

Predator experience on cryptic prey affects the survival of conspicuous aposematic prey

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Initially, aposematism, which is an unprofitable trait, e.g. noxiousness conspicuously advertised to predators, appears to be a paradox since conspicuousness should increase predation by naive predators. However, reluctance of predators for eating novel prey (e.g. neophobia) might balance the initial predation caused by inexperienced predators. We tested the novelty effects on initial predation and avoidance learning in two separate conspicuousness levels of aposematic prey by using a 'novel world' method. Half of the wild great tits (*Parus major*) were trained to eat cryptic prey prior to the introduction of an aposematic prey, which potentially creates a bias against the aposematic morph. Both prey types were equally novel for control birds and they should not have shown any biased reluctance for eating an aposematic prey. Knowledge of cryptic prey reduced the expected initial mortality of the conspicuous morph to a random level whereas control birds initially ate the conspicuous morph according to the visibility risk. Birds learned to avoid conspicuous prey in both treatments but knowledge of cryptic prey did not increase the rate of avoidance learning. Predators' knowledge of cryptic prey did not reduce the predation of the less conspicuous aposematic prey and additionally predators did not learn to avoid the less conspicuous prey. These results indicate that predator psychology, which was shown as reluctance for attacking novel conspicuous prey, might have been important in the evolution of aposematism.

Keywords: aposematism; novelty; neophobia; initial evolution; signal conspicuousness; predator psychology

1. INTRODUCTION

A combination in which prey species advertise their unprofitability to potential predators with conspicuous signals is called aposematism (Poulton 1890). Warning colours, which are a form of aposematism, are colours that usually contrast with the background (Cott 1940; Edmunds 1974; Endler 1978), since predators learn to associate conspicuous rather than cryptic patterns and colours with unprofitability more easily (Gittleman & Harvey 1980; Sillén-Tullberg 1985*a,b*; Roper & Wistow 1986; Alatalo & Mappes 1996; Lindström *et al.* 1999*a*). Predators also remember this association for longer (Roper & Redston 1987). Although aposematism has been shown to be selectively advantageous against experienced predators it bears an evolutionary problem. Conspicuousness increases the initial predation risk (Gittleman & Harvey 1980; Alatalo & Mappes 1996) since predators can detect conspicuous prey more easily. Thus, how did conspicuousness evolve, since the first pioneers were prone to predation due to increased visibility and encounter rate and, therefore, were most probably sampled and killed during the training of predators?

Although learning (Cott 1940; Gittleman & Harvey 1980) has been attributed as being the main factor facilitating the evolution of aposematism, it is not the only potential aspect of predator psychology that can influence the signals used by prey species. If predators already have some preferences (Guilford & Dawkins 1991) when they encounter possible new prey types for the first time, this could make a difference in the evolutionary scenario. Predator preferences may be innate (see Lindström *et al.*

(1999*b*) and references therein) or unlearned and triggered by novelty (Schuler & Roper 1992) or they may be learned or be the result of a search image (Tinbergen 1960).

Neophobia, i.e. the fear of anything new, has been shown to affect the food choices made by many generalist predators (Barnett 1958). Rats show hesitancy in eating novel food and even familiar food paired with novel cues. Coppinger (1969) showed that the diet history of birds affects the choices they make when presented with novel conspicuous colours. He suggested that neophobia might therefore be important in the evolution of warning signals. Marples *et al.* (1998) proposed that diet conservatism, where neophobia plays a role, could provide a mechanism for the initial increase in aposematic prey types. Therefore, a preference for cryptic prey could reduce the predation risk of even conspicuous aposematic prey since predators may fail to recognize new conspicuous types as prey or learn to avoid novel conspicuous unpalatable prey more quickly.

However, a predator's reaction towards novel prey is not fixed but can be altered by changes in rearing environment and by the experiences of an individual (Braveman 1978). Generalist and specialist predators are also known to behave differently towards novel prey (Greenberg 1983). Generalists are bolder in including novel food in their diets compared to specialist species (Marples *et al.* 1998). Novel food consumption may also differ between the sexes. Female chickens tend to be less neophobic than males although there are differences in different chick strains (Jones 1986). Novelty has also been shown to enhance avoidance learning (Shettleworth 1972; Roper & Marples 1997; but see Roper 1994). Furthermore, novel odours can elicit an avoidance of coloured

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food even when the colour pattern is relatively familiar (Rowe & Guilford 1999) indicating differences between signal modalities.

