



# Did aggregation favour the initial evolution of warning coloration? A novel world revisited

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From experiments using novel prey signals to avoid innate reactions to traditional signals, [Alatalo & Mappes \(1996, \*Nature\*, 382, 708–710\)](#) concluded that gregariousness would have selected for warning coloration as it originated for the first time, whereas a solitary prey distribution would not. We have investigated this suggestion in experiments using the same novel prey and background symbols and wild-caught great tit, *Parus major*, predators. We compared the attack rate on cryptic unpalatable and aposematic unpalatable prey in either a solitary or an aggregated treatment. In the aggregated treatment we found no difference in attack rate on cryptic and aposematic prey. In the solitary treatment the attack rate on aposematic prey was significantly lower after one attack and at the end of the experiment. Thus, we conclude that, in so far as these experiments mimic an original predator–prey relationship, they do not give support to the idea that aggregation would have favoured the evolution of warning coloration in unpalatable prey.

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The evolution of unpalatability and aposematic coloration has long been a subject of debate. An important question has been whether these traits evolved in solitary or in aggregated prey ([Guilford 1990](#)). [Fisher \(1930\)](#) suggested that unpalatability may evolve in kin-grouped prey, and kin selection has been applied to the evolution of aposematic coloration as well. On the other hand, experiments on live prey ([Wiklund & Järvi 1982](#); [Sillén-Tullberg 1985](#)) as well as phylogenetic work ([Tullberg & Hunter 1996](#)) suggest that both of these traits can evolve in solitary prey.

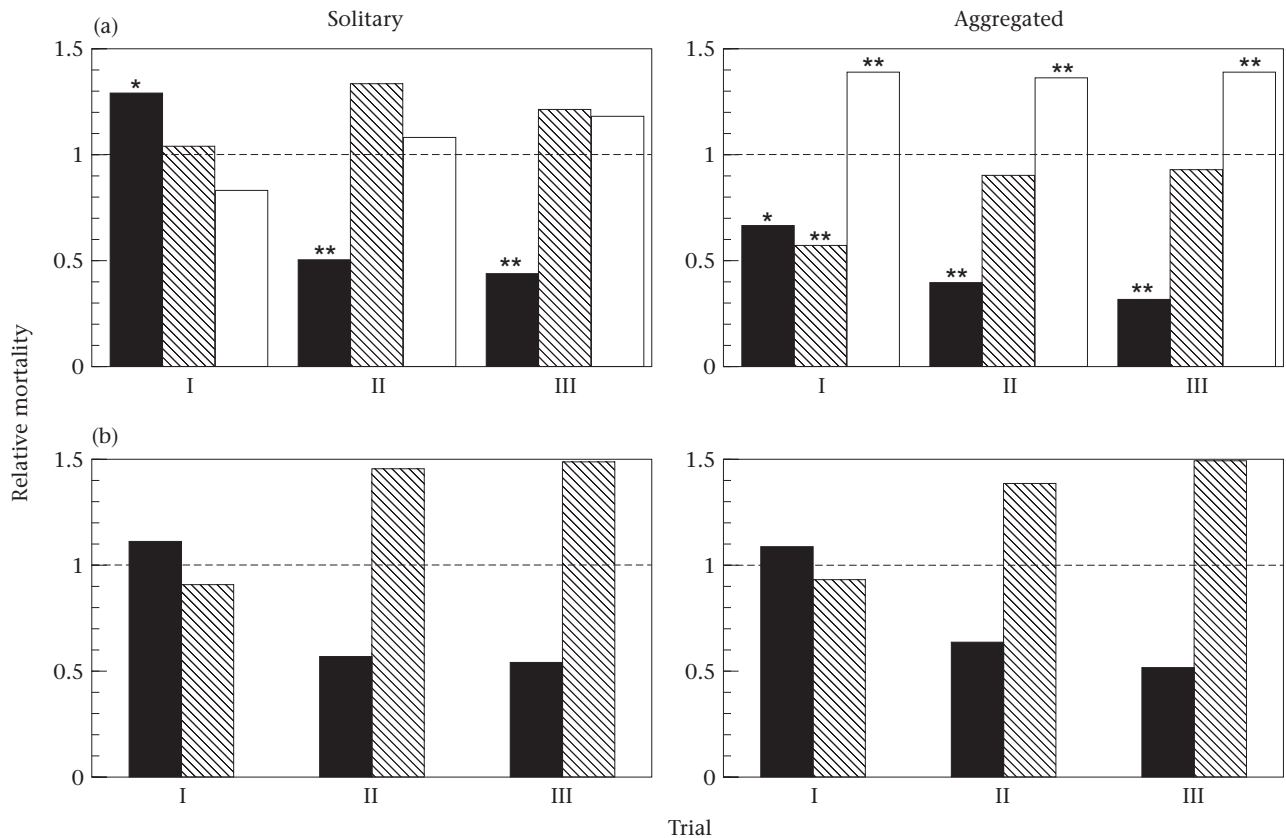
One argument that can be raised against experiments using extant predators and prey is that extant predators are not evolutionarily naïve. They may have innate biases against traditional aposematic signals, acquired through a long process of predator–prey coevolution. This, in effect, would increase the benefit of evolving such signals today, compared with an initial stage in the evolution of life where presumably no such predator biases existed. To circumvent the problem of innate predator biases, [Alatalo & Mappes \(1996\)](#) performed a series of experiments using novel, nontraditional prey signals. From one of these experiments, ‘the initial origin experiment’, they concluded that, when warning coloration first arose, gregariousness would have selected for warning coloration, whereas solitary living would not.

