in

signal) and variation in palatability contribute to the generalization ability and memory of the predators.

METHODS

These experiments were carried out at Konnevesi Research Station, central Finland, from February to April 2002. We used wild great tits, *Parus major*, as predators, captured from feeding sites around the station. We used a prebaited trap (a box 15×15 cm and 40 cm high containing peanuts) which had an entrance that could be closed with a trap door. The size of the entrance was such that only great tits could enter the trap. The traps were placed so that we could see when birds entered them. We used the trap door only when capturing birds, and we shut it by pulling a string attached to the door. Each bird was removed immediately after capture. This method allowed us to capture only unringed great tits that had not been used in previous experiments. Central Finland Regional Environment Center gave us permission to capture and keep the birds and the Ethical Committee of the University of Jyväskylä gave permission for the study. Birds were kept individually in illuminated plywood cages (65×65 cm and 80 cm high) on a diet of sunflower seeds and tallow at a temperature of $10°C$. Each cage contained three perches. Birds were food deprived 2 h before being tested but fresh water was available ad libitum. The experiments were done in February−April to avoid disturbing the birds' breeding. Birds were kept an average $\pm$ SE of 17.98 ± 0.57 days in captivity. None of the birds showed any signs of ill health. After the study, all birds were released to the sites from which they were originally captured.

Experimental Aviaries

The predation experiment was run in a large aviary (58 m^2) and the memory experiment in a small aviary (13 m^2). A novel world with a landscape of crosses (Alatalo & Mappes 1996; Lindström et al. 1999) was set up in both aviaries. The floor was covered with white European standard A3 size paper sheets, which were glued together and covered with adhesive plastic. On each sheet were 71 randomly printed crosses and 10 crosses cut out of white cardboard and glued randomly on the sheet. The cardboard crosses represented fake prey, whose purpose was to make the background three-dimensional, so that cryptic prey items (see below) would not be too discernible. The novel landscape of the large aviary consisted of 15 rows and 22 columns, that is, 330 sheets of A3 paper (size 42×29.6 cm), covering an area of 41 m^2 of the floor. Between the rows were wooden planks along which the birds could move. The rows and columns were assigned letters and numbers and this information was noted on the side of the planks, allowing us to determine where birds were feeding. The aviary contained 12 equally distributed perches for birds to handle the prey items (see below). Four sheets under each of the eight perches that were attached to the wooden planks and two sheets under each wall-attached perch were left empty of prey. This was done to ensure that the handled prey items were not mixed up with the unconsumed prey when we were making observations. Thus, there were 290 possible sheets upon which prey items could be placed. In the small aviary, the landscape was formed of eight rows and 10 columns (80 A3 sheets in total). Four handling perches were provided, two on each side of the aviary. As the small size made for easier observation, prey items could be placed on all 80 sheets.

Prey Items

We used artificial prey items consisting of a piece of almond glued between two pieces of paper with a symbol printed on each side (Lindström et al. 2001b; Ihalainen & Suutari 2003). We made these prey items by gluing a tiny slice (ca. 8 mg) of almond between two 10×10-mm pieces (width 2 mm) of white paper which formed a 'shell' that birds had to open to get the almond. These black and white symbols were either cryptic or conspicuous. Cryptic symbols were similar to the crosses on the paper background (Lindström et al. 1999, 2001b). Two aposematic symbols, an irregular star and a square (Fig. 1), were dissimilar to the background symbols and therefore effectively conspicuous (Ihalainen & Suutari 2003; see also Lindström et al. 1999, 2001b). These two symbols, stars and squares, were chosen on the basis of three criteria: (1) birds should have no prior preference for either symbol; (2) they should be equally conspicuous; and (3) signals should be slightly distinguishable and thus different. We tested these assumptions in different experiments (Ihalainen & Suutari 2003). We made aposematic prey items unpalatable by soaking the sliced almonds in two concentrations of Heliopar solution (active ingredient chloroquinine, 250 mg/tablet; mild: 1 tablet/30 ml; strong: 8 tablets/30 ml). The pieces of almond were then dried and glued between the two pieces of paper. Birds were taught to open palatable artificial prey items without symbols (Lindström et al. 2001b) before the experiments.

Predation Experiment

We scattered prey items randomly in eight blocks with no more than one prey item per sheet of paper. We marked prey types on a map of the aviary to keep track of which prey was which, because it was not possible to identify the prey by sight from a distance. Each bird was offered 200 randomly placed prey items (100 palatable cryptic prey and 100 unpalatable conspicuous prey; see below) of which it was allowed to eat only 30. Each trial lasted until the bird had eaten 30 prey items ($\overline{X} \pm \text{SE} = 1$ h 13 min $\pm$ 385 s). Depending on the bird's performance we ran one to five trials per day (median 2).

