

Higher survival of aposematic prey in close encounters with predators: an experimental study of detection distance

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Aposematic animals are often conspicuous. It has been hypothesized that one function of conspicuousness in such prey is to be detected from afar by potential predators: the 'detection distance hypothesis'. The hypothesis states that predators are less prone to attack at long detection range because more time is allowed for making the 'correct' decision not to attack the unprofitable prey. The detection distance hypothesis has gained some experimental support in that time-limited predators make more mistakes. To investigate effects of prey presentation distance we performed two experiments. First, in experiment 1, we investigated at what distance chicks, *Gallus gallus domesticus*, could see the difference in colour between aposematic and plain mealworms. Birds chose the correct track in a two-way choice when prey were at 20, 40 and 60 cm distance but not at 80 cm. Second, in experiment 2, fifth-instar larvae of the aposematic bug *Lygaeus equestris* were presented to experienced chicks at 2, 20 or 60 cm distance. We found no difference in attack probability between distances. However, prey mortality was significantly lower for the shortest presentation distance. In conclusion, we found no support for the hypothesis that aposematic prey benefit from long-range detection; in fact they benefit from short-distance detection. This result, and others, suggests that the conspicuousness of aposematic prey at a distance may simply be a by-product of an efficient signalling function after detection.

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Defensive coloration can be divided into two broad categories, where one (crypsis or camouflage) functions to avoid detection, whereas the other (warning or aposematic coloration) functions to avoid attack after detection in unpalatable prey (Cott 1940; Edmunds 1974; Evans & Schmidt 1990; Ruxton et al. 2004). There are strong indications that unpalatable insects can use a combination of these strategies, being cryptic when viewed from afar and aposematic when viewed from a close distance (Tullberg et al. 2005), but as a rule aposematic animals are more easily discovered than cryptic ones. Evolutionary biologists understand this heightened detectability as the main cost of warning coloration (Ruxton et al. 2004). The cost can be balanced in several ways by the signalling of a defence, which in effect decreases predator attacks through unlearned or learned avoidance (see references in e.g. Ruxton et al. 2004). It has been shown that stronger signals elicit stronger avoidance reactions in predators (Gamberale & Tullberg 1996; Forsman & Merilaita 1999; Gamberale-Stille & Tullberg 1999; Riipi et al. 2001).

So, when discovered by a predator, aposematic prey benefit from having a strong and efficient signal. Such a signal may also make prey more easily detected from afar than a weaker signal. But could there be a benefit for aposematic prey to be discovered from afar? Based on the fact that many predators are time limited and therefore prone to make mistakes while foraging, Guilford (1986, 1989) suggested that the longer viewing distance that aposematic coloration entails also allows for more time to make the correct decision about prey quality. According to this 'detection distance hypothesis' (Guilford 1986, 1989) aposematic prey should benefit from being detected from afar because it increases the chance that the predator makes the 'correct' decision not to attack or aborts an initiated attack. That is, on average aposematic prey will be discovered at a greater distance than cryptic prey of the same size, shape and orientation. After discovery, the predator must approach the prey prior to making a physical attack. The process of approach will take longer when it begins from a greater distance. This approach time gives the predator time to inspect the prey (from ever closer range as it approaches) and perhaps search its memory to try to reach the correct decision as to whether to attack the prey or not. For defended prey the correct decision is to decline to attack. Thus the detection distance hypothesis predicts that aposematic prey are less likely to be mistakenly attacked by predators than same-sized, similarly defended cryptic prey.

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The core of the detection distance hypothesis is the time factor, and there is a growing literature demonstrating that organisms with more time at their disposal make more accurate decisions (e.g. Ings & Chittka 2008). There is also experimental support for this idea in that a longer time for decision making results in fewer attacks on aposematic prey (Guilford 1986; Gamberale-Stille 2000, 2001). However, there is less experimental support for the idea that detection distance itself results in a positive effect on decision making; in fact, the only study carried out so far seems to contradict the hypothesis (Guilford 1989). Thus, it is not at all established which role detection distance has in the behaviour of predators vis-à-vis aposematic prey (see also Ruxton et al. 2004, page 99).

