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Unlearned responses of chicks, *Gallus gallus domesticus*, towards aposematic insect-like stimuli

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Many predators avoid aposematic prey that possess conspicuous warning displays. This aversion can include innate and learned components, either of which could be exploited by profitable Batesian mimics that resemble aposematic prey. The perceptual bias hypothesis proposes that predators' unlearned aversions may not correspond exactly with the patterns of aposematic prey, and that inaccurate Batesian mimics gain a fitness advantage by maximizing the unlearned aversion of their predators rather than their similarity to the model. This would provide a particular advantage when faced with naïve predators that have not yet had the opportunity to learn an association between the warning patterns and defences of the prey they encounter. We tested this hypothesis in the context of hoverflies that mimic stinging Hymenoptera: do naïve predators avoid wasp-like stimuli, and, if so, is this bias stronger when encountering inaccurate mimics? We presented domestic chicks, *Gallus gallus domesticus*, with arrays of 3D-printed stimuli each of which concealed a mealworm, *Tenebrio molitor.* Each array included control nonmimetic flies and alternative warning-coloured stimuli drawn from a set of wasps and honey bees (models), hoverflies (mimics) and artificially generated intermediates. The chicks had never encountered insect-like prey or stimuli (other than mealworms) prior to these trials. We found no difference in the order in which the stimuli were attacked in different treatments, but did find that chicks were slightly slower to open dishes with aposematic as opposed to control stimuli. Our results do not provide strong support for the perceptual bias hypothesis in the case of hoverflies, but we do find evidence of variation in the unlearned response towards insect stimuli dependent on appearance. These differences illustrate the importance of defensive signals, both honest and deceptive, in influencing predator behaviour even from the first encounter.

Many predators are hesitant to attack aposematic prey with conspicuous warning displays (Poulton, 1890). This behaviour often provides a fitness advantage to the predator due to the association between warning displays and prey defence (Ruxton et al., 2004). Even naïve predators have unlearned biases in their selection of prey that can promote avoidance of patterns commonly used by aposematic prey (Schuler & Hesse, 1985; S. M. Smith, 1975; Wiklund & Järvi, 1982), and these initial biases can then be refined (Aronsson & Gamberale-Stille, 2012; Fay et al., 2024; Halpin et al., 2008; Taylor et al., 2015) through direct learning from encounters.

Aversion to aposematic prey, whether innate or learned, is of mutual benefit to predators and aposematic prey, but it can also be exploited by harmless Batesian mimics (H. W. Bates, 1862; Hetz & Slobodchikoff, 1988; Lindström et al., 1997). If predator avoidance of aposematic patterns is largely due to learning, then we usually predict that the protection a Batesian mimic receives from predation will improve with increasing similarity to the aposematic model (Getty, 1985; but see Johnstone, 2002; Oaten et al., 1975). However, if predators have strong unlearned biases leading to avoidance of certain colours and patterns, then to gain optimal levels of protection, a Batesian mimic could benefit from displaying a pattern that corresponds to the peak of those biases. This optimal pattern does not necessarily match the phenotype of the model; although the model could similarly benefit from exploiting any bias, it may be constrained by different selective pressures from the mimic, such as trade-offs with other functions of colour

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pattern. The exploitation of predators' unlearned biases has been referred to as the ‘perceptual exploitation’ (Kikuchi & Pfennig, 2013) or ‘perceptual bias’ (McLean et al., 2019) hypothesis. Evidence for exploitation of unlearned biases by mimetic prey is currently lacking, but examples are known from other forms of deceptive mimicry (O'Hanlon et al., 2014; Vereecken & Schiestl, 2008). If Batesian mimics have evolved in appearance to exploit predator biases rather than to be indistinguishable from their models, this could help to explain the persistence of inaccurate mimicry, a long-standing puzzle in evolutionary ecology (Dittrich et al., 1993; Gilbert, 2005; Kikuchi & Pfennig, 2013; Taylor et al., 2025).

Naïve avian predators have been shown to avoid prey that possess several pattern characteristics often found in aposematic prey, such as yellow and black stripes (Lindström et al., 1999; Roper & Cook, 1989; Schuler & Hesse, 1985), red and yellow rings (S. M. Smith, 1975, 1977), high levels of achromatic contrast (Halpin et al., 2020) or solid yellow or red coloration (Gamberale-Stille & Tullberg, 2001; Protti-Sánchez et al., 2023; Rowe & Guilford, 1996). However, results are not consistent across experiments and unlearned biases appear to be highly context dependent (Fischer et al., 1975; Roper & Marples, 1997). For example, biases can become more evident when associated with particular odours (Jetz et al., 2001; Rowe & Guilford, 1996), bitter-tasting toxins (Rowe & Skelhorn, 2005; Skelhorn et al., 2008) or shapes (Gamberale-Stille & Tullberg, 2001).

It has been suggested that unlearned avoidance is limited to patterns typical of the most dangerous types of prey, such as coral snakes (genus *Micrurus*), where the cost of learning through direct experience would be prohibitively high (Brodie & Brodie, 1999). When dealing with prey that impose a lower fitness cost, a predator may gain from adopting a more exploratory approach that improves knowledge of the relative costs and benefits of a range of possible prey (Kikuchi & Sherratt, 2015). However, experimental evidence suggests that unlearned avoidance can apply more widely. While some examples of patterns innately avoided by birds in experiments have clear similarity to snakes (e.g. Schuler & Hesse, 1985; S. M. Smith, 1975), others do not have an obvious resemblance to highly dangerous prey (e.g. Gamberale-Stille & Tullberg, 2001; Halpin et al., 2020).

Given the observed variability in the presence and extent of unlearned bias depending on context, we have limited ability to generalize across study systems, and conducting experiments with realistic stimuli is of great importance. To manipulate visual phenotypes in a controlled manner, studies of visual preference often use entirely artificial prey (S. M. Smith, 1975), or simple manipulations of real organisms such as painting (Exnerová et al., 2007) or covering (Veselý et al., 2013) colour patterns. Increased realism is possible through 3D printing, allowing manipulation of some stimulus features while keeping others true to life (Plate & Rößler, 2024; Policha et al., 2016; Scharf et al., 2019; Taylor et al., 2025). Here, we use scanned 3D images of prey to produce both realistic replicas and artificial intermediates that vary in their levels of mimetic accuracy (Taylor et al., 2025).

