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The effect of distastefulness and conspicuous coloration on the post-attack rejection behaviour of predators and survival of prey

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Aposematic insects use bright colours and/or distinct markings to advertise their toxins to potential predators. When toxins are bitter-tasting and detectable upon attack, birds are able to use taste when making decisions about whether or not to eat defended prey. Taste-rejection behaviour, when birds taste but do not ingest a prey item, is often assumed to increase the survival of defended prey, yet few empirical studies have investigated the post-attack survival rates of live defended insects. We used naïve domestic chicks (*Gallus gallus domesticus*) foraging on live waxmoth larvae (*Galleria mellonella*) in a laboratory setting, where conspicuousness and distastefulness could be controlled and manipulated to investigate the effects of taste-rejection behaviour, as well as the associated handling behaviour, on post-attack survival of prey. We found that being distasteful increased the probability of being rejected by naïve chicks, and taste-rejection behaviour tended to be more frequent when distasteful prey were conspicuous compared with when they were cryptic. Conspicuous coloration also appeared to affect predators' assessment of prey distastefulness, with past experience strongly influencing the probability that conspicuous (but not cryptic) prey were rejected. However, in contrast to previous findings, there was no evidence that either distastefulness or conspicuousness altered how predators handled the prey before making a decision about whether or not to eat it, in any way that enhanced prey survival post-attack. Therefore, taste-rejection behaviour appears to be a useful measure of prey survival. Our results provide novel insights into the potential importance of signal conspicuousness for prey populations with variable defences, and highlight the need to consider the role of taste-rejection behaviour in mimicry dynamics. © 2016 The Authors. *Biological Journal of the Linnean Society* published by John Wiley & Sons Ltd on behalf of Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, **00**, 000–000.

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INTRODUCTION

Insects display a diverse range of defence mechanisms, including adaptations to avoid being detected or caught by predators (Cott, 1940; Cuthill *et al.*, 2005), as well as physical and chemical defences to deter ingestion if discovered (Atkins, 1980; Bowers, 1992; Cott, 1940; Eisner & Meinwald, 1966; Friedlander, 1976; Guilford, 1988; Hauglund *et al.*, 2006). Species that use chemical defences are often brightly coloured, or have other conspicuous signals, to advertise their unpalatability to potential predators; a mode of defence referred to as 'aposematism' (Atkins, 1980; Cott, 1940; Friedlander, 1976; Guilford, 1988; Mappes *et al.*, 2005; Poulton, 1890; Rowe & Halpin,

2013). Conspicuous coloration has been shown to be advantageous in reducing attack rates on defended prey, with naïve predators learning to avoid aposematic prey and remember to avoid them for longer compared with cryptically coloured prey (e.g. Gittleman & Harvey, 1980; Guilford & Dawkins, 1991; Kaplan & Rogers, 2001; Krebs *et al.*, 1996; Roper & Wistow, 1986).

However, conspicuous coloration can also change the post-attack behaviour of predators, and specifically, can increase the probability that a distasteful prey item is released. Many aposematic insects produce externally detectable bitter-tasting chemicals (Nishida, 2002), and predators can reject prey post-attack on the basis of their distastefulness (Gamberale-Stille & Guilford, 2004; Halpin, Skelhorn & Rowe, 2008a,b; Sillén-Tullberg, 1985; Skelhorn &