This study focused on how the knowledge of a predator and the conspicuousness of an aposematic prey affect its initial predation and a predator's avoidance learning. Our aim was to test (i) whether predators' knowledge of cryptic prey and signal conspicuousness affect the survival of a novel aposematic prey on its introduction, (ii) whether the relative novelty of an aposematic prey affects the learning process, and (iii) whether learning is more dependent on a signal's conspicuousness. We were able to do this by creating a 'novel world' (Alatalo & Mappes 1996) for birds where the background was formed of symbols and where artificial prey also wore symbols. By using this method the impact of colours, towards which birds have been repeatedly shown to have preferences (see the references in Lindström *et al.* (1999b)), can be diminished.

2. MATERIALS AND METHODS

The study was carried out at Konnevesi Research Station in central Finland. We used wild great tits (*Parus major*) as predators in our experiments. Central Finland Regional Environment Centre gave us permission to mist-net and keep the birds (LS-36/98, Dnro 0998L0540/253) and the Ethical Committee of the University of Jyväskylä gave us permission to perform the experiment (nro 12 21.9.98). Birds were individually housed in illuminated plywood cages (65 cm × 80 cm × 65 cm). It is essential to keep birds in captivity calm. Birds cannot see out in these plywood cages and, therefore, they do not continuously try to escape. Birds also retain good plumage conditions much better in plywood cages compared to any cages with a view to the outside. The birds had access to sunflower seeds, peanuts and fresh water *ad libitum*. The experimental aviary was 3.4 m × 3.9 m (height 2.5 m) in size. In order to habituate birds feeding from the aviary, the floor was covered with sunflower seeds and peanuts. Two handling perches were provided on both sides of the room. After the experiment the birds were released at the same location as where they were captured.

(a) Training

Birds were divided into two groups after capture, i.e. to a preference and visibility experiment ($n = 22$) and to a learning experiment ($n = 56$). First, all birds were taught to handle artificial prey items. For the preference, experiment birds were gradually trained to open almond-filled white-paper prey items. Birds were first offered pieces of plain almond. After they had eaten the almonds they were offered a piece of almond glued to a piece of white paper and then a piece of almond inserted between two white papers, but with the almond clearly visible. Finally, a tiny slice of almond (*ca.* 8 mg) was glued between two 10 mm × 10 mm pieces of paper, which birds had to open in order to get access to the almond. In each training stage, birds had to eat five artificial prey items before they were upgraded to the next stage.

(b) Preference experiment

The preference experiment was conducted in order to see whether wild birds had any prevailing biases towards the artificial symbols used in this experiment. If the birds had had a preference for or avoidance towards the symbols we would not have overcome

the evolutionary history of the birds' preferences. Birds that were assigned to the preference experiment were further divided into two groups according to the aposematic symbols (see figure 1), i.e. either 'weak' symbols (filled boxes with crosses) or 'strong' symbols (filled boxes) and these groups were also retained in the visibility experiment. Both groups were offered the 'cryptic' symbol (crosses) along with either of the 'aposematic' symbols, i.e. the weaker ($n = 11$) or the stronger ($n = 11$). This was performed in cages (30 cm × 24 cm × 40 cm) illuminated with light bulbs (75 W) that had a white plastic cover and, thus, there was no ultraviolet light present. The birds were provided a perch and the offering of two signalling prey items was performed on a tray that was placed *ca.* 10 cm from the perch (see Lindström *et al.* (1999b) for details). Two symbols (the cryptic symbol and either of the aposematic symbols) were offered side by side and the order in which the bird took the prey items was recorded. The birds were offered a total of 20 pairs. Pairs were presented in four consecutive sessions that were separated by a break.

(c) Visibility of the aposematic signal

A visibility experiment using the same birds was carried out after the preference experiment. This was done in order to determine the possible visibility risks for the two different conspicuousness levels of aposematic prey on the novel landscape. Two novel landscapes were created on two similar aviary floors (covering an area of 9.57 m²). The landscapes were divided into seven rows and ten columns of A3-size (*ca.* 42 cm × 29.6 cm) paper sheets (altogether 70) that each had 66 cross symbols irregularly orientated and spaced. The paper sheets were covered with transparent self-adhesive book covering film (Pelloplast). Ten fake, cryptic prey items (a cryptic symbol glued to a paper-board) were glued on the film of each A3 paper sheet. This was done in order to make the landscape three-dimensional and to make it more difficult for the birds to find the cryptic prey. There was a wooden blank between each row along which the birds could move and handle the prey. The aviaries were illuminated with four bulbs (75 W) each having a white plastic cover, which was similar to the preference experiment.