Hoverflies (Diptera: Syrphidae) are a classic study system for Batesian mimicry, being a diverse and abundant taxonomic group that includes both nonmimics and mimics of Hymenoptera with varying degrees of mimetic accuracy (Gilbert, 2005; Leavey et al., 2021; Penney et al., 2012). Birds (Dittrich et al., 1993) and humans (Taylor et al., 2017) will, in experiments, learn to avoid wasps and generalize this avoidance to some hoverflies. Wild predators including birds (Dlusski, 1984), crab spiders (Morris & Reader, 2016) and dragonflies (Rashed et al., 2005) have been found to show aversion to hoverflies or hoverfly-like patterns. However, there is little evidence as to whether unlearned biases contribute to aversion in any of these cases, and, if so, which mimics might receive the greatest protection from naïve predators. Elucidating any such unlearned preferences will reveal whether inaccuracy in mimetic hoverflies could have evolved to take advantage of predator biases, and will also serve as an important baseline against which the results of learning experiments involving the same predators and prey can be compared.

We tested the unconditioned responses of naïve domestic chicks, *Gallus gallus domesticus*, towards a range of wasp-like and hoverfly-like stimuli. Chicks are frequently used as model predators when studying unlearned visual biases (e.g. Fischer et al., 1975; Protti-Sánchez et al., 2023; Roper & Marples, 1997) because, being precocial, their early life experience can be closely controlled to minimize any effect of direct learning, or social learning from experienced conspecifics, on foraging behaviour. Their closest wild relatives have a generalist diet including insects (Klasing, 2005), and would be expected to encounter a range of aposematic, mimetic and nonmimetic prey.

Chicks were presented with an array of eight probe stimuli (each chick receiving a single type from one of eight treatments) and eight control stimuli (an alternative, nonmimetic fly stimulus). Treatments included stimuli based on three species of Hymenoptera (in nature, aposematic models), three mimetic species of hoverfly and two novel intermediates between pairs of models and mimics. The intermediates represented mimics that are more accurate than the extant hoverflies on which they were based, and were included to allow us to explore the potential effects of perceptual bias on hypothetical phenotypes of higher mimetic accuracy than our hoverfly study species.

Each stimulus had to be ‘attacked’ (lifted off a dish) to obtain a mealworm reward that the chicks had learned to associate with the dishes. We assumed stimuli that were attacked later in the sequence, and those that took longer to be attacked, received greater protection from predation.

Our experiment allows us to distinguish four alternative hypotheses (H0—H3) relating to the chicks' unlearned biases.

H0: chicks are not biased towards or against any of our presented stimuli, which all receive equivalent levels of protection.

H1: chicks are biased against attacking the probe stimuli, all of which have some form of aposematic coloration, but with no biases among the different treatments.

H2: chicks are most strongly biased against the hymenopteran stimuli, which would limit the need for costly mistakes when learning in the wild.

H3: chicks are most strongly biased against the hoverfly stimuli. This would support the perceptual bias hypothesis that mimetic inaccuracy is (at least partly) adaptive in eliciting maximum aversive bias from predators.

In addition to these main hypotheses, our experiment also allows us to test for other differences between treatments, such as whether predators show stronger unlearned biases against stimuli in the wasp mimicry complex than those in the honey bee mimicry complex.

METHODS

Stimulus Design

Experimental stimuli were based on real wasp (Hymenoptera) and fly (Diptera) taxa chosen to represent different levels of mimetic accuracy, as well as some novel stimuli created using combinations of traits from two different specimens (Fig. 1). To generate intraspecific variation, we used two or three different individuals from each taxon to produce separate stimuli.

Treatment	Species	Category and description	*N* variants	*N* chicks	Image
Control, included in all treatments	*Mesembrina meridiana*	Nonmimic: fly expected to elicit no avoidance	3	75	
Solitary wasp	*Argogorytes mystaceus*	Model: aversive hymenopteran with black and yellow stripes	3	9	
Common wasp	*Vespula vulgaris*	Model: common aversive hymenopteran	3	10	
Wasp mimic intermediate	*50% V. vulgaris, 50% Syrphus ribesii*	Intermediate: novel mimetic stimulus with increased accuracy compared with *S. ribesii*	3	9	
Wasp mimic *Syrphus*	*Syrphus ribesii*	Mimic: common hoverfly thought to be Batesian mimic of *V. vulgaris*	3	9	
Wasp mimic *Chrysotoxum*	*Chrysotoxum arcuatum* and *C. verralli*	Mimic: hoverfly, accurate Batesian mimic of *V. vulgaris*	2 + 1	10	
Honey bee	*Apis mellifera*	Model: Common aversive hymenopteran	2	10	
Bee mimic intermediate	*50% A. mellifera, 50% Eristalis tenax*	Intermediate: novel mimetic stimulus with increased accuracy compared with *E. tenax*	2	9	
Bee mimic *Eristalis*	*Eristalis tenax*	Mimic: hoverfly, accurate Batesian mimic of *A. mellifera*	2	9	

Figure 1. Treatments and stimuli used in the experiment. Note that the two species of *Chrysotoxum* (wasp mimics) are visually highly similar and so were grouped together under the same treatment.

Insect specimens were collected between June 2020 and August 2021 from various locations in England using a hand net. Specimens were euthanized by freezing at −18 °C for approximately 30 min. They were then pinned through the thorax and positioned into a natural-looking posture before drying for 6–24 h.

We created plastic, 3D printed, life-sized, full colour stimuli based on these specimens following methods described in detail in Taylor et al. (2025). Briefly, we obtained 3D digital images of the insect specimens via photogrammetry, using a protocol adapted from Nguyen et al. (2014).

