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THE EFFECT OF ALTERNATIVE PREY ON THE DYNAMICS OF IMPERFECT BATESIAN AND MÜLLERIAN MIMICRIES

LEENA LINDSTRÖM,[1] RAUNO V. ALATALO,[2] ANNE LYYTINEN,[3] AND JOHANNA MAPPES[4]
Department of Biological and Environmental Science, Konnevesi Research Station, P. O. Box 35,
FIN-40014 University of Jyväskylä, Finland
[1]*E-mail: lilema@cc.jyu.fi*
[2]*E-mail: alatalo@bytl.jyu.fi*
[3]*E-mail: alyytine@bytl.jyu.fi*
[4]*E-mail: mappes@bytl.jyu.fi*

Abstract.—Both Batesian and Müllerian mimicries are considered classical evidence of natural selection where predation pressure has, at times, created a striking similarity between unrelated prey species. Batesian mimicry, in which palatable mimics resemble unpalatable aposematic species, is parasitic and only beneficial to the mimics. By contrast, in classical Müllerian mimicry the cost of predators' avoidance learning is shared between similar unpalatable co-mimics, and therefore mimicry benefits all parties. Recent studies using mathematical modeling have questioned the dynamics of Müllerian mimicry, suggesting that fitness benefits should be calculated in a way similar to Batesian mimicry; that is, according to the relative unpalatability difference between co-mimics. Batesian mimicry is very sensitive to the availability of alternative prey, but the effects of alternative prey for Müllerian dynamics are not known and experiments are rare. We designed two experiments to test the effect of alternative prey on imperfect Batesian and Müllerian mimicry complexes. When alternative prey were scarce, imperfect Batesian mimics were selected out from the population, but abundantly available alternative prey relaxed selection against imperfect mimics. Birds learned to avoid both Müllerian models and mimics irrespective of the availability of alternative prey. However, the rate of avoidance learning of models increased when alternative prey were abundant. This experiment suggests that the availability of alternative prey affects the dynamics of both Müllerian and Batesian mimicry, but in different ways.

Key words.—Aposematism, coevolution, imperfect mimicry, novel world, *Parus major*, predation pressure, warning coloration.

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The striking similarity of color patterns in *Heliconius* butterflies or the imitation of wasps by hoverflies are considered to beautifully illustrate natural selection. It is assumed that the predators are the selective agent acting to promote similarity (i.e. mimicry) in these species (Bates 1862; Müller 1879; Fisher 1930). This is because some predators can learn to avoid unprofitable prey that use aposematic signals (unpalatable conspicuous prey, after Poulton 1890) and, subsequently, predators generalize this avoidance to similar color patterns. Imitation basically falls into two distinct categories, which are named after their discoverers: Batesian mimicry (Bates 1862) and Müllerian mimicry (Müller 1879). The key difference between these two mimicry types is which party benefits from the resemblance. In Müllerian mimicry all prey are unprofitable and thus co-mimics draw mutual benefit by aiding the predator avoidance learning (as in *Heliconius*). By contrast, in Batesian mimicry, mimics (e.g. hoverflies) rely on deception; they would (without mimicry) be profitable to a potential predator. Therefore selection acts differently in the two different mimicry systems (Fisher 1930; Nur 1970; Matthews 1977; Turner 1987).

Bates drew his conclusions about mimicry from field observations (Bates 1862). He collected strikingly similar butterflies from the Amazon forests and realized, after capture, that they belonged to different families. He suggested that a perfectly palatable prey could escape predation by imitating the color pattern of an unpalatable prey that predators had already learned to avoid. Bates therefore considered mimicry to be based on a deception that would only be possible if the predators generalized their learned avoidance. Three components are key to the dynamics of Batesian mimicry and the success of deception: the unpalatability of the model, the frequency of mimics, and the availability of the alternative prey. These components affect the level of similarity between models and mimics. The more unpalatable or toxic the model, the more imperfect mimics are avoided by the predator (Duncan and Sheppard 1965; Goodale and Sneddon 1977; Lindström et al. 1997). Similarly, the mimicry is least harmful to models and more beneficial to mimics if the mimics are relatively rare (Fisher 1930; Nur 1970; Lindström et al. 1997; but see Brower 1960) since the more common the mimic, the more unstable is the mimicry (Lea and Turner 1972; Lindström et al. 1997). Additionally, availability of alternative prey affects the degree of similarity. When alternative prey are abundant, predators can also choose nonmimetic prey, which reduces predation on both models and mimics (Holling 1965; Getty 1985; Nonacs 1985; Hetz and Slobodchikoff 1988) and selection is likely relaxed.

Müller based his theory of mimicry on both observations and mathematical modeling (1879). According to Müller's original idea, similarity in Müllerian mimicry is caused by the fact that predators need to be educated to avoid unpalatable prey. By sharing a similar color pattern, prey species would reduce the education costs since predators would need to learn to avoid a single color pattern only. Müller considered that the benefit for each co-mimic could be calculated by their frequencies in the prey population. This predicts positive frequency-dependent selection and monomorphism in color pattern among co-mimics (Turner 1987; Joron and Mallet 1998; Mallet and Joron 1999), since any deviation from the common warning pattern would be selected against (Mallet and Barton 1989; Kapan 2001).