One important reason for the lack of experimental evidence of effects of detection distance per se may be that it is very difficult to test since it is difficult to discern the precise moment that a predator actually discovers the prey. Therefore, in the present study we investigated the role of presentation distance of aposematic prey as an approximation of detection distance. We presented real live aposematic bugs to domestic chicks, *Gallus gallus domesticus*, at different distances whereupon the chicks at least had the opportunity to view the prey for different durations while approaching it. We used chicks with previous experience of the aposematic prey. In a separate experiment, we also investigated at what distances chicks are able to differentiate between aposematic and palatable prey.

METHODS

Predators and Prey

We used domestic chicks, under permission from Stockholms djurförsöksetiska nämnd, in two consecutive experiments (1 and 2). The experimental birds arrived from the hatchery in batches of 22–33 individuals. At arrival they were less than 18 h old and had not yet eaten. Each batch was housed in a cage with a 100 × 55 cm steel-net floor and wooden sides 20 cm high. The roof of the cage was made partly of wood and partly of chicken wire. The cage was heated with a 60 W carbon light bulb and the floor of the cage was covered with wood chips. All chicks were fed chick starter crumbs (Pullfor) and water ad libitum, and from the day of arrival (Day 1) they were also handfed with mealworms, *Tenebrio molitor*, on several occasions. After taking part in the experiments, all birds were put down by cervical dislocation and immediate decapitation, according to the national standard procedure for laboratory animals.

In experiment 1 we investigated at what distances the birds were able to discern the warning coloration. We used dead mealworms as prey because it was necessary to be able to manipulate both the coloration and the palatability of the test insects. After killing the mealworms by freezing, we painted aposematic mealworms 'Brilliant Red' with children's paint (Gouache Tempera, Color & Co, Lefranc and Bourgeois, Le Mans, France). They were made unpalatable by covering them with 'Stop n Grow' (Mentholum, East Kilbride, U.K.), which is bitter tasting. As control prey we used nonmanipulated dead mealworms.

In experiment 2 we investigated the effects of prey presentation distance on the chicks' attacking behaviour and prey survival. We used the fifth-instar larva of the heteropteran bug *Lygaeus equestris*, which had been reared on a mixture of seeds from *Vincetoxicum hirundinaria*, the main natural host plant, and sunflower, *Helianthus annuus*. The larvae used in the experiment were of a similar red coloration, with black wing-buds, legs, antennae and parts of the head. This prey has been used in several previous experiments and is distasteful to chicks (e.g. Tullberg et al. 2000).

Predator Training and Experimental Procedure

Experiment 1

This experiment took place in an L-shaped arena consisting of two corridors extending in a 90° angle from each other, both 15 cm wide, 30 cm high and 120 cm long. The arena was made of wood, but was completely covered with white paper as a background.

Prior to the experiment the birds were trained to forage in the arena on their fourth and fifth day after arrival. On Day 4, birds were trained to forage on dead mealworms scattered on the floor. Birds were first trained in groups of five, then, in a second session, in pairs. On Day 5 the birds were trained singly in the following way. One chick at a time was placed behind a gate in the corner where the two tracks met. One dead mealworm was placed in one of the tracks in the arena. We opened the gate when the chick faced in between the two tracks, and the chick was allowed to choose a track and eat the mealworm. For each chick during training the location of the mealworm was alternated between tracks and it was placed at 20, 40, 60 and 80 cm from the gate. Each chick was trained on two occasions, each time with one mealworm at each of four distances, so all chicks ran eight times singly for prey in the arena prior to the experiment. If a chick chose the wrong track, it was allowed to correct its mistake, that is, go back and enter the correct track and retrieve the mealworm.

