



Behavioral Ecology (2015), 00(00), 1–7. doi:10.1093/beheco/arv135

Original Article

Multicomponent deceptive signals reduce the speed at which predators learn that prey are profitable

John Skelhorn,^a Grace G. Holmes,^a Thomas J. Hossie,^b and Thomas N. Sherratt^c

^aInstitute of Neuroscience, Centre for Behaviour & Evolution, Newcastle University, Henry Wellcome Building, Framlington Place, Newcastle upon Tyne NE2 4HH, UK, ^bDepartment of Biology, Trent University, Peterborough, Ontario K9J 7B8, Canada, and ^cDepartment of Biology, Carleton University, Ottawa, Ontario K1S 5B6, Canada

Received 13 May 2015; revised 23 July 2015; accepted 27 July 2015.

Many prey use multicomponent deceptive signals to fool predators into mistaking them for inedible objects, toxic prey, or dangerous animals. However, recent experiments have suggested that multicomponent deceptive signals are no more effective in deterring predators than single-component signals, making it difficult to understand how they have evolved. Here, we use an established experimental system in which naive domestic chicks are presented with models of snake-mimicking caterpillars to test the idea that multicomponent deceptive signals reduce the speed at which predators learn that prey are profitable. We presented chicks with a series of 4 trials in which they encountered a single type of caterpillar model. The type of model differed among our 4 experimental groups that were arranged in a 2×2 factorial design: models either possessed eyespots or did not and were in either the resting or defensive posture. Chicks' responses to the same model prey were then retested following an extended 72-h retention period. Chicks rapidly attacked prey with no defensive traits and initially showed similar levels of wariness to prey with either 1 or 2 deceptive traits. However, chicks learned that single-trait caterpillars were profitable more quickly than 2-trait caterpillars and retained their learned responses better. This suggests that prey with multicomponent deceptive signals may have a selective advantage over prey with single-component deceptive signals when predators repeatedly encounter such prey.

Key words: antipredator, caterpillar, eyespots, learning, mimicry, predation.

INTRODUCTION

Prey have evolved a wide variety of antipredator defenses that reduce the likelihood of them being eaten (Ruxton et al. 2004). Many forms of antipredator defense rely on deceiving predators into forgoing their attack: masquerading prey resemble inedible objects (Skelhorn et al. 2010a, 2010b; Skelhorn 2015); undefended Batesian mimics resemble prey with noxious secondary defenses (Bates 1862); palatable deimatic prey produce startling/intimidating displays that are believed to elicit fear responses in predators (Maldonado 1970; Vallin et al. 2005; Langridge et al. 2007); and a number of prey species appear to mimic dangerous vertebrates such as snakes (Cott 1940; Bates 1862; Weismann 1882; Poulton 1890).

Intriguingly, deception is rarely based on a single trait. Batesian mimics often resemble their models in terms of color, pattern,

and shape (Norman et al. 2001; Bain et al. 2007; Valkonen et al. 2011; O'Hanlon 2014); deimatic displays are often composed of signals in multiple sensory modalities (Umbers et al. 2015); and many prey species possess behavioral adaptations that appear to enhance the likelihood of predators being deceived (McIver and Stonedahl 1993). For example, some mimetic butterflies fly in a manner that closely resembles the characteristic flight behavior of their defended models (Srygley and Ellington 1999; Srygley 2004); some wasp-mimicking hoverflies position their legs over their heads giving the impression that they possess wasp-like antennae (Penney et al. 2014); and some snake-mimicking caterpillars inflate the anterior or posterior segments containing eyespots when attacked by predators, thereby increasing the degree to which they resemble snakes (Hossie and Sherratt 2014; see Figure 1b).

In many cases, the possession of multiple deceptive traits is easily explained: they act additively or synergistically to increase the chance of the deception being successful (Kappan 2001; Skelhorn and Rowe 2010; Iserbyt et al. 2011; Skelhorn et al. 2011; Skelhorn and Ruxton 2013; Finkbeiner et al. 2014), or

Address correspondence to J. Skelhorn. E-mail: john.skelhorn@ncl.ac.uk.