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Rowe, 2006a,d; Wiklund & Järvi, 1982), particularly when they are conspicuous compared with cryptic (Halpin *et al.*, 2008a,b). Whilst these experiments suggest a selective advantage to distasteful prey having aposematic coloration, they have mostly used artificial prey (chick crumbs), and cannot measure how the process of being tasted and rejected, and the handling behaviour involved, affects the post-attack survival of live prey. Indeed, very few studies have investigated the post-attack survival of live defended insects (see Järvi *et al.*, 1981; Sillén-Tullberg, 1985; Wiklund & Järvi, 1982), and out of these, only one has looked specifically at the survival benefits of being conspicuous compared with being cryptic (Sillén-Tullberg, 1985). Sillén-Tullberg (1985) found that great tits (*Parus major*) taste-rejected both conspicuous (red) and cryptic (grey) forms of a distasteful seed bug (*Lygaeus equestris*) after attacking them, but that the cryptic form was less likely to survive once rejected. It was suggested that the difference in survival was due to birds being more cautious when attacking the aposematic morph, and thus handled this prey type more gently than the cryptic prey prior to making a decision about whether to eat the prey or reject it (Sillén-Tullberg, 1985). However, alternative explanations exist. It is possible that the aposematic morph was more resilient to being handled than the cryptic morph (Cott, 1940), as is known to be the case in some butterfly species (e.g. Carpenter, 1942; DeVries, 2002). The findings may also have been due to differences in colour rather than conspicuousness per se, as the birds may have had an unlearned bias against red prey and handled them more cautiously (Exnerova *et al.*, 2006; Roper & Cook, 1989; Roper & Marples, 1996; Rowe & Guilford, 1996), which might also have been exacerbated by the bitter taste of the insects (Rowe & Skelhorn, 2005). There may also have been differences between the two seed bug morphs which were not obvious to the experimenter but that were detectable to the birds, for example, in their texture, odour or taste. Therefore, currently we do not know if avian predators handle conspicuous and cryptic prey differently when they are distasteful, or whether conspicuousness per se affects the post-attack survival of live prey.

Since learning and memory play a major part in the foraging decisions of birds, prey coloration and distastefulness probably both influence how birds forage on aposematic prey based on their past experience. This will be particularly relevant in populations where there is variability in chemical defences (e.g. Brower *et al.*, 1970; Moranz & Brower, 1998; Skelhorn & Rowe, 2006b,c, 2007). In the case of mimicry complexes, for example, where different prey species share the same colour patterns but may be unequally defended (Joron & Mallet, 1998; Lindström *et al.*, 1997; Rettenmeyer, 1970), prey may be distinguishable on the basis of their defence where defences are externally detectable; birds, and other predators, could use taste to discriminate between unequally toxic prey and select those that are less defended (Halpin & Rowe, 2010; Skelhorn & Rowe, 2010). Whilst there have been studies of how previous experience with prey of a mimicry complex affects future foraging decisions based on shared coloration (e.g. Brower *et al.*, 1964, 1968; Lindström *et al.*, 2006; Speed *et al.*, 2000), we do not know how previous experience might influence the handling or taste-rejection behaviour of predators, and in turn the survival of prey in future encounters (Holen, 2013). These predatory behaviours could have a significant impact on mimicry dynamics, and this is therefore a knowledge gap that needs to be filled. This experiment used naïve domestic chicks (*Gallus gallus domesticus*) foraging on live waxmoth larvae (*Galleria mellonella*) in a laboratory setting. Waxmoth larvae are an attractive food for chicks, and we were able to carefully control and manipulate their conspicuousness and distastefulness. We first tested whether or not prey conspicuousness altered the way in which avian predators handled prey after attacking them, and the likelihood that they would reject a prey after attacking and tasting it, and if so, how this influenced prey survival. We subsequently also tested whether the conspicuousness of prey affected birds' foraging behaviour when faced with a visually similar prey in future.

MATERIALS AND METHODS

EXPERIMENTAL SUBJECTS AND HOUSING

Fifty-six domestic chicks (*Gallus gallus domesticus*) of mixed sex were used as experimental subjects, and eight were used as buddy chicks. All chicks were hatched in the laboratory and housed in cages measuring $100 \times 50 \times 50$ cm. They were maintained at a room temperature of 25°C and kept on a constant 14 L:10 D cycle, using fluorescent lights with no UV component. Water was available ad libitum, as were unmanipulated (brown) chick starter crumbs, except during training and experimental periods when food deprivation was necessary. All chicks were marked with non-toxic child-friendly marker pens and weighed each day for chick welfare purposes. The experiment was carried out in accordance with ASAB and Home Office guidelines for animal research. Chicks were donated to free-range farms at the end of the experiment.