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Here we examine this suggestion in an experiment using a similar novel world setting. In their initial origin experiment, [Alatalo & Mappes \(1996\)](#) compared the attack rates of great tits, *Parus major*, on three types of prey, palatable cryptic, unpalatable cryptic and unpalatable aposematic, in either a solitary or an aggregated treatment. However, to investigate the adaptive significance of aposematism in unpalatable prey, it is crucial that only unpalatable prey are compared with respect to attack rates. Thus, in this study we compared the fate of aposematic and cryptic unpalatable prey in either a solitary or an aggregated treatment.

## BACKGROUND

The results of the initial origin experiment ([Alatalo & Mappes 1996](#)) included the first few attacks in each of three trials (on consecutive days) and were interpreted as showing differential advantage for the aposematic form in the two treatments. Thus, for unpalatable aposematic prey there was an initial disadvantage in the solitary treatment, owing to their higher mortality in the first trial, and an advantage in the aggregated treatment, owing to their lower mortality in the first trial ([Fig. 1a](#)). However, the presence of palatable prey, which were attacked at a higher rate in the aggregated treatment, influenced this result, which can be seen in an analysis that disregards attacks on palatable items and considers only attacks on unpalatable prey in the two treatments



**Figure 1.** (a) Relative mortality of aposematic (■), unpalatable cryptic (▨) and palatable cryptic (□) prey items when presented solitarily and aggregated in the 'initial origin' experiment of Alatalo & Mappes (1996) (an attacked prey item is counted as 'killed'). Mortalities are standardized by dividing the observed mortality by the randomly expected mortality; horizontal lines show the point at which observed matches expected mortality. Significant deviations from randomly expected mortality are denoted by asterisks ( $*P < 0.05$ ;  $**P < 0.01$ ). (b) Relative mortality of aposematic (■) and cryptic unpalatable (▨) prey items (i.e. excluding the attacks on palatable cryptic items from the analysis) when presented solitarily and aggregated in the 'initial origin' experiment. Mortalities are standardized as in (a). The original data on relative mortalities were kindly provided by R. Alatalo & J. Mappes.

(Fig. 1b). Thus, comparing the relative attack rates on cryptic and signalling unpalatable prey in this experiment, we can see that the patterns are quite similar in the solitary and aggregated treatments. In both treatments there were slightly more attacks on the aposematic form in the first trial, whereas in the second and third trials, attack rate on the cryptic form was much higher. Our interpretation of this is that, because all signalling prey were unpalatable, the birds learned to associate the signal with unpalatability in both treatments. However, because some of the cryptic prey were palatable and indistinguishable from the unpalatable prey, the birds continued to attack cryptic unpalatable prey in both treatments. Thus, we suggest that the presence of such palatable cryptic prey determined the fate of the unpalatable cryptic prey.

First, to investigate the adaptive significance of aposematic coloration in already unpalatable prey, only unpalatable prey should be compared with respect to their attack rates. Encounters with palatable prey could take place in a separate training trial before encounters with unpalatable prey in the experimental trial. This would mimic a seemingly realistic situation where predators first have some experience of palatable cryptic prey and then

encounter a population with two unpalatable prey types, one signalling and the other not. In one treatment the unpalatable prey have previously evolved gregariousness and in the other they live solitarily. The specific question then is whether the relative benefit of being aposematic is higher when the prey have already evolved gregariousness. This is the question we addressed in our first experiment.