On Day 6, prior to the experiment, all chicks were presented with aposematic mealworms. These presentations took part in a small arena, 40 cm long, 25 cm wide and 25 cm high, with walls and floor covered with the same white paper as the experimental arena. The chicks were placed into the arena approximately 15 cm from a prey item that was already present in the arena. Birds were presented with palatable and aposematic mealworms in an alternating manner for a maximum of 60 s per presentation, until they avoided the aposematic mealworms. This training started and ended with a palatable mealworm to test whether the chicks were still hungry for prey.

Directly after the aposematic presentations, the chicks took part in the experiment. The chicks were divided into one of four groups that corresponded to prey distances of 20 cm ($N = 18$), 40 cm ($N = 17$), 60 cm ($N = 18$) and 80 cm ($N = 18$). The experiment was designed as a choice between the two tracks, with a palatable prey in one track and an aposematic prey in the other, at the same distance from the gate. The location of the aposematic prey was decided by flipping a coin. As in training, the chick was placed behind the gate and when it was facing forward in between the two tracks, the gate was opened. We registered whether or not the chick made the correct decision to run down the track with the palatable prey.

Experiment 2

This experiment was carried out in a wooden arena with a total length of 120 cm and total width of 40 cm and with walls 30 cm high (Fig. 1). The arena was divided into two tracks, one slightly wider (21 cm) than the other (16 cm). The wall between the tracks was made partly of wood and partly of chicken wire. The chicken wire enabled the chicks to view their companions in the parallel track during training, but these parts were covered with wood during the experiment. The broader track A was the experimental track, and the other, track B, was used for a companion chick during training. After 2 days of training the chicks performed well in the experiment, that is, they ran along the track and ate control food, also without the presence of a companion.

Both tracks in the arena had a start gate at 20 cm distance from one end. These gates, behind which a chick had been placed, were opened at the start of training sessions and experiments. The experimental track had two additional gates, one at a distance of

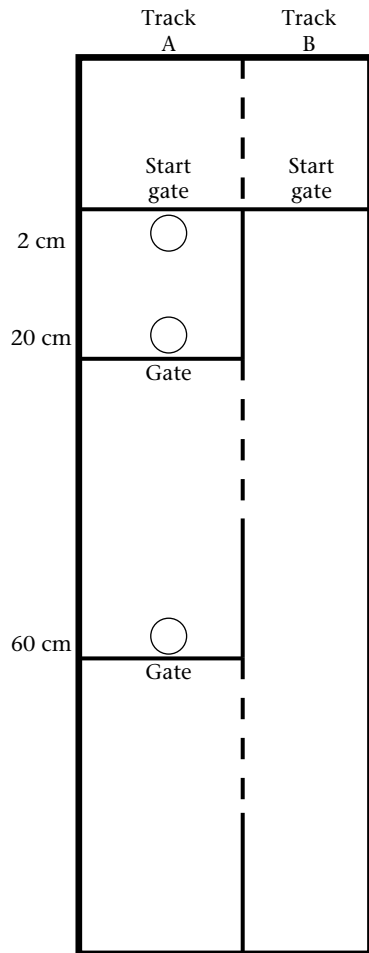


Figure 1. The arena of experiment 2, with the experimental track (track A) and a training track used for companion chicks (track B). Circles indicate the placement of prey. The wall between the two tracks was made partly of wood (continuous line) and partly of chicken wire (dashed line) during training and completely covered with wood during the experiment.

20 cm and the other at 60 cm from the start gate. We used three prey distances, 2 cm, 20 cm and 60 cm, in the experiment. We chose the longest and the shortest distances used in experiment 1 that lay within the visible range for the chicks (20 cm and 60 cm) and added a very close distance of 2 cm to investigate possible nonlinear distance effects. For the shortest experimental distances, 2 cm and 20 cm, we retained the gate at 20 cm from the start gate. For the longest experimental distance, 60 cm, the gate at 20 cm from the start gate was removed. The longest possible track in the arena, 100 cm, made by removing both gates after the start gate, was used during training but not in the experiment (see below).

