ANIMAL BEHAVIOUR, 2008, **75**, 417–423
doi:10.1016/j.anbehav.2007.05.006

Available online at www.sciencedirect.com
ScienceDirect

Domestic chicks primarily attend to colour, not pattern, when learning an aposematic coloration

MARIANNE ARONSSON & GABRIELLA GAMBERALE-STILLE
Department of Zoology, Stockholm University

(Received 6 March 2007; initial acceptance 7 April 2007; final acceptance 10 May 2007; published online 22 October 2007; MS. number: 9299)

Aposematic conspicuous coloration consists of one or a few bright colours, often in combination with a black defined internal pattern. The function of conspicuousness in aposematism has been ascribed to signal efficacy, based on experimental evidence involving prey items with uniform colour that contrast with the background. Although there are several hypotheses about the existence of internal contrasts within warning coloration, little experimental evidence has been presented. Here we used domestic chicks, *Gallus gallus domesticus*, to investigate the relative importance of colour and pattern in avoidance learning. Birds in two groups were first trained to discriminate between a grey positive stimulus and a cyan negative stimulus with either black dots or stripes. Pieces of mealworms, untreated and palatable or made unpalatable by soaking in quinine were used as reinforcers. Secondly, to determine what birds had attended to when learning the discrimination, colour and/or pattern, we compared how they generalized their avoidance of the 'training stimulus' to either a 'colour only' or 'pattern only' stimulus. The chicks learned to avoid the unpalatable prey items but showed no difference in behaviour depending on the type of pattern presented. The generalization test showed that birds avoided the novel 'colour only' stimulus at least as much as the 'training stimulus', and did not generalize their avoidance to the 'pattern only' stimulus. We conclude that birds do not necessarily attend to complex patterns when learning a warning signal, and domestic chicks primarily learn a bright colour rather than an equally novel conspicuous black pattern.

Keywords: colour patterns; domestic chick; *Gallus gallus domesticus*; generalization behaviour; internal pattern contrast; signal design; signal evolution

There are two main strategies for a prey species to avoid predation, by hiding through crypsis or by signalling unprofitability as prey through warning coloration. Animals that signal their unprofitability to potential predators usually use a conspicuous colour pattern. Thus, aposematic animals often have a bright red, orange, yellow or white colour in combination with black (Cott 1940). Such colours contrast strongly against the green and brown natural background, making them easily recognizable and discriminable both from the background and from the palatable and camouflaged prey that the predators usually hunt (Turner 1975; Sherratt & Beatty 2003). The function of this conspicuousness of aposematic colours has been ascribed to signal efficacy, and as all signals, warning signals need to be easy to detect, discriminate and memorize by the intended receivers (Guilford & Dawkins 1991). Evidence for this function has been found as prey items with a colour that contrast against the background increase the speed and durability of avoidance learning (Roper & Wistow 1986; Roper & Redston 1987), elicit avoidance in naive predators (Lindström et al. 2001), and increase the probability of recognition in already experienced predators (Gamberale-Stille 2001). However, these studies only explain the bright colours of aposematic prey, and not why they often also have internal contrasting patterns.

There are several suggested hypotheses about the function of internal contrasts within warning colour patterns, with only very little suggestive evidence in support. It has been argued that some patterns and colours used in aposematic signalling are specifically memory stimulating and facilitate avoidance learning (Rothschild 1984; Kaye et al. 1989). This could be the case if there are patterns

Correspondence: M. Aronsson, Department of Zoology, Stockholm University, 106 91 Stockholm, Sweden (email: marianne.aronsson@zoologi.su.se).