However, there are also examples of polymorphic Müllerian mimicries (e.g. Brown and Benson 1974) that are difficult to explain by Müller's original theory (Joron and Mallet 1998). Experimental evidence for Müllerian mimicry is based largely on field studies (Benson 1972; Mallet and Barton 1989; Kapan 2001), in which predator behavior is not directly observed. Despite the lack of understanding of exactly how predators promote similarity in Müllerian co-mimics, predator behavior forms a basis of the mathematical models (e.g., Speed 1993; Turner and Speed 1996; Speed and Turner 1999; Mallet and Joron 2000). There is a clear need for more detailed studies of predator behavior (e.g., Alatalo and Mappes 1996; Speed et al. 2000; Rowe et al. 2004).

Müller's theory was based on equally unpalatable co-mimics, which is probably an unrealistic assumption. Unconventional mimicry theory has focused on the effects of probable difference in palatabilities between models and mimics (Huheey 1976; Turner 1987; Speed 1993). These unconventional mimicry theories are termed quasi-Batesian mimicry, and the more unpalatable species are designated ''models'' and the less unpalatable species are designated ''mimics'' (Speed 1993, 1999; Mallet 1999). According to quasi-Batesian mimicry theory, the dynamics of Müllerian mimicry should resemble parasitic Batesian mimicry dynamics, in which the mimics (or the less toxic prey) benefit at a cost to the models. Quasi-Batesian mimicry dynamics could explain the existence of polymorphic Müllerian mimics because the selection tends to be diversifying rather than purifying (Turner and Speed 1996).

If Müllerian mimicry is more similar to Batesian mimicry than conventional theory assumes (Joron and Mallet 1998; Mallet and Joron 1999), then the availability of alternative prey might also affect Müllerian mimicry dynamics. It is known that alternative prey affects the mortality rates of Batesian mimics and their models (Getty 1985; Hetz and Slobodchikoff 1988) and also the mortality rates of aposematic prey (Lindström et al. 2001a). For instance, when alternative prey is abundantly available, Batesian mimics need not accurately resemble their unpalatable models. This contrasts with strong selection pressure on imperfect mimics when alternative prey is scarce (Mappes and Alatalo 1997; but see Dittrich et al. 1993). Another possible effect of alternative palatable prey is that when such prey are abundantly available predators might learn to avoid unpalatable prey from less experience (in terms of number eaten; Lindström et al. 2001a). This challenges Müller's assumption that predators learn from a fixed number of prey eaten (see discussion in Joron and Mallet 1998; Mallet and Joron 1999). Additionally, alternative prey can convert a mutualistic Müllerian relationship into a parasitic quasi–Batesian one depending on the predator behavior (Kokko et al. 2003).

We set out to test the fitness benefits for *imperfect* Batesian and Müllerian mimics when different amounts of palatable prey were available using a ''novel world'' method (Alatalo and Mappes 1996). In addition, we used imperfect mimicry to assess the importance of the signal in the mimicry systems. This was done by using symbols that were different; that is, predators could potentially separate the mimics from the models. Additionally, imperfect mimicry allows us to identify maximal selection pressures created by predators in a mimicry system. However, our models and mimics were necessarily similar in order to produce mimetic advantage even though they were not classical mimics (i.e., indistinguishable). We analyzed the mimicry when there were equal frequencies of models (50) and mimics (50) but differing numbers of alternative prey. Batesian mimicry theory assumes that the scarcity of alternative prey increases the relative predation of imperfect mimics, whereas an abundance of alternative prey should decrease the predation pressure and increase the mimetic advantage. Conventional Müllerian mimicry theory has focused on the model-mimic relationship, overlooking the effects that alternative prey might have on Müllerian mimicry dynamics. Because we presented the models and the mimics in equal frequencies, the fitness benefits for mimics and models are assumed to be equal (Müller 1879; Marshall 1908) since purifying selection should be at its minimum.

MATERIALS AND METHODS

Birds and Aviary

This study was carried out at Konnevesi Research Station (central Finland) in the autumn of 2000. Wild great tits (*Parus major*) were caught around the research station and kept in individually illuminated cages ($65 \times 80 \times 65$ cm^3) on a diet that contained sunflower seeds, peanuts, and fresh water ad libitum. Birds were habituated to feed on sunflower seeds and peanuts from the floor of an experimental aviary (57.7 m^2 × 3.5 height). Twelve perches were equally distributed within the aviary: eight perches (height 45 cm) were attached to wooden planks (see below) and one to each of the four walls. Observations of a bird's behavior were made through a one-way mirror from an adjoining observation room without disturbing birds.

Training

Birds were considered ready for the experiment when they had learned to open artificial prey items they had never seen before. These prey items were made by gluing a tiny slice (about 8 mg) of almond between two 10×10 mm pieces of white paper that formed a ''shell'' that birds had to open in order to access the almond. We taught birds to open these artificial prey items before the experiment (see Lindström et al. 2001a,b). Birds that failed to learn to open these artificial prey items were released without performing the experiment. On average, birds learned to open the prey items in 1.4 days ($n = 62$, SE $= 0.76$).

