

Imperfect Batesian mimicry—the effects of the frequency and the distastefulness of the model

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SUMMARY

Batesian mimicry is the resemblance between unpalatable models and palatable mimics. The widely accepted idea is that the frequency and the unprofitability of the model are crucial for the introduction of a Batesian mimic into the prey population. However, experimental evidence is limited and furthermore, previous studies have considered mainly perfect mimicry (automimicry). We investigated imperfect Batesian mimicry by varying the frequency of an aposematic model at two levels of distastefulness. The predator encountered prey in a random order, one prey item at a time. The prey were thus presented realistically in a sequential way. Great tits (*Parus major*) were used as predators. This experiment, with a novel signal, supports the idea that Batesian mimics gain most when the models outnumber them. The mortalities of the mimics as well as the models were significantly dependent on the frequency of the model. Both prey types survived better the fewer mimics there were confusing the predator. There were also indications that the degree of distastefulness of the model had an effect on the survival of the Batesian mimic: the models survived significantly better the more distasteful they were. The experiment supports the most classical predictions in the theories of the origin and maintenance of Batesian mimicry.

1. INTRODUCTION

Bates (1862) was one of the first to describe interesting relationships between conspicuously coloured butterflies. He suggested that there were unpalatable species (models) which were ‘imitated’ by unrelated species though they were palatable (mimics). According to Bates the predators (namely birds) learn to avoid these unpalatable models using visual cues and thus also avoid palatable mimics. His observations were considered as adaptations developed by natural selection. Batesian mimicry was and is cited as one of the first examples of Darwin’s theory of evolution by natural selection (see Fisher 1930).

The Batesian mimicry complex includes a predator, a model and a mimic. The predator acts as a selective agent (see Edmunds 1966; Bowers *et al.* 1985; Mallet & Barton 1989) in this complex since it affects the mortality of both the model and the mimic. The model is an aposematic species, which conspicuously advertises its unprofitability to the predator. The predator learns to avoid the model species as a result of the warning signal, e.g. conspicuous coloration (Gittleman & Harvey 1980; Roper & Redston 1987; Guilford 1990; Endler 1991). A palatable mimic, which resembles a model, gains protection by deceiving the same predators to avoid it along with the model. The classic

example of Batesian mimicry with close similarity between model and mimic is the coloration between monarchs (*Danus plexippus*) and viceroys (*Limenitis archippus*) (Brower 1958, but see Ritland & Brower 1991). The black-and-yellow warning coloration shared between hoverflies (Diptera) and wasps (Hymenoptera) is an example of Batesian mimicry, where the resemblance between the model and the mimic is much less perfect (see Dittrich *et al.* 1993).

The main feature of Batesian mimicry is deception of the predator’s senses, e.g. sight. The protection of the mimic is gained by diminishing the attack rate by the predator, because the predator mixes up unpalatable models and mimics and leaves both untouched. For example, the Batesian mimic can gain protection by sharing a colour pattern with the model (Sternburg *et al.* 1977). Since predators commonly learn (Mallet & Singer 1987, but see Schuler & Hesse 1985) to avoid aposematic species, this resemblance, favourable to the mimic, is unprofitable to the model (Fisher 1930; Lea & Turner 1972). The encounter rate by the predator is increased since palatability of the mimic is associated with the signal shared with the model. This conflict between the mimic and the model is considered to be a result of natural selection acting more strongly on the mimic than on the model (Nur 1970; Huheey 1984; Turner 1987).

Batesian mimicry has probably evolved more frequently in the presence of highly unprofitable models (Endler 1991). The unprofitability of the model may also affect the degree of the imitation. There is also

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evidence that an imperfect mimic can survive if the model is highly unpalatable (Duncan & Sheppard 1965; Goodale & Sneddon 1977), however, nearly perfect mimicry is to the mimic's advantage as long as the mortality of the mimic is higher than that of the model (Fisher 1930; Nur 1970).

If the predators have to learn to avoid the aposematic models, the mimics might disturb the learning process unless they are relatively rare. Bates (1862) argued that the imitation could be advantageous to mimic species only if the models highly outnumber them. The fundamental experiment by Jane Brower (1960), however, indicated that perfect Batesian mimics can gain some protection even when the prey included only 10% models. Similar findings have also been made in other studies with visually perfect (Huheey 1980; Avery 1985; Nonacs 1985) but not with imperfect (Pilecki & O'Donald 1971) mimicry. These findings are therefore more applicable to automimicry (see Brower *et al.* 1970; Rettenmeyer 1970), where individuals within the same species differ according to the distastefulness (Alonso-Meja & Brower 1994). In the early evolution of Batesian mimicry the mimics were probably imperfect, and later improved by selection.