0003–3472/08/$34.00/0

or colour combinations that are easier for a predator to discriminate and memorize than others, or if the signal salience is increased by the internal colour boundaries (Guilford 1990). Rowe & Guilford (2000) suggested that by having contrasts in a warning pattern the learning of a specific hue is facilitated, so one function of internal patterns might be to direct the predators' attention to the warning colour itself. Osorio et al. (1999) suggest that different parts of a prey colour pattern play different roles in a predators' foraging behaviour, the contrasting pattern attracts attention while specific colours signal specific information and are remembered accurately. They also suggest that high contrasting patterns may be beneficial and evolve because of predators' supernormal responses to contrasting patterns. Another way that internal pattern contrasts could increase signal salience is via the mechanism of lateral inhibition in the nervous system of the retina. Simplified, lateral inhibition makes the eye detect changes in brightness, such as edges between differently bright areas, by making the contrast even stronger. It is thus possible that a highly contrasting internal pattern, with a lot of edges between areas, is more stimulating than a uniform coloration. Another reason for increased salience would be if predators find certain shapes or patterns more attention grabbing. This could for instance be if they have biases for certain pattern-shapes or if these patterns make the prey more different from cryptic palatable prey. In a study using wild-caught Redwing blackbirds, Mason (1988) showed that a more complex stimulus (colour and pattern) in a one-trial avoidance-learning test produced a greater resistance to extinction than either colour or pattern alone. However, whether this effect of complexity is because of an increased salience of the stimulus or some other effect is unknown.

A pattern may also increase the symmetry of the signal, and hence influence prey detection and the association with unpalatability (Forsman & Herrström 2004). Delius & Nowak (1982) showed that pigeons more easily detect, learn and reproduce patterns from their memory when the patterns are symmetric than when they are asymmetric. Recent findings suggest that an otherwise strong signal is weakened by asymmetries in pattern, colour or in the shape of the signalling pattern elements (Forsman & Merilaita 1999; Forsman & Herrström 2004). Also, with a chaotic environment as a background, a regular pattern may stand out and therefore improve recognition and detection (Kenward et al. 2004). However, these are more or less experimentally untested hypotheses, and may only explain why patterns are regular or symmetrical, not why they would function better than a uniform conspicuous coloration.

Previous studies with bird predators suggest that only parts of a warning signal are used as cues and generalized while others are ignored (Schmidt 1960; Terhune 1977; Evans et al. 1987). Also, bird attention is biased towards the most salient component within a multicomponent colour pattern when learning to avoid prey with one of two patterns. Less salient components are not as efficient as cues, and may only be attended to if they solely predict the profitability of the prey (Gamberale-Stille & Guilford 2003).

The aim of the present study is to investigate the relative importance of colour and pattern in avoidance learning, by investigating which aspects a bird predator attends to when learning a warning colour pattern. The experimental colour patterns consist of a bright colour and a contrasting black pattern that both predict the unpalatability of the prey. We also investigate if birds may find one pattern more attention grabbing than another by comparing differences in discrimination learning between patterns consisting of dots and stripes. We investigate this by measuring the speed of discrimination learning in young domestic chicks, *Gallus gallus domesticus*, followed by a generalization test to determine what birds learn about the colour pattern. In this study we use an experimental method where we present a paper stimulus in association with a rewarding or punishing food item. This is a method commonly used in the field of experimental psychology where the focus is on animal learning mechanisms. Similar methods also have a long tradition in aposematic and mimicry research (e.g. Schmidt 1960; Terhune 1977; Mason 1988; Osorio et al. 1999; Gamberale-Stille & Guilford 2003; Forsman & Herrström 2004), and these studies have provided much important knowledge about predator reactions to warning signals.

METHODS

Subjects and Housing

As predators we used domestic chicks under permit from Stockholms norra djurförsöksetiska nämnd (D.nr. 185/04). Fifty-seven newly hatched and unfed male chicks arrived from a commercial hatchery in batches of about 20 individuals. The chicks were housed in cages ($115 \times 60 \times 20$ cm, length × width × height) with the floor covered with wood chips and heated with a carbon-filament lamp. The room used for housing and experiments was lit by daylight from the windows and old daylight-strip lights (BIOLUX L36W/72, OSRAM, München, Germany) between 0800 and 1800 hours. Measuring the light spectra in the room by the arena with a spectrometer showed that no ultraviolet light was present. Birds were fed chick starter crumbs and water ad libitum. On the day of arrival the chicks were individually marked with numbers on their backs using a black marker pen. The markings did not cause any increased pecking by other individuals on this area. After taking part in the experiment, all birds were put down by dislocation and immediate decapitation, according to the national standard procedure for laboratory animals.

The Experimental Arena

The preexperimental training and the experiment took place in a square arena ($120 \times 120 \times 30$ cm high) made of wood, with a 25-cm-wide runway surrounding a smaller enclosure with net walls. This enclosure was used during the preexperimental training for companion chicks. There were 32 circular wells, 4 cm in diameter, sunk about 1.5 cm into the floor, and spaced uniformly along the runway. The bottom of these wells was painted white and the