Second, one might want to explain the difference in relative attack rate on cryptic palatable and cryptic unpalatable prey in the two treatments of the 'initial origin experiment'. Thus, why was the attack rate on cryptic palatable prey much higher in the aggregated treatment (Fig. 1a)?

A possible behavioural explanation is that in the solitary treatment the birds were never able to differentiate between cryptic palatable and cryptic unpalatable prey. However, in the aggregated treatment, where groups of palatable prey were presented together with groups of unpalatable prey, perhaps the birds left an unpalatable aggregation after tasting one item, whereas they continued to attack additional items of a palatable group. We investigated this possibility in experiment 2.

## METHODS

The novel world, that is, novel background and prey types, was created following Alatalo & Mappes (1996). Artificial prey were made of a 6-mm-long rye straw filled with animal fat and with paper wings marked with a symbol at each end. Unpalatable items had a 12% concentration of chloroquine. Because there was no difference in bird behaviour between two reciprocal settings in Alatalo & Mappes (1996), we chose one of these settings, namely a background of crosses on white paper, palatable cryptic items with crosses, and unpalatable items with either crosses (cryptic) or squares (aposematic/signalling). We have followed Alatalo & Mappes in referring to prey marked with the background symbol as cryptic, but since the rye straws are easy to detect on the background paper, this crypsis does not entail camouflage. Thus, it might have been preferable to refer to the prey items as 'ordinary' and 'different' instead of as 'cryptic' and 'aposematic'.

We carried out the experiments at Tovetorp field station, 100 km south of Stockholm, from November 1998 to February 1999. Male great tits caught in the vicinity of the field station were used as predators (under permit from Linköpings djurförsöksetiska nämnd). They were kept individually in cages measuring 50 × 70 cm and 50 cm high. The cages were made of a wooden frame and thick white cotton cloth sides. The tits were kept in these cages under ambient daylength conditions and a temperature of 10°C for about 5 days and given water and sunflower seeds ad libitum before participating in the experiment. Before the birds could attack the artificial prey items in the experiment, they had to learn to eat from straws filled with animal fat. Thus, in addition to sunflower seeds they were given a few such straws (without wings) each day.

Experiments took place in a room measuring 230 × 240 cm and 195 cm high, lit by six daylight lamps. Temperature was held at 10°C and drinking water was provided in a jar. To make the experimental birds more comfortable in the room we placed an artificial Christmas tree, a tree branch and a ray of perches, in three different corners. A wooden frame, measuring 180 × 128 cm, on to which the background paper was glued, was pushed towards the fourth corner of the room. Birds were tested individually and moved to the test room in a box that we could attach from the outside to one of the walls in which a hole had been drilled. A sliding door on the box made the room directly accessible to the bird. Two of the walls, furthest from the background frame, were provided with one-way glass windows (78 × 48 and 88 × 48 cm, respectively), making it possible to observe a bird from two angles. Data were collected simultaneously by two observers, so that if behaviour was obscured by the body of the bird for one observer, it could be readily observed by the other.

The birds were first acclimatized to the test room, and also taught to eat from straws filled with animal fat in that room. Each bird was deprived of food for 1 h, put in the transport box, and allowed to forage in the room for 1 h where straws (without wings) were presented against a

white background (without symbols). Only birds that ate from at least one straw during this pretraining period were used in the experiment.

After each experiment the birds were given mealworms along with sunflower seeds. They were let free the following morning at the same place that they were originally caught. Each bird took part in only one experiment.

### Experiment 1

The experiment consisted of two trials on 2 consecutive days. Birds were deprived of food for 2 h prior to each trial. In the training trial on the first day each bird ( $N=21$ ) was given 32 palatable cryptic items, that is, with wings with a cross against a background with crosses. To make sure that they experienced both solitary and grouped prey, 16 items were presented solitarily and 16 items were presented in tight groups of four. The birds were allowed to take 10 items, but the trial was interrupted after 40 min even if fewer items had been taken. For each item taken, we recorded if it was solitary or grouped.

