Animal Behaviour 81 (2011) 825–829

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Colour biases are a question of conspecifics' taste

John Skelhorn [a,b,*]

[a] Centre for Behaviour & Evolution, Institute of Neuroscience, Newcastle University
[b] Centre for Research in Animal Behaviour, College of Life & Environmental Sciences, University of Exeter

ARTICLE INFO

Article history:
Received 10 September 2010
Initial acceptance 15 November 2010
Final acceptance 11 January 2011
Available online 12 February 2011
MS. number: 10-00607

Keywords:
aposematism
chemical defence
disgust
distasteful
domestic chick
evolution
Gallus gallus domesticus
innate bias
social learning
warning coloration

Toxic prey often advertise their defences to predators using conspicuous colours, such as red and yellow; and predators exhibit unlearned biases against warningly coloured food. These biases are particularly evident when other components of warning displays, such as sounds and odours, are present. Predators are thought to use additional signal components to reduce their attack rates on warningly coloured prey when the risk of them being defended is perceived to be high. If this is the case, any cue that allows predators to predict the presence of defended prey reliably should incite biases against warningly coloured food. Using domestic chicks, *Gallus gallus domesticus*, as predators and coloured crumbs for prey, I tested whether observing a conspecific's distaste response caused predators to bias their foraging decisions away from warningly coloured prey. Chicks observed a conspecific that had been given either a drop of water or a drop of Bitrex (a bitter-tasting solution). They were then offered a choice of either red and green, or yellow and green crumbs. Chicks that observed a conspecific's reaction to Bitrex attacked fewer red and yellow crumbs, and more green crumbs, than chicks that observed a conspecific's reaction to water. Observing conspecifics' disgust responses therefore caused birds to bias their foraging preference away from warningly coloured food and towards food of a more neutral colour. This suggests that predators' social systems may play a more important role than previously thought in the evolution of prey defences.

Aposematic prey use conspicuous colour patterns to advertise their chemical or physical defences to potential predators (Poulton 1890; Cott 1940). The conspicuous colour patterns used by aposematic prey are thought to speed up the avoidance learning process by being particularly salient to predators (Gittleman & Harvey 1980; Roper & Wistow 1986; Guilford 1992). In addition, many studies have shown that predators can have unlearned aversions to particular colours and patterns associated with warning signals (e.g. Schuler & Hesse 1985; Sillén-Tullberg 1985; Roper & Cook 1989; Mastrota & Mench 1995; reviewed in Schuler & Roper 1992), although the results of these studies are not always consistent (e.g. Fischer et al. 1975; Roper 1990; Roper & Marples 1997; Jones & Carmichael 1998).

However, in nature, the warning displays of aposematic prey rarely depend on coloration alone. Many prey use sounds and odours as part of their displays (Cott 1940; Haskell 1966; Edmunds 1974); and it has been consistently found that the presentation of a novel sound or odour causes naïve foraging predators to bias their behaviour against food with visual traits typically associated with aposematism, such as food that is conspicuous, red or yellow, or novel (Rowe & Guilford 1996; Marples & Roper 1996; Rowe & Guilford 1999a, b; Jetz et al. 2001; Lindström et al. 2001). One explanation for these findings is that the additional signal components provide cues that predators can use to reduce their attack rates on coloured prey that are more likely to be defended (Rowe & Guilford 1999b; Gambarale-Stille & Tullberg 2001). These incited biases could therefore allow birds to sample potentially valuable novel prey items when the risk of them being defended is perceived to be low, while also allowing them to avoid novel prey items when the risk of them being toxic is perceived to be high.

If this explanation is correct, any cue that predators can use to predict the presence of toxic prey in the environment reliably should cause predators to bias their foraging decisions away from warningly coloured prey. Birds shake their heads and wipe their beaks vigorously after sampling distasteful food (Johnston et al. 1998; Sherwin et al. 2002), and if these highly stereotyped distaste responses provide reliable information about prey quality, they could alert conspecifics to the presence of distasteful prey in the environment. Predators could then alter their foraging decisions in an adaptive manner, becoming more wary of prey with visual signals typically associated with aposematic prey, when the risk of them being unprofitable is perceived to be higher.

I used naïve domestic chicks as predators and artificially coloured crumbs for prey, to ask whether observing conspecifics'

* Correspondence: J. Skelhorn, Centre for Research in Animal Behaviour, College of Life & Environmental Sciences, University of Exeter, Washington Singer Laboratories, Perry Road, Exeter EX4 4QG, UK.
E-mail address: J.P.Skelhorn@Exeter.ac.uk.

0003-3472/$38.00 © 2011 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
doi:10.1016/j.anbehav.2011.01.017

distaste responses, but not the prey that elicited these responses, caused naïve birds to bias their attacks away from red crumbs (a colour typically associated with insect warning patterns) and towards food of a more neutral colour (green) in experiment 1; and away from yellow crumbs (also associated with insect warning patterns) and towards green crumbs in experiment 2.