Treatments

We used a three by three factorial design (Fig. 1) in which we varied both the signal and the taste of the unpalatable prey. In nine treatments that tested each of these factors against the others, birds were presented with the

Signal	Mildly unpalatable	Variably palatable (both tastes)	Strongly unpalatable
Irregular star	Group 1 N = 12 100 / 100	Group 2 N = 11 50:50 / 100	Group 3 N = 7 100 / 100
Square	Group4 N = 11 100 / 100	Group 5 N = 11 50:50 / 100	Group 6 N = 7 100 / 100
Both signals	Group 7 N = 12 50:50 / 100	Group 8 N = 14 50:50 / 100	Group 9 N = 13 50:50 / 100

Figure 1. The set-up for the predation experiment, sample sizes and the frequencies of different (aposematic/cryptic) prey types. We used a 3 by 3 design, to test the effects of signal (irregular star, square, both) and unpalatability levels (mildly unpalatable, both tastes, strongly unpalatable) on the overall predation of Müllerian comimics. Shaded cells indicate mimetic treatments. The treatment where both unpalatability and signals varied (group 8) is formed of two groups where the star was strongly unpalatable and the square mildly unpalatable or the square was strongly unpalatable and the star mildly unpalatable. There was no difference in the total number of unpalatable items eaten in these two groups (Mann–Whitney test: $Z = -0.258$, $N_1 = N_2 = 7$, $P = 0.796$) and so these two groups were pooled in the complete analysis.

prey with irregular stars, squares, or both symbols in three configurations of taste. The aposematic prey were mildly unpalatable, strongly unpalatable or a mixture of these two levels of unpalatability. When the level of unpalatability was kept constant, we assessed the importance of the signal, and when the signal was kept constant, we assessed the importance of palatability to bird predation on this mimicry complex.

We assigned 98 great tits to the nine experimental groups (Fig. 1). The treatments were undertaken in parallel to avoid possible seasonal effects, with each bird tested individually. Thus, all nine treatments lasted over the course of the experiment (67 days). Groups 1–6 were offered prey with a constant signal (groups 1–3: irregular stars; groups 4–6: squares), but with taste varying between the treatments (mildly unpalatable, highly unpalatable or both tastes). Birds were offered prey with both irregular stars and squares together in groups 7–9, with the taste varying between the treatments as in groups 1–6.

As the encounter rate of alternative prey directly influences the number of aposematic prey types eaten (Lindström et al. 2001a, 2004), we kept the number of aposematic prey constant (at 100) for all treatments. In the treatments with variation in signal, palatability level or both (i.e. the shaded cells in Fig. 1), the different types of aposematic prey were offered in an equal 50:50 ratio. In other words, when birds faced variation in palatability, but not in signal, they were presented with stars (or squares), half of which were strongly unpalatable and the other half mildly unpalatable. When the birds faced variation in signal but not in palatability, they were presented with strongly (or mildly) unpalatable stars and squares in a 50:50 ratio. Experimental group 8, which received both signals and both unpalatability levels, was constructed from two different treatments, as the

unpalatability level was kept constant within a signal. Thus, one set of birds received 50 highly unpalatable stars and 50 mildly unpalatable squares, and the other 50 strongly unpalatable squares and 50 mildly unpalatable stars. For the overall predation pressure, counted as the total number of aposematic prey eaten, there was no effect of which signal was the original 'model' and which was the 'mimic' (Mann–Whitney test: $U = -0.258$, $N_1 = N_2 = 7$, $P = 0.796$) and therefore these two groups were pooled for complete analysis.

The three by three experimental design allowed us to test the overall effects of how signal, unpalatability and variation in both of these factors affected the total number of prey eaten. However, it revealed little about the differences in mortality rates between the two comimics and, therefore, we compared 'mimicry' treatments to each other (Fig. 1) to test different hypotheses (Table 1).