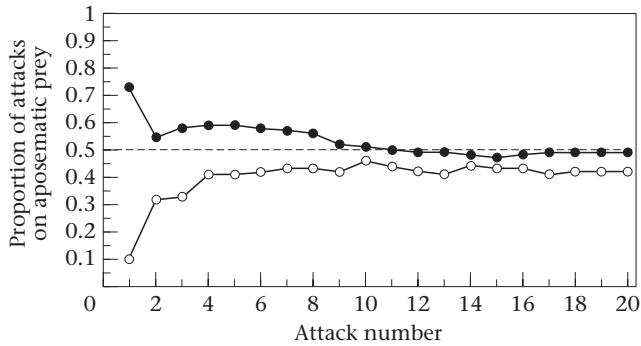
In the experimental trial on the second day, we randomly assigned the birds to one of two treatments, solitary and aggregated. In the solitary treatment ( $N=10$ ) birds were presented with 16 aposematic and 16 cryptic unpalatable prey items that had been randomly distributed over the background with crosses. In the aggregated treatment ( $N=11$ ) birds were presented with four groups each with four cryptic unpalatable items and four groups each with four aposematic unpalatable items, the eight groups being randomly distributed over the same background as in the solitary treatment. Birds were deprived of food for 2 h prior to the trial, which lasted for 20 min. The reason for the shorter time in this trial was to avoid the birds going without food for long in a situation where all prey items were inedible. We recorded all attacks during the trial.

### Experiment 2

Great tits were presented with groups of palatable cryptic prey together with groups of unpalatable cryptic prey, the two prey types being visually indistinguishable. Two groups each with eight palatable cryptic items and two groups each with eight unpalatable cryptic items were placed on the background with cross symbols in the form of a square of 40 × 40 cm. The exact placement of palatable and unpalatable groups varied between experimental birds. Birds ( $N=8$ ) were deprived of food for 2 h and then allowed to forage for 30 min in the experimental arena. We noted the sequence of attacks on items from the four groups and the total number of palatable and unpalatable items taken.

### Statistics and Data Analysis

We used the Wilcoxon signed-ranks test with the individual bird as unit, to evaluate the significance of variation in attack rates. When reporting a comparison we indicate the number of birds showing a difference in



**Figure 2.** Proportion of attacks on aposematic prey items during the first 20 attacks by great tits in experiment 1. For a given attack number, the proportion was computed from all attacks up to and including this number. Ten birds were presented with solitary prey (○) and 11 with aggregated prey (●). The two treatments differ with respect to prey taken in the first attack (Fisher exact test:  $P=0.008$ ).

attack rate ( $N_{\text{diff}}$ ), since these birds provide all the data actually used by the test.

We calculated relative mortality as follows. For a bird with  $x$  attacks on cryptic and  $y$  attacks on aposematic prey, the random expected attacks on each prey form is  $z=(x+y)/2$ , and the relative mortalities are then  $x/z$  and  $y/z$  for the two prey forms.

## RESULTS

### Experiment 1

In the training trial we found no difference in the tendency to attack aggregated and solitary palatable prey. In the very first attack eight birds took an item from an aggregation and 13 birds took a solitary prey item (chi-square test:  $\chi^2_1=1.19$ ,  $P=0.275$ ). Moreover, for the 10 attacks allowed in the trial there was no significant difference between the number of solitary and aggregated prey attacked (Wilcoxon signed-ranks test:  $T=22.5$ ,  $N_{\text{diff}}=12$ ,  $P>0.2$ ).

In the experimental trial 11 birds received aggregated and 10 birds received solitary unpalatable prey. Most prey items were quickly dropped after being picked up, and there was thus a chance for the same prey item to be handled more than once. The total number of attacks ranged from one to 41, but there was no significant difference in total attacks between the treatments (Mann-Whitney  $U$  test:  $U=53$ ,  $N_1=10$ ,  $N_2=11$ ,  $P=0.888$ ; solitary treatment:  $\bar{X} \pm \text{SD}=15.2 \pm 11.6$ ; aggregated treatment:  $15.3 \pm 12.7$ ).