Training sessions started on Day 2 (that is, the day after arrival at our facility). First, three chicks were placed behind the start gates in each of the tracks. The other two gates had been removed so that both tracks measured 100 cm. Four small petri dishes (3.5 cm diameter) with several mealworms in each had been placed along each track. The six chicks were allowed to walk the whole track and eat mealworms along the way. This training session lasted 7–10 min. The procedure was then repeated, but now with only two chicks in track A and none in track B. Next, the procedure was repeated with one chick in track A and one in track B, and now with only one mealworm in each petri dish. Lastly, each chick was trained in the other track in the same way. Thus, on this first day of training, each chick was trained in the arena four times.

The training continued on Day 3. Each chick was first trained on the 20 cm track with a petri dish with one mealworm at 2 cm from the gate. A companion chick was held in track B but given no food. Next, the chick was trained on the 20 cm track with the prey at the end of the track (20 cm from the gate), and then on the 60 cm track in the same manner. Later the same day each chick was trained in the same way but without a companion chick. Thus, on this second day of training each chick was allowed a total of six training sessions.

Also on training Day 3, after the training in the arena, we presented the chicks with live aposematic prey (the *L. equestris* bugs). Each chick was trained individually in a cage measuring 30 × 55 cm, made from part of a housing cage. First, the chick was placed about 10 cm from a petri dish with a mealworm which was always immediately consumed. The chick was then lifted from the cage, the petri dish was exchanged for one containing an aposematic prey, and the chick was again placed about 10 cm from the petri dish. The chick was given a maximum of 60 s to attack the prey, and its behaviour was recorded. If a bird attacked the aposematic prey it was not trained further. Otherwise it was trained again, and, if it did not attack the prey, it was trained for a third time. Of 87 chicks, 47 attacked aposematic prey during training, but all chicks were tested in the experiment the next day.

The experiment was carried out on Day 4. We randomly allocated the chicks into three experimental groups, 2 cm, 20 cm and 60 cm, and each chick was only tested once. The chick was first given a mealworm, then an aposematic bug, and then a mealworm again. All prey items were alive and were always presented in a petri dish at the designated distance. The chick was placed behind the start gate before each prey presentation. In the case of mealworms these were always eaten in an attack. Chicks varied in their response to aposematic prey and, if they attacked, whether they swallowed prey. In the case of attacked but not eaten prey we noted its condition after the attack, that is, whether it was mortally wounded or killed. We measured the time it took between gate opening and attack of prey. If no attack had occurred within 60 s the presentation was terminated.

Statistical Analyses

The number of birds making correct decisions in experiment 1 and the number of attacking birds and birds killing prey in experiment 2 were compared using contingency tables (Fisher's exact test for 2 × 2 tables, and the Freeman–Halton extension of the Fisher's exact test for 2 × 3 and 2 × 4 tables; Freeman & Halton 1951). In experiment 1, we also used goodness-of-fit tests to compare the proportion of birds making the correct decision to a null hypothesis of 0.5. In experiment 2, we used a Kruskal–Wallis test to compare the time to attack between treatments.

RESULTS

Experiment 1

The distance to prey had an effect on the proportion of birds that made the correct decision to run down the track with the palatable prey (Fisher's exact test: $P = 0.011$; Fig. 2). Fewer than half of the birds with prey at 80 cm distance made the correct decision (7/18), and the result is not significantly different from a random choice of tracks (50:50, goodness-of-fit test: $\chi^2_1 = 0.5$, $P = 0.479$). On the other hand, most birds in the 20, 40 and 60 cm groups made the correct decision, and these results were significantly different from random (50:50, goodness-of-fit tests: 20 cm: 17/18, $\chi^2_1 = 12.5$, $P = 0.0004$; 40 cm: 14/17, $\chi^2_1 = 5.88$, $P = 0.015$; 60 cm: 15/18, $\chi^2_1 = 6.72$, $P = 0.010$), and there was no significant difference