To generate novel mimetic forms, we identified points in 3D morphological space that were equidistant between two endpoints chosen from among the real specimens. Intermediate points were calculated from separate parameterizations of shape, pattern, colour and size. All 3D meshes, including the real specimens, were processed in the same manner so that each stimulus would include comparable levels of detail. Due to difficulties in both processing and printing of thin and elongated structures, legs, wings and antennae were given simplified shapes of uniform thickness. A grey circular base was added to strengthen the legs and provide a mounting point.

We printed physical 3D representations of these digital insects on a HP Jet Fusion 580 machine at Matsuura Machinery (Coalville, U.K., https://www.matsuura.co.uk) using polyamide 12 powder (CB PA12) and colour cosmetic settings. Stimuli were then given

VaporFuse Surfacing treatment in a DyeMansion Powerfuse S (https://dyemansion.com), which created a less grainy, slightly glossier finish.

Study Organisms and Housing

Domestic chicks, *G. g. domesticus* (Ross strain; P. D. Hook Hatcheries Ltd., U.K., https://pdhook.co.uk), were acquired immediately following hatching, transported by car (2 h) and housed in a laboratory at Newcastle University. Chicks were mixed sex, but we were unable to determine individual sex noninvasively. Mean weight (± SD) on arrival was 37.8 ± 3.4 g and on the last day of the experiment was 134 ± 23.3 g. Chicks were housed communally in two nonconcurrent batches of 64 and 66 in a floor pen measuring approximately 2 m^2. The floor was covered in wood shavings and hay. Food (HPS Starter Crumb, Special Diets Services, Witham, U.K., https://sds-diets.com) was provided ad libitum in a green feeding trough as well as smaller white circular dishes, and water was provided ad libitum from free-standing drinkers with green bases. Mealworms were provided each morning in small grey food dishes attached to a grey board to familiarize the chicks with experimental equipment (see below). The pen included unpainted wooden perches for enrichment and suspended ceramic heaters. The room was kept at 25°C and with a 14:10 h light:dark cycle.

Experimental Arena

The experiments took place in an arena with white plastic lining the floor and walls, measuring 115 × 70 cm and 40 cm high, and divided into two sections of lengths 25 and 90 cm, separated by a mesh barrier such that each section was visible from the other. The first section formed a buddy area to house two buddy chicks (from a stock of eight, rotated every hour) during all sessions. Buddy chicks were never used for experimental testing, but instead ensured that experimental chicks were always able to see and hear conspecifics, to reduce stress. The larger section of the arena was the experimental area, which included, at the end closer to the buddy area, a removable 60 × 60 cm board (surfaced with a mottled grey vinyl tile). Grey opaque food dishes (4 cm diameter) with removable lids were mounted on the board at 15 cm intervals in a 4 × 4 array. A video camera (Panasonic HC-V180, https://www.panasonic.com) was positioned above the arena aimed downwards with a view of the whole experimental area, and was used to record all trials. The arena was in the same laboratory as the chicks were housed, but raised height (about 1 m) and opaque walls ensured that experimental chicks did not see the stimuli, or conspecific behaviour in the arena, prior to their trials. To view the experimental arena, see the supplementary video.

Habituation and Training Phase

The two batches of chicks were further split (randomly) into two groups, which began the experiment on consecutive days: one on the day after arrival and the other group 2 days after arrival. This staggering of start times eased time pressure on certain days, ensuring that all chicks had time during light periods before and after trials when they could feed freely. On the first day, chicks received six 2 min trials in the experimental area, foraging from 16 open dishes containing mini mealworms, *Tenebrio obscurus*. Chicks were first grouped in threes, then pairs, then individually (two trials each). Prior to the last three sessions on day 1, and all following sessions, chicks were food-deprived for 60 min to ensure motivation to forage. In these and all subsequent trials, chicks were initially released into the arena by placing them at the opposite end to the board with the dishes.

Over the course of the following 7 days, chicks received one further trial each day following the same format as above, but with the addition of opaque lids to the dishes. Initially, lids were placed adjacent to the dishes, so that mealworms were still visible and accessible. Each day, the lids were placed increasingly covering the dishes until the lids were fully on and the mealworms were completely hidden, teaching chicks to lift off a lid to obtain a mealworm. On day 5, mini mealworms were replaced with the larger yellow mealworm, *T. molitor.* While mini mealworms were easier for small chicks to handle, we wanted to maintain motivation for the rapidly growing chicks, many of which gained more than 300% in body mass during the course of the experiment. Trials continued until all mealworms had been consumed, or 10 min had elapsed, whichever was sooner.

Testing Phase

Chicks were considered to have succeeded in the training if, on the final trial, they opened all lids and consumed all mealworms within 10 min. These chicks were stratified into groups of eight according to the time taken to complete the final training trial, and within each stratum, chicks were assigned to one of the eight treatments at random (each chick being presented with an array of eight probe stimuli of a single type from that treatment, plus eight control stimuli). In this way, each treatment included chicks with approximately the same mean speed of progressing through a trial. Treatments corresponded to different probe stimuli representing a range of real model, real mimic and novel mimic stimuli (Fig. 1). Experimenters were not blind to the treatment type; however, key behavioural events (opening of dishes) were unambiguous to observe and not subject to experimenter bias.

On the day following training, these chicks completed a single testing trial, which followed the same format as training but with the addition of 3D printed stimuli on the lids of the dishes. Eight dishes had control (fly) stimuli and eight had probe stimuli matching the assigned treatment, with each set including multiple variants (see Stimulus Design, above). Stimuli were reused for multiple chicks, after spraying with 70% ethanol between trials to sterilize and remove odours. Occasionally, pecking from the chicks damaged legs, wings or antennae of the stimuli, which were then replaced with new stimuli. At the time of the trial, we recorded the order in which dishes were opened and the time taken to open all 16 dishes. Chick behaviour was scored by watching video playback of the testing trials using BORIS software (Friard & Gamba, 2016), following the ethogram in Table 1, with each behaviour also listing the dish number with which the chick was interacting. Those coding behaviour from video footage were not given details of the trial-level treatment, nor of the stimuli on each dish. It was not practical to carry out the behavioural coding entirely blind to treatment, since the stimuli are visible in the video footage, but their identity was difficult to discern at the given resolution. Note that two videos were missing due to errors with recording; therefore, for these detailed behavioural scores, sample size was slightly smaller ($N = 73$) than the trial-level data ($N = 75$). For an example video of the test phase, see Supplementary Material.