In the visibility experiment four cryptic and four aposematic (either filled boxes with crosses or filled boxes) prey types were randomly distributed to five blocks (each block was 14 sheets) (a total of 20 + 20 prey items). In this experiment all paper prey items were palatable in order to allow us to estimate the visibility risk for each prey type. Birds were allowed to eat 15 prey items. We performed direct behaviour observations without disturbing the birds through a one-way mirror glass. The order in which the birds ate the prey items was recorded.

(d) The learning experiment

In order to assess the impact of prior knowledge of cryptic prey on avoidance learning a new set of birds ($n = 56$) was divided into four treatments ($n = 14$ for each treatment) according to 'knowledge' level and the type of aposematic symbol (filled boxes with crosses or filled boxes). We used two conspicuousness levels since there have been indications (Lindström *et al.* 1999a) that relatively inconspicuous novel prey benefit more from novelty effects than highly conspicuous prey. The 'control' group of birds was taught to open artificial white prey items as in the preference experiment. These birds should not show an initial aversion to the aposematic prey types, but should eat cryptic and conspicuous prey according to the visibility difference and, thus, should not show biased reluctance for eating the aposematic type. The 'experienced' group was

trained to open prey items that had the cryptic symbol (crosses) printed on them. This group potentially shows a bias against novel aposematic prey and should not eat the prey according to their visibility difference. Their training was performed similarly to that for the control group except that experienced birds were allowed to eat 15 one-sided paper prey items (stage 2 in the training process). The enhancement of the cryptic signal was performed in this phase since it would least affect the birds' ability to handle the paper prey items.

Before the actual experiment, birds were habituated to eating the artificial prey items in the aviary in order to reduce the possible effects of the novelty of foraging from the novel landscape. Fifteen prey items were placed into five groups in such a way that one prey item of the group was on the wooden blank, one was next to it and one was in the middle of the A3 paper. The control group was given white prey items and the experienced group cryptic prey from the novel landscape. Altogether, each experienced bird ate 40 cryptic prey items prior to the learning experiment.

In the experiment, 20 palatable, cryptic symbols and 20 unpalatable (almonds soaked in 67 g l^{-1} of chloroquine-phosphate solution for 1h) of either the weaker or stronger aposematic symbols were randomly scattered to five equal blocks (each of the 14 A3 papers). Birds were allowed to eat 15 prey items and the order in which they took the prey items was recorded. The same procedure was repeated on five consecutive days. The statistical tests were performed by using an SPSS v.9.0 statistical package. Parametric statistics were used when the data met the assumptions (a two-factorial ANOVA and repeated-measures ANOVA), otherwise non-parametric statistics were applied. All p -values are two-tailed.

3. RESULTS

(a) Preference

Birds captured from the wild can have either inherited or learned preferences. Therefore, birds' preferences towards the symbols used in the experiment were tested. We compared the number of conspicuous (either filled boxes with crosses or filled boxes) prey types versus the number of cryptic (crosses) prey types taken as the first in a pair. The birds showed no preference, as measured as the mean of the 20 pairs presented, towards the less conspicuous signal (filled boxes with crosses) ($\bar{x} = 10.72$ and $\text{s.e.} = 0.75$) or the cryptic signal (crosses) ($\bar{x} = 9.27$ and $\text{s.e.} = 0.75$) (Wilcoxon $Z = -1.136$, $n = 11$ and $p = 0.256$). This was true also for the more conspicuous prey types (filled boxes and crosses) ($\bar{x} = 9.45$ and $\text{s.e.} = 1.2$, and $\bar{x} = 10.55$ and $\text{s.e.} = 1.22$, respectively) (Wilcoxon $Z = -0.358$, $n = 11$ and $p = 0.721$).

(b) Visibility

There was a tendency towards the birds eating the less conspicuous (filled boxes with crosses) signal (Wilcoxon $Z = -1.860$, $n = 11$ and $p = 0.063$) more often than the cryptic prey when they were presented against the cryptic background. The median for the visibility risk (number of signalling prey taken divided by number of cryptic items taken) was 1.50 for the less conspicuous signal. When more conspicuous prey (filled boxes) was offered with cryptic prey on the crossed background, the birds took the conspicuous prey items more often ($Z = -2.941$, $n = 11$ and $p = 0.003$). Some birds might have developed a