METHODS

Subjects and Housing

Forty-five domestic chicks, *Gallus gallus domesticus*, that were hatched in the laboratory served as experimental subjects in experiment 1 (30 experimental chicks and 15 demonstrator chicks; see below for details); and a further 24 served as experimental subjects in experiment 2 (16 experimental chicks and eight demonstrator chicks). 'Experimental chicks' observed the responses of 'demonstrator chicks' to either a palatable or a bitter solution. The food colour preferences of experimental chicks were then measured. In both experiments, chicks were housed in two cages measuring 100 × 50 cm and 50 cm high. One cage housed the experimental chicks, and the other the demonstrator chicks. They were all subject to a 14:10 h light:dark cycle using uncovered fluorescent lights with no UV component, and temperatures were maintained at 24–25 °C using room heaters and heat lamps. All subjects were marked with nontoxic 'child-friendly' coloured marker pens, which did not appear to have any adverse effects on chick behaviour. Water was provided ad libitum, as were brown chick starter crumbs except during training and experimenting when food deprivation was necessary. When being food deprived, chicks had access to water, but not food. Weights were monitored for welfare purposes throughout the experiment, and all chicks gained weight as the experiment progressed. All deprivation periods were in accordance with Home Office regulations and guidelines, and the experiment was approved by Newcastle University's Comparative Biology Centre ethics committee. At the end of the experiment all chicks were donated to freerange smallholdings.

Artificial Prey

Red, yellow and green palatable crumbs were produced by spraying 150 g of brown chick starter crumbs with either 2 ml of Supercook red food dye (Supercook, Leeds, U.K.), 5 ml of Supercook yellow food dye, or 0.5 ml of Sugarflair spruce-green food dye (Sugarflair, Benfleet, Essex, U.K.) all diluted to 90 ml with tap water. These concentrations were chosen because they produced a similar degree of colour saturation in the crumbs. All crumbs were allowed to dry for 24 h before being sieved to ensure they were of similar size.

Experimental Arena

The arena consisted of a cage similar to the housing cages, with a section measuring 25 × 50 cm and 50 cm high, partitioned off using a wire-mesh screen to create a separate 'observation chamber'. Chicks placed in the observation chamber could observe the behaviour of birds placed in the experimental section of the arena through the wire-mesh screen. The floor of the experimental arena was covered in white paper that was changed every trial. The purpose of the white paper was to ensure crumbs of different colours appeared equally conspicuous.

Training

During the first 2 days posthatch, the experimental chicks were habituated to the observational chamber of the arena, and trained to eat brown crumbs from the white floor of the experimental section of the arena. On the first day posthatch, chicks were placed in the experimental section of the arena for three training sessions in groups of three, followed by one session in pairs: each session lasted 5 min. While one group of experimental chicks was placed in the experimental section of the arena, another group containing the same number of experimental chicks was placed in the observation chamber. This meant that each chick experienced four trials in the observation chamber and four trials in the experimental section of the arena on its first day of life. These trials allowed chicks to habituate to the arena and no food deprivation was necessary.

On day 2, chicks were given four trials designed to train chicks to eat brown crumbs in the experimental arena. To motivate chicks to eat, they were food deprived for approximately 90 min before each training session. This short deprivation period does not distress the chicks, nor does it have any adverse effects on their daily weight increases. In the first of these trials, chicks were placed in the arena in pairs, while in the following three trials chicks were placed in the arena individually: all training sessions lasted for approximately 3 min. In the first three trials, while experimental chicks were placed in the experimental section of the arena, the same number of experimental chicks was again placed in the observation chamber. However, in the final training trial, in which birds foraged individually in the experimental section of the arena, no bird was placed in the observation chamber. Thus, by the end of training, all birds had experience of observing birds forage in the experimental section of the arena, and of foraging completely alone in the experimental arena. All chicks ate readily in the arena in the final training trial, and no chick showed any sign of distress. The demonstrator chicks received no training in the experimental arena.

Testing

On day 3, the experimental chicks were divided into two equally sized groups. Chicks in the Water group observed a demonstrator that had been given 0.05 ml of water, and chicks in the Bitrex group observed a demonstrator that had been given 0.05 ml of a solution of 8 drops of 2% Bitrex solution in 100 ml of water. In experiment 1, experimental chicks in both groups were then given a choice between red and green crumbs; and in experiment 2, experimental chicks in both groups were then given a choice between yellow and green crumbs.

Twenty palatable green crumbs and 20 palatable warningly coloured crumbs (red in experiment 1, yellow in experiment 2) were scattered in the back two-thirds of the experimental arena (furthest away from the observation chamber). After approximately 90 min of food deprivation, experimental chicks were individually placed in the observational chamber of the experimental arena. A demonstrator chick was then given 0.05 ml of either water or Bitrex solution depending on which group the experimental chick was in. The drop of water or Bitrex solution was either offered to chicks on the end of a 1 ml pipette (from which many chicks readily drank) or was dropped onto the end of their beaks while they were in the home cage (see Rowe & Skelhorn 2004). Chicks were able to drink the drop from the end of their beaks, or shake their heads and wipe it off. No chick refused to drink the drop given to them. The demonstrator was then immediately placed in the front third of the experimental arena between the experimental chick and the coloured crumbs. The experimental chick was allowed to watch the demonstrator for 2 min before it was returned to its home cage. None of the demonstrators attacked the coloured crumbs since they had not been habituated to feed in the experimental arena. The experimental chick was then immediately removed from the observation chamber and placed into the experimental section of the arena, where it was allowed to attack (peck or eat) 16 of the 40 coloured crumbs before being removed from the arena. Each demonstrator chick demonstrated to one chick