LIVE PREY

For this experiment we required live prey that could be manipulated to be either conspicuous or cryptic against the background, and either distasteful or undefended. Live waxmoth larvae (waxworms) are completely palatable and readily eaten by chicks (pers. obs.). We made waxworms distasteful by coating them with a Bitrex solution (1 drop in 100 mL water), which is non-toxic but tastes bitter to birds (Skelhorn & Rowe, 2009), or left them undefended by coating them with water. Each solution was applied to the waxworms using small paintbrushes immediately before they were placed in the experimental arena. The waxworms were also pale in colour making it easy to manipulate their coloration with either green or purple non-toxic child-friendly pens. Each prey was coloured in the same way, with four pen strokes being added to each waxworm's dorsal surface and sides, to ensure that all prey were uniformly coloured.

EXPERIMENTAL ARENA

The experimental arena was a cage identical to the ones used to house the chicks. An area measuring $25 \times 50 \times 50$ cm was fenced off from the rest of the arena using wire mesh, to form the buddy area, which contained two buddy chicks during training and experimental trials. Buddy chicks were in constant view of chicks in the experimental area to prevent them from becoming potentially stressed from isolation. Buddy chicks had food and water available to them at all times, and were replaced every three trials from a pool of non-experimental birds. The floor of the entire arena was covered with laminated paper, which was coloured either purple or green, using the same non-toxic pens that were used to colour the live prey.

TRAINING

Training trials took place on the first 7 days after the chicks hatched. These trials ensured that the chicks were familiar with the experimental arena and eating out of Petri dishes, and also that they had experience of eating live prey prior to the experiment. In alternating trials, experimental chicks were trained on a white background (making brown crumbs and mealworms relatively conspicuous), or a brown background (making the brown crumbs and mealworms relatively cryptic). This was to ensure that all chicks had equal experience of both relatively cryptic and conspicuous prey prior to the experimental trials.

On Days 1–3 post-hatch chicks were allowed to forage on starter crumbs presented in Petri dishes. On Day 1, chicks received two trials where they were put into the experimental arena in groups of 3 for 10 minutes. On Day 2, they were put in the arena in groups of three for one trial, then in pairs for two trials. On Day 3, and on all of the following training days, the chicks were food-deprived for one hour before being put into the experimental arena. They then received one trial where they were placed into the arena in pairs, followed by three trials throughout the day where they spent 5 minutes foraging alone in the experimental arena.

On Days 4–7, live mealworms were placed in Petri dishes on the floor of the experimental arena. On Day 4, two 'mini-mealworms' (13–18 mm in length) were placed in each of three Petri dishes and chicks were put in the arena in groups of three for three trials. On Day 5, two mini-mealworms were placed in each of two dishes and chicks were put in the arena in pairs for two trials. On Days 6 and 7, two 'regular mealworms' (20–25 mm in length) were placed in two Petri dishes and chicks were put in the arena in pairs for three trials on Day 6 and for one trial on Day 7. The chicks were also placed in the arena individually for three trials on Day 7, with one mealworm in each of the two dishes. At the end of the training period, all chicks were readily eating live prey from the Petri dishes.

EXPERIMENTAL TRIALS

Following training, we conducted one experimental trial per day for two consecutive days. In these trials, which we will refer to as Day 1 and Day 2 from this point onwards, two Petri dishes were placed approximately 10 cm away from the buddy area, and 12 cm apart, and each contained a single waxworm. All birds received a green and a purple waxworm, but we manipulated the relative conspicuousness of the two waxworms by presenting them on either a purple or a green background. Although we gave birds two waxworms, we ensured that they could attack only one of them by placing a transparent lid over the top of one of the dishes. We used this design in order that each chick could make a visual comparison between a cryptic and a conspicuous waxworm, but it could only taste one prey type, thus ensuring that we collected the same number of data points for each prey type.

