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Non-warning odors trigger innate color aversions—as long as they are novel

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Warning signals made by unpalatable insects to potential predators commonly target more than one sense: such signals are ''multimodal.'' Pyrazines are odors produced by warningly colored insects when attacked, and have been shown to interact with food coloration, biasing avian predators against novel and typically aposematic food. However, at present it is not known whether this is an adaptation by prey to exploit a general feature of avian psychology, or an evolutionary response by birds to enhance their avoidance of unpalatable prey. Here we investigate the effect of other odors on the innate responses of naive domestic chicks (*Gallus gallus domesticus*) to food that is of novel color, or of a color that is associated with warning coloration, yellow. In the first experiment, we demonstrate that natural and artificial odors that have no association with aposematism in the wild can produce biases against both novel colored foods and yellow colored foods. In a second experiment, we also show that odor novelty is vital for eliciting such effects. These results support the idea that warning odors have evolved in response to preexisting psychological biases against novel odors in predators, rather than predators evolving specific responses against odors associated with unpalatable prey. *Key words:* antipredator; aposematism; foraging; innate aversions; multimodal signals; neophobia; signal design. *[Behav Ecol 12:134–139 (2001)]*

Many unpalatable prey animals signal their unpalatability to predators with conspicuous coloration—a phenomenon known as ''aposematism'' (Cott, 1940; Poulton, 1887). Although theory is predominately concerned with explaining aposematic colors or patterns in terms of their ability to facilitate avoidance learning (Guilford, 1990; Schuler and Roper, 1992; Wickler, 1968), evidence is accumulating that animals can also have innate aversions to aposematically colored prey (e.g., Schuler and Roper, 1992; Smith, 1980). Domestic chicks have been shown to prefer olive mealworms to black, yellow-and-black striped, or red ones (Roper and Cook, 1989; Schuler and Hesse, 1985), while red and yellow are the most aversive colors for naïve northern bobwhites (Mastrota and Mench, 1995) and zebra finches (Sillèn Tullberg, 1985), and evoke the most intense startle responses in hand-reared blue jays (Ingalls, 1993). It would appear that certain coloration, especially conspicuous colors and patterns used in aposematic signaling, can have an intrinsic aversive value and be avoided more than others.

However, visual warning signals do not always occur in isolation, and are often combined with acoustic or olfactory cues, that is, they are multimodal. For example, the seven-spot ladybird (*Coccinella septempunctata*) is not only distinctively black-and-red colored, but also emits pyrazine odor when attacked (Marples et al., 1994; Rothschild and Moore, 1987). Pyrazines are extremely volatile compounds and occur alongside warning coloration in insects from widely differing taxonomic groups (Moore et al., 1990; Rothschild et al., 1984). Interestingly, while pyrazines are not apparently aversive themselves (Guilford et al., 1987), they can interact with visual cues in non-experienced predators to induce or enhance unlearned responses. It has been shown in domestic chicks that pyrazine can increase the latency with which novel food is accepted (Marples and Roper, 1996), and that it can trigger aversions against yellow and red food that are not evident in the absence of the odor (Rowe and Guilford, 1996). It could be that these foraging biases are specific to pyrazines, suggesting a co-evolved response by predators against the odor, or that it is a more general response evoked by any odor, with the emphasis then being that insects had evolved pyrazine to exploit a general feature of avian psychology. Marples and Roper (1996) showed that almond odor (which is associated with plant toxins) increased the latency to eat novel foods, although odors of vanilla and thiazole, an artificial compound, had no such effect. This led to their conclusion that odors associated with toxicity, like warning colors, can have a special intrinsic warning value and trigger innate aversions against aposematically colored prey (see also Woolfson and Rothschild, 1990).

The experiments presented here investigate the apparent ''warning'' function of pyrazine, comparing its ability to induce foraging biases in chicks with two ''non-warning'' odors: methyl salycilate which is a plant compound associated with pathogen resistance (Shulaev et al., 1997), and ethyl acetate which is an organic solvent with no known signaling function. The first experiment tests whether these odors also induce foraging biases against novel and yellow (aposematically) colored food in domestic chicks, or whether such a role is particular to pyrazine odor.

