



Avian predators change their foraging strategy on defended prey when undefended prey are hard to find



Thomas Carle*, Candy Rowe

Centre for Behaviour & Evolution, Institute of Neuroscience, Newcastle University, Newcastle, U.K.

ARTICLE INFO

Article history:

Received 9 January 2014
Initial acceptance 11 February 2014
Final acceptance 17 April 2014
Published online
MS. number: 14-00023R

Keywords:

aposematism
camouflage
concealment nutrient–toxin trade-off
crystallisation
foraging

Visually hunting predators forage on prey possessing a range of different defence strategies. The two most commonly studied defence strategies are camouflage (in which palatable and undefended prey have colour patterns to minimize detection) and aposematism (in which toxic prey advertise their defences using conspicuous warning signals). Typically, these two defence strategies are studied in isolation, but when multiple prey species are eaten by the same predators, changes in the defence strategy of one species could affect the selection pressures acting on the defensive strategy of another. In this experiment, we tested this idea by investigating whether predators increased their foraging behaviour on prey that they knew to be toxic when undefended prey were better concealed. European starlings, *Sturnus vulgaris*, were allowed to forage freely for undefended (water-injected) and defended (quinine-injected and coated) mealworms, *Tenebrio molitor*, in bowls containing woodchip (prey type was signalled by bowl colour). Toxic prey were always covered with 30 ml of woodchip, while undefended prey were covered with either 30 ml or 150 ml of woodchip (all birds received both woodchip depths). Increasing the amount of woodchip covering the undefended prey made them harder to find, but did not affect birds' propensity to search for toxic prey. However, birds did attack and eat more toxic prey, but only when they received the 150 ml treatment before the 30 ml treatment. Our experiment shows that better concealed palatable prey can increase predation of toxic prey, with implications for the study of prey defences.

© 2014 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Predators have exerted strong selection pressures on their prey, leading to the many different defence strategies that are employed by prey in the wild (Cott, 1940; Mappes, Marples, & Endler, 2005). One common way that palatable prey attempt to avoid predation is through concealment, i.e. decreasing the likelihood that they are discovered by predators. Prey can conceal themselves by hiding, for example in rock refuges (e.g. Cooper, 2008) or under leaf litter (e.g. Van Buskirk, 2001), masquerading as a nonfood item, such as a twig (e.g. Skelhorn, Rowland, Speed, & Ruxton, 2010), or being camouflaged against the background (e.g. Stevens & Merilaita, 2009). What these adaptive defensive strategies have in common is that they reduce the probability that a visually hunting predator finds the prey (e.g. Cuthill et al., 2005; Otis, Santana, Crawford, & Higgins, 1986) and increase predators' search times when foraging (e.g. Dimitrova, Stobbe, Schaefer, & Merilaita, 2009; Skelhorn et al., 2010). Therefore, these strategies increase not only prey survival, but also the search costs for foraging predators.

However, some prey do not attempt to conceal themselves and are much easier to find. Aposematic prey are highly visible through their use of conspicuous warning coloration to advertise their chemical or physical defences to predators (Cott, 1940; Poulton, 1890). Distinctive conspicuous coloration ensures that aposematic prey are not easily confused with more palatable prey in the environment (Beatty, Beirincx, & Sherratt, 2004; Mappes et al., 2005; Niskanen & Mappes, 2005; Sherratt & Beatty, 2003; Valkonen, Niskanen, Bjorklund, & Mappes, 2011; Wuster et al., 2004): naïve predators are more cautious when attacking conspicuous prey (Halpin, Skelhorn, & Rowe, 2008; Lindström, Rowe, & Guilford, 2001) and can easily learn to reduce their attacks on toxic prey that are aposematically coloured (Gittleman & Harvey, 1980; Lindström, Alatalo, & Mappes, 1999). Aposematic prey are therefore costly to predators but in a different way: their defences are harmful to the predator and should be avoided if possible.

Concealment and aposematism are generally considered to be very distinct defensive strategies (e.g. Stevens, 2007; but see Johansen et al., 2010; Tullberg, Merilaita, & Wiklund, 2005). Therefore, it is not surprising that selection pressures exerted by predators on each type of coloration have been studied independently of one another (Mappes et al., 2005; Stevens & Merilaita,

* Correspondence: T. Carle, Centre for Behaviour & Evolution, Institute of Neuroscience, Newcastle University, Henry Wellcome Building, Framlington Place, Newcastle, NE2 4HH, U.K.

E-mail address: th.carle@gmail.com (T. Carle).

2009). However, generalist predators (such as insectivorous birds) are often seen foraging on multiple prey species that have different defensive strategies (e.g. Chai, 1986; Pinheiro, 1996). Therefore, they will be exerting selection pressures simultaneously on prey species that defend themselves through concealment and on others that invest in toxins. This is likely to lead to coevolutionary changes between species with different defence strategies.

One way in which this could occur is by undefended prey becoming better concealed, meaning that predators find it harder to acquire nutrients from palatable prey. When nutrients available from palatable prey become increasingly scarce, predators are more willing to consume toxic prey (e.g. Barnett, Bateson, & Rowe, 2007; Barnett, Skelhorn, Bateson, & Rowe, 2012; Chai, 1986; Chatelain, Halpin, & Rowe, 2013; Gelperin, 1968; Pinheiro, 1996; Sexton, Hoger, & Ortleb, 1966). A reduction in nutrient acquisition from undefended prey can occur when they are less abundant or smaller (Halpin, Skelhorn, & Rowe, 2013; Lindström, Alatalo, Lyytinen, & Mappes, 2004), but could also occur if they are better concealed. Therefore, we would expect that increasing the level of concealment in undefended prey would increase the selection pressures acting on toxic prey. This is important to know because it would indicate that defensive strategies in sympatric species could coevolve, and specifically that improvements in concealment in palatable prey could alter the selection pressures acting on aposematically coloured prey.