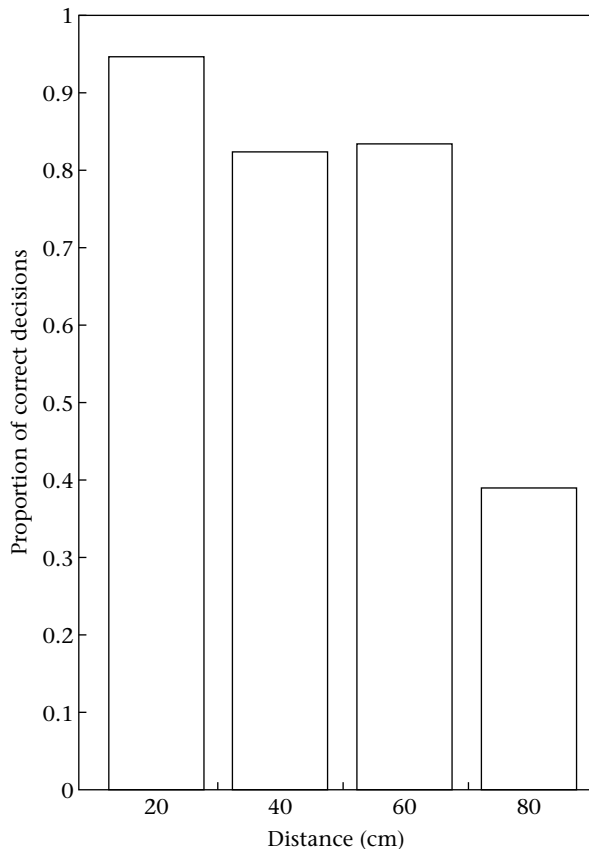


Figure 2. The proportion of birds making the correct decision to approach the palatable prey in a choice situation between palatable and aposematic prey presented at the distances of 20 cm ($N = 18$), 40 cm ($N = 17$), 60 cm ($N = 18$) and 80 cm ($N = 18$) from the birds.

between the three shorter distances (Fisher's exact test: $P = 0.603$). Thus, we conclude that chicks were able to discern the warning coloration at the distances 20, 40 and 60 cm, but not at 80 cm. All birds ran all the way up to the prey, independently of distance or choice of track.

Experiment 2

The chicks in all experimental groups approached the aposematic prey and there was no significant difference between the experimental groups in the number of chicks that attacked the aposematic prey (Table 1). All of the birds that attacked aposematic prey in the experiment had also attacked the prey during training. Thus, the birds that had only viewing experience from the previous day never attacked prey during the experiment and in the following we only include birds with previous attacking experience in the analysis. Again, there was no significant difference between the distance groups in the tendency to attack (Table 1, Fig. 3).

None of the birds ate any aposematic prey in the experiment. However, the three experimental groups differed in the number of chicks that killed prey (Table 1) with a greater risk of death for prey at the furthest distance (2 cm versus 60 cm; Fisher's exact test: $P = 0.035$; Fig. 3). Also, when we considered only attacks, the proportion of attacks ending with prey mortality differed between experimental groups (Table 1), with the highest mortality at the longest distance.

There was a difference between treatment groups in how much time elapsed between the opening of the gate and attack by the bird.

Table 1

Attacking behaviour of birds in experiment 2 with statistical comparisons

Comparison	Distance (cm)			Fisher's exact P
	2	20	60	
Proportion of birds in total that attacked in the experiment	5/29	7/29	6/29	0.853
Proportion of birds with previous attacking experience that attacked prey	5/15	7/19	6/13	0.806
Proportion of birds with previous attacking experience that killed prey	0/15	1/19	4/13	0.026
Proportion of attacks ending in mortality	0/5	1/7	4/6	0.032

Bold text indicates $P < 0.05$.

As expected, it took longer for birds with the 60 cm track to reach and attack the aposematic prey (60 cm: $\bar{X} \pm SE = 3.64 \pm 0.39$ s, $N = 6$; 20 cm: $\bar{X} \pm SE = 1.76 \pm 0.46$ s, $N = 7$; 2 cm: $\bar{X} \pm SE = 1.50 \pm 0.21$ s, $N = 5$; Kruskal–Wallis test: $H_2 = 11.73$, $P = 0.003$).