Neophobic responses are a general and well-investigated aspect of food choice behavior in animals (e.g., Tarpy, 1997), and their role in visual warning signal function is well established (e.g., Coppinger, 1970; Roper, 1994). In a second experiment, therefore, we investigate the role of odor novelty. These experiments together aim to uncover whether ''warning odors'' have an intrinsic value to birds in association with novel and warningly colored foods, or whether instead they have evolved to make use of a general neophobic response in avian predators.

MATERIALS AND METHODS

Predators and prey

At the start of each experimental week, we obtained day-old male Ross 1 domestic chicks (*Gallus gallus domesticus*) in

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batches of 30–40 from a commercial hatchery. They were kept in metal cages (80 × 45 × 35cm) in groups of 15 to 20 at approximately 20°C under heat lamps, and subject to a 12:12 light:dark cycle. Water and food (untreated brown chick starter crumbs) was offered ad libitum. At the end of each experimental week, chicks were donated to small free-range holdings.

The prey used during the experiments were also brown starter crumbs, sieved to ensure that all crumbs were approximately 2 mm in diameter. Green and yellow crumbs were dyed by spraying brown crumbs with water-soluble food colorants and drying them under heat lamps. Brown crumbs were left undyed but sprayed with water and dried to control for processing effects on texture. All crumbs were palatable.

Table 1
Sample sizes in the twelve different treatment groups of experiment 1

	Pyrazine		Methyl salycilate		Ethyl acetate	
Color choice	(a)	(b)	(a)	(b)	(a)	(b)
Odor present	15	15	17	13	14	13
Odor absent	16	18	15	11	14	16

The two color choices offered were (a) green versus brown (i.e., novel versus familiar color) and (b) yellow versus green (i.e., novel + aposematic versus novel color).

General methods and experimental apparatus

An experimental week consisted of 4 days of training with the experiment conducted on day 5. On days 1 and 2, we trained single chicks to eat brown crumbs scattered on the white floor of a simple circular training arena (diameter 80 cm, walls 30 cm).

Two duplicate testing arenas were placed in the center of the two experimental chambers, which were olfactorily, visually, and acoustically separated from each other and from the room where the chicks were housed. The air in each room was filtered through an extraction unit, minimizing odor contamination between rooms. Each testing arena consisted of a high-walled circular runway (approximately 20 cm in width with walls of 25 cm in height and curved along the perimeter of an 80 cm-diameter circle) placed on a wooden platform. Each was lit by three 60-W incandescent desk lamps positioned 50 cm above the runway. The runway was a series of 16 sunken, uniformly spaced wells of 5 cm diameter. At the bottom of each well, was a petri dish containing cotton wool that would receive the experimental odors; each petri dish had a hole pierced in its lid to allow odors to permeate into the air above. The lid was also covered with a piece of porous, white filter paper that provided a uniform non-reflective white background for food presentation, but which also allowed odors to pass through. Each petri-dish closed very tightly and personal inspection confirmed that odor concentration was highest close to the middle of the dish and decreased with distance from there. In any training session, a chick crumb was placed on each lid, and chicks learned to eat the crumbs in succession. There was no time limit on any session and a piece of cardboard was moved behind them to obstruct the way back. Any chick that could not learn this task by the end of the fourth day (see below) was excluded from the experiment.

At the end of day 2, chicks were put in pairs into a testing arena and given food in order to familiarize them to the testing arena. No odor was present. Further training of single chicks took place on days 3 and 4 (particular to each experiment, see below).

Experiment 1: the effect of odor type

On days 3 and 4, we gave each chick three training sessions with a brown crumb placed in each of the 16 wells. No odor was present. Training took place in the arenas that chicks were later tested in. After the final training session on the fourth day, chicks were randomly assigned to one of four groups (two color choices in each of two odor treatments) and individually marked. Chicks were food deprived overnight (12 h, dark period) before the experimental session on day 5.