Ethical Note

Our experiment followed all U.K. Home Office guidelines and those laid out by the ASAB Ethical Committee/ABS Animal Care Committee (2024). Our protocol was approved by Newcastle University AWERB committee (project ID 966), and reporting follows the ARRIVE 2.0 guidelines. Chicks always had visual contact

Table 1
Ethogram used in scoring chick behaviour

	Behaviour	Description
Frequent	Look	Initial fixing of gaze on a particular dish, often associated with movement towards that dish
	Peck lid	A single peck at a dish lid or attached stimulus
	Remove lid	Lifting or knocking lid with beak to open a dish enough to reveal the mealworm inside
	Shake lid	Rapid side-to-side shaking of the head while holding lid in beak
	Peck worm	A single peck at a mealworm
	Shake worm	Rapid side-to-side shaking of the head while holding mealworm in beak
	Eat worm	Mealworm consumed and swallowed
	Leave	Walking away from a dish or mealworm and moving attention to another part of the arena. Used to define the endpoint of interactions with a particular dish
Rare	Retreat	Stepping away from a dish while still fixing attention on that dish (i.e. not leaving for another dish, see above)
	Foot remove lid	Knocking off lid with a foot (possibly accidently) while moving past a dish
	Bill wipe	Beak wiped against foot or part of the arena

Behaviours listed as frequent were observed in at least 80% of trials, while rare behaviours were observed at most 11 times across all trials. Frequent behaviours are listed in the order that they would appear in a typical behavioural interaction with a single dish.

with conspecifics, including with buddy chicks in the experimental arena. Food deprivation lasted 1 h (which was the minimum necessary to ensure chicks were motivated to forage), during which time chicks retained access to water ad libitum and were never kept singly. The main floor pen, food deprivation pen and experimental arena were all within the same laboratory, to minimize stress associated with handling. Chicks were weighed daily and inspected visually to monitor health; one chick, which showed low weight gain, was excluded from all experimentation to avoid it experiencing food deprivation. We aimed for $N = 10$ per treatment based on prior experience with similar experiments (e.g. Schmidt & Schaefer, 2004; Skelhorn, 2011; Skelhorn et al., 2008). Unfortunately, it was not possible to reduce sample size by presenting individual chicks with multiple treatments, since only the first would reflect unlearned behaviour. At the end of the experiment, chicks were euthanized by cervical dislocation by a trained animal technician, with death confirmed by exsanguination. Rehoming was not possible due to avian influenza restrictions in place at the time.

Live mealworms were used as rewards since previous experience has shown that chicks are more motivated to attack live prey. Flies, bees and wasps had to be euthanized before photogrammetry to ensure zero movement between photographs. Our use of 3D printed stimuli meant that instead of collecting dozens of individuals to provide replicate stimuli, only small numbers of flies and wasps ($N < 10$ for each species) were required to generate the images on which stimuli were based.

Statistical Analyses

Analysis was carried out in R version 4.4.2 (R Core Team, 2024), using generalized linear models (GLMs) and generalized linear mixed models (GLMMs; Bates et al., 2015). At the level of individual chicks, three parallel models were fitted to explain chick behaviour in the testing phase with response variables of trial duration, mean rank of probe dishes (with ‘rank’ being the ordinal position within the sequence of 16 dishes opened) and stimulus of first dish opened (control or probe). We predicted that treatments eliciting an aversive response towards the probe stimuli should have a higher mean rank for probe dishes, should lead to a longer overall trial duration and be more likely to feature the control as the first dish opened.

For all three responses, the same set of predictors was used: treatment (eight-level factor), batch (four-level factor, to allow for differences between start days and cohorts) and duration of final training trial (continuous, accounting for repeatable differences in how quickly chicks completed trials). Model families were Gaussian with a log link for trial duration, Gaussian for mean rank and binomial for first dish (probe or control). Model fit was assessed visually for normality of residuals and homoskedasticity using residual plots. The contribution of the treatment term was assessed by comparing Akaike information criterion values (AICc, calculated using the package MuMIn; Bartoń, 2023) between models including and excluding the term, and was considered significant if the inclusive model had $\Delta\text{AICc} \leq -2$.

At the level of individual stimuli/dishes, we fitted two further models to explain chick behaviour towards those stimuli, with time to opening and number of lid pecks. Time to opening was measured from the first behaviour towards that dish (usually ‘look’) to the point at which the dish was opened, not counting any time when the chick was interacting with other dishes. We excluded the nine instances when a chick removed a lid with its foot, as these appeared to be accidental, often while the chick was looking at or interacting with another dish, and therefore did not reflect a response to the stimulus in question. Lid pecks were common behaviours that might reflect hesitancy or exploration on the part of the chick, as opposed to immediate opening of the lid. Model families were gamma for time to opening and Poisson for number of pecks. Each model included chick as a random effect, and each was repeated using four different levels of grouping of the stimuli: no stimulus term (testing H0), probe versus control (two levels, testing H1), category (four levels: nonmimic/control, mimic, intermediate and model, testing H2 and H3) and all stimuli (nine levels, one for each stimulus type, testing for other mixed, idiosyncratic patterns of variation). These model variants were compared using AICc values as described above.

We also tried fitting an equivalent model (Poisson family) using the response variable ‘number of attempts’, defined as the number of times that a chick approached a dish, separated by behaviours directed towards other dishes. Due to low levels of variation in the response variable (80% of stimuli were opened after a single attempt) this model did not fit well, with warnings of singular fit, so we do not present the results in detail. However, with this substantial caveat, we note that the null model (no effect of stimulus) was the best supported of the models.

RESULTS

Of an initial 114 chicks, 75 successfully completed training and progressed to the testing trial, giving $N = 9$ or 10 for each treatment (Fig. 1). All 75 chicks opened all 16 dishes during the testing trial, in a median time of 125 s (range 69−373 s). Chicks showed significant repeatability when comparing times taken during final training trial and testing trial (Spearman rho $= 0.37$, $P = 0.001$, $N = 75$).