DISCUSSION

This experiment provides no evidence of benefits to aposematic prey being discovered at a distance as hypothesized by Guilford (1986, 1989, 1990). On the contrary, although there was no significant difference in attack probability between distances, prey were more likely to be killed when presented at longer distances. Thus, the results show that it can be more advantageous for aposematic prey to be detected at a closer range which was also the finding in Guilford (1989) where experienced great tits, *Parus major*, made more mistakes (i.e. attacked more aposematic prey) at the longer of two distances. The difference in prey survival between distances in the experiment presented here was not so much an effect of the probability of attack as of handling of prey during an attack.

This study is not the first to note a difference between treatments in how birds handle prey in an attack. In a study by Schuler & Hesse (1985; see also Schuler & Roper 1992), using dead coloured mealworms as prey, a lower tendency to handle (i.e. pick up and carry and/or beat to the ground) and eat prey in an attack was interpreted as a measure of a lower motivation to feed on the prey. In contrast, in a different experimental situation, comparing predator behaviour towards solitary and grouped aposematic prey, Skelhorn & Ruxton (2006) interpreted a greater mortality in grouped prey after attack as a measure of greater fear, since it also correlated with a lower attack probability measured as latency to attack. However, also when comparing effects of aggregations in aposematic prey, Gamberale-Stille (2000) found the opposite pattern, that a lower mortality of grouped than solitary prey was correlated with a lower attack probability. However, from the results of our present study we cannot deduce whether or not the greater mortality of prey presented at longer distances is due to a fear response or a feeding response. In any case, it is apparent that being discovered at a greater distance is not favourable to the survival of prey.

In experiment 1, we found that chicks could readily distinguish between the aposematic and plain mealworms at distances up to 60 cm that were then used in experiment 2. We wanted to use live aposematic prey with real warning colours when testing the effect of distance, but we did not have any palatable prey similar to the aposematic bugs in shape. This made it necessary to use different prey in the two experiments. The *L. equestris* larvae, used in experiment 2, are shorter but wider than the mealworms used in experiment 1, and probably have a somewhat smaller visible area. However, it is unlikely that the use of the slightly larger mealworms instead of shield bugs in this case would result in too large an

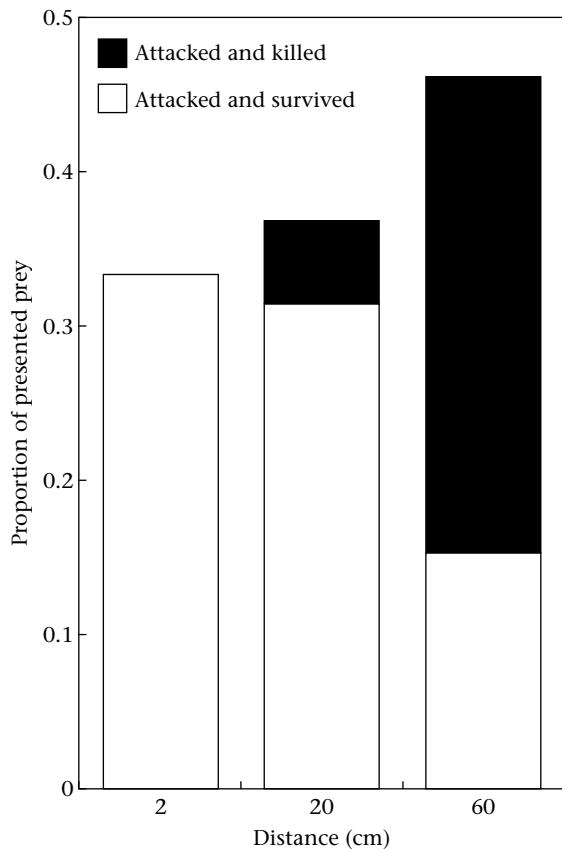


Figure 3. The proportion of chicks with prior attacking experience that attacked aposematic fifth-instar *Lygaeus equestris* at three different distances: 2 cm ($N = 15$), 20 cm ($N = 19$) and 60 cm ($N = 13$). Attacked prey survived or were killed but none were eaten.