Most mimicry experiments have been done by using a method in which the perfect mimic has been presented to a predator simultaneously with alternative prey (Brower 1960; Pilecki & O'Donald 1971; Lea & Turner 1972; Goodale & Sneddon 1977; Avery 1985; Nonacs 1985). However, in the field, prey are not usually encountered exactly simultaneously. Simultaneous choice designs might thus underestimate the mortality risks for both Batesian mimics and models (see Hetz & Slobodchikoff 1988).

Our aim was to investigate what effects the level of unpalatability and the frequency of a model have on its imperfect Batesian mimic in a sequential choice situation. The predators thus only had one prey option at a time: model, mimic or control, since when estimating survival chances in the field a sequential choice is more realistic than the simultaneous choice. For a solitary model or mimic it is crucial that previous encounters are remembered when a predator encounters them singly.

2. MATERIALS AND METHODS

(a) Predator

This experiment was carried out during autumn 1995 at Konnevesi Research Station, central Finland. Wild great tits (*Parus major*), which are abundant in the area, were used as predators. Birds ($n = 76$) were captured with a mist net and kept individually in cages ($15 \times 15 \times 25 \text{ cm}^3$) for a few days and released after the experiment. Each cage was individually illuminated and covered with paper sheets to keep the birds calm. At first, the birds were kept in continuous light to ensure that they were feeding in the cages. Birds were provided with sunflower seeds and nuts as food, and fresh water *ad libitum*. Not all the birds were suitable for the experiment, since some (7) refused to forage in the cages and were therefore released without using them in the experiment. Ten birds failed to eat the mealworms. In the final

experiment, 59 birds were used (28 females and 31 males, of which there were 45 yearlings and 14 adults).

The experimental cages were larger in size ($30 \times 20 \times 40 \text{ cm}^3$). The cage had no bottom, but was placed on a plywood board. There was a hole ($r = 3 \text{ cm}$) in the plywood, under which a tray could be placed. The birds were trained to feed from the hole. The experimental prey was presented on a petri dish on the tray. The birds were isolated from the observer by a plywood screen in front of the cage and observations were made through a hole in the screen. The birds were allowed to habituate to experimental cages for at least a day before the experiment. Since birds have tetrachromatic vision, cages were illuminated with non UV-emitting bulbs to minimize effects invisible to man. There was fresh water available continuously, but there was food only during the habituation time.

(b) Prey

The prey used in this experiment were final instar mealworm larvae (*Tenebrio molitor*). The birds had no previous experience with the prey since it is not naturally available in this area. The aposematic models were first injected with 0.1 ml of chloroquine solution and also dipped into the solution. Three light-blue nonpareils (1.5 mm sized small sugarballs normally used in cake decoration) were used as a signal and glued (with animal fat) on the head end of each larva's body. The use of nonpareils instead of paints was to ensure no change in the palatability of the mimics. Birds did not eat the nonpareils, and usually removed them before eating the prey type. Since light blue is not a common warning colour, it was used to minimize previous learning with aposematic coloration. The novel colour was also used to test if an imperfect signal alone can support mimicry. The Batesian mimics to the chloroquine-flavoured models were larvae with three nonpareils in the middle of the body (figure 1). Controls were mealworm larvae without the signal. All models, mimics and controls were reduced to a length of ca. 2 cm by removing segments from the tail end of the body.

There were two levels of chloroquine solution and hence two levels of distastefulness: palatability 1 = 17% and palatability 2 = 63% solution. Both solutions were unpleasant to humans and had a gradient in unpalatability (personal observations), which we assumed to be so for birds also.

(c) Training

As is likely that Batesian mimicry evolved after the aposematic coloration, the predators were first allowed to encounter the models. The birds were divided into two groups according to palatability treatments and trained first to avoid the aposematic models by giving them control-model couplets. For motivation, birds were deprived of food for 1 h before training. At first six pairs of control and model larvae were presented simultaneously for 3 min each. After a pause of 20 min, 4 models and controls were presented individually one at a time in a random sequence at two-minute intervals to the birds.

(d) Experiment

The experiment was carried out 1 h after training. During this hour birds were offered three sunflower seeds to ensure that they were not too hungry and were able to make a real choice.