There were no significant differences between treatments in terms of trial duration (treatment term $\Delta\text{AICc} = 4.4$, $df = 7$; Fig. 2a, Table A1), mean probe rank ($\Delta\text{AICc} = 8.0$, $df = 7$; Fig. 2b, Table A2) or first dish opened ($N = 37$ controls, $N = 38$ probes; $\Delta\text{AICc} = 13.3$,

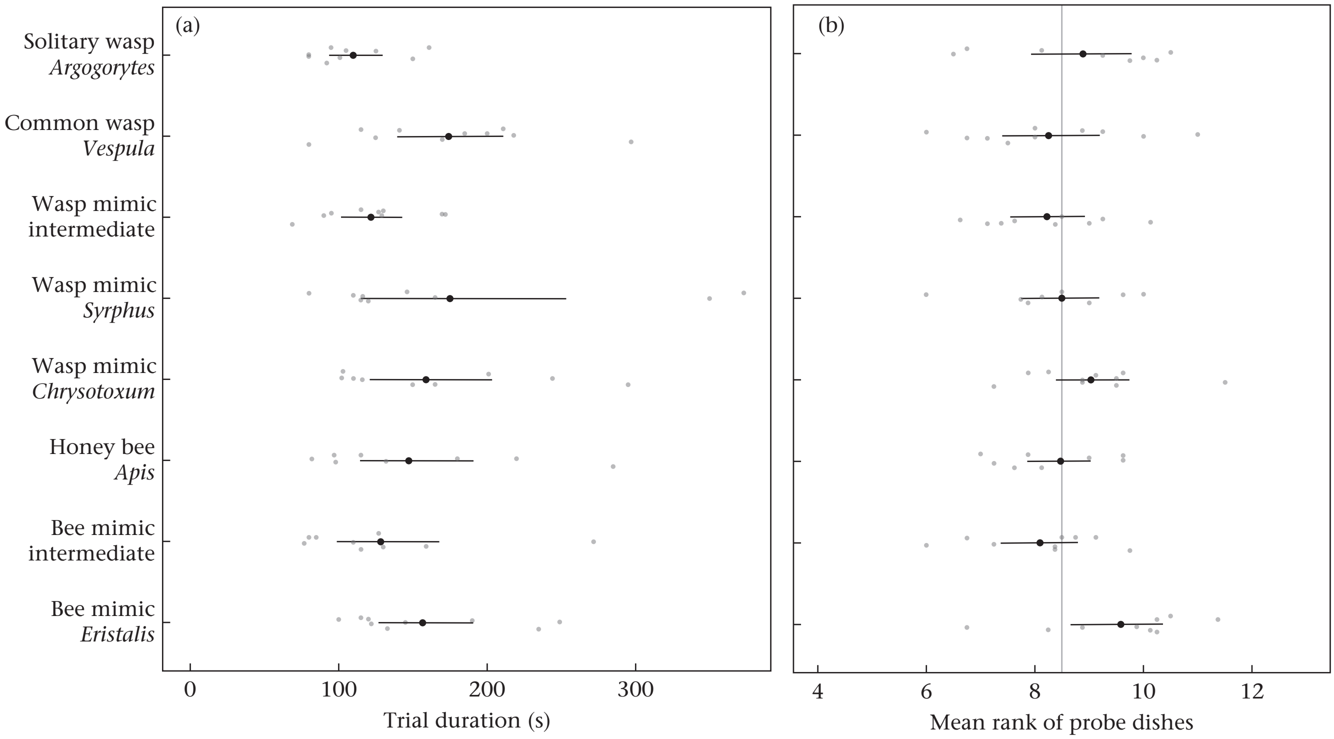

Figure 2. Chick behavioural responses to treatments involving eight different probe stimuli. Grey points show individual chicks, black points are the means and horizontal lines show 95% bootstrapped confidence intervals. (a) Time taken for chicks to open all 16 dishes in the trial. (b) Mean rank of the eight probe dishes within the sequence of 16. Vertical line at 8.5 shows the expectation from random chance.

$df = 7$; Table A3). Grouping all probe stimuli together, there was no significant difference in mean probe rank from the expected value of 8.5 if the order of probe and control attacks were random (two-tailed *t* test: $t_{74} = 0.86$, $P = 0.39$).

Chicks were slightly slower to open probe dishes compared with controls (model prediction for probes: 1.04 s (95% confidence interval, CI = [0.93, 1.17]) and for controls: 0.89 s (95% CI = [0.76, 1.06]); ΔAICc = −18.4, $df = 1$ compared with null model; Fig. 3b, Table A4). Chicks did not peck at the majority (83%) of dishes, but the number of pecks did vary according to stimulus category (ΔAICc = −12.4, $df = 3$ compared with null model; Fig. 3a, Table A5), with control (model prediction = 0.15, 95% CI = [0.11, 0.21]) and wasp stimuli (0.18, 95% CI = [0.09, 0.34]) receiving more pecks than mimics (0.09, 95% CI = [0.02, 0.18]) and intermediates (0.06, 95% CI = [0.04, 0.17]).

Behaviours that might have been indicative of an aversive reaction towards stimuli, such as retreat or bill wiping, were rare ($N = 11$ and 5 respectively), limiting the quantitative analysis possible. Within the small sample sizes, there was no evidence of difference in frequency between control and probe dishes (retreat: 3/11 control, binomial test $P = 0.11$; bill wipe: 4/5 control, binomial test $P = 0.19$).

DISCUSSION

We found some evidence that chicks have unlearned preferences among fly- and wasp-like prey. When presented with these novel stimuli, chicks consumed the associated prey in all cases. Rare instances of overtly negative behaviours (retreat, bill wiping) were not directed preferentially towards particular stimuli, and there was no preference towards probe or control stimuli in the order in which chicks opened dishes. However, we did find that chicks were slightly faster to open dishes that featured nonmimetic stimuli as opposed to those resembling Hymenoptera, mimetic hoverflies or those designed to be intermediate between the two. These results are consistent with H1: chicks are biased against attacking the probe stimuli, all of which have some form of aposematic coloration, but with no biases among the different treatments. We did not find any evidence to support the perceptual bias hypothesis in this context: there was no advantage to hoverfly, as opposed to hymenopteran, stimuli in terms of eliciting greater avoidance from our predators.