Memory/Generalization Experiment

We carried out the memory/generalization experiment 1 week after the predation experiment with the same set of birds. Birds were now offered only two types of prey (cryptic and irregular stars) regardless of their previous treatment. We randomly scattered 30 prey items of each type in five blocks. Birds received only palatable prey items to prevent any further avoidance learning. For statistical analysis, we divided birds into six groups according to their experience (no experience/experience of the stars) and the unpalatability treatment they were in originally (mild, strong, both tastes). Birds were allowed to eat 10 prey items and we recorded the order in which they took them. Thus, we tested whether birds that had previously encountered unpalatable stars remembered to avoid this particular prey

Table 1. Summary of mimetic treatments where conspicuous unpalatable prey varied in signal but the unpalatability level was kept identical (groups 7 and 9), varied in palatability but the signal was kept identical (groups 2 and 5) and varied in both signal and palatability level (groups 8a and 8b)

Group	Signal	Taste	Number eaten	Percentage conspicuous (expected 50)	Frequency (expected 1)	Without mimicry (expected 1)
				Assessment of mimicry advantage		
7	Star	Mild	6.42±1.00	46±5	0.86±0.13	0.89±0.14
	Square		7.00±0.71	54±5	0.93±0.09	**0.78±0.08**
9	Star	Strong	5.15±0.76	**38±4**	**0.69±0.10**	0.96±0.14
	Square		7.54±0.48	**62±4**	1.01±0.06	1.01±0.06
2	Star	Mild	8.82±1.09	54±4	1.18±0.15	1.22±0.15
		Strong	7.55±0.87	46±4	1.01±0.12	**1.40±0.16**
5	Square	Mild	8.45±0.89	55±3	1.13±0.12	0.94±0.10
		Strong	6.73±0.59	45±3	0.90±0.08	0.91±0.08
8a	Star	Strong	5.29±0.99	**36±4**	0.70±0.13	0.99±0.19
	Square	Mild	8.71±0.47	**64±4**	**1.16±0.06**	0.97±0.05
8b	Square	Strong	6.71±1.48	52±6	0.91±0.17	0.92±0.17
	Star	Mild	6.86±1.24	48±6	0.90±0.20	0.93±0.17

The mimetic advantage between the comimics was assessed in three ways. Number eaten: the total number of a particular prey type eaten in the experiment. Percentage conspicuous: the proportion of that particular prey type eaten from all unpalatable prey items eaten. Frequency: whether a particular prey type was over- or underpredated in relation to its frequency in the whole prey population. Without mimicry: the mortality of the particular prey type in a mimicry treatment divided by the mortality of that prey type without mimicry (i.e. nonmimetic treatments). Values below one indicate that mimicry is beneficial for that prey type whereas values above one indicate that mimicry is not beneficial. Bold numbers indicate the statistical significance from random, using one-sample *t* test against 50% in proportion and 1.0 in relative predation. Means are given ± SEM. Since we chose to use several approaches in analysing the mimetic advantage, increasing the number of tests also increased the likelihood that some tests were significant just by chance.

type. We also assessed whether birds that had encountered only squares as unpalatable generalized their avoidance towards another conspicuous signal, the stars.

Statistical Analysis

First we tested whether birds showed a bias against either of our conspicuous signals by calculating how many birds chose the square or star first (groups 7−9). We also assessed possible inherent bias by testing whether the latency to start the trial depended on the signal (square versus star; analysed from groups 1−6).

For the overall predation pressure, we used two-way analysis of covariance (ANCOVA) where the number of aposematic prey eaten was a dependent variable and the aposematic signal (star, square, both) and the level of unpalatability of aposematic prey (mild, strong, both) were fixed factors. As there was a negative correlation between the date of the trial and the number of aposematic prey items eaten (Spearman rank correlation: $r_S = -0.374$, $N = 98$, $P < 0.001$), indicating that the predators ate fewer aposematic prey from the novel landscape towards the end of the experiment, we used the experimental day (first day = 1) as a covariate. There was no three-way interaction between the covariate and the fixed factors (ANOVA: signal * unpalatability * covariate: $F_{4,80} = 0.336$, NS) nor any two-way interactions (signal * covariate: $F_{2,80} = 0.677$, NS: unpalatability * covariate: $F_{2,80} = 0.256$, NS; all $P > 0.511$), which allowed us to use the experimental day as a covariate. As all treatments were done in parallel, there was no difference in the mean experimental day between the treatments (one-way ANOVA: $F_{8,97} = 0.302$, $P = 0.963$).

To test learning, we divided the total number of conspicuous prey eaten during each trial into three (first part: 1−10 prey items eaten, second part: 11−20 prey items eaten; third part: 21−30 prey items eaten). Then we calculated how many conspicuous prey items birds ate during each part. This gives us a measure of learning during the trial. We used the number of aposematic prey eaten in each part as a dependent variable in the repeated measures ANOVA, where the between-subject factors were the signal of the prey (star, square, both) and the unpalatability level of the prey (mild, strong, both). We included the experimental day as a covariate.