Birds were habituated to forage in an artificial environment before the learning experiment was performed. Novel landscapes were created on the floors of two smaller aviaries. The landscapes comprised seven rows and 10 columns of A3 size sheets of paper (European standard, size 42×29.6 cm^2). Each sheet had 70 crosses (cryptic symbols) printed on it under a layer of self-adhesive book covering film (Pelloplast, Pello, Finland) (see Lindström et al. 2001). To make the landscape three-dimensional, each piece of A3 paper also had 10 fake cryptic prey, which were a background symbol glued

TABLE 1. The mean total sum of prey types eaten in two trials of both experiments. In Batesian mimicry experiments birds were allowed to eat 100 prey items whereas in Müllerian mimicry they were allowed to eat 60 prey items. The prey items we used were either green or blue squares with four arms extending diagonally from each corner on the same plane as the square (for an example of the crossed square, see Rowe et al. 2004). In Batesian mimicry, when models were green (represented here by black squares), mimics were blue (light squares) and vice versa. In the Müllerian mimicry experiment, models were green and mimics were blue. The standard errors of the mean are given in brackets.

Alternative prey	Batesian mimicry: Models ■/▨	Batesian mimicry: Mimics ▨/■	Batesian mimicry: Controls ×	Müllerian mimicry: Models (greens)	Müllerian mimicry: Mimics (blues)	Müllerian mimicry: Controls
Scarce	20.00 (3.37)	43.25 (1.57)	36.00 (4.72)	8.43 (1.35)	14.36 (1.84)	37.21 (2.54)
Abundant	13.75 (2.69)	24.53 (1.75)	61.63 (3.91)	4.50 (0.53)	6.50 (1.20)	49.00 (1.64)
Control	—	—	—	6.75 (0.55)	14.50 (2.40)	36.25 (3.06)

to paperboard and stuck on top of the film. The addition of fake prey items ensured that the birds learned to pay attention to the symbols. A wooden plank along which birds could move and handle the prey lay between each A3 row. During the test trial, birds were allowed to eat 12 white and three cryptic paper prey items (prey printed with cross symbols) from the landscape. The trial was conducted to ensure that the birds were able to learn to eat artificial prey items from the novel landscape. Birds had to complete this test trial before starting the experiment.

Prey Items

Experimental prey items were similar to the training items, but all experimental prey items had a signal. Cryptic, alternative prey items had a single cross that was similar to that printed on the landscape. Both signaling prey (models and mimics) had symbols that were colored squares with four arms extending diagonally from each corner on the same plane as the square (for an example of the crossed square, see Rowe et al. 2004). Conspicuous symbols used in this experiment were chosen on the basis of three criteria: (1) they should be equally conspicuous, (2) signals should be slightly distinguishable and thus different, and (3) birds should be able to generalize an avoidance of one signal toward the other signal. We tested these assumptions in different experiments that will be reported elsewhere (J. Mappes, R. V. Alatalo, L. Lindström, and A. Lyytinen, unpubl. ms.). Since it was difficult to match a pair of symbols in their general similarity, conspicuousness, and birds' abilities to learn to avoid them, we used squares colored either light green or light blue. However, it is likely that both symbols were novel for the birds since they had not encountered this prey in the wild before and indeed both signals were equally preferable when given to birds. These two signals were equally conspicuous against the novel world background (X). Birds were also able to learn to discriminate between them when one color was made unpalatable and the other was palatable. Additionally, if a bird was taught to avoid the blue signal, it later generalized this avoidance to green and vice versa. Thus, these symbols were different but generalizable to great tits, although they appear very different to us (see also Dittrich et al. 1993). These symbols fulfill the criteria of imperfect mimicry.

Alternative cryptic prey were always palatable. In both the Batesian and the Müllerian mimicry experiments models were made unpalatable by soaking the almonds in a chloroquinine solution (2 g of chloroquinine dissolved in 30 ml of water). The almonds were then dried and glued between pieces of paper that had been printed with the conspicuous symbols. Previous experiments (Lindström et al. 2001a,b), established that this dosage makes the prey items highly unpalatable, and birds are able to learn to avoid unpalatable prey with a conspicuous signal. Models were either green or blue. In the Batesian mimicry experiment, mimics were palatable and were either blue or green. The mimics in the Müllerian mimicry experiment were made unpalatable by soaking the almonds in a chloroquinine solution (250 mg of chloroquinine dissolved in 30 ml of water) that was eight times lower in concentration than that of the models. This difference was sufficient to produce a difference in learning rates (L. Lindström, A. Lyytinen, J. Mappes, and K. Ojala, unpubl. ms.).

Experimental Aviary

The novel landscape was set up in a large aviary (size 57.7 m^2, height 3.5 m) and consisted of 15 rows and 22 columns (i.e. 330 sheets) of A3 paper covering an area of 41 m^2. Four sheets under each of the eight perches in the aviary and two sheets under each of the wall-attached perches were left empty. This was done to ensure that the handled prey items were not mixed up with the unconsumed prey while making the observations. Thus, there were 290 possible sheets upon which prey items could be placed.