Figure 2 shows the proportion of attacks on aposematic prey items over the first 20 attacks in the two treatments. For the solitary treatment the proportion was always less than 0.5. For the aggregated treatment the proportion changed during the experiment from above to slightly below 0.5 (Fig. 2). We compared the number of attacks on the two prey types at four points in the experiment: after one, six, 10 and the total number of attacks (Table 1). For the aggregated treatment there were no significant differences in attack rate on cryptic and aposematic prey at any

**Table 1.** Test for the effect of prey signal (aposematic or cryptic) on attack rate in solitary and aggregated prey

Number of attacks	Solitary prey ( $N=10$ )	Aggregated prey ( $N=11$ )
1	$P=0.02$	$P=0.23$
6	$P>0.2$ ( $T=9$ , $N_{\text{diff}}=8$ )	$P>0.1$ ( $T=13$ , $N_{\text{diff}}=10$ )
10	$P>0.2$ ( $T=15$ , $N_{\text{diff}}=9$ )	$P>0.5$ ( $T=21.5$ , $N_{\text{diff}}=9$ )
All	$P=0.03$ ( $T=4$ , $N_{\text{diff}}=9$ )	$P>0.2$ ( $T=16$ , $N_{\text{diff}}=10$ )

Statistical tests are based on differences (i.e. attacks on aposematic minus attacks on cryptic prey) after one, at most six, at most 10, and for the total number of attacks by great tits presented with solitary or aggregated prey items. Two-tailed  $P$  values refer to the Wilcoxon signed-ranks test, except for the first attack for which the binomial distribution was used.  $N$  refers to the number of birds in each treatment,  $N_{\text{diff}}$  is the number of birds differing in number of attacks on aposematic and cryptic prey.

of these points. For the solitary treatment there were significantly fewer attacks on aposematic than cryptic prey after one attack and for all attacks in the trial, but no significant difference after six or after 10 attacks (Table 1). Figure 3 shows the total number of attacks on the two prey types for each bird in the two treatments (see Table 1). In the solitary treatment, seven out of 10 birds attacked more cryptic than aposematic prey, and in the aggregated treatment six out of 11 birds attacked more cryptic than aposematic prey (Fig. 3). In conclusion, we found no support for aggregation favouring aposematism in unpalatable prey.

### Experiment 2

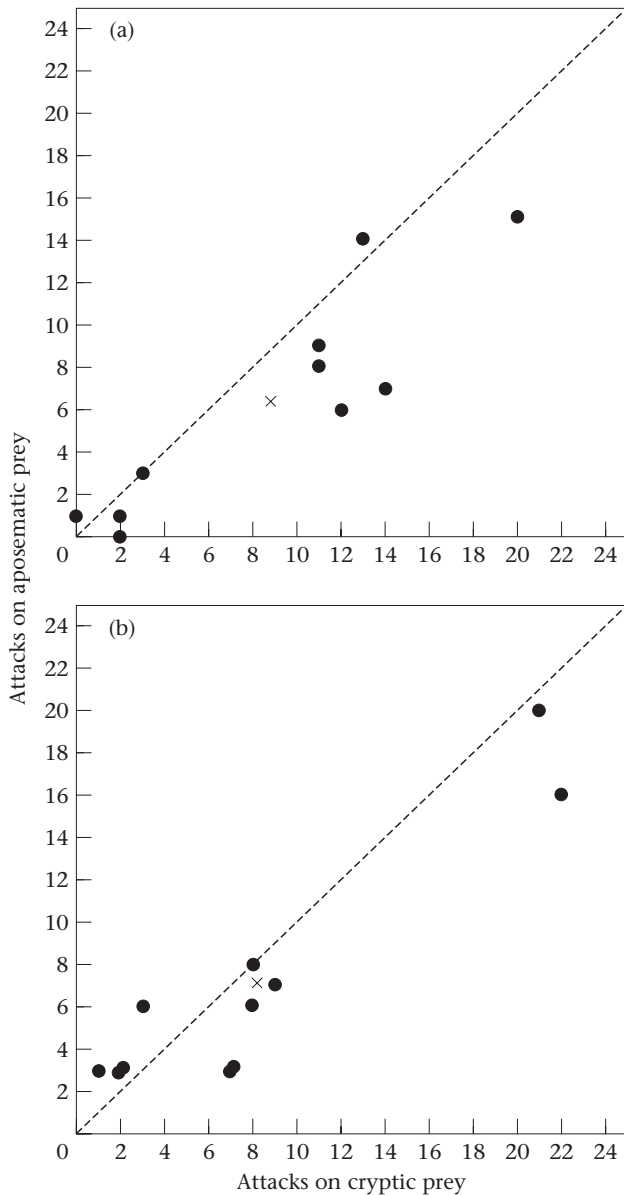
All eight birds visited all four prey groups at least once. The total number of attacks ranged from 19 to 41 and, as in the previous experiment, some prey items were quickly dropped after being picked up and might thus be handled more than once in the trial. The birds attacked significantly more palatable items (Wilcoxon signed-ranks test:  $T=0$ ,  $N_{\text{diff}}=8$ ,  $P=0.008$ ; Fig. 4).