There are several ways to analyse the mimetic advantage and the outcome of this advantage depends on which of these comparisons one chooses. We chose three ways (Table 1). First, we tested whether birds ate the different comimics in the same proportion as they were presented. Deviation from 50:50% would indicate that one type benefited more in the system and the overpredated form would disappear from the prey population. Second, we analysed whether birds ate the mimetic prey in relation to the frequency at which they were presented. If the birds ate the mimetic forms by their frequencies, predation would be random and there would be no selection against these types compared to the cryptic type. Any deviation from the frequencies would indicate that the prey would be selected against (overpredated) or selected for (underpredated). Third, we assessed quasi-Batesian mimicry dynamics by comparing the mortality rates (which take into account the different densities of prey) of nonmimetic groups (i.e. perfect mimicry, groups 1, 3, 4, 6) to those of mimetic groups (Fig. 1) within the signal. Any deviation from this analysis would reveal what in this

particular system contributes more to the learning process of predators. All analyses were one-sample t tests to an expected value. Because we chose to use several approaches in analysing the mimetic advantage, we also increased the likelihood that some tests were significant just by chance. However, by carrying out all these analyses, we also wanted to draw attention to the fact that there are several ways of assessing the mimetic advantage and selection pressures and this could affect the way we think about the benefits of mimicry.

We used the number of stars eaten as a dependent variable in a two-way ANOVA in the memory/generalization experiment. The factors in this experiment were predators' experience of the signal (i.e. experienced versus no experience) and the level of unpalatability (mild, strong, both tastes) the birds faced in the predation experiment.

When the data did not meet the assumptions of parametric statistics we applied parametric statistics. All statistical analysis was performed with SPSS (SPSS Inc., Chicago, IL, U.S.A.) and all P values are two tailed.

RESULTS

Predation Experiment

There was no initial bias for either of the symbols since birds attacked both aposematic symbols (star versus square) equally as their first choice (analysed from groups 7−9: $\chi_1^2 = 0.64$, $P = 0.42$). Indirectly measured, there was no difference in preference between the aposematic signals, as the birds' latency to feed did not differ significantly between signal groups (analysed from groups 1−6: Mann−Whitney test: $Z = -0.56$, $N_1 = N_2 = 26$, $P = 0.58$). Therefore, all differences between the signals in the predation experiment were due to the introduction of unpalatability.

We compared the overall effects of the two factors, palatability and signal, on the total number of conspicuous prey eaten. In the ANCOVA model, experimental day was highly significant ($F_{1,88} = 19.21$, $P < 0.001$), indicating a seasonal effect on the number of aposematic prey items eaten. There was no two-way interaction between palatability and signal ($F_{4,88} = 1.71$, $P = 0.156$). The signal of the unpalatable prey had a significant effect on the number of unpalatable prey items eaten ($F_{2,88} = 4.42$, $P = 0.015$). Pairwise comparisons between estimated marginal means showed that the squares were predated most heavily (square alone versus star alone, post hoc least-significant difference: LSD = 2.31, $P = 0.029$; square versus both signals: LSD = 2.77, $P = 0.005$). This indicates that the star was a more effective signal than the square. Stars alone were predated at the same rate as the mixture of stars and squares presented simultaneously (stars alone versus both signals: LSD = 0.46, $P = 0.633$), indicating that variation in signal did not increase overall predation against a strong signal but decreased the predation against a weak signal (square). There was a nonsignificant tendency ($F_{2,88} = 2.76$, $P = 0.069$) for the level of unpalatability to have an effect on the total number of unpalatable prey items eaten (Fig. 2). The pairwise comparisons
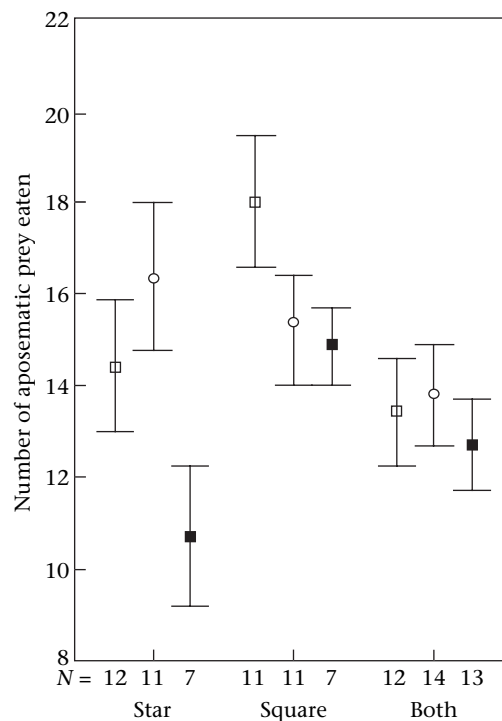