While we detected significant variation in chick behaviour according to prey stimulus, it is notable that the differences were very slight. These unlearned responses were not sufficient to deter chicks from interacting with our stimuli, or to provide protection for the associated prey, which were all ultimately consumed. However, flies are capable of very rapid escape responses (Card & Dickinson, 2008; Thyselius et al., 2018), so in real ecological contexts, even small amounts of hesitation on the part of a predator might increase the opportunity for prey to escape (Chittka & Osorio, 2007). In a similar experiment involving learned avoidance, we also found that chick response to stimuli varied but only by fractions of a second (Taylor et al., 2025). Especially given the short duration, we cannot be sure that the chicks' hesitation was related to caution or aversion elicited by the aposematic patterns. It is possible that the delay was instead related to simple sensory factors, with the patterned stimuli perhaps harder to process or target. Of course, in the wild, delayed attack represents a potential survival advantage for the prey regardless of the mechanism by which it is caused.

Our results showed varying numbers of pecks directed towards different stimulus types, with models and nonmimics being pecked the most. These results, while significant, should be regarded cautiously due to the low frequency of pecking; in most encounters, chicks did not peck at the dish or stimulus prior to

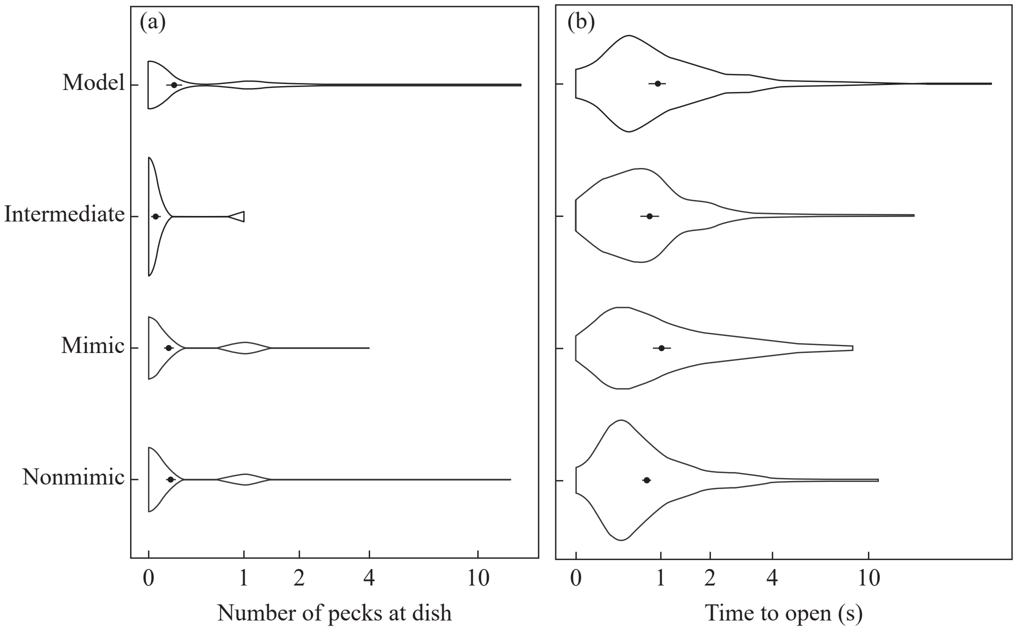

Figure 3. Chick behaviour at each dish according to stimulus type. Grey lines are violin plots of the distribution of values, black points are the means and horizontal lines show 95% bootstrapped confidence intervals. (a) Number of pecks at each dish prior to opening the lid. (b) Time from first interaction with the dish to opening the lid (excluding time interacting with other dishes). Note log scale of *X* axis in both panels has been adjusted to include plotting of zero values, which would not normally appear on a log scale.

opening the dish. Furthermore, in the context of a predator–prey interaction, it is difficult to know whether an increased number of pecks represents hesitancy, and hence an advantage to the prey, or a higher level of motivation from the predator, which would be disadvantageous to the prey.

We have not found any evidence supporting the perceptual bias hypothesis in hoverflies, although given the small effect sizes observed for other stimulus comparisons, we cannot rule out that it might be evident in other contexts where aversive reactions are more pronounced. Existing evidence suggests that unlearned aversion to aposematic prey is variable depending on prey type. Elongated prey with yellow and/or red rings have repeatedly been shown to elicit avoidance from birds, which has been attributed to the snake-like appearance (Roper & Cook, 1989; Schuler & Hesse, 1985; S. M. Smith, 1975, 1977). The potential cost of even a single attempted attack on prey such as a coral snake is high enough that there will be a strong evolutionary advantage to evolving innate avoidance (Brodie & Brodie, 1999). When the stakes are less high, there are potential advantages for a generalist predator to sampling a wide range of prey types to improve knowledge of the relative frequencies, costs and benefits of the prey population (Kikuchi & Sherratt, 2015; Skelhorn et al., 2016), so unlearned biases against such prey should be weaker. Birds show unlearned aversion to some aposematic bugs (Exnerová et al., 2007; Gamberale & Tullberg, 1996), and sometimes to uniform yellow or red prey (Gamberale-Stille & Tullberg, 2001; Mastrota & Mench, 1995; Rowe & Guilford, 1996), but such results are less consistent than those showing aversion to snake-like patterns (Fischer et al., 1975; Roper & Marples, 1997). To our knowledge, among published studies of unlearned responses, Mostler (1935) is most closely comparable to ours in terms of prey types. Mostler (1935) found that young birds attacked and fed on both hymenopteran and syrphid prey with little hesitation, unless they had already encountered noxious models. These results imply a lack of bias in relation to the presented insects, but leave open the possibility that the birds were influenced by early-life provisioning while still in the nest, or that subtle biases like those from our experiment were in play but not detected.