The higher attack rate on the palatable items, even though they were visually indistinguishable from the unpalatable items, may be explained by bird foraging behaviour. Thus, birds usually picked only one item per visit to an unpalatable aggregation, whereas they tended to attack two or more consecutive items in a visit to a palatable aggregation. To test this we measured the number of consecutive attacks in the first visit to each of the four aggregations for each bird, and found that this number was significantly higher for the palatable aggregations (Wilcoxon signed-ranks test:  $T=0$ ,  $N_{\text{diff}}=8$ ,  $P=0.008$ ).

## DISCUSSION

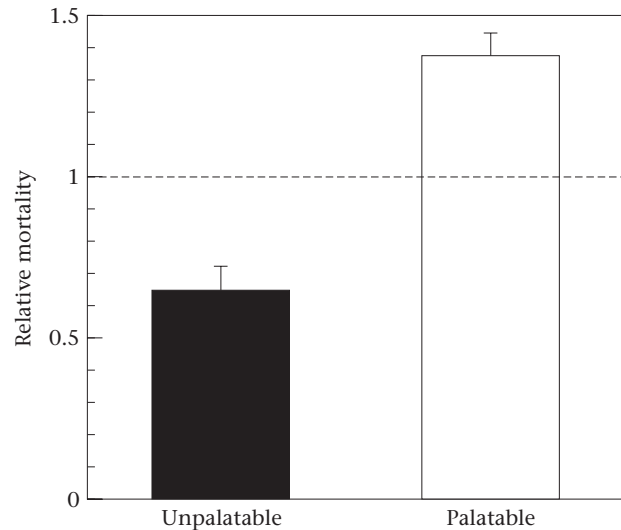
### Experiment 1

The two treatments differed, for instance, in the kind of prey taken in the very first attack (Fig. 2), and we may ask why birds should prefer to attack the novel aposematic



**Figure 3.** The total number of attacks on aposematic and cryptic prey for individual birds (●) in (a) the solitary prey treatment ( $N=10$ ), and (b) the aggregated prey treatment ( $N=11$ ) in experiment 1. Crosses represent means of total attacks on aposematic and cryptic prey, respectively. The dotted lines correspond to equal attacks on the two prey types.

prey in the aggregated treatment but the cryptic form in the solitary treatment. One might have expected them to prefer the cryptic form in both treatments, because of a positive reinforcement from the training trial. A possible reason for our result is to be found in the relative conspicuousness of the two prey forms in the two treatments. As mentioned, the cryptic prey in the novel world are cryptic only in the sense that the wing pattern matches the background pattern and not in the sense that they are difficult to find (because the straw is apparent). However, the aposematic items are more conspicuous in the sense that they stand out more markedly against the background and attract attention, at least to the human



**Figure 4.** Relative mortalities of unpalatable and palatable cryptic prey when presented in groups to great tits ( $N=8$ ) in experiment 2. Bars show mean+SE of relative prey mortality for the eight birds. Mortalities are standardized so that equal mortality for the two forms is given by the horizontal line.

eye. This relative conspicuousness of aposematic prey may have been accentuated in the aggregated treatment and could have caused a higher initial attraction. However, our results differ from what has been found in experiments using live prey, where aggregations produced stronger aversion in naïve predators than did solitary aposematic prey (Gamberale & Tullberg 1998).

## Experiment 2

The reason for the higher attack rate on palatable items was that, on the one hand, the birds tended to leave a group of unpalatable prey after one attack and, on the other, they tended to make several consecutive attacks on prey in a palatable aggregation. This is a likely explanation of the results in Alatalo & Mappes (1996; see also Fig. 1), but it also exemplifies a more general principle.