Figure 2. The mean $\pm$ SEM total number of aposematic prey types eaten depending on their signal (star or square) and unpalatability level. □: Mild; ○: variable; ■: strong unpalatability.

suggest that the strongly unpalatable prey were predated at a lower level than both the mildly unpalatable prey (LSD = −2.13, $P = 0.041$) and the prey with varying levels of unpalatability (LSD = −2.15, $P = 0.038$). This indicates that the unpalatability levels were different and variation in taste increased predation compared to that on highly unpalatable prey presented alone. This is in accordance with quasi-Batesian mimicry theory, although it did not have the same effect in all signal groups (Fig. 2). The mildly unpalatable prey was predated at the same rate as prey with both levels of unpalatability (LSD = −0.19, $P = 0.983$).

Learning was significant (repeated measures ANCOVA: $F_{2,88} = 15.23$, $P < 0.001$) indicating that, overall, birds avoided the unpalatable prey more at the end of the trial (Fig. 3). Since the aposematic prey was conspicuous, the birds attacked these prey types more at the beginning of the trial but attack rates were reduced towards the end of the trial (Fig. 3). There were no two-way interactions (learning $*$ palatability level: $F_{4,176} = 0.79$, $P = 0.53$; learning $*$ signal: $F_{4,176} = 1.18$, $P = 0.32$; learning $*$ covariate: $F_{2,88} = 1.66$, $P = 0.19$) or three-way interaction (learning $*$ palatability level $*$ signal: $F_{8,176} = 1.10$, $P = 0.38$), indicating that the reduction was similar in all groups (Fig. 3).

Mimicry Treatments

To assess the mimetic benefits, we compared groups that varied in signal (groups 7 and 8), palatability (groups 2
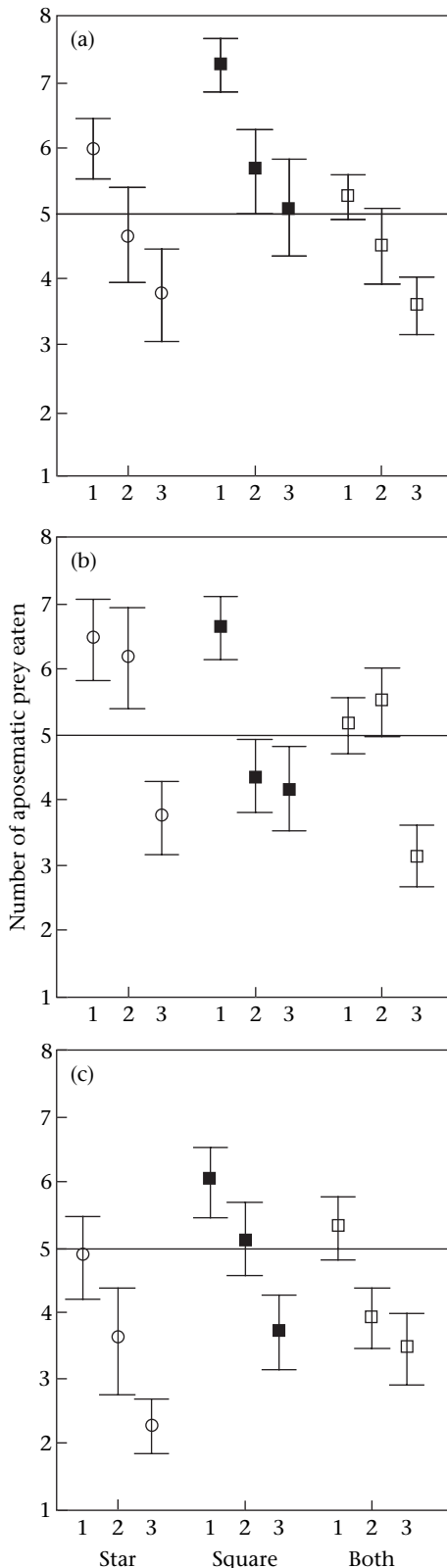
Figure 3. The learning curves of birds ($\overline{X} \pm$ SEM number of aposematic prey eaten) depending on the signal of the aposematic prey ($\bigcirc$: star; $\blacksquare$: square; $\square$: both) when (a) aposematic prey was mildly unpalatable, (b) there was variation in taste or (c) aposematic prey was strongly unpalatable. To test learning, we divided the total number of aposematic prey eaten during each trial into three: (1: 1−10

and 4) or both (group 9). As described above, we analysed the benefits of mimicry in several ways. First, we calculated in which proportion the birds ate a particular prey type from all aposematic prey items they ate. As the prey items were presented in 50:50 frequencies, we tested whether the percentages differed from 50. Only when strongly unpalatable stars were presented with squares (which were either strongly or mildly unpalatable: group 8a and 9 in Table 1) was the proportion of stars from all unpalatable prey eaten lower than 50% (one-sample t test: group 9: $t_{12} = -2.69$, $P = 0.02$; group 8a: $t_6 = -3.08$, $P = 0.022$; Table 1). This indicates that, with respect to each other, the squares survived poorly when they were paired with strongly unpalatable stars.