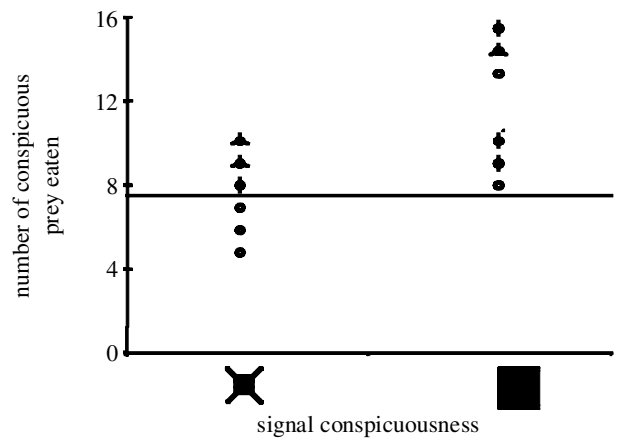


Figure 1. Distribution of the number of conspicuous prey items eaten in the visibility experiment. Each petal in the sunflowers indicates an individual bird. The reference line indicates where conspicuous prey were eaten at the same rate as cryptic prey.

search image for the conspicuous prey (since two ate conspicuous prey only) and, thus, the visibility risk was nearly sixfold higher when compared to the cryptic prey ($M_d = 6.50$) (figure 1).

(c) Learning experiment

In order to assess the initial risk for the aposematic prey type entering a cryptic population, we counted the number of aposematic prey items eaten within the first five prey items taken. The interaction between experience and signal conspicuousness was significant (ANOVA, $F_{1,52} = 15.73$ and $p < 0.001$) when the number of unpalatable prey items eaten within the first five prey items consumed was a dependent variable (figure 2). This indicates that knowledge of the cryptic prey acted differently between the two signal levels. While experience decreased consumption of the more conspicuous morph ($t = 4.16$, $\text{d.f.} = 26$ and $p < 0.001$ after Bonferroni correction), knowledge of the cryptic prey did not affect the survival of the less conspicuous morph ($t = -1.16$, $\text{d.f.} = 26$ and $p = 0.518$ after Bonferroni correction). However, by comparing the mortality to the visibility experiment there was no initial cost for the weaker signal in either treatment (Mann–Whitney U -test, control $Z = -1.34$ and $p = 0.222$, and experienced $Z = 0.82$ and $p = 0.467$), indicating no cost of visibility to this morph. Instead, the predation of the more conspicuous prey by control predators did not differ from the estimated visibility risk (Mann–Whitney U -test, $Z = -1.01$ and $p = 0.373$), but the mortality was less than expected when the predators had experienced cryptic prey prior to the experiment (Mann–Whitney U -test, $Z = -3.17$ and $p = 0.001$) (figure 2).

In order to test learning, we used the amount of unpalatable prey eaten in every trial as the dependent variable. There was a significant three-way interaction between the trial number, signal conspicuousness and experience (repeated-measures ANOVA, $F_{4,49} = 2.76$ and $p = 0.038$) (figure 3). This indicates that both the conspicuousness of the signal and experience affected learning. When both signal conspicuousness levels were

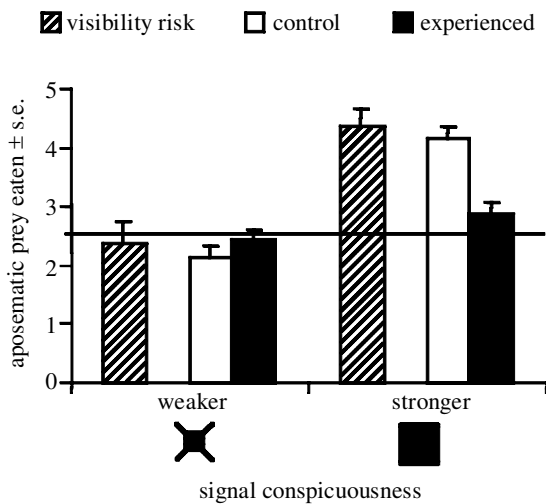


Figure 2. The mean number of aposematic prey eaten (\pm s.e.) within the first five prey consumed in the visibility experiment (hatched bars) and in the first trial of the learning experiment (open and closed bars). Hatched bars indicate the visibility risk of conspicuous prey attained from the visibility experiment. Open bars indicate the control group, which had no prior knowledge of the cryptic prey and the closed bars the experienced group, which knew the cryptic prey prior to the introduction of aposematic prey in the learning experiment.