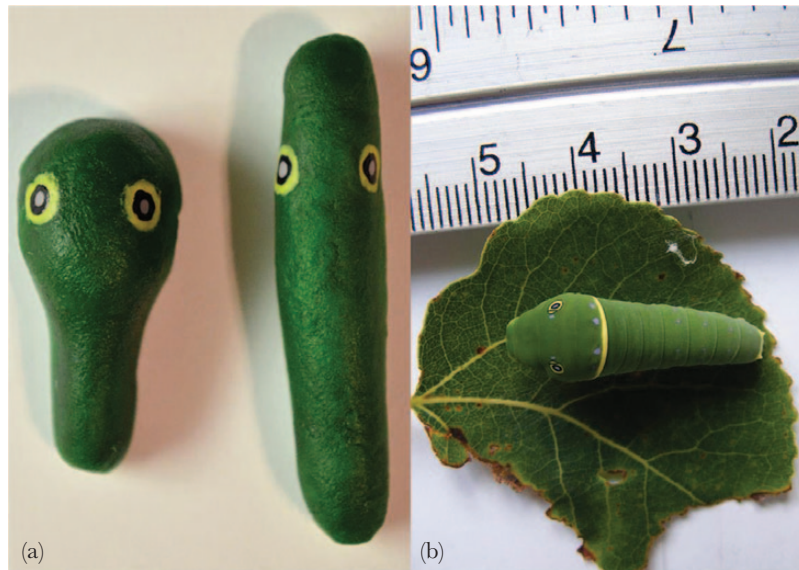


Figure 1

(a) Examples of the artificial prey types used in this experiment: a resting posture caterpillar with eyespots (right) and a defensive posture caterpillar with eyespots (left). (b) Final instar Canadian tiger swallowtail (*Papilio canadensis*) caterpillar in its defensive posture (models were loosely based on this species). Images by T.J.H.

different components deter different types of predators (Pearson 1989) or act at different stages of the predation process (Endler 1991). However, explaining the evolution of additional traits is challenging in cases where 1 or both traits enhance prey survival when found in isolation, but there is no additional benefit to possessing both traits concurrently. In particular, studies have found that 1) although artificial Batesian mimics that resemble the color of their models gain protection from avian predators, there is no additional benefit to matching both color and pattern (Kazemi et al. 2014); 2) although the visual components of the deimatic display of peacock butterflies enhance survival when performed in isolation, there is no additional benefit to producing both the visual and the auditory components of the display (Vallin et al. 2005); 3) although model snakes with triangular heads or viper-like zigzag patterned bodies are protected from snake-eating birds, snake models with both traits gain no additional protection (Valkonen et al. 2011); and 4) although both the eyespots and the defensive posture of putative snake-mimicking caterpillars have been shown to protect caterpillar-like models from attack by avian predators, models with both the defensive posture and eyespots survive no better than models with only 1 of these traits (Hossie and Sherratt 2012, 2013; Skelhorn et al. 2014). It is therefore difficult to understand how these multicomponent deceptive signals evolve, given that once 1 trait has evolved, additional traits seemingly provide no additional survival benefit.

One potential explanation for the above observations is that the survival benefit of a secondary defensive or mimetic trait is smaller than the survival benefit of a primary trait, and so it is harder to reject the null hypothesis of no difference even if there was one (a type II error). Alternatively (or in addition), earlier studies such as those listed above may have failed to capture the full extent to which defensive traits influence prey survival. In particular, experiments have primarily monitored the effects of defensive traits on predators' initial decisions to attack novel prey. Laboratory studies have monitored predators' responses to a single prey item (Vallin

et al. 2005; Skelhorn et al. 2014) or a small number of prey items (Kazemi et al. 2014), and field studies typically monitor prey survival over a relatively short time period (often ≤ 3 days: Valkonen et al. 2011; Hossie and Sherratt 2012, 2013). This gives predators little or no opportunity to encounter multiple prey items and learn about their profitability. Consequently, we do not know whether or how specific deceptive traits combine to influence either the rate at which predators learn that prey are profitable or the length of time for which this information is retained.

Failure to consider how predators react after repeated interactions with prey is a potentially important oversight. In more honest signaling contexts, such as when toxic prey advertise their defenses to predators, different signal components have been shown to interact to enhance the speed at which predators learn that prey are unprofitable (Rowe 1999; Lindstrom et al. 2001; Franks and Sherratt 2007; Siddall and Marples 2007). Intuitively, one might predict the converse when signaling is dishonest, namely that possessing multiple deceptive traits would reduce the speed at which predators learn that prey are undefended and shorten the duration that this information is retained. If true, then the deceptive traits discussed above could, after all, have an additive effect on survival in cases where predators repeatedly encounter deceptive prey. This would help to explain how multiple deceptive traits have evolved in the same species. It is thus vital we understand how the multiple components of deceptive signals interact to influence the cognitive processes of predators if we are to explain how such signals have evolved and are maintained.

Here, we address this challenge using an established experimental system in which naive domestic chicks are presented with caterpillar-like model prey (Skelhorn et al. 2014; Hossie et al. 2015). Using a 2×2 factorial design in which model caterpillars either possess eyespots or do not and are in either the resting or defensive posture, we determine the effects of eyespots, inflated anterior body segments, and their interaction on: 1) predators' initial wariness to attack prey, 2) the rate at which predators learn that prey are profitable, and 3) how predators retain this information over time.