The waxworm that was uncovered and accessible to the chick was one of four types: cryptic undefended, cryptic distasteful, conspicuous undefended or conspicuous distasteful. On Day 1, chicks were randomly assigned to receive one of these prey types, and thus there were four experimental groups ($N = 14$, with similar numbers of males and females in each group), named after the prey type given on

Day 1 (Cryptic Undefended, Cryptic Distasteful, Conspicuous Undefended and Conspicuous Distasteful). We also ensured that within each group, half the chicks received a green waxworm and the other half received a purple waxworm, and changed the background colour accordingly. Therefore conspicuousness was independent of colour per se.

Each chick was food-deprived for approximately one hour before being placed in the arena, where it remained until it had attacked and/or eaten the waxworm, but for no longer than 5 min. After the trial, any remaining waxworm that had not been attacked, or that had been attacked then rejected, was kept in its Petri dish, with a piece of wet paper to prevent the larvae from dehydrating, to enable us to record post-attack survival in the following 48 h. Notably, any prey that were attacked but not eaten will be referred to simply as 'rejected' from this point onwards.

On Day 2 of the experimental trials, the chicks received an identical presentation of the waxworms, but now the distastefulness of the uncovered waxworm was reversed. This meant that chicks that were given a distasteful waxworm on Day 1 were given an undefended waxworm on Day 2, and chicks that were given a undefended waxworm on Day 1 were given a distasteful waxworm on Day 2. The waxworms and laminated floors were the same colours on both days.

RESULTS

We used Fisher's exact test to analyse the data since this gives a more accurate analysis of categorical data than the chi-squared test when sample sizes are relatively small, and is also appropriate for those comparisons when the data are unbalanced between groups (Fisher, 1954).

EXPERIMENTAL DAY 1: ATTACK BEHAVIOUR OF INEXPERIENCED PREDATORS

On Day 1, the chicks attacked the cryptic and the conspicuous waxworms with equal probability ($P > 0.05$). However, the mortality of prey (the number eaten plus those that died after being rejected) differed depending on whether they were distasteful or not: the mortality of distasteful prey was significantly lower than that of undefended prey ($P = 0.035$; see Table 1A). This appeared to be due to whether or not a prey was rejected rather than the ways in which predators handled the prey prior to rejection: the distasteful prey had an overall higher probability of being taste-rejected than the undefended prey ($P = 0.032$; see Table 1A), but there was no difference in the proportions of distasteful and undefended prey that survived after being rejected ($P > 0.05$; see Table 1A). Overall, these data confirmed that tasting bitter was an effective defence for the prey as the birds were more likely to reject a distasteful prey than an undefended one.

Whilst the taste of prey did affect rejection rates, the conspicuousness of prey did not. Amongst the undefended prey, the conspicuous and cryptic waxworms were rejected similarly ($P > 0.05$; see Table 1A). There was a tendency for the distasteful prey to be rejected more when they were conspicuous than when they were cryptic but this was not significant ($P = 0.078$; see Table 1A). There was also no significant difference in the survival of rejected conspicuous and cryptic distasteful prey ($P > 0.05$; see Table 1A).

These results suggest that being distasteful or conspicuous did not affect the birds' handling behaviour of the prey in any way that affected post-attack survival. However, we also kept all the waxworms that were not attacked by chicks (six conspicuous and six

Table 1. Numbers of prey that were attacked, eaten, and rejected post-attack, along with rejection- and mortality rates for each of the four prey types on (A) Day 1 and on (B) Day 2. Notably, on Day 2 prey were visually the same as on Day 1, but undefended prey were now faced with predators that had experienced a distasteful prey on Day 1 and *vice versa*.