Batesian Mimicry

To test the effects of alternative prey on Batesian mimicry, birds were divided into four groups according to the availability of alternative prey (scarce or abundant) and the color of the model (green or blue). In the scarce treatment, birds (n = 8) were offered a choice of 50 unpalatable models, 50 palatable mimics, and 50 palatable alternative cryptic prey. In the abundant treatment, birds (n = 8) were given 50 unpalatable models, 50 palatable mimics, and 100 palatable alternative cryptic prey. Prey types were scattered randomly in eight blocks to ensure interspersion. Birds were allowed to eat 50 prey items in a trial. The prey was considered ''killed'' if the birds ate, took bites from, or tasted the prey. If birds took the prey and dropped it immediately, it was considered to have survived the encounter. However, birds dropped the prey items rarely. Models and mimics were always different colors (i.e. blue vs. green, and green vs. blue), and so we did not test the perfect mimicry (where models and mimics are the same color). An identical trial with a new set of prey items was repeated with each bird the next day.

Müllerian Mimicry

To test how the availability of alternative palatable prey affects the dynamics of Müllerian mimicry we divided a different set of birds into four groups depending on the color of the model (green or blue) and the frequency of alternative prey (scarce or abundant). In the scarce treatment ($n = 14$), we gave birds 50 unpalatable models, 50 mildly unpalatable mimics, and 50 palatable cryptic prey. In the abundant treatments ($n = 12$), birds were given 50 models, 50 mimics, and 150 palatable cryptic prey. The conventional theory predicts that the alternative prey are unlikely to cause an effect, therefore to increase a likelihood of detecting any effects we increased the abundance of alternative prey in the Müllerian mimicry experiment. As we increased the number of prey considerably, we also included a control treatment to separate density effects from frequency effects. We also had a treatment ($n = 12$) of 83 models, 83 mimics, and 83 palatable cryptic prey to control for the different amount of prey items presented in the experiment. Therefore, the density of prey items was similar to the 50:50:150 abundant alternative prey treatment, but the frequency of prey was the same (1:1:1) as in the 50:50:50 scarce alternative prey treatment. Models and mimics were always different colors as we were not interested in testing perfect mimicry.

During each trial a bird could choose 30 prey items from prey items that were scattered randomly in eight blocks to ensure an even distribution (treatment: scarce 150, abundant 250, and control 249). The prey type and the order in which they were killed were recorded. To assess learning, we repeated the experiment on a consecutive day with a full set of prey presented to the birds.

Statistical Analyses

To assess fitness effects of all three prey types (models, mimics, and cryptic prey), we chose random predation as our null hypothesis because it is the most conservative. Because cryptic prey was presented in different frequencies (scarce vs. abundant treatment), we calculated the relative predation on each prey type to compare fitness effects between models, mimics, and cryptic prey. Because the birds were allowed to eat a fixed number of prey in each trial (50 in Batesian mimicry experiment and 30 in Müllerian mimicry experiment), we calculated relative predation for each prey type by deviating the observed predation (i.e. the number eaten of a particular type) by the expected predation of that prey type (i.e. the number expected by prey frequency). This index takes into account that the likelihood of a predator encountering a given prey changes between the treatments as the total number of prey changes. A value of one indicates that the prey type is predated at random; that is, at a level that would be expected by its frequency. Any value less than one indicates that a particular prey benefits from lowered predation pressure, and a value above one indicates that the prey is suffering from overpredation. Thus, although the mortality of a given prey may differ between treatments, they may still be predated relatively at the same level.

First we assessed whether the overall predation of these three prey types differed from random, by performing one sample *t*-test and correcting the *P*-values by the number of tests (Rice 1989). To test learning we used a double multivariate generalized linear model (GLM) for repeated measure designs, since models and mimics are presented to the birds simultaneously on two consecutive days. The relative predation of models and mimics eaten on both days was used as the dependent variable for analysis in both experiments. The within-subject factor in the double multivariate GLM is time (i.e. day 1 to day 2) for these two measures, model and mimic, and between-subject factor is the availability of alternative prey (scarce/abundant) and the color of the model species (green/blue). Last, we tested the mimetic advantage by directly comparing the survival of the models to the mimics. Where pairwise analyses were applied, we used either parametric or nonparametric analysis according to whether the data met the assumptions of the test. All *P*-values are two-tailed. Statistical analyses were performed using SPSS (Release 11.01; SPSS 1997.).

RESULTS

Batesian Mimicry

We analyzed the overall relative predation pressure (i.e. the total number of a particular prey type eaten during the whole experiment/the expected predation for that prey type) on models, Batesian mimics, and cryptic prey. When tested against random predation (value 1), models were eaten at a lower rate than expected in both alternative prey treatments (sequential Bonferroni corrected: $t_7 = -3.96$, $P = 0.02$; $t_7 = -4.18$, $P = 0.02$ respectively), indicating that they benefited from their conspicuous signal and unpalatability (Fig. 1). Batesian mimics, in turn, were overpredated when alternative prey were scarce (sequential Bonferroni corrected: $t_7 = 6.33$, $P < 0.001$), but predated at a random level when alternative prey were abundant (sequential Bonferroni corrected: $t_7 = -0.21$, $P = 0.837$). This indicates that when the alternative prey were abundant, selection against imperfect mimics was relaxed (see Figs. 1, 2) identifying a clear benefit in relation to the visibility of the signal. Cryptic prey were eaten at random when they were scarce (sequential Bonferroni corrected: $t_7 = 0.57$, $P = 1.0$), although there was a tendency for them to be eaten at a higher rate than expected when they were abundant (sequential Bonferroni corrected: $t_7 = 2.97$, $P = 0.063$).