METHODS

Subjects and housing

Forty-eight newly hatched female domestic chicks (*Gallus gallus domesticus*) of the “Novo Brown” strain were purchased from a commercial hatchery in Lancashire, UK. They were transported to the laboratory by car, where they were housed in 3-floor pens measuring 120 cm × 70 cm. The floor of the pens was covered with wood chips and each pen contained a food hopper, a water hopper, and a plastic shelter. Birds were subject to a 14:10h light cycle under florescent lighting, and the temperature of the laboratory was maintained at 24–27 °C using 2 room heaters. Water was provided ad libitum, as were chick starter crumbs, except during training and experimenting when brief periods of food (but not water) deprivation were necessary to ensure chicks were motivated to forage. All chicks were marked with nontoxic “child-friendly” colored marker pens to allow individuals to be identified: this did not have any adverse effect on chick behavior. Chicks were weighed and visually inspected by JS daily: all chicks gained weight as the experiment progressed. At the end of the experiments, the chicks were donated to free-range small holdings. The experiments were conducted under local ethical approval from Newcastle University (ERC Project ID No. 340) and complied with both UK Home Office regulations and the Association for the Study of Animal Behavior’s Guidelines for the Treatment of Animals in Research and Teaching.

Artificial prey

We followed Hossie and Sherratt’s (2013) method of producing countershaded (dark dorsal and light ventral sides) pastry caterpillars, based loosely on the appearance of the late instars of *Papilio canadensis* and *Papilio glaucus* caterpillars. We used the same pastry recipes as Hossie and Sherratt (40 mL of lard, 118 mL of flour, and either 3 drops of Leaf Green food dye in 20 mL of water to produce light green pastry or 6 drops of the same dye in 15 mL of water to produce dark green pastry). Indeed, to facilitate comparability all the dyes, paints and plaster of Paris moulds used by Hossie and Sherratt (2013) were shipped to the UK from Canada and used in these experiments. Our previous experiments have shown that chicks find pastry caterpillars highly palatable, and tend to consume them immediately on attack (Skelhorn et al. 2014).

We produced 4 types of artificial caterpillars: 1) no eyespot-resting posture; 2) no eyespots-defensive posture; 3) eyespots-resting posture; and 4) eyespots-defensive posture (see Figure 1a). To create countershaded caterpillars in a resting posture, we pressed together dark and light pastry cylinders (4-cm long with a diameter of ≈0.5 cm) to produce caterpillars 4-cm long with a diameter of ≈0.7 cm. Caterpillars made in this way were then pressed into plaster moulds with anterior thickening to create caterpillars with a defensive posture. Thus, caterpillars with a defensive posture had the same volume and color as caterpillars in a resting posture but were just 3 cm in length. Caterpillars with eyespots were produced by painting 2 yellow circles (≈0.45 cm diameter) dorsolaterally on the prey 0.4 cm apart. Since resting- and defensive-posture caterpillars were different lengths (4 and 3 cm, respectively), we painted eyespots ≈0.7 cm from the anterior tip of resting-posture caterpillars and ≈0.5 cm from the anterior tip of defensive-posture caterpillars. A black circle (≈0.3 cm diameter) was then painted inside each of the yellow circles, and finally, a small white spot of paint (≈0.1 cm diameter) was added to the center of the black circles.

Training

On day 1 posthatch, chicks were left to acclimatize to the laboratory. The following day, 36 experimental chicks were trained to eat chick starter crumbs from the white paper-covered floor of an experimental arena. Two identical arenas were used, each consisting of a cage measuring 120 cm × 50 cm × 50 cm, with a section measuring 20 cm × 50 cm × 50 cm partitioned off using wire mesh to create a separate “buddy arena.” In all training and experimental trials, 2 chicks were placed in the buddy arena to reduce any potential distress from placing experimental chicks alone in the arena. These buddy chicks were selected from a stock of 12 individuals and were changed every 3 trials. These chicks were not given access to artificial prey at any point during the experiment.

Chicks received 6 training trials at regular intervals: 3 on day 2 posthatch and 3 on day 3. In all trials, chick starter crumbs were scattered over the floor of the experimental arena, and chicks were then placed in the arena for approximately 2 min. In the first 2 training trials, chicks were placed in the arena in groups of 3; in the following 2 trials, chicks were placed in the arena in groups of 2; and in the final 2 trials, chicks were placed in the arena individually. In the final trial, a sycamore (*Acer pseudoplatanus*) branch (≈50 cm long) complete with leaves was placed in the center of the arena. This was to familiarize chicks with branches in order that they did not show a neophobic response when presented with a branch in the subsequent test trials (see below). Chicks were food deprived for 30 min before each of the training trials on day 2 to ensure they were motivated to forage. During all training trials, the 2 arenas were used simultaneously. However, during the test trials, only 1 subject performed the experiment at any one time, in order to ensure that measurements were taken accurately. By the end of the training trials, all chicks had pecked the branch and were eating crumbs in the experimental arena.