Prey type	Attacked	Eaten	Rejected Died	Rejected Survived	Rejection rate (%)	Mortality rate (%)
(A)						
Cryptic undefended	9	6	1	2	33	78
Cryptic distasteful	13	6	1	6	54	54
Conspicuous undefended	11	7	1	3	36	73
Conspicuous distasteful	11	1	2	8	91	27
(B)						
Cryptic undefended	8	5	2	1	38	88
Cryptic distasteful	7	4	0	3	43	57
Conspicuous undefended	7	1	0	6	86	14
Conspicuous distasteful	9	8	1	0	11	100

cryptic prey). Unlike the rejected waxworms, all these waxworms survived in the 48 h following the trial (100% survival). Therefore, there does appear to be a potential cost of being attacked even if rejected.

EXPERIMENTAL DAY 2: ATTACK BEHAVIOUR OF EXPERIENCED PREDATORS

On Day 2, whilst the coloration of the covered and uncovered waxworms were the same as on Day 1, the distastefulness of the uncovered waxworm was now reversed. Only experienced chicks, that is, those that had attacked the waxworm on Day 1, were tested on Day 2. We predicted that chicks' experiences on Day 1 would influence their attack rates on Day 2. However, there were no significant differences in the proportion of prey attacked on Day 1 and Day 2 for any of the four prey types ($P > 0.05$ for all comparisons; see Table 1). So, experience with a Bitrex-coated waxworm on Day 1 did not reduce the probability of attack on Day 2. However, when we analysed the rejection rates of each prey type on Day 1, and compared them with those on Day 2 we found that prior experience did have a surprising effect on the taste-rejection behaviour of the birds.

Conspicuous distasteful waxworms had a lower probability of being rejected on Day 2 when given to chicks that had previously experienced a conspicuous undefended waxworm, compared with when they were presented to naïve chicks on Day 1 ($P < 0.01$; see Fig. 1). When conspicuous undefended prey were given to chicks that had previously experienced a conspicuous distasteful prey, there was a tendency for them to be rejected more than when they were given to naïve chicks, but this was not significant ($P = 0.06$; see Fig. 1). Intriguingly, there were no differences between Day 1 and Day 2 in the rejection of undefended cryptic prey ($P > 0.05$) or distasteful cryptic prey ($P > 0.05$; see Fig. 1).

Similarly to Day 1, the survival of rejected prey after 48 h was high and there was no difference in the survival of any of the prey types between the 2 days (post-rejection survival on Day 2: conspicuous undefended (6/6), conspicuous distasteful (0/1), cryptic undefended (1/3), cryptic distasteful (3/3); $P > 0.5$ for all comparisons; see Table 1). Any waxworms that were not attacked also survived ($N = 13$).

DISCUSSION

As found in previous experiments, distastefulness can be an effective deterrent to naive avian predators (Gamberale-Stille & Guilford, 2004; Halpin & Rowe, 2010; Halpin *et al.*, 2008a,b; Sillén-Tullberg,
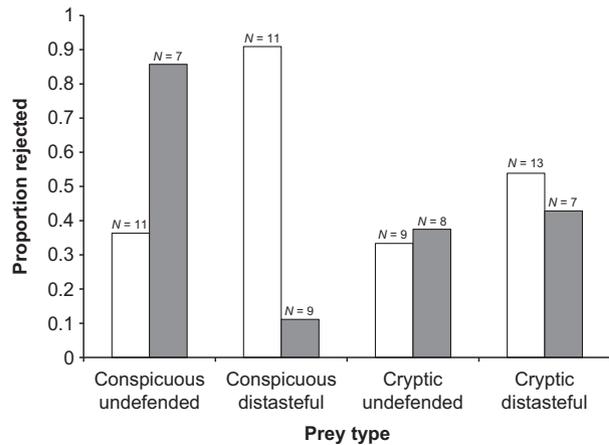

Figure 1. Proportion of attacked prey for each of the four prey types that were rejected on Day 1 (white bars), and on Day 2 (grey bars). Note that on Day 2, the appearance of the prey did not change, but undefended prey were now faced with predators that had experienced a distasteful prey on Day 1 and *vice versa*.