Because the double multivariate GLM for repeated design analysis allows us to test the predation on two consecutive days on both models and mimics separately, we found that there was significant predator avoidance learning of models ($F_{1,12} = 12.74$, $P = 0.004$) but not of mimics ($F_{1,12} = 0.25$, $P = 0.630$). This indicates that the birds learned to avoid models but mimics were eaten at the same level on both days (see Fig. 2). There were no interactions between learning and availability of alternative prey for models or mimics. There was a main effect of alternative prey on predation of mimics ($F_{1,12} = 14.46$, $P = 0.003$) but not on that of models ($F_{1,12} = 0.14$, $P = 0.718$). This suggests that mimics were less

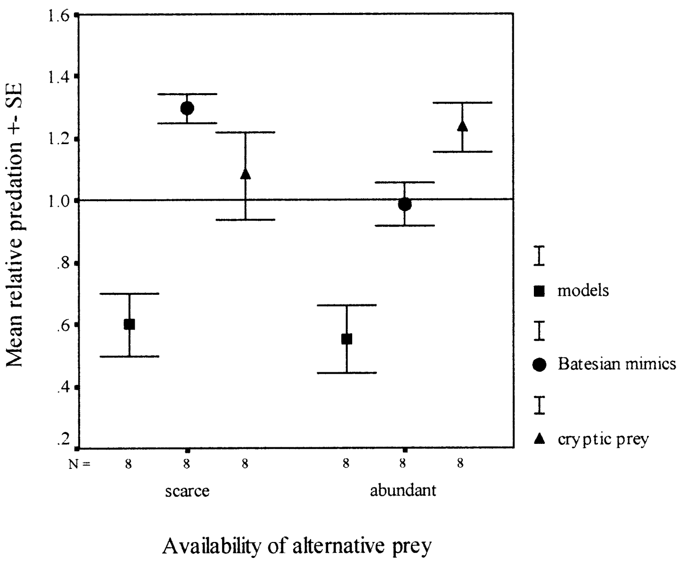

FIG. 1. The mean relative predation of models (squares), Batesian mimics (circles), and cryptic (triangles) alternative prey depending on the availability of alternative prey. A line represents a random predation, with values above the line indicating higher predation and values below the line indicating lower predation against the prey type in relation to their frequencies. The bars represent standard errors of the mean.

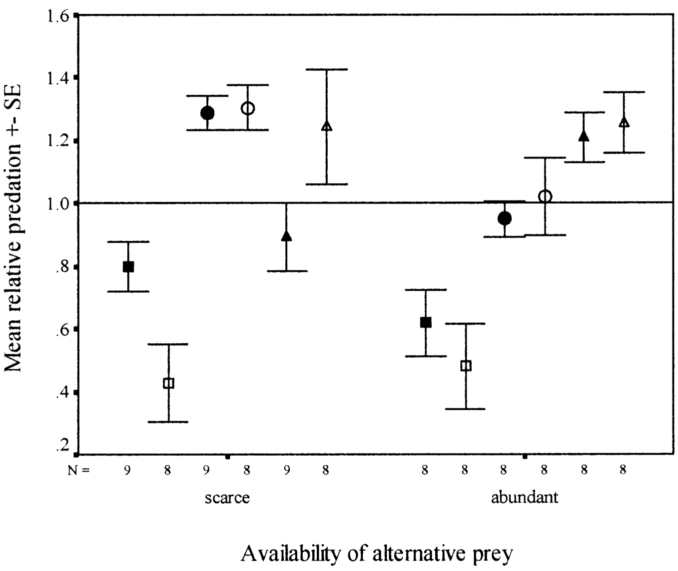

FIG. 2. The relative predation of models (squares), mimics (circles), and cryptic (triangles) prey in the two alternative prey treatments in Batesian mimicry. Filled symbols indicate the relative predation in the first trial and open circles in the second trial. A line represents random predation. The bars represent standard errors of the mean.

predated when alternative cryptic prey were abundant (Fig. 2). The color had a marginally nonsignificant main effect on models ($F_{1,12}$ = 3.84, P = 0.074) but not on mimics ($F_{1,12}$ = 2.31, P = 0.154). This indicates that the colors tended to be treated differently when they signaled unpalatability. Birds seemed to eat more blue than green unpalatable prey, but there was no interaction between color, alternative prey, or learning.

To assess the relationship between models and mimics, we compared the absolute numbers eaten between alternative prey treatments. Models were eaten at the same rate irrespective of the frequency of alternative prey (total sum: t_{14} = 1.45, P = 0.169), whereas the surplus of alternative prey directly decreased the total sum of mimics eaten (t_{14} = 7.92, $P < 0.001$). Predators ate the models within both treatments at a lower rate than they ate the mimics (scarce: $t_8 = -10.97$, $P < 0.001$, abundant: $t_8 = -4.63$, P = 0.002) indicating that the mimics were indeed imperfect. However, the ratio of eaten models to eaten mimics remained similar between the two treatments (Mann-Whitney U = 22.5, P = 0.318). This indicates that the predators, although separating the mimics from the models, ate them in similar proportions between the treatments.