The selective advantage for cryptic, palatable prey to be well spaced out was demonstrated by Tinbergen et al. (1967) and Croze (1970); one reason for the advantage is that many predators adopt an area-restricted search strategy. Thus, not spacing out, even when avoiding aggregating in a strict sense, could be disadvantageous for prey encountering such predators (see Edmunds 1990). Also aggregation in a strict sense should be disadvantageous for prey that cannot flee or protect themselves (see Vulinec 1990 and references therein), and our experiment illustrates that predators tend to concentrate foraging on such groups. However, when some kind of protection has evolved, the road to gregariousness as an antipredator strategy is in principle open, although its evolution ultimately depends on whether the combined risk of discovery and attack at discovery is reduced (Turner & Pitcher 1986; Sillén-Tullberg & Leimar 1988).



## General Discussion

Alternative evolutionary pathways leading from palatability and crypsis to unpalatability and warning coloration have been suggested. Based on the results from their experiment with three prey types, Alatalo & Mappes (1996) proposed a route for the initial evolution of aposematism: 'Unpalatability alone selected for gregariousness, as predators would just leave the aggregation after tasting the first items. Once the prey were aggregated, selection would have instantly favoured the appearance of a warning signal to allow the predators to learn to associate the signal with unpalatability.' Thus, they suggested the following sequence of events, starting with palatable, cryptic and solitary prey: (1) palatability→unpalatability; (2) solitary→aggregated; (3) cryptic→aposematic.

In our opinion their experiments were not designed to test each step in this sequence, because three prey types (palatable cryptic, unpalatable cryptic and unpalatable aposematic) were present simultaneously in either a solitary or aggregated distribution. Instead, to test the first step, palatable cryptic prey should be compared with unpalatable cryptic prey, both types presented in a solitary distribution. To test the second step, the comparison should be between solitary and aggregated prey, both types being unpalatable and cryptic. The third step should be tested by comparing cryptic and aposematic unpalatable and aggregated prey. For the whole sequence of events to be held plausible, each of these steps should be verified experimentally.

In our experiment we did not test this sequence. Instead we tested whether the second step is necessary for the third step to take place. Thus, given that unpalatability has evolved from palatability we compared cryptic and aposematic prey in either a solitary or an aggregated distribution. Our experiment indicates the possibility of the following route to aposematism from palatable, cryptic and solitary prey: (1) palatability→unpalatability; (2) cryptic→aposematic.

As mentioned we did not test the first step, but that unpalatability has to precede warning coloration may be regarded as less controversial in the present context. Thus, for the initial origin of aposematism we may disregard the possibility that unpalatability evolves after warning coloration, that is, via Batesian mimicry.

Where does aggregation fit into our scenario? On the one hand, the evolution of gregariousness may or may not occur as a third step in our sequence. On the other, aggregation could also evolve directly after unpalatability (Sillén-Tullberg & Leimar 1988; Vulinec 1990), in which case aposematism may or may not occur as a third step. The important point we make, however, is that we found no evidence that aggregation facilitated the evolution of warning coloration. Aggregation cannot therefore be regarded as a prerequisite for the evolution of aposematism.

In their experiments, Alatalo & Mappes (1996) set out to shed light on an historical event, namely the initial origin of aposematism. As much as we are in favour of the ingenuity of their novel world, we question whether this setting helps to increase our understanding of the

historical event. First, predation as a phenomenon arose in the sea no later than the Cambrian period, well over 500 million years ago (Futuyma 1998), and along with predation arose counteradaptations to predation. Many of today's marine invertebrates are toxic (Bakus 1981) and several species are conspicuous against their natural background (Edmunds 1987; Rosenberg 1989) and are avoided after experience by predators (Tullrot & Sundberg 1991). It may be that unpalatability, sometimes coupled with warning signals, arose in the sea soon after the evolution of predation. At least, the sea is the most likely place for these strategies to have evolved for the very first time. If so, groups of kin are less likely to be involved because planktonic larval dispersal excludes kin grouping in most marine organisms (Rosenberg 1989).

Second, for whatever predators the very first aposematic signal evolved, it is unlikely that these signals were arbitrary. Thus, whether the signals were conspicuous (Roper & Redston 1987), of a specific colour or pattern (Schuler & Hesse 1985; Roper 1990), or otherwise different looking from edible prey (Turner 1975), they ought to have explored some sensory bias in the predator psychology, because 'the limitations of the sensory apparatus will necessarily introduce such biases' (Guilford 1990, page 35). The sensory biases of past predators may have been different from those of present-day predators, or they may have been similar, provided that the general outline of the sensory apparatus has not changed. To shed light on this question, deep phylogenetic insights would be needed.

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