Prior to testing on the fifth day, control or experimental solutions were added to each of the 16 petri dishes in both arenas. It was impossible to test all odors in a single week, and therefore in each week, one arena was treated with only one of the three test solutions. There were 3 weeks of pyrazine experiments, and 2 weeks each of ethyl acetate and methyl salicylate experiments. In all weeks the second testing arena contained an appropriate control solution (10 ml absolute ethanol dissolved in 990 ml distilled water in the case of pyrazine, and distilled water for the other two odors). Stimulus intensity between odors could only be controlled subjectively, and odor solutions were therefore added to petri dishes to produce a similar strength: four drops of pyrazine solution (0.1 ml 98% 2-isobutyl-3-methoxypyrazine dissolved in 10 ml absolute ethanol and diluted with 990 ml distilled water), six drops of pure ethyl acetate, and six drops of pure methyl salicylate (2-hydroxybenzoicacid-methylester, or ''Oil of Wintergreen'').

In all weeks there were two color choice groups in each odor treatment: (a) eight brown (familiar) versus eight green (novel) crumbs, and (b) eight green (non-aposematic, novel) versus eight yellow (aposematic, novel) crumbs. The sequence of the colors in the arena was alternated, with successive chicks starting with a different color. An experimental session consisted of a single chick proceeding along the runway in one direction, eating or rejecting each crumb as it was encountered. There was no time limit in any session, and chicks were not allowed to return to rejected crumbs. For each well we recorded whether a crumb was eaten or not.

The experiments lasted between 1.5 and 2 h, depending on the number of chicks being tested: a total of 189 chicks were tested in batches of 20 to 28 per week. Of these, 12 showed various signs of distress before and during the testing and did not eat any crumbs: these were excluded from the experiments. Table 1 details the sample sizes for the twelve treatment groups.

Experiment 2: the effect of odor novelty

To test whether odor novelty is important in eliciting food biases, we repeated experiment 1 using only ethyl acetate, but this time included groups that experienced the odor prior to testing on day 5. Again, there were two color treatments: (a) green versus brown crumbs, and (b) yellow versus green crumbs. However, as well as having test groups that had either novel odor or no odor (repeating the four ethyl acetate groups in experiment 1), two groups of chicks (one of each color choice) were given their three training sessions on days 3 and 4 with ethyl acetate added to all 16 wells of the experimental arena (familiar odor).

Therefore, after training on day 2, chicks were randomly assigned to one of six groups and marked. The odor novel and odor absent groups were trained in one testing arena to which no odor was added, while odor familiar groups received the same training but in the other testing arena where six drops of ethyl acetate had been added to the cotton wool pads in each petri dish before training. Because one chamber had

Table 2
Results of ANOVA on chicks' attack biases against the novel color or the aposematic color in the presence or absence of three odors

Effects	df	*F*	*p*
Odor presence (OP)	1	48.83	<.0001
Odor type (OT)	2	0.66	.52
Color choice (CC)	1	2.83	.09
OT * OP	2	0.11	.89
OT * CC	2	1.17	.31
OP * CC	1	0.19	.67
OT * OP * CC	2	0.51	.60

The two color choices offered were (a) green versus brown (i.e., novel versus familiar color) and (b) yellow versus green (i.e., novel + aposematic versus novel color); $n = 177$.

to be odorless for the entire training and experiment, while the other contained odor, the odor novel chicks could not be trained in the room that they would later be tested in. Consequently, during training and testing, care was taken to minimize visual cues perceived from the surroundings by transferring chicks from the home cage to the arenas in a closed box, and put into the arena with their eyes obstructed.