Müllerian Mimicry

As our experimental groups (scarce vs. abundant alternative prey) involved different total numbers of prey presented in the aviary, we tested whether this difference alone had an impact on the number of unpalatable prey eaten the experiment. Therefore, we included a control treatment (83 mimics: 83 models:83 cryptic prey) in the experiment, with frequencies equal to those of our scarce treatment (50:50:50) and simultaneously with a density equal to that of our abundant alternative prey treatment (50:50:150). We performed a two-factorial ANOVA in which the color of the model (green, blue) and the treatment type (scarce, control, abundant) were used as factors. The availability of alternative prey had an effect on the total number of aposematic prey eaten ($F_{2,32}$ = 6.73, P = 0.004), but neither the signal color of the model nor the interaction between the availability of alternative prey and color ($F_{1,32}$ = 0.81, P = 0.375; $F_{1,32}$ = 0.46, P = 0.635 respectively) were significant. Post-hoc tests reveal that the birds ate unpalatable prey according to their frequency (scarce vs. control Bonferroni mean difference = 1.53, P = 1.000) rather than density (abundant vs. control Bonferroni mean difference = -10.25, P = 0.021; see Table 1 for sums).

The Batesian mimicry experiment suggested that the birds ate more blue than green unpalatable models. Therefore, we performed a multivariate two-factorial ANOVA for the total relative predation on highly unpalatable models and mildly unpalatable mimics using the color of the model and the availability of alternative prey as factors. The multivariate tests revealed a significant effect on the color of the model ($F_{2,21}$ = 7.46, P = 0.004), indicating that the color indeed was more important than the unpalatability of the prey items. When the same analysis was conducted using the relative predation on the different colors as the dependent variables (i.e. greens vs. blues rather than between the two different tastes), there was no apparent effect for the tastes ($F_{2,21}$ = 0.39, P = 0.681). This means that predators differentiated prey types according to their colors rather than their palatability. Therefore, in line with the theory models are the prey types that are more effective in producing predator avoidance (Mallet 1999). A more meaningful analysis would be to test the fitness effect separating the colors rather than the tastes. In the following analyses we have considered greens as models and blues as mimics.

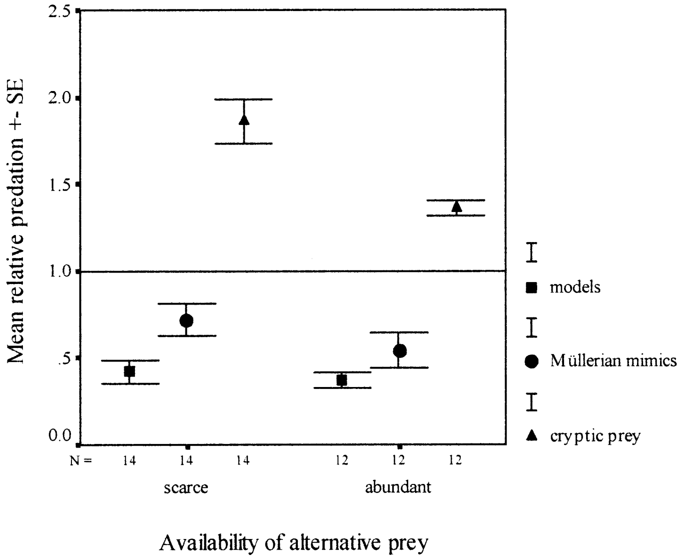

FIG. 3. The mean relative predation of greens as models (squares), blues as Müllerian mimics (circles), and cryptic alternative prey (triangles) depending on the availability of alternative prey. A line represents a random predation, with values above the line indicating higher predation and values below the line indicating lower predation against the prey type in relation to their frequencies. The bars represent standard errors of the mean.

When the overall relative predation pressure was tested against random predation (value 1), models (greens) were eaten at a lower rate than expected in both alternative prey treatments (sequential Bonferroni corrected: $t_{13} = -8.55$, $P < 0.001$; $t_{11} = -14.17$, $P < 0.001$ respectively), indicating that they benefited from their conspicuous signal and unpalatability (Fig. 3). The same was true for Müllerian mimics (blues) also, which were under-predated in both alternative prey treatments although the effect was more clear when alternative prey were abundant (sequential Bonferroni corrected: $t_{13} = -3.07$, $P = 0.054$; $t_7 = -4.57$, $P = 0.006$, respectively). Cryptic prey was overpredated in both treatments (sequential Bonferroni corrected: scarce $t_{13} = 6.77$, $P < 0.001$: abundant $t_{11} = 7.94$, $P < 0.001$,).

To assess the learning in the mimicry experiment we performed a double multivariate GLM for repeated design. There was significant avoidance learning of both models (greens) and mimics (blues) ($F_{1,22} = 41.35$, $P < 0.001$, and $F_{1,22} = 53.38$, $P < 0.001$ respectively; Fig. 4.). There was an interaction between the availability of alternative prey and learning ($F_{1,22} = 5.05$, $P = 0.035$) for the models, with birds learning to avoid them better when alternative prey were more abundant (see Fig. 4). There was no such effect for mimics ($F_{1,22} = 1.91$, $P = 0.181$). There was a marginal but nonsignificant interaction between the level of palatability and learning for the models ($F_{1,22} = 3.23$, $P = 0.086$) but not for mimics. The availability of alternative prey did not have a main effect for either models ($F_{1,22} = 0.31$, $P = 0.586$) or mimics ($F_{1,22} = 0.41$, $P = 0.907$) indicating that the predators ate the prey types according to their frequencies. There were no three-way interactions between learning, taste, and availability of alternative prey for either models or mimics. Furthermore, there were no main effects of unpalatability level or availability of alternative prey for either models or mimics (Fig. 4).