There were three levels of model-mimic frequencies (model frequencies of the model-mimic complex: 25%, 50% and

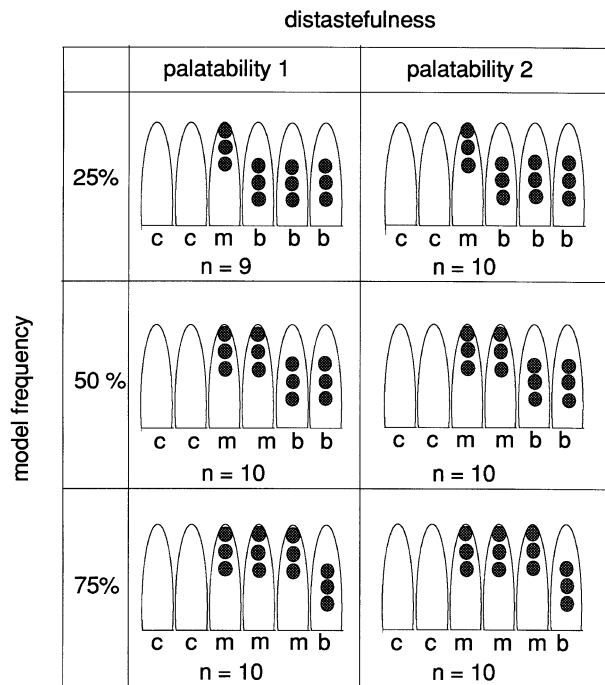


Figure 1. The experimental design. There were two treatments: the frequency of the model and the distastefulness of the model. The frequencies of the model are calculated within the mimic-model complex. The levels of distastefulness are palatability 1 = 17% and palatability 2 = 63% of chloroquine solution. For each bird five trials, where prey items were in random sequence, were presented. The letters 'c' represent the control, 'm' the model and 'b' the Batesian mimic.

75%) at both palatability levels (figure 1). Each bird was assigned to one of these treatments. Treatments consisted of five trials each lasting for 15 min, with a 15 min interval between the trials. In a trial, six prey items (two of which were controls) were offered to a bird in a random sequence, one at a time. Each item was presented to a bird for 30 s. If the bird did not take the prey it was removed from the cage. The bird was allowed 2 min to handle each prey item. Between trials all leftover food was removed from cages. To equalize hunger levels we made sure that birds ate at least three prey items in each trial; thus if a bird ate only two controls it was offered one extra mealworm immediately after the trial.

The prey was considered as 'killed' if the birds ate, took bites from the prey, or were hammering the prey. If the birds took a larva and dropped it immediately it was considered to have survived (in each experimental series only an average of 1.30, s.d. = 1.53 mealworms were dropped). Mortalities were calculated over trials as percentages and transformed into arcsin squareroot to normalize the data. Statistical tests, which are all two-tailed, were performed by using a PC version of SPSS (SPSS 1992).

3. RESULTS

(a) Training

There was no preference in the first choice (model = 28, control = 31, binomial test, $p = 0.79$), which indicates that the signal was indeed novel at first. In the final couplet the first choice was mainly for the control mealworm (palatability 1: $n_{\text{model}} = 9$, $n_{\text{control}} = 20$, binomial test, $p = 0.063$; palatability 2:

$n_{\text{model}} = 3$, $n_{\text{control}} = 27$, binomial test, $p < 0.001$). The birds seemed to learn more quickly to avoid the model at the higher distastefulness level (Fisher exact test, $p = 0.058$).

Although the birds learnt to avoid aposematic prey in the couplets there were only a few birds which rejected all individually presented models. The mean mortality of the models in the training was 42% ($n = 29$, s.d. = 21%) for the less distasteful and 41% ($n = 30$, s.d. = 30%) for the more distasteful model; mean mortalities of the controls were 67% (s.d. = 26%) and 78% (s.d. = 25%) respectively, to palatability. Birds learned to avoid aposematic models since they killed more controls than models (palatability 1: Wilcoxon matched pairs, $Z = -3.24$, $p = 0.0012$; palatability 2: Wilcoxon matched pairs, $Z = -3.91$, $p < 0.001$).

(b) Experiment

The experimental data were analysed by using an ANOVA model, where the frequency and the palatability of the model were categorical factors. Each prey type was analysed separately as the dependent factors in two-way ANOVAs. No interactions between palatability and frequency were found (Batesian mimic: $F_{(2,53)} = 0.46$, $p = 0.616$; model: $F_{(2,53)} = 0.14$, $p = 0.868$; control $F_{(2,53)} = 0.44$, $p = 0.643$). The treatments had no effect on the mortality of the control (frequency: $F_{(2,55)} = 0.31$, $p = 0.734$; palatability: $F_{(1,55)} = 0.02$, $p = 0.889$).

The frequency of the models had a significant effect on the mortality of the mimics ($F_{(2,55)} = 3.47$, $p = 0.038$). The mimics survived better the more abundant the models were. There were also indications that the distastefulness of the models affected the mortality of the mimics ($F_{(1,55)} = 3.17$, $p = 0.081$) (figure 2).