We then tested whether the prey types were predated randomly by calculating the relative predation in relation to the frequency of presentation. Predation is random when prey types are eaten according to their frequencies, taking into account the frequency of the cryptic prey. As the predators were allowed to eat 30 prey items during each trial, the expected predation for squares and for stars (or for the different taste levels) was 7.5 and for the cryptic prey 15. Only strongly unpalatable stars were eaten at a lesser rate than expected by their frequency when they were paired with strongly unpalatable squares (one-sample t test: $t_{12} = -3.09$, $P = 0.009$; group 9 in Table 1). Furthermore, the mildly unpalatable squares were overpredated when they were presented with strongly unpalatable stars ($t_7 = -2.56$, $P = 0.043$; group 8a in Table 1).

Finally, we tested whether mimicry was beneficial by dividing the mortality of each prey type in each mimetic combination by the mortality of that particular prey type without mimicry. From this point of view, mimicry was costly only for the strongly unpalatable stars when they were mimicked by identical, but mildly unpalatable, prey ($t_{10} = -2.53$, $P = 0.03$; Table 1). This is in line with the quasi-Batesian hypothesis. Imperfect mimicry was more beneficial than being alone for mildly unpalatable squares when they were mimicked by mildly unpalatable stars ($t_{11} = -2.83$, $P = 0.016$; Table 1). This suggests a classical Müllerian mimicry benefit for the poor signal. However, for the remaining groups there were no costs or benefits from mimicry.

Memory/Generalization Experiment

We tested whether the birds remembered to avoid stars ('experience', groups 1−3, 7−9) and whether they generalized their avoidance of squares to stars ('no experience', groups 4−6). There was an interaction between experience of the stars and the taste treatment (two-way

prey items eaten; 2: 11−20 prey item eaten; 3: 21−30 prey item eaten). Then we calculated how many aposematic prey items birds ate during each part of the trial. The reference line at 5 indicates when birds ate cryptic prey and aposematic prey at the same rate. Any values below this line indicate that birds ate fewer aposematic than cryptic prey and values above the line indicate that birds ate more aposematic prey than cryptic prey.
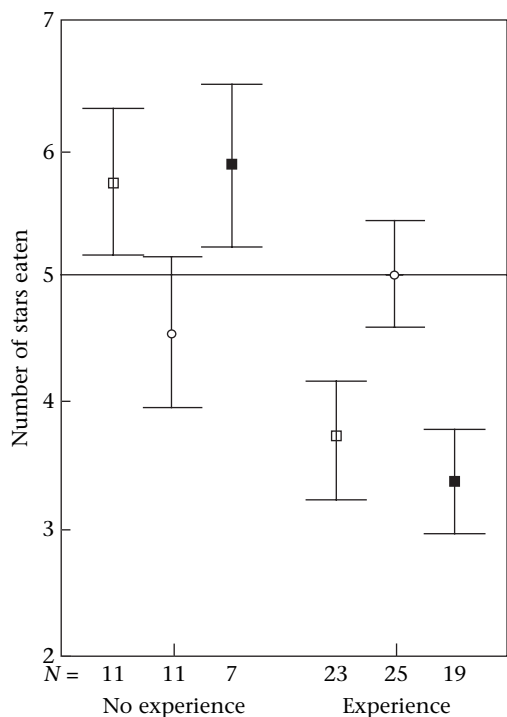
Figure 4. The number of stars eaten $\pm$ SE in the memory experiment according to birds' experience and the unpalatability level in the predation experiment. When birds had no experience of stars, they had encountered only squares before; when birds had experience of stars, they had encountered either only stars or both stars and squares before. Different taste levels indicate the differences in the predation experiment. The line at 5 represents random predation, with values above the line indicating higher predation and values below the line indicating lower predation against the prey type. □: Mild; ○: variable; ■: strong unpalatability.