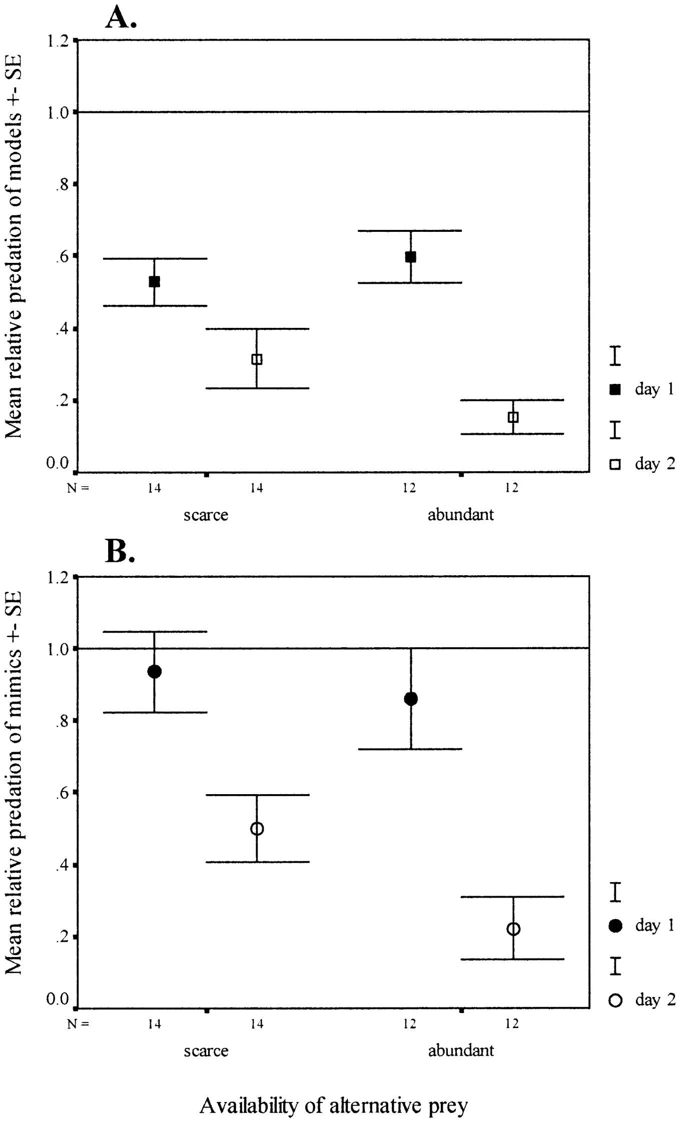

FIG. 4. The mean relative predation on (A) the models (i.e. greens) and (B) the mimics (i.e. blues) during the two trials (day 1 and day 2) with the two different treatments of alternative prey availability.

Fewer models and mimics were eaten when the alternative prey were abundant (total sums: (Mann Whitney $U = 44$, $P = 0.041$; Mann Whitney $U = 26.5$, $P = 0.002$ respectively). Although models were eaten at both alternative prey treatments at a lower level than mimics (scarce: $t_{13} = -2.987$, $P = 0.010$, abundant: $t_{11} = -2.275$, $P = 0.044$) the ratio models to mimics was not altered by the availability of alternative prey ($t_{24} = -0.133$, $P = 0.895$). These results indicate that although the models were eaten at a lesser rate, predators ate the models and the mimics at the similar proportions.

DISCUSSION

These experiments propose that it is important to take alternative prey into account in calculations of the predation pressures for both Batesian and Müllerian mimicry. The effects of alternative prey were not, however, the same on both mimicry types. The availability of alternative prey increased the survival of mimics (see Table 1) as birds fed more heavily on the alternative prey than either the Batesian or Müllerian mimics. However, when we calculate whether this difference affected the relative predation we observed that the availability of alternative prey had different effects in the two mimicries. In Batesian mimicry, the availability of alternative prey affected the relative mortalities of the mimics (Figs. 1, 2). Batesian mimics were heavily overpredated when alternative prey were scarce, but predation on mimics was random when alternative prey were abundant. This indicates that abundant alternative prey decreases selection on imperfect mimics (see also Hetz and Slobodchikoff 1988). In Müllerian mimicry the availability of alternative prey had an effect on the total number of co-mimics eaten but not on their relative predation indicating that, although the mortality rates changed, the selection by predation when all three prey types are taken into account would remain similar (see Figs. 3, 4). However, there was some benefit for models in Müllerian mimicry as predators learned more easily to avoid Müllerian models when alternative prey were abundant. Therefore, our results indicate that the availability of alternative prey is more crucial for the pure Batesian mimics, as has previously been suggested (Holling 1965; Getty 1985; Nonacs 1985; Hetz and Slobodchikoff 1988), and that Müllerian mimicry is not as strongly influenced by the availability of alternative prey, as predicted by conventional Müllerian mimicry theory (Joron and Mallet 1998; Mallet and Joron 1999).