The effects of the experiment on the models were more obvious than on the mimics. Both the models frequency ($F_{(2,55)} = 12.03$, $p < 0.001$) and distastefulness ($F_{(1,55)} = 5.32$, $p = 0.025$), significantly affected the mortality of the models. The higher the models' frequency, the better was the survival of the models (figure 2). The more distasteful models also survived better than the less distasteful models.

4. DISCUSSION

This experiment demonstrates that there is space for the evolution of Batesian mimicry. Imperfect Batesian mimics gained most in terms of low mortality when the models outnumbered them (figure 2). The experiment with the novel signal also suggests that the more unpalatable the models were, the better the mimics seemed to survive. The high frequency and unprofitability of the models seems to be crucial for the introduction of imperfect Batesian mimics, which confirms the existing theory (Fisher 1930; Nur 1970). The introduction of Batesian mimics increased the mortalities of the models. After the introduction of mimics the models survived better the more abundant they were. More unpalatable models also had higher survival rates than less unpalatable models, indicating

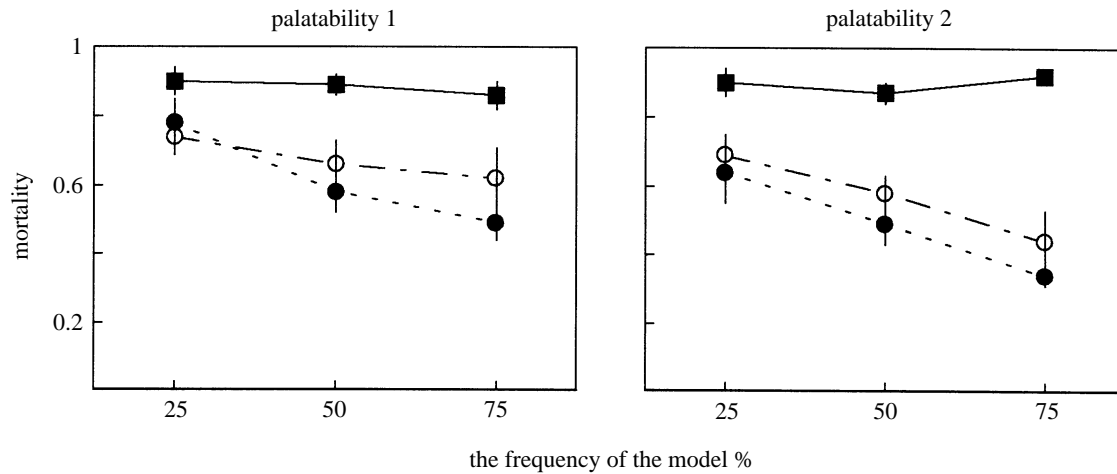


Figure 2. The mortalities of controls (filled squares), mimics (open circles) and models (filled circles) according to the frequency and palatability of the model. The bars represent the \pm s.e. of means.

that the fitness loss to models at low mimic frequencies is not particularly severe if the models are highly unpalatable. The introduction of a Batesian mimic into the prey population seems to have least effect on relatively common and highly unprofitable models.

There is evidence that perfect mimics (automimicry) can gain protection from their resemblance to the models even when they outnumber the models (Brower 1960; Nonacs 1985). The relationship between hoverflies and wasps is considered as an example of imperfect Batesian mimics outnumbering their models. This might be explained by the innate tendency of birds to avoid yellow-black colour patterns (Schuler & Hesse 1985, but see Dittrich *et al.* 1993). Alternatively, Howse & Allen (1994) have suggested that this imperfection is due to the satyric mimicry, where there is ambiguity of the signal. Waldbauer (1988) has also suggested that the mimics and models can spread through time to avoid predation. He observed that Batesian mimics of some models fly before the fledging time of local birds and thus avoid naive predators.

Our experiment also demonstrates the conflict between models and mimics, which becomes apparent in sequential, as opposed to simultaneous choice experiments (Brower 1960), since the predators have no alternative prey presented at the same time. The occurrence of the mimics strongly affects the survival of the models, particularly when they are common. At low model frequencies the mortality of the models is over 70%, which suggests that in this situation, mimicking these models might not be profitable. If the predation among models is high, it will also lead to high predation among Batesian mimics. As Nonacs (1985) points out, the mimicry complex should be seen as dynamic. Selection pressure is strongest on the prey type which suffers highest mortality. Therefore, if mortality of the mimic is highest, selection will drive the resemblance towards the model. In contrast, if mortality of the model is high it might be beneficial to the model to become more unpalatable since the visual image of the model is not likely to alter (see Turner 1987). This would also benefit the mimics.

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