Avoidance of aposematic prey is not an all-or-nothing response, with predators sometimes willing to consume relatively unpalatable prey depending on its value (Halpin et al., 2014; Smith et al., 2014), what alternatives are available (Carle & Rowe, 2014; Halpin et al., 2013) and their current toxin burden and energetic state (Barnett et al., 2011; Skelhorn & Rowe, 2007). Being more willing to sample a wide range of prey types is especially favoured in more complex or variable environments (Greenberg & Mettke-hofmann, 2001). While a predator might avoid a small cost by innately avoiding moderately defended prey, the benefit might be outweighed by the reduced information and flexibility in foraging strategy. In a system such as the hoverfly–wasp mimicry complex, where Batesian mimics are common and models are only moderately aversive, selection might therefore act against predators that maintain unlearned biases, or favour those that moderate such biases using additional signals such as odour.

The predators and stimuli used in our experiments differ from those in typical bird–insect interactions in the wild in several ways, which could mean that predators show different (probably higher) levels of aversion in such natural interactions. Our 3D printed stimuli were designed to be as accurate as possible in their representation of the visual appearance of real insects, and other work has shown similar learned responses to such stimuli and real, dead specimens (Taylor et al., 2025). Nonetheless, it is not possible to match appearance precisely, so there may be details of real insect appearance that would elicit stronger behavioural responses than we observed. For example, our stimuli had slightly lower colour contrast than real specimens (Fig. A1), and contrast is known to affect unlearned colour biases in chicks (Halpin et al., 2020). We also did not attempt to recreate other traits such as movement, scent or sound. While similar investigations to ours have also successfully demonstrated unlearned biases based purely on visual cues (Lindström et al., 1999; Roper & Cook, 1989;

Schuler & Hesse, 1985), the avoidance of warning-coloured prey items can be enhanced in the presence of other multimodal signalling elements such as scent (Rowe & Guilford, 1996) or sound (Rowe & Guilford, 1999). In the case of Hymenoptera and their mimics, there are no known olfactory components to the display, but there is some evidence that buzzing sounds enhance the protection received by aposematic prey (Brower & Brower, 1965; Moore & Hassall, 2016; Rowe & Guilford, 1999); it would be interesting to investigate the interaction between auditory and visual cues in future work, but here we focus on visual biases alone.

Chicks are well established as laboratory models of bird foraging behaviour, including for studies of aposematism (e.g. Aronsson & Gamberale-Stille, 2012; Gamberale & Tullberg, 1998; Jetz et al., 2001; Roper, 1990). Nonetheless, they have diverged from wild insectivores through both natural and artificial selection, which may among other changes have reduced their degree of dietary neophobia (Rose et al., 1985) since they are less likely to encounter unpalatable food items in captivity. Future experiments following similar methodology with other avian predator species could be useful in establishing how generally our conclusions apply. Predators can also vary within species in their responses to prey (Exnerová et al., 2010). Here, our conclusions do not cover those individuals that failed to complete training, but if anything, we would expect those chicks to show greater hesitation in the face of unfamiliar or aposematic prey.

Predators starting with a weak aversion towards wasp-like aposematic patterns are likely to enhance that aversion using social information from conspecifics or heterospecifics (Hämäläinen et al., 2020; Landová et al., 2017; Skelhorn, 2011; Thorogood et al., 2018) or by learning from direct experience. Given that our evidence suggests limited initial protection, mimics are still vulnerable while predators are naïve, a problem exacerbated if mimics are encountered at high frequency compared to models (Lindström et al., 1997). One way that mimics can minimize this problem is to reduce emergence at times when naïve predators such as fledgeling birds are most abundant (Mappes et al., 2014; Waldbauer, 1988).

The results of our experiment will provide an important reference point for any future experiments involving predator learning of wasp-like patterns, showing that predators may have subtle biases that exist prior to any experience with aposematic stimuli.

Author Contributions

Christopher H. Taylor: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. David J.G. Watson: Methodology, Investigation. Francis Gilbert: Writing – review & editing, Funding acquisition, Conceptualization. David J. Pritchard: Supervision, Formal analysis. John Skelhorn: Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. Tom Reader: Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Data Availability

Trial-level behavioural data from the experiment are available from the NERC EDS Environmental Information Data Centre (see Taylor et al., 2024; https://doi.org/10.5285/2348b53a-77f7-4293-8060-1a66fe4cea93).

Declaration of Interest

John Skelhorn works as Managing Editor at Animal Behaviour, but was not involved on behalf of the journal in any capacity at any stage of peer review or production of the article.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2026.123479.

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Appendix

Table A1
Coefficient estimates from GLM of trial duration

	Estimate	SE	*z*	Lower CI (2.5%)	Upper CI (97.5%)
Intercept	2.51	0.5	5.04	1.55	3.46
T:*Argogorytes*	0.41	0.2	2.11	0.05	0.85
T:*Chrysotoxum*	0.23	0.2	1.14	−0.15	0.67
T:*Eristalis*	0.15	0.21	0.73	−0.25	0.61
T:*Eristalis* intermediate	0.12	0.22	0.57	−0.3	0.59
T:*Apis*	0.23	0.2	1.12	−0.16	0.67
T:*Syrphus*	0.35	0.2	1.72	−0.02	0.79
T:*Syrphus* intermediate	−0.12	0.24	−0.49	−0.6	0.38
Log (duration from training)	0.46	0.1	4.75	0.27	0.64
Batch 1b	0.13	0.11	1.16	−0.09	0.35
Batch 2	−0.22	0.13	−1.6	−0.49	0.05
Batch 2b	−0.14	0.13	−1.03	−0.41	0.12

Fitted model was: glm(duration ~ treatment + log(duration_train) + batch, family = Gaussian(link = 'log')). The baseline treatment is *Vespula*. Note that z scores from this model output were not used to assess significance. Instead, significance of the treatment term was assessed by comparison of AICc values between this and a nested model without the term. See Methods for further details. T = treatment, CI = 95% confidence interval.