ANOVA: $F_{2,90} = 4.24$, $P = 0.02$). The unpalatability level that the birds had experienced in the predation experiment affected their reactions to prey in the memory experiment (Fig. 4). Birds with no experience of the stars ate more of them than birds that had faced them previously (one-sample t test: $t_{94} = 2.62$, $P = 0.010$). This indicates that birds remembered to avoid stars if they had experienced them as unpalatable prey, but birds without experience of stars did not generalize their acquired avoidance of squares to stars.

When experience levels were analysed separately, the birds with no experience of the stars ate stars at the same rate regardless of the unpalatability level of the aposematic prey in the predation experiment (one-way ANOVA: $F_{2,26} = 1.48$, $P = 0.246$). However, when birds had experience of the stars, the previous unpalatability level affected the number of stars they ate in the memory experiment (one-way ANOVA: $F_{2,64} = 3.97$, $P = 0.024$). Post hoc tests showed that the difference is due to variation in taste increasing the number of stars eaten in the memory experiment (both unpalatability levels versus mildly unpalatable: LSD = 1.30, $P = 0.033$; both unpalatability levels versus strongly unpalatable: LSD = 1.63, $P = 0.012$). The single taste treatments did not differ from each other (strongly unpalatable versus mildly unpalatable: LSD = -0.32, $P = 0.613$).

DISCUSSION

Our results suggest that both the signal and the taste of prey affect the predation pressure on Müllerian comimics. The signal denoting unpalatability is not irrelevant; the irregular star was much more effective at causing avoidance by birds than the square, even though there was no initial bias against either signal. Surprisingly, when both stars and squares were presented to the birds, the predation pressure was not significantly increased compared to perfect mimicry (Fig. 2), which is suggested by classical Müllerian mimicry theory (Müller 1879; Joron & Mallet 1998; but see Beatty et al. 2004; Rowe et al. 2004). This implies that although the prey items were clearly different, their conspicuous resemblance to each other seemed to be to some extent mutually beneficial. There was a tendency for unpalatability to affect the predation pressure and there were some suggestions that strongly unpalatable prey was avoided more than mildly unpalatable prey. The variation in the unpalatability levels increased predation against strongly unpalatable prey as suggested by quasi-Batesian theory (Speed 1993), but this tendency was not apparent at all signal levels (Fig. 2, Table 1). Taken together, these results suggest that the signals and the unpalatability levels can produce different effects depending on the configuration of the whole mimicry complex.

Although birds reduced the consumption of the conspicuous prey during the trial (Fig. 3), there was no evidence for an interaction between the learning curves and the prey's signal or unpalatability. This indicates that birds learned similarly in all treatments. Similarly, Rowe et al. (2004) reported that increasing the signal difference between comimics did not create selection against imperfect mimicry, contrary to the classical theory (Müller 1879; Joron & Mallet 1998). In our predation experiment it seemed that predation pressure tended to decrease for the mildly unpalatable weaker signal (square) when it was paired with the strong signal, indicating that for this prey type even imperfect Müllerian mimicry would be a more beneficial strategy than perfect mimicry (Speed et al. 2000). The mechanism for this benefit in the predation experiment may be either the broad generalization of the predators, which seems to depend on the signal strength, or 'the neighbour effect' where less defended prey benefits from its defended neighbour regardless of the signal (e.g. Mappes et al. 1999). Alternatively, learning three things (avoid models, avoid mimics and prefer cryptic prey) at the same time may not be difficult for these birds (see discussion in Rowe et al. 2004 and Beatty et al. 2004) and therefore we do not see strong selection for pattern similarity at the beginning of the learning process.

Despite the small differences in our predation experiment, we analysed the mimetic advantage in three ways (Table 1). These calculations were made to emphasize that, as fitness is always relative, it is crucial to pay attention to the comparison point we choose. First, we compared the relative fitness of mimics to models (whether mortality deviates from 50:50%), and in our analysis only when the strongly unpalatable stars were presented with squares, did selection favour stars to squares (Table 1, groups 8a and 9). Then we compared the fitness benefits of both

signal types to their frequency in the prey population. Only when the strongly unpalatable stars were presented with the strongly unpalatable squares (group 9) were the stars underpredated, suggesting that this prey type was predated at a lower rate than the cryptic prey. However, squares were predated at an expected rate and therefore would not be selected against if our comparison point were against cryptic prey, but would be selected against if the comparison point were stars. Similarly, when the mildly unpalatable squares were presented against the strongly unpalatable stars the squares were overpredated (group 8a) and thus would be selected against, unless we compare their (mild square) survival to perfect mimicry (see last column in Table 1). These analyses underline that there are more benefits of mimicry than only a comparison to perfect mimicry. It could be that the reason for problematic variation in signals in the Müllerian mimicries (e.g. Brown & Benson 1974) is that selection is not acting against imperfect mimics promoting perfect mimicry, since these imperfect mimics might not be selected against the alternative prey (see also Kokko et al. 2003; Lindström et al. 2004).