Learning trials

On day 4, the 36 experimental chicks were randomly assigned to 1 of the 4 experimental groups ($n = 9$ per group). Birds in all 4 groups were subject to a series of 4 trials: 2 on day 4 and 2 on day 5. In each trial, chicks were food deprived for 30 min before being placed in the experimental arena individually. Here, each chick encountered a sycamore branch (≈50 cm in length) supporting a single pastry caterpillar. Caterpillars were presented on a branch to increase comparability with previous studies (Hossie and Sherratt 2012, 2013) and to ensure chicks did not stand on prey (which could potentially have caused prey to become misshapen). The branch was located in the center of the arena: one end was 25 cm from the buddy arena and the other 25 cm from the rear wall. Chicks were placed in a central position immediately in front of the rear wall of the experimental arena. The pastry caterpillars were attached to the branches using pins pushed into the branches in random positions. The tops of the pins were cut off leaving approximately 3 mm protruding from the branches, onto which pastry caterpillars were impaled.

Each chick received the same type of caterpillar in all 4 trials. However, the type of caterpillar that birds encountered differed among our 4 experimental groups: 1 group received caterpillars with no eyespots in a resting posture; 1 group received caterpillars with no eyespots in a defensive posture; 1 group received caterpillars with eyespots in a resting posture; and 1 group received caterpillars with eyespots in the defensive posture. Birds remained in the arena until they attacked the caterpillar (maximum time = 600 s).

The latency to first inspect the caterpillar (an unambiguous behavior in which chicks tilt their head dramatically to one side and view the caterpillar monocularly), the latency to attack the caterpillar (here, we use the latency to first peck the pastry caterpillar, but note that all birds subsequently ate them), and the presence/absence of approach–retreat behavior (repeatedly approaching and retreating from the caterpillar) were recorded. These measures were chosen because they were unambiguous and have been used in previous studies investigating the antipredator efficacy of both eyespots and the defensive posture (Skelhorn et al. 2014; Hossie et al. 2015).

Retention trial

On day 8 of life (≈ 72 h after the final learning trial), all experimental chicks received a single retention trial. This was identical to the learning trials, and its purpose was to establish whether birds' behaved in the same way toward caterpillars after a short interval (i.e., 72h) in which they did not encounter any further model caterpillars.

Statistical analysis

All analyses were conducted in R version 2.13.2. Given the repeated measures design, variation in the latency of chicks to first inspect and first attack artificial caterpillars over the 5 repeated trials were analyzed by fitting a general linear mixed effects model using the lme function of the nlme package. Here, individual chick was treated as a random factor, whereas caterpillar posture (resting/defensive), eyespot (present/absent), trial (1–5), and their interactions were treated as fixed factors. Trial was treated as categorical rather than a covariate predictor due to the evident nonlinear relationship of trial to latency (a phenomenon confirmed by the significantly improved fit of the higher parameter categorical model using log-likelihood ratio tests). We ascertained whether the random effect of the individual should be accounted for by an intercept only term or an intercept with a separate adjustment for each trial, using a log-likelihood ratio test. Likewise, we identified the appropriate covariance assumption by comparing the fit of models with autoregressive, compound symmetry, general correlation, and no within-group correlation structures using log-likelihood ratio tests. Given the prevalence of interactions, post hoc multiple comparisons were restricted to comparing the latency of chicks to inspect (or attack) specific caterpillar phenotypes across different trials (necessarily assuming an intercept only random effect). These tests were based on Tukey Honest Significant Difference and conducted using the glht function of the multcomp package. Model criticism (evaluating normality and homogeneity of error) was performed by inspecting the residual plots of fitted models, which indicated a need for square root transformations prior to analysis.

The presence or absence of approach–retreat behavior per trial was a binary (0/1) response variable. Given the binomial error distribution, we fitted a generalized linear mixed effects model using the glmer function of the lme4 package with a logit link function. Once again, the individual chick was included as a random factor in our analysis, whereas posture, eyespot, trial, and their interactions were treated as fixed factors. The decision to treat trial as a categorical variable was again supported by log-likelihood ratio tests, although this in turn necessitated considering that each chick provides only an intercept term (a robust assumption given that a random slope was not justified when trial is treated as continuous). Model simplification was conducted through log-likelihood ratio tests, whereas the covariance matrix was assumed unstructured.

RESULTS

Inspection time

The most parsimonious model was identified as a full-factorial Anova with no within-group correlation structure and individual accounted for through both a random intercept and an individual-specific adjustment for trial. In this best-fitting model, the responses of chicks to caterpillars varied significantly with the presence/absence of eyespots, the caterpillar posture, and with trial, while many interactions were also highly significant (Table 1). The main effects and interactions show that the average time chicks took to inspect the artificial caterpillars not only varied with the caterpillar phenotype and trial but that the change in the response of chicks over trials depended on the caterpillar phenotype. Caterpillars in defensive posture and with eyespots elicited the longest initial inspection times and the slowest attenuation in response over time (Figure 2, top panel). Conversely, caterpillars in resting posture and without eyespots were inspected rapidly throughout all 5 trials. Post hoc multiple comparisons revealed that the inspection times for caterpillars in defensive posture with eyespots differed significantly between the first trial and the third and fourth trials (each $P < 0.05$), whereas the inspection times on the first and fifth trial (i.e., the retention trial) did not differ significantly ($P = 0.397$). Likewise, post hoc multiple comparisons on the responses of chicks to the remaining 3 phenotypes indicated that the inspection time was always significantly higher on the first trial than all the other trials (all $P < 0.05$), but there were no other significant differences.