overestimation of how far the birds could see the prey. In experiment 2, the experimental prey were alive and moved around and were therefore probably more eye catching than dead mealworms. Also, the difference in both colour and shape between experimental and control prey in experiment 2 could further facilitate recognition at a greater distance. In any case, we can never control for when the experimental birds actually detect the prey and/or the warning coloration at any distance, and, as mentioned earlier, the experiment is designed only to allow for detection at different maximum distances.

In both experiments, all birds ran all the way up to the prey, independently of prey quality and distance. Thus, no birds aborted their approach in the present experiments, as was suggested by the detection distance hypothesis (Guilford 1986). However, this could be a result of our training procedure to acclimatize the birds to the arena. By training them to run all the way in the arena for palatable mealworms they may have learned to expect palatable prey at the end of the track. However, the results of the choice experiment, experiment 1, also show that since birds were able to discriminate between prey and choose the palatable mealworm at distances up to 60 cm, they can already make decisions about prey quality before approaching the prey.

The detection distance hypothesis is based, not on distance itself, but on the increased time allowed for making a decision about prey quality (Guilford 1986). Accordingly, more time elapsed before attacks in the longer distance treatments. Although previous experiments have shown that time available for making a decision is important (Guilford 1986; Gamberale-Stille 2000, 2001), other factors may also have indirect effects through distance. One such

factor could be an uncertainty about reaching prey in time, perhaps before a competitor (Gamberale-Stille 2000, 2001) or before the prey escapes. Another factor that may interact with distance is that the birds that forage for insects are also often prey themselves. They must always divide their attention between being vigilant for predators and other tasks (Dukas & Kamil 2000, 2001; Kaby & Lind 2003). Thus, not all the time available while approaching prey from a distance can be spent focusing on the prey and deciding about profitability.

One antipredator strategy for which distance between predator and prey in itself ought to be important is startle/intimidation, where relative proximity to the predator is likely to be a prerequisite for its efficiency (e.g. Sargent 1990; Ruxton et al. 2004; Vallin et al. 2006). Previous work has shown that size and strength of aposematic signals are important for predator avoidance (e.g. Gamberale & Tullberg 1996; Forsman & Merilaita 1999; Gamberale-Stille & Tullberg 1999; Riipi et al. 2001). Therefore, one possibility is that an aposematic signal is more intense and/or involves an element of intimidation at a close distance. The more careful handling resulting in lower prey mortality at the closer distances is consistent with such an effect. It is possible that such a startle-like effect of aposematic signals may affect a predator-prey interaction at several levels, such as neophobia, avoidance learning, memorability, etc. (e.g. Ruxton et al. 2004). It may be that approach from a greater distance causes a decrease in wariness, perhaps simply because wariness declines over time from initial detection of the stimulus. Additionally or alternatively, it may be that initial detection at a greater distance induces less wariness, because of the smaller visual impact of a more distant object.

Various authors have hypothesized that not all aposematic animals maximize conspicuousness, and that some prey seem to combine crypsis at a distance with aposematism close up (Edmunds 1974; Rothschild 1975; Papageorgis 1975; Endler 1978; Endler & Mappes 2004), and this idea has recently received experimental support (Tullberg et al. 2005). This implies a warning function designed for the identification of, and association with, a noxious quality after discovery, not for discovery as such. However, the conspicuousness of warning colours varies considerably and it would be simplifying to make the assumption that they were all designed for the same basic purpose. Thus, in the future other types of aposematic prey, varying in size, colour and pattern, and different predator models should be tested in different experimental set-ups for the effect of detection distance. In view of the existing evidence, signalling at short range may be the foremost function of aposematism.

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