Table A2
Coefficient estimates from linear model of sequence of dishes opened

	Estimate	SE	*z*	Lower CI (2.5%)	Upper CI (97.5%)
Intercept	9.97	1.99	5.01	5.99	13.95
T:*Argogorytes*	−0.62	0.6	−1.02	−1.82	0.59
T:*Chrysotoxum*	0.17	0.61	0.29	−1.05	1.4
T:*Eristalis*	0.82	0.64	1.28	−0.46	2.1
T:*Eristalis* intermediate	−0.73	0.62	−1.17	−1.98	0.52
T:*Apis*	−0.41	0.61	−0.67	−1.62	0.8
T:*Syrphus*	−0.24	0.65	−0.38	−1.54	1.05
T:*Syrphus* intermediate	−0.55	0.64	−0.86	−1.82	0.72
Log (duration from training)	−0.25	0.41	−0.6	−1.07	0.58
Batch 1b	0.24	0.42	0.57	−0.59	1.07
Batch 2	0	0.44	−0.01	−0.89	0.88
Batch 2b	0.14	0.47	0.3	−0.79	1.07

Fitted model was: lm(sequence ~ treatment + log(duration_train) + batch). The baseline treatment is *Vespula*. Note that *z* scores from this model output were not used to assess significance. Instead, significance of the treatment term was assessed by comparison of AICc values between this and a nested model without the term. See Methods for further details. T = treatment, CI = 95% confidence interval.

Table A3
Coefficient estimates from GLM of first dish opened

	Estimate	SE	*z*	Lower CI (2.5%)	Upper CI (97.5%)
Intercept	0.11	3.19	0.04	−6.24	6.43
T:*Argogorytes*	−0.28	0.95	−0.3	−2.19	1.58
T:*Chrysotoxum*	−0.36	0.95	−0.38	−2.27	1.52
T:*Eristalis*	0.52	1.04	0.5	−1.5	2.65
T:*Eristalis* intermediate	−0.08	0.98	−0.08	−2.04	1.88
T:*Apis*	−1.22	0.99	−1.23	−3.27	0.67
T:*Syrphus*	0.02	1.02	0.02	−2.01	2.06
T:*Syrphus* intermediate	−0.94	1.03	−0.91	−3.06	1.05
Log (duration from training)	0.12	0.66	0.18	−1.19	1.44
Batch 1b	−0.53	0.66	−0.79	−1.86	0.77
Batch 2	−1.15	0.72	−1.59	−2.64	0.23
Batch 2b	−0.07	0.75	−0.09	−1.54	1.41

Fitted model was: glm(first_dish ~ treatment + log(duration_train) + batch, family = ‘binomial’). The baseline treatment is Vespula. Note that *z* scores from this model output were not used to assess significance. Instead, significance of the treatment term was assessed by comparison of AICc values between this and a nested model without the term. See Methods for further details. T = treatment, CI = 95% confidence interval.

Table A4
Coefficient estimates for fixed terms from GLMM of time taken to open dish

	Estimate	SE	*z*	Lower CI (2.5%)	Upper CI (97.5%)
Intercept	0.96	0.06	16.85	0.85	1.08
Nonmimic	0.16	0.04	4.43	0.09	0.24

Fitted model was: glmer(latency ~ type + (1|chick), family = ‘gamma’). The baseline type is probe. Note that *z* scores from this model output were not used to assess significance. Instead, significance of the type term was assessed by comparison of AICc values between this and a null model without the term, as well as two further models with stimuli split by different numbers of levels. See Methods for further details. 95% CI = confidence interval.

Table A5
Coefficient estimates for fixed terms from GLMM of number of pecks prior to opening dish

	Estimate	SE	*z*	Lower CI (2.5%)	Upper CI (97.5%)
Intercept	−1.89	0.17	−10.82	−2.23	−1.55
C:Mimic	−0.55	0.17	−3.16	−0.89	−0.21
C:Hybrid	−0.92	0.38	−2.43	−1.66	−0.18
C:Model	0.16	0.16	1.04	−0.14	0.47

Fitted model was: glmer(n_pecks ~ category + (1|chick), family = ‘Poisson’). The baseline category is nonmimic. Note that *z* scores from this model output were not used to assess significance. Instead, significance of the category term was assessed by comparison of AICc values between this and a null model without the term, as well as two further models with stimuli split by different numbers of levels. See Methods for further details. C = category, CI = 95% confidence interval.

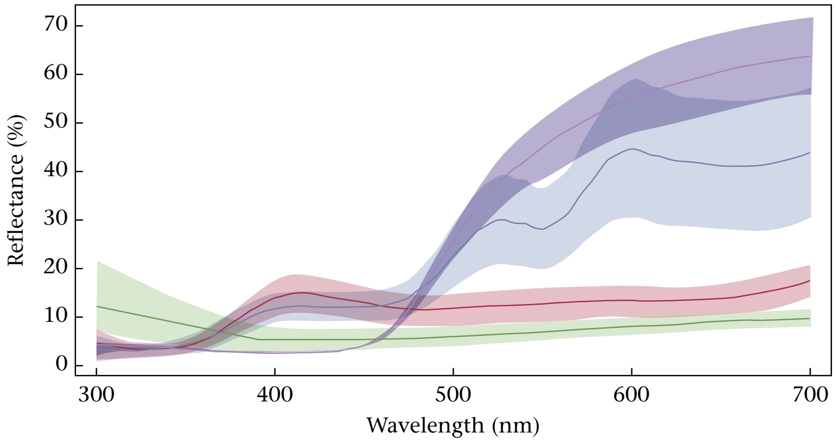

Figure A1. Spectral reflectance curves comparing real specimens with 3D printed stimuli. Specimens and stimuli were the common wasp, *Vespula vulgaris.* Three readings were taken from both yellow and black regions of each pattern, and processed using locally estimated scatterplot smoothing (LOESS) with a span of 0.25. Lines show the mean of those three readings, shaded regions show ± standard deviation. Purple line: yellow region of pattern on real specimen. Blue line: yellow region of pattern on printed stimulus. Green line: black region of pattern on real specimen. Red line: black region of pattern on printed stimulus.