Latency to attack

As might be expected, a chick's latency to inspect a model caterpillar and its latency to attack were not independent end points (overall product moment correlation of an individual's latencies across all trials and experimental treatments $r = 0.876$, degrees of freedom [df] = 178, $P < 0.001$). Once again a full-factorial Anova with no within-group correlation structure and a random intercept with adjustment for trial was identified as the most parsimonious model to explain variation in attack latencies. As above, the responses of chicks to caterpillars varied significantly with the presence/absence of eyespots, posture, and trial, whereas many interactions were also highly significant (Table 2). Caterpillars in defensive posture with eyespots again elicited the longest times to attack and showed the slowest attenuation (Figure 2, middle panel). Likewise, caterpillars in resting posture and without eyespots were attacked rapidly

Table 1
Hypothesis tests following the fit of a linear mixed effects model to explain variation in the root transformed inspection time

	Numerator df	Denominator df	F value	P
Inspection latency				
(Intercept)	1	128	140.05	<0.0001
Posture	1	32	108.39	<0.0001
Eyespot	1	32	82.91	<0.0001
Time	4	128	56.15	<0.0001
Posture \times eyespot	1	32	78.95	<0.0001
Posture \times time	4	128	0.57	0.6857
Eyespot \times time	4	128	2.46	0.0489
Posture \times eyespot \times time	4	128	11.75	<0.0001

The most parsimonious model (shown) assumed no within-group correlation structure and a random intercept and trial adjustment for each individual tested.

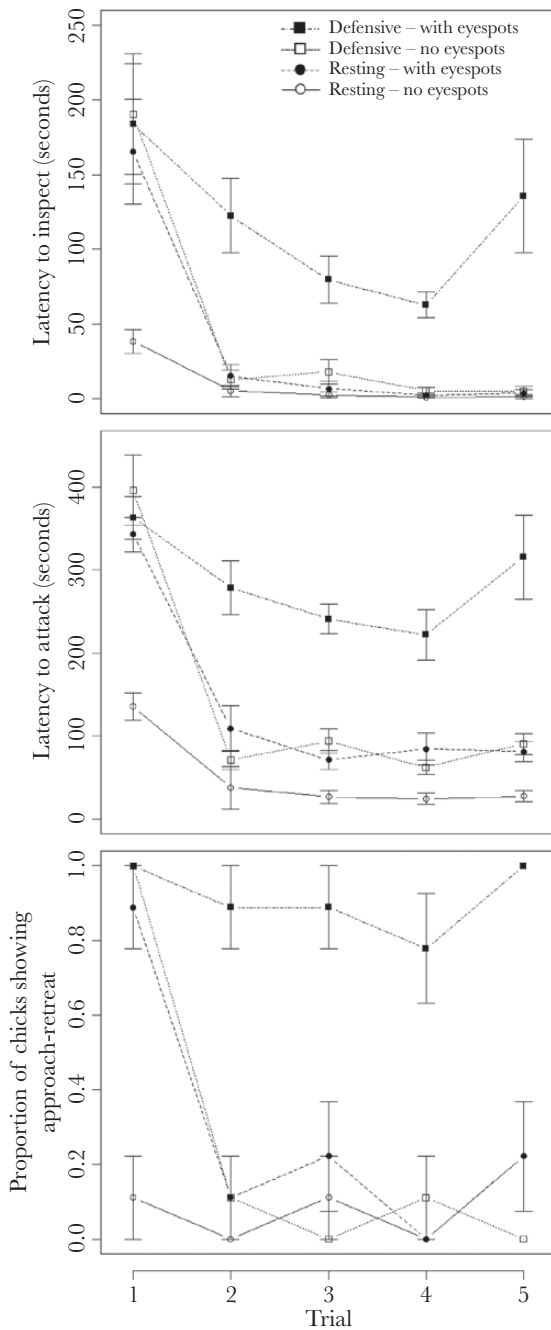


Figure 2
 The mean (± 1 SE) times in seconds for chicks to inspect (top panel) and attack (middle panel) the 4 types of artificial caterpillar (defensive posture with eyespots, defensive posture without eyespots, resting posture with eyespots, and resting posture without eyespots) over the 5 separate trials (trials 1–4 were the learning trials that took place on days 4 and 5 of the chicks’ lives; trial 5 was the retention trial that took place on day 8 of their lives), and the proportion of chicks (± 1 SE) showing approach–retreat behavior (bottom panel) toward the 4 types of artificial caterpillars over the 5 separate trials. SE = standard error.

throughout all 5 trials. Post hoc multiple comparisons revealed precisely the same patterns as noted above for inspection latency. Thus, the time to attack all phenotypes, except the defensive posture with eyespot phenotype, was significantly higher on the first trial than all the other trials (all $P < 0.05$), but no other differences

