



## 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

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