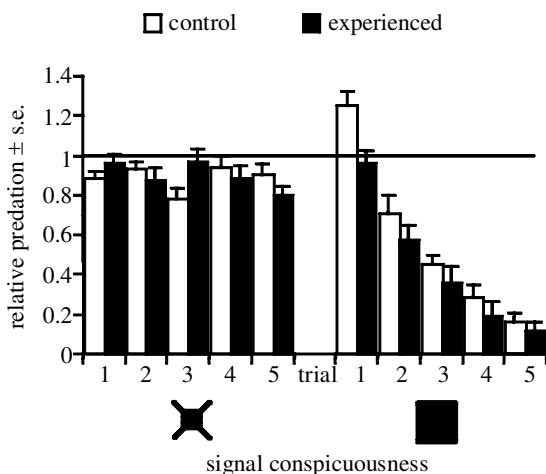


Figure 3. The relative predation risk of aposematic prey for both conspicuousness levels in relation to cryptic prey. Open bars indicate the control group, which did not have prior knowledge of the cryptic prey and closed bars the experienced group, which had experience of the cryptic prey prior to the learning experiment. At the random line predators eat cryptic and aposematic prey with the same probability. Above the random line predators eat more aposematic than cryptic prey and below the random line predators prefer cryptic prey.

compared separately the interaction between experience and learning was non-significant at both conspicuousness levels (repeated-measures ANOVA, weaker $F_{4,23} = 2.03$ and $p = 0.123$, and stronger $F_{4,23} = 1.165$ and $p = 0.352$). The birds did not learn to avoid the less conspicuous prey during the five-day period (repeated-measures ANOVA, $F_{4,23} = 0.88$ and $p = 0.498$) and experience did not play a role in the experiment ($F_{1,26} = 0.63$ and $p = 0.803$).

However, the more conspicuous prey was learned ($F_{2,23} = 70.622$ and $p < 0.001$) and there seemed to be a main effect of experience ($F_{1,26} = 3.719$ and $p = 0.065$), indicating that knowledge of the cryptic prey affected learning but that learning was due more to the conspicuousness of the aposematic prey.

4. DISCUSSION

A novel, highly conspicuous aposematic signal did not suffer from the expected visibility risk when predators had prior knowledge of the cryptic prey (figure 2). The reduction in the potential visibility risk (figure 2) was most apparent in the early encounters of the conspicuous aposematic prey. Although there was a higher visibility cost for the conspicuous prey when predators did not know the cryptic prey, this led to faster avoidance learning of the birds. Since there was no interaction between learning and experience, our experiment suggests that relative novelty does not increase the learning process (figure 3), although this has been previously found in some (Shettleworth 1972; Roper & Marples 1997) but not all experiments (Roper 1994). These results indicate that exploiting predator behaviour towards novelty might have played an important role in the evolution of aposematism.

There was no initial cost for the weaker signaller from the visibility risk but there was no gain in the predator familiarity with the cryptic prey either. There seems to be a threshold in signal conspicuousness that has to be attained before predators are able to associate unpalatability with the signal and learn to avoid the signalling prey (Lindström *et al.* 1999a). This experiment also suggests that predators' knowledge of cryptic prey does not alter this threshold which sets yet another difficulty in conspicuousness gradually evolving under a learning scenario (Lindström *et al.* 1999a).

The fact that conspicuousness is not the only property of aposematic prey (Sillén-Tullberg 1985b; Roper 1994), but that the actual colouring itself may account for novelty effects should also be taken into account (see Schuler & Roper 1992). A slight dissimilarity from the background but yet different colour might create novelty benefits for the prey since birds have been shown to remember and separate colours accurately but not contrast (Osorio *et al.* 1999). Since learning seemed to be more important in the avoidance of conspicuous aposematic prey, it does not seem likely that novelty effects alone are responsible for the evolution of aposematism (see Mallet & Joron (1999) for a discussion). However, dietary conservatism may provide time-windows for prey that allow them to develop aposematic coloration (Marples *et al.* 1998). Therefore, novelty effects might have been spatially important in the evolution of aposematism if predator individuals (Jones 1986) or species (Marples *et al.* 1998) differ in their neophobia levels (see Turner & Mallet 1996).

Conspicuous aposematic signalling has been considered to have evolved in a gregarious prey species since gregariousness conveys multiple benefits. For instance, grouping increases the avoidance learning of predators, but it also reduces the visibility risks (Gagliardo & Guilford 1993; Alatalo & Mappes 1996, 2000; Gamberale & Tullberg

1996a). While the benefits of grouping have been studied, phylogenetical data have suggested that aposematism evolved in a solitary prey and that grouping was attained later (Sillén-Tullberg 1988, 1993). Mechanisms for the evolution of conspicuousness among solitary prey include peak shift or generalization, e.g. learned aversion is shifted towards more conspicuous prey (Gamberale & Tullberg 1996b; Yachi & Higashi 1998; Lindström *et al.* 1999a) and gradual change (Lindström *et al.* 1999a). However, predator behaviour (Guilford & Dawkins 1991) in terms of novelty effects against new aposematic morphs combined with learning can provide an additional mechanism for the initial increase in conspicuous morphs within a cryptic population without the need for grouping.

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