Table 2
Hypothesis tests following the fit of a linear mixed effects model to explain variation in the root transformed latency to attack

Attack latency	Numerator df	Denominator df	F value	P
(Intercept)	1	128	3514.033	<0.0001
Posture	1	32	134.373	<0.0001
Eyespot	1	32	104.536	<0.0001
Time	4	128	70.322	<0.0001
Posture \times eyespot	1	32	4.463	0.0425
Posture \times time	4	128	1.885	0.1170
Eyespot \times time	4	128	3.211	0.0150
Posture \times eyespot \times time	4	128	10.172	<0.0001

The most parsimonious model (shown) assumed no within-group correlation structure and a random intercept and trial adjustment for each individual tested.

were significant. The attack latencies for caterpillars in defensive posture with eyespots differed significantly between the first trial and the third and fourth trials (each $P < 0.05$), whereas the attack latencies in the first and fifth trial (i.e., the retention trial) did not differ significantly ($P = 0.412$).

Approach–retreat behavior

The most parsimonious model for the incidence of approach–retreat behavior involved posture, eyespot, time, posture \times eyespot, and posture \times time (the remaining pairwise interaction and the 3-way interaction were dropped). Log-likelihood ratio tests comparing this most parsimonious model with the reduced model lacking the factor entirely or specific interaction confirmed the overall importance of posture (likelihood ratio chi squared = 54.54, $df = 6$, $P < 0.001$), eyespot (likelihood ratio chi squared = 49.38, $df = 2$, $P < 0.001$), and time (likelihood ratio chi squared = 58.10, $df = 8$, $P < 0.001$), as well as the specific pairwise interactions (posture \times eyespot: likelihood ratio chi squared = 49.38, $df = 2$, $P < 0.001$; posture \times time likelihood ratio chi squared = 58.10, $df = 8$, $P < 0.001$). Overall, the caterpillars in defensive posture with eyespots elicited a high frequency of approach–retreat behavior, which continued throughout the trials. Resting caterpillars with eyespots evoked a similar initial reaction, but this response waned over time. Post hoc testing for differences in the tendency of chicks to engage in approach–retreat behavior across trials revealed a significant fall in approach–retreat tendency from trial 1 to 2 in eyespotted caterpillars in resting posture ($P = 0.033$), but there were no other significant differences (Figure 2, bottom panel).

DISCUSSION

Our results clearly demonstrate that caterpillars with either eyespots or a defensive posture initially elicit levels of predator wariness similar to that of caterpillars with both traits, whereas caterpillars that have no such traits are rapidly inspected and attacked. Importantly, however, we found that predator wariness was not fixed and decayed much more markedly over time for 1-trait mimics than 2-trait mimics. Moreover, although chicks presented with single-trait mimics retained their learned responses following an extended period (i.e., 72 h) without encountering the prey items, chicks’ wariness of 2-trait mimics was effectively reset. In short, there is a clear benefit to possessing multicomponent deceptive signals: they reduce the speed at which predators learn that prey are profitable and shorten the duration that this information is retained compared with single-component signals.

This suggests that prey with multicomponent deceptive signals may have a selective advantage over prey with single-component deceptive signals in situations where predators repeatedly encounter such prey. This observation helps to explain why prey do not always rely on a single deceptive trait to fool their predators and illustrates that predation experiments run over relatively short periods of time may underestimate the protective value of multicomponent deceptive signals.

The behavior of the chicks in our experiment may represent an adaptive foraging strategy common to many predators. Theoretical work has shown that initial wariness of a novel prey type, and subsequent decisions to sample it, can be explained by assuming that predators trade-off the likelihood that prey are unprofitable (e.g., toxic or dangerous), and the probability of seeing the prey type in the future (Sherratt 2011). Chicks may have shown initial wariness of all prey types that were perceived to pose any risk because, having encountered the prey type only once, the probability of seeing it again in the future was likely to be low. Subsequent decisions can then be explained by assuming that predators more heavily weighed the risk of the prey type being defended/dangerous for 2- than 1-trait mimics: they effectively needed more information before being convinced that 2-trait mimics posed little/no risk. Intriguingly, our findings also suggest that the retention of information about prey profitability may be influenced by similar trade-offs to those that influence their decisions to sample novel prey, and it would be interesting to incorporate such biases in information retention into theoretical models of predator decision making.