1985; Skelhorn & Rowe, 2006a,d; but see Skelhorn & Rowe, 2009; Wiklund & Järvi, 1982). The data from Day 1 showed that being distasteful increased the probability of being rejected by naïve chicks, and demonstrates the potential for individual survival advantages to possessing externally detectable defences (Leimar *et al.*, 1986; Sillén-Tullberg, 1985). We have previously found that naïve predators will reject distasteful prey at a higher rate when they are conspicuous compared with when they are cryptic (Halpin *et al.*, 2008a,b), which supports the idea that predators may 'go slow' and be more attentive to the distastefulness of conspicuous compared with cryptic prey (Guilford, 1994). This would give a selective advantage for being conspicuous once distastefulness has evolved. Here, however, although there was a tendency for distasteful prey to be rejected more often when conspicuous compared with cryptic, there was no significant difference between the two. It is possible that may have been due to the reduced sample size, resulting from not all chicks attacking the waxworms, since the tendency for distasteful prey to be rejected more frequently when they are conspicuous compared with cryptic is consistent with findings in previous studies (Halpin *et al.*, 2008a,b).

Of course, rejection rates may not reliably measure survival rates, and it is therefore important to measure the post-attack survival of prey to fully understand selection pressures on prey defences. For the first time, using controlled laboratory manipulations, we were able to test whether conspicuousness affected prey handling and post-attack survival of prey. On Day 1, the post-attack survival rates of all

four prey types remained high (between 71% and 86%), and we found no differences in the survival rates in the 48 h following attack. Therefore, we found no evidence for conspicuousness or distastefulness altering the attack behaviour of naïve predators in any way that enhanced the survival of rejected prey. This is in contrast to Sillén-Tullberg's (1985) previous study, which showed higher survival in a conspicuous red seed bug compared with a cryptic grey morph. However, there are several differences between our two studies. Importantly, neither conspicuousness nor distastefulness were controlled in Sillén-Tullberg's original study, since this used natural variation in morphology and defence strategy within a species. Although it is clearly valuable to study natural prey systems, we cannot be sure that differences in predator behaviour were not affected by other factors, for example variability in prey toxicity (e.g. Exnerova *et al.*, 2006; Smith, 1975). Therefore, perhaps rather than the predators' handling behaviour affecting survival, the aposematic morphs may have been more defended and resilient to attack than cryptic conspecifics (Carpenter, 1941; DeVries, 2002). Certainly, our data do not support the idea that conspicuousness affects how cautious or voracious predators are when they are attacking and handling prey (but see Skelhorn & Ruxton, 2006).

Another possible reason that our findings differ is that there could be differences in the foraging behaviour of great tits and chickens. Domestic chicks and great tits are both widely used as predators in research investigating the evolution of prey defences, and have been important in demonstrating general principles of how predators use warning signals to learn about and reduce their attack rates on defended and aposematic prey (e.g. Alatalo & Mappes, 1996; Halpin *et al.*, 2008a; Lindström *et al.*, 2001). However, they can also exhibit differences in their foraging behaviour. For example, aposematic prey are less likely to survive being attacked by domestic chicks when they are aggregated compared with solitary prey (Skelhorn & Ruxton, 2006), whilst the reverse has been reported for gregarious and solitary aposematic prey faced with great tits (Mappes & Alatalo, 1997). This could be due to species differences, or simply reflect the past foraging of the birds: notably, hand-reared great tits behave differently to wild-caught ones (Exnerova *et al.*, 2006). Our results serve to highlight the need to test different predator species in order to get a broader understanding of the varying selection pressures that prey may be faced with.