The palatability of the prey also tended to affect the predation pressure on the comimics. The presence of mildly unpalatable mimics seemed to increase the total number of aposematic prey eaten compared to a situation without the mimics, which is suggested by quasi-Batesian mimicry theory. The theory further suggests that it is the more unpalatable prey that is paying the cost of predator education (Speed 1993, 1999). It could be argued that our experiment does not directly test quasi-Batesian dynamics as we kept the density of aposematic prey constant in relation to cryptic prey by manipulating model:mimic frequencies, whereas the mathematical models keep densities of the model species constant (Speed 1993, 1999). We were interested in testing whether the quasi-Batesian dynamics exist at all when the pure frequency-dependent Müllerian benefit (50:50) is at its minimum. Therefore, only by keeping the density of aposematic prey constant can we test whether the unequal benefits occur and whether the presence of a less protected mimic (whether it is a weaker signal or a milder unpalatability) alone is harmful to the model. We could detect weak quasi-Batesian effects only on the strongly unpalatable stars, which seemed to suffer from increased predation when they were paired with the mildly unpalatable stars (Table 1). No such effect was found when the predators encountered squares as aposematic prey. This suggests that quasi-Batesian effects may depend more on the signal than on the taste of the unpalatable prey.

Even though we did not find strong evidence that learning promotes similarity in mimicry (see also Rowe et al. 2004), mark–recapture experiments on butterflies give a very different view, showing that perfect mimics are recaptured at a higher rate than those with deviating signals which are supposedly predated and therefore heavily selected against (Benson 1972; Mallet & Barton 1989; Kapan 2001). It is likely that mark–recapture experiments test predator generalization and learnt avoidance rather than the learning process itself. Our memory/generalization experiment mimics a similar situation, where predators encounter a familiar prey type or a new one. In general, birds remembered to avoid stars if they had experienced them as unpalatable prey (Fig. 4). Nonexperienced birds also ate conspicuous stars by their frequency not by their visibility, indicating that there might be some weak benefit of the resemblance. Although squares and stars were mutually beneficial during the learning process, when birds had experienced only the squares as unpalatable prey, they did not generalize their avoidance of these prey types to stars, which corresponds to the findings from the field (Benson 1972; Mallet & Barton 1989; Kapan 2001). Alternatively, it could be that the generalization was weak, because birds in the square treatment had most difficulties in learning to avoid the squares as aposematic prey (Fig. 2).

A more interesting result from our memory experiment, consistent with quasi-Batesian theory, was that the variation in taste affected the memory of the predators (Speed & Turner 1999; see also Macdougall & Dawkins 1998). In other words, when predators had previously encountered strongly and mildly unpalatable aposematic prey together, they remembered poorly to avoid the stars a week later (Fig. 4). Perhaps the difference in palatability encouraged birds to test more of the conspicuous prey in the memory experiment. Alternatively, the predators might not have reached the same asymptote in learning, as we allowed the birds to eat a fixed number of aposematic prey.

The decreased attack rate on aposematic prey towards the end of the experiment was unexpected. One possible explanation is that the observed pattern is due to real seasonal effects. As the season progresses, and the snow melts (the experiment was done between February and April), the motivation to search for insect prey is likely to change, which might affect the willingness of birds to eat unpalatable prey. Alternatively, either hormonal changes or nutritional needs might have changed. However, this pattern did not affect the model:mimic dynamics.

Overall, these results indicate that imperfect mimicry (conspicuousness) between comimics is not always harmful for prey, particularly in comparison with perfect mimicry (see also Rowe et al. 2004). In some cases, imperfect mimicry even seemed to be a more beneficial strategy than perfect mimicry (Table 1). The memory experiment also suggests that the learning process alone might not promote similarity between two aposematic signals (see also Ihalainen & Suutari 2003; Rowe et al. 2004), but that selection against imperfect mimicry might be more pronounced when predators do not generalize their avoidance, as has been shown in mark–recapture studies (Benson 1972; Mallet & Barton 1989; Kapan 2001). The unpalatability difference between comimics might also increase the likelihood of predators sampling the mimetic prey community, suggesting that, in some situations, the dynamics might indeed be more Batesian than classically Müllerian. These results only emphasize the need for more accurate assessment of predator behaviour to understand the evolution of Müllerian mimicry and mimicry systems.

Acknowledgments

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