Irrespective of the underlying mechanism, it is clear that predators' initial reactions to novel or deceptive prey will not necessarily be the same as their long-term reactions: although our birds were initially equally wary of 1- and 2-trait mimics, they took longer to learn that the 2-trait mimics were profitable and forgot this more quickly. Intriguingly, a recent field study using similar caterpillar models found no difference in mortality between 1- and 2-trait mimics (Hossie and Sherratt 2013), indicating that free-living birds in these short-term experiments may behave in a manner analogous to the initial reactions of naive chicks. Several studies have also failed to find additive effects of multicomponent signals in other deceptive signaling systems (e.g., Vallin et al. 2005; Valkonen et al. 2011; Kazemi et al. 2014). This failure to find additive effects of multiple signaling components in previous studies, in contrast to ours, can be explained in several possible ways, which are not mutually exclusive: 1) earlier studies were too short in duration to allow individual predators to repeatedly encounter the deceptive prey; 2) lacked the power to detect relatively small effect sizes; or 3) used inedible model prey which prevented predators from learning they were palatable. Alternatively, the birds in our experiment may have learned about the profitability of mimics quickly 4) because we did not allow them to encounter the model species that the mimics are thought to resemble or 5) because, unlike in many natural situations, there were no alternative prey available to them, and the number and type of alternative prey available is known to influence predators foraging decisions (Skelhorn and Rowe 2009; Ihalainen et al. 2012; Halpin et al. 2013).

If models are sufficiently abundant or toxic (perhaps even lethal) to prevent predators from learning that mimics are profitable, then predators' longer-term reactions may have little effect on prey mortality and will not select for multiple deceptive traits. However, if mimics are sufficiently common that predators repeatedly encounter deceptive prey, and/or models are relatively uncommon or even absent then predators' longer-term responses may be the primary selective force shaping antipredator traits. Under these circumstances, individuals with multiple deceptive traits will have a selective

advantage over those with just one, and this will lead to the evolution of multicomponent deceptive signals. It is therefore clear that we need to measure the efficacy of defensive traits over ecologically realistic timescales in order to gain a full appreciation of the mechanisms through which defensive traits deter would-be predators.

In recent years, there has been a great deal of emphasis on the evolution and maintenance of imperfect mimics, and a number of theories have now been presented to help understand why predators do not see through these poor disguises (see Kikuchi and Pfennig 2013 for review). Here, we examine the reverse, asking why mimicry is frequently extremely high quality, involving multiple dimensions of color, pattern, behavior, and sound. Our work demonstrates that apparently superfluous defenses can hold hidden adaptive value that may only be revealed by examining outcomes over an ecologically appropriate timescale. Whether the time-mediated protective effects of multicomponent signals observed here are widespread remains to be seen: if they are, this may have wide-ranging implications for the interpretation of experiments that purport to show that perfect and imperfect mimics are equally protected from predators.

FUNDING

Funding for this research was provided by a Discovery Grant (NSERC) awarded to T.N.S., and a start-up package was awarded to J.S. by Newcastle University.

We thank M. Waddle for her expert care of the chicks, J. Mappes and 2 anonymous reviewers for their helpful comments on an early version of the manuscript.

Handling editor: Johanna Mappes

REFERENCES

- Bain RS, Rashed A, Cowper VJ, Gilbert FS, Sherratt TN. 2007. The key mimetic features of hoverflies through avian eyes. *Proc Biol Sci.* 274:1949–1954.
- Bates HW. 1862. Contributions to an insect fauna of the Amazon Valley, Lepidoptera: Heliconiidae. *Trans Linn Soc Lond.* 23:495–566.
- Cott HB. 1940. Adaptive coloration in animals. New York: Oxford University Press.
- Endler JA. 1991. Interactions between predators and prey. In: Krebs JR, Davies NB, editors. *Behavioural ecology*. Oxford: Blackwell Scientific. p. 169–196.
- Finkbeiner SD, Briscoe AD, Reed RD. 2014. Warning signals are seductive: relative contributions of color and pattern to predator avoidance and mate attraction in *Heliconius* butterflies. *Evolution.* 68:3410–3420.
- Franks DW, Sherratt TN. 2007. The evolution of multicomponent mimicry. *J Theor Biol.* 244:631–639.
- Halpin CG, Skelhorn J, Rowe C. 2013. Predators' decisions to eat defended prey depend on the size of undefended prey. *Anim Behav.* 85:1315–1321.
- Hossie TJ, Sherratt TN. 2012. Eyespots interact with body colour to protect caterpillar-like prey from avian predators. *Anim Behav.* 84:167–173.
- Hossie TJ, Sherratt TN. 2013. Defensive posture and eyespots deter avian predators from attacking caterpillar models. *Anim Behav.* 86:383–389.
- Hossie TJ, Sherratt TN. 2014. Does defensive posture increase mimetic fidelity of caterpillars with eyespots to their putative snake models? *Curr Zool.* 60:76–89.
- Hossie TJ, Skelhorn J, Breinholt JW, Kawahara AY, Sherratt TN. 2015. Body size affects the evolution of eyespots in caterpillars. *Proc Natl Acad Sci USA.* 112:6664–6669.
- Ihalainen E, Rowland HM, Speed MP, Ruxton GD, Mappes J. 2012. Prey community structure affects how predators select for Mullerian mimicry. *Proc Biol Sci.* 279:2099–2105.
- Iserbyt A, Bots J, Van Dongen S, Ting JJ, Van Gossum H, Sherratt TN. 2011. Frequency-dependent variation in mimetic fidelity in an intraspecific mimicry system. *Proc Biol Sci.* 278:3116–3122.