Traditionally, Batesian mimicry at high frequencies is considered to be harmful for the model (Nur 1970; Turner 1987; Lindström et al. 1997; but see Brower 1960) unless there is a surplus of alternative prey available (Holling 1965; Getty 1985). In our experiment, birds learned to avoid models but there was no effect of availability of alternative prey on the relative survival rates of the models. Since birds were able to separate the conspicuous palatable prey (mimics) from the models when alternative prey were scarce, mimics did not derive Batesian benefit from their resemblance to the models and were indeed predated at a higher rate than cryptic prey (Fig. 2). This would imply that the imperfect mimicry would be a highly unsuccessful strategy when alternative prey are scarce and imperfect mimics would be quickly selected out from the prey population (cf. Mappes and Alatalo 1997; Caley and Schluter 2003). This is probably because the unpalatability of the models was not severe enough to maintain imperfect mimicry (see Duncan and Sheppard 1965) and the mimic was as valuable as the cryptic alternative prey (see Sherratt 2002) and, therefore, in a scarce food situation the predators could not afford to ignore that prey type (see Kokko et al. 2003).

It should also be noted that most Batesian mimicry experiments test the memory and/or generalization ability of the predator rather than the interference of mimics in the learning process. Birds are usually taught initially to avoid the models (see e.g. Brower 1960; Lindström et al. 1997) and this decreases the predation of the mimics. However, because recent debate suggests that Müllerian dynamics are similar to Batesian dynamics, we studied both mimicry systems under similar conditions; that is, when predators learn to avoid the aposematic signal. Our experiment shows that when alternative prey were abundantly available, birds decreased their relative predation pressure on imperfect mimics, suggesting a Batesian benefit even to an imperfect mimic. This further suggests that imperfect mimics might benefit from a high availability of alternative prey, and that we might not need to provoke strong selection pressures to explain imperfect Batesian mimicry (see Edmunds 2000; Johnstone 2002).

In our Müllerian mimicry experiment, the most apparent result was that the birds seemed to find the color signals more important than the taste cues. Therefore, we analyzed the results using green prey as models and blue prey as mimics. Greens were avoided more rapidly indicating that green color is a stronger signal and therefore more likely to act as a model in this system (see Mallet 1999). Overall the results would have been similar even if they were analyzed according to taste differences, but the variances would have increased considerably. Both unpalatable prey types benefited from their unpalatability even at the very beginning of the experiment but the availability of alternative prey affected how quickly predators learned to avoid the models (Fig. 4). Although availability of abundant alternative prey had an effect on the total number of aposematic prey items eaten, the relative predation was the same (Fig. 4). These results suggest that Müllerian dynamics do not resemble Batesian dynamics in relaxing the predation pressure on mimics in proportion to the increasing availability of alternative prey. Thus, Müllerian co-mimics experienced similar predation in the experiment irrespective of the abundance of alternative prey. The availability of alternative prey did, however, affect the mortality rates (see Table 1.).

When mimics and models were compared to each other, mimics in both Batesian and Müllerian (blues) mimicries were eaten at a higher rate than models. This is most likely a result of the fact that the mimics were imperfect. Therefore they did not fully drive benefits from their resemblance to the models while predators were learning to avoid the mimicry complex. However, when we consider fitness effects against random predation only, Batesian mimics in the scarce alternative prey treatment were eaten at a higher rate than expected (see Figs. 2 and 4). This would suggest that predators could select imperfect mimics out from the prey population. Because predation in Müllerian mimicry did not significantly differ from random predation, this suggests that even imperfect mimics would not be selected against. Birds apparently generalized more broadly between the models and the mimics when the mimics were unpalatable (i.e. Müllerian co-mimics).

According to quasi–Batesian mimicry theory, the models should suffer an increased predation cost as the more palatable mimics present in the prey population slow down the avoidance learning of the predators (Speed 1993, 1999). In contrast, Batesian mimicry theory predicts that this loss might be balanced to some extent by an excess of alternative prey in the prey population (Holling 1965; Getty 1985; Hetz and Slobodchikoff 1988). Therefore, it is reasonable to question whether the availability of alternative prey also affects dynamics of Müllerian mimicry, as the conventional theory has ignored its effects. In this paper we suggest that abundant alternative prey have a more profound impact on imperfect Batesian than on Müllerian mimicry, suggesting that the dynamics of the two systems indeed differ (compare Figs. 2 and 4). This is most likely due to the fact that Batesian mimics are profitable prey, whereas Müllerian mimics are not, and the question is whether it is to the predators benefit to separate the models from the mimics in the first place (see also Kokko et al. 2003). We did not directly test quasi-Batesian mimicry theory, as it is based on an accurate resemblance between models and mimics. Interestingly, however, our data shows that the signal seemed to be more important to the avoidance learning of the predators than the relative unpalatability difference of the prey, suggesting that the variability in taste might not be as significant for the Müllerian mimicry systems as suggested by unconventional theory (Speed 1993; Speed and Turner 1999; Turner and Speed 1996). Although our results illuminate the effects alternative prey can have in both Batesian and Müllerian mimicries, our focus was on testing imperfect mimicry. It is clear that more experiments on different degrees of signal similarity and unpalatability differences are needed.

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Corresponding Editor: M. Björklund