Similarly to Sillén-Tullberg's (1985) experimental design, we presented our birds with two prey simultaneously. However our designs differed in that she presented each bird with either a cryptic or conspicuous prey, alongside a familiar edible prey item that was conspicuous against the background, whilst we consistently presented a cryptic and a conspicuous prey to each bird, although only one was obtainable, in order to ensure that all birds had the same visual experience. The way in which prey are presented visually, can affect findings; for instance, predators have been shown to attack aposematic prey more forcefully when they are aggregated compared with solitary (Skelhorn & Ruxton, 2006). So, it is possible that the way in which the chicks saw both prey in our experiment could have influenced their foraging behaviour in some way. However we actually know very little about how the way in which prey are viewed in natural systems influences predator foraging decisions, and future experiments investigating whether foraging behaviour towards cryptic and conspicuous prey differs when these are presented together compared with separately would be informative. Nevertheless, we do know that there are prey populations existing in nature where some individuals are cryptic whilst others are conspicuous (e.g. Andrés & Rivera, 2001; Sword, 1999; Willink *et al.*, 2013), and our design reflects a scenario where predators may see two phenotypes of the same prey species.

However, in comparing rejection behaviour between our two experimental days, we did find that conspicuousness affected how birds tasted and rejected prey across multiple encounters. Birds rejected cryptic prey on Day 2 according to their distastefulness rather than using their previous experience on Day 1. In contrast, chicks that were given conspicuous prey rejected them with a similar probability on Day 2 as on Day 1, seemingly ignoring the change in distastefulness. This intriguing result suggests that a bird's response to a prey's distastefulness is significantly affected by its past experience but only when the prey are conspicuous and not when they are cryptic. One possibility for why this difference occurs is that by being more attentive to the level of distastefulness of novel conspicuous prey on Day 1, birds form stronger memories which impact their expectations in future encounters, and their judgements and decisions to reject prey on Day 2. Conspicuousness certainly does affect learning and taste-rejection behaviour (e.g. Gittleman & Harvey, 1980; Halpin *et al.*, 2008a,b), so it is perhaps not surprising to find another way in which predators' behaviour is affected by prey coloration. There is currently much debate among psychophysicists about the impact of coloration on human taste perception (see Spence *et al.*, 2009 for a recent review), and we should not be surprised to find 'multimodal' interactions affecting foraging decisions in other animals (Rowe, 1999; Rowe & Halpin, 2013). However, our

data cannot identify the specific perceptual or cognitive mechanisms underlying this behaviour, which will require further research.

Regardless of the exact mechanism, this behaviour has potential implications for populations of prey that share the same conspicuous warning pattern, but vary in their level of defence (Brower *et al.*, 1970; Guilford, 1994; Moranz & Brower, 1998). For example, in Batesian mimicry, undefended mimics may benefit from being tasted and rejected if predators have previously encountered models (see also Skelhorn & Rowe, 2006a, 2007). However, if palatable mimics are encountered before distasteful models, this could be extremely costly for defended individuals. Although previous theoretical and empirical studies of mimicry have mainly focussed on the role of avoidance learning in mimicry dynamics (Gavrilets & Hastings, 1998; Lindström *et al.*, 1997; Simmons & Weller, 2002; Speed, 1999; Turner, 1987), our data suggest that taste-rejection behaviour could also be important in fully understanding the selection pressures involved (see also Holen, 2013).

To conclude, this experiment demonstrates the importance of distastefulness and conspicuousness on the rejection behaviour of avian predators, but finds no effect of either on post-attack survival rates of prey. Therefore, it seems likely that previous data suggesting that post-attack survival was better for conspicuous than for cryptic prey may be due to differences in prey morphology and not due to differences in handling behaviour by predators. Our findings provide novel insights into the potential importance of the conspicuousness of signals in the evolution of mimicry, and suggest we need to fully consider the role of taste-rejection behaviour in the evolutionary dynamics of prey defences.

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