- Kappan DD. 2001. Three-butterfly system provides a field test of Mullerian mimicry. *Nature*. 409:388–340.
- Kazemi B, Gamberale-Stille G, Tullberg BS, Leimar O. 2014. Stimulus salience as an explanation for imperfect mimicry. *Curr Biol*. 24:965–969.
- Kikuchi DW, Pfennig DW. 2013. Imperfect mimicry and the limits of natural selection. *Q Rev Biol*. 88:297–315.
- Langridge KV, Broom M, Osorio D. 2007. Selective signalling by cuttlefish to predators. *Curr Biol*. 17:R1044–R1045.
- Lindstrom L, Rowe C, Guilford T. 2001. Pyrazine odour makes visually conspicuous prey aversive. *Proc Biol Sci*. 268:159–162.
- Maldonado H. 1970. The deimatic reaction in the praying mantis *Stagmatoptera biocellata*. *Z Vergl Physiol*. 68:60–71.
- McIver JD, Stonedahl G. 1993. Myrmecomorphy: morphological and behavioural mimicry of ants. *Annu Rev Entomol*. 38:351–379.
- Norman MD, Finn J, Tregenza T. 2001. Dynamic mimicry in an Indo-Malayan octopus. *Proc Biol Sci*. 269:1755–1758.
- O'Hanlon JC. 2014. The roles of colour and shape in pollinator deception in the orchid mantis *Hymenopus coronatus*. *Ethology*. 120:652–661.
- Pearson DL. 1989. What is the adaptive significance of multicomponent defensive repertoires? *Oikos*. 54:251–253.
- Penney HD, Hassall C, Skevington JH, Lamborn B, Sherratt TN. 2014. The relationship between morphological and behavioural mimicry in hover flies (Diptera: Syrphidae). *Am Nat*. 183:281–289.
- Poulton EB. 1890. The colours of animals: their meaning and use especially considered in the case of insects. Chicago (IL): D. Appleton.
- Rowe C. 1999. Receiver psychology and the evolution of multicomponent signals. *Anim Behav*. 58:921–931.
- Ruxton GD, Sherratt TN, Speed MP. 2004. Avoiding attack: the evolutionary ecology of crypsis, warning signals and mimicry. New York: Oxford University Press.
- Sherratt TN. 2011. The optimal sampling strategy for unfamiliar prey. *Evolution*. 65:2014–2025.
- Siddall EC, Marples NM. 2007. Better to be bimodal: the interaction of color and odor on learning and memory. *Behav Ecol*. 19:425–432.
- Skelhorn J. 2015. Masquerade. *Curr Biol*. 25:R643–R644.
- Skelhorn J, Dorrington G, Hossie TJ, Sherratt TN. 2014. The position of eyespots and thickened segments influence their protective value to caterpillars. *Behav Ecol*. 25:1417–1422.
- Skelhorn J, Rowe C. 2009. Distastefulness as an antipredator defence strategy. *Anim Behav*. 78:761–766.
- Skelhorn J, Rowe C. 2010. Birds learn to use distastefulness as a signal of toxicity. *Proc Biol Sci*. 277:1729–1734.
- Skelhorn J, Rowland HM, Delf J, Speed MP, Ruxton GD. 2011. Density-dependent predation influences the evolution and behaviour of masquerading prey. *Proc Nat Acad Sci USA*. 108:6532–6536.
- Skelhorn J, Rowland HM, Ruxton GD. 2010a. The evolution and ecology of masquerade. *Biol J Linn Soc*. 99:1–8.
- Skelhorn J, Rowland HM, Speed MP, Ruxton GD. 2010b. Masquerade: camouflage without crypsis. *Science*. 327:51.
- Skelhorn J, Ruxton GD. 2013. Size-dependent microhabitat selection by masquerading prey. *Behav Ecol*. 24:89–97.
- Srygley RB. 2004. The aerodynamic costs of warning signals in palatable mimetic butterflies and their distasteful models. *Proc Sci Biol*. 271:589–594.
- Srygley RB, Ellington CP. 1999. Discrimination of flying mimetic, passion vine butterflies *Heliconius*. *Proc Sci Biol*. 266:2137–2140.
- Umbers KDL, Lehtonen J, Mappes J. 2015. Deimatic displays. *Curr Biol*. 25:R58–R59.
- Vallin A, Jakobsson S, Lind J, Wiklund C. 2005. Prey survival by predator intimidation: an experimental study of peacock butterfly defence against blue tits. *Proc Biol Sci*. 272:1203–1207.
- Valkonen JK, Nokelainen O, Mappes J. 2011. Antipredatory function of head shape for vipers and their mimics. *PLoS One*. 6:e22272.
- Weismann A. 1882. Studies in the theory of decent. London: Sampson Low, Marston, Searle, & Rivington. Translated by Meldola R.