In this experiment, we investigated how birds changed their foraging behaviour on undefended and defended prey when undefended prey became harder to find. We developed a novel experimental protocol in which European starlings, *Sturnus vulgaris*, foraged freely for undefended (water-injected and palatable) and defended (quinine-injected and distasteful) mealworms, *Tenebrio molitor*, individually placed in dishes on the floor of a laboratory. The mealworms were placed in the bottom of the dishes and covered in woodchip where the prey type (undefended or defended) that each bowl contained was signalled by the colour of the dish. The defended mealworms were always relatively easy to find, and were covered by a small amount of woodchip. As it had low search costs and a chemical defence, we considered this prey type to have similar properties to an aposematic prey species. The undefended mealworms varied in the depth of woodchip covering them in order to manipulate the ease with which they were found and the search costs for the predator. We predicted that when undefended prey were better concealed by being covered with more woodchip, search times for undefended prey would increase and fewer would be found and eaten. As a consequence, we also predicted (1) that birds would choose to forage more often in bowls containing defended prey that were easier to find and (2) that the number of defended prey attacked and eaten would increase.

METHODS

Subjects and Housing

Fifty European starlings were caught from the wild in Northumberland, U.K. (Natural England Licence Number 20103688) during September and October in 2010. They were caught using a whoosh net, and transferred in ringing bags within an hour to laboratories at Newcastle University. The birds (35 juveniles and 15 adults, 18 males and 32 females) were health checked upon arrival (all birds arrived in good health) and were individually marked using numbered plastic rings. When not used in experiments, they were housed in free-flight rooms (215 × 340 cm and 220 cm high) in groups of 25 individuals. The rooms were environmentally enriched with ropes, branches and wood bark on the floor for foraging, as well as the daily provision of water for bathing. The

ambient temperatures of the free-flights were checked daily and were maintained between 15 and 21 °C between December and May. Birds were maintained on a 14:10 h light:dark cycle under high flicker rate (100 Hz) fluorescent lighting, and food (fruit, mealworms and poultry maintenance diet) and water were available ad libitum. Birds were weighed each week and visually inspected daily by a trained technician during their time in captivity to ensure that they remained in good health.

We selected 16 adult starlings (14 females and two males) that were naïve to the task for our experiment, by catching them in the dark from the free-flight (all birds underwent a detailed health check at the same time). The birds were individually housed in wire cages (75 × 50 cm and 50 cm high) in a separate room that allowed visual and acoustic interaction between individuals. The cages were enriched with a bowl of water used for bathing, a litter tray containing woodchips for foraging and branches as perches. The light:dark cycle was 14:10 h and the temperature was similar to that of the free-flight. We carried out the experiment in December 2010 ($N = 8$) and in May 2011 ($N = 8$); the mean maximum laboratory temperature was different for birds in December 2010 (17 °C) and May 2011 (22 °C). Birds had constant access to water, and were fed chick crumbs and fruit ad libitum, except during food deprivation periods prior to the training and experimental trials (see below). A piece of apple was also given at the end of each daily session. To habituate birds to the bowls that would be used in the experiment, two circular white plastic bowls (diameter: 9.5 cm; height 4.5 cm) were added to each cage for 3 consecutive days. On each day, the bowls were filled with 30 ml of sand in the bottom and with 30 ml of woodchips containing four mealworms. The sand served to weight the bowls and to prevent them from tipping over, and the woodchips covered the mealworms so that the birds had to forage in the bowls to find prey.

After the experiments, all birds were health checked by a trained veterinary surgeon to ensure that they were at normal weight, in good condition and disease free. They were then BTO ringed and released at their site of capture under our Natural England Licence (June 2011). Although we were unable to monitor the birds following their release and subsequent dispersal, we have seen and recaptured birds that we have previously released, demonstrating their ability to survive in the wild. The experiments were conducted under local ethical approval from Newcastle University (ERC Project ID No. 266) and all procedures adhered to ASAB/ABS's Guidelines for the Treatment of Animals in Behavioural Research and Teaching.

Prey

We used mealworms of similar length (approximately 20 mm) as prey in our experiment. Mealworms that were given to birds in their home cages and during the training phase were not manipulated in any way. However, during the learning and test trials, we gave birds undefended prey (injected with 0.02 ml of water) and defended prey (injected with 0.02 ml of 4% quinine dihydrochloride solution). Defended mealworms used in the learning and test trials were also coated with a drop of the 4% quinine dihydrochloride solution to make them distasteful, making it easier for the birds to learn the difference between the two types of mealworm.

Training Trials

After 3 days of habituation to the bowls containing mealworms in their home cages, birds were trained to forage from bowls placed on the floor of an adjacent laboratory (Fig. 1). Each day, they were food deprived for 2 h before a single 30 min trial. Twenty circular white plastic bowls (diameter: 9.5 cm; height: 4.5 cm) were placed

Download English Version:

<https://daneshyari.com/en/article/8490438>

Download Persian Version:

<https://daneshyari.com/article/8490438>

[Daneshyari.com](https://daneshyari.com)