On day 5, two replicate experimental sessions were conducted (i.e., approximately 1 h later the same chicks were subjected to the same experiment), with ethyl acetate as the test odor (six drops per well). We tested the groups in a rotating order and in the familiar testing arena they had already been trained in, that is, arenas were swapped between the chambers with a slight pause to minimize the possibility of odor being transferred to the non-odor room. As the chemical used is an organic solvent with high volatility, we reapplied four drops per petri dish before performing the second session 1 h later. Overall we tested 57 chicks in 2 experimental weeks: nine in each of the three treatment groups of color choice (a) and 10 in each group of color choice (b).

Data analysis

Since two colors were offered simultaneously in each color choice group, the reaction towards one cannot be treated independently from the other. Therefore, as a combined measure of the relative aversion, for every chick, the "attack bias" against a particular color was calculated. For color choice (a) chicks scored +1 for eating a brown (familiar) crumb and −1 for eating a green (unfamiliar) crumb, while in color choice (b) a chick scored +1 for eating a green (non-aposematic) crumb and −1 for eating a yellow (aposematic) crumb. This is a measure of foraging bias against a predicted color (novel green crumbs in color choice [a] and yellow "aposematic" crumbs in color choice [b]), where equal preference is indicated by a score of 0. As there were always eight crumbs of each color, a value of +8 indicates a chick eating only one color and avoiding all crumbs of the other color in the predicted direction (i.e., against novel green crumbs or yellow "aposematic" crumbs), while −8 shows an absolute discrimination between crumb colors but a bias in the reverse direction.

RESULTS

Experiment 1: the effect of odor type

We found that the presence of odor had a significant effect on prey choice (ANOVA: see Table 2). Although there was no effect of odor type (see also Figure 1), the presence of any of the three tested odors resulted in attack biases significantly

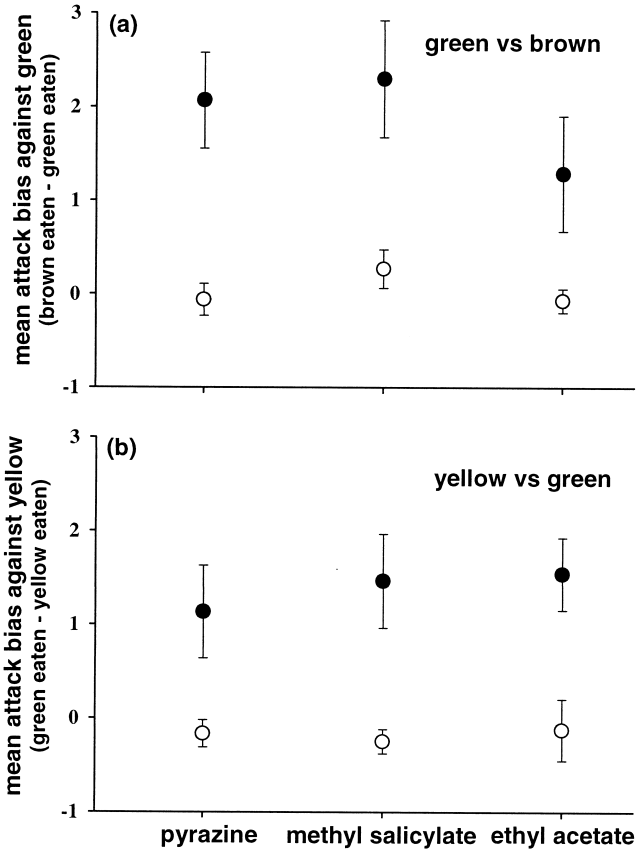

Figure 1
(a) Mean attack bias (± SE) of 5-day old birds against the novel color in the choice experiment of green (novel) versus brown (familiar) crumbs in the presence (closed circles) or absence (open circles) of odors. (b) Mean attack bias against the specific color yellow in the choice experiment of yellow (aposematic and novel) versus green (novel) crumbs. A positive attack bias indicates avoidance, a negative indicates preference.

different from the non-odor groups. Table 3 shows that, on average, chicks avoided one or two more green than brown crumbs (see also Figure 1a), and one or two more yellow than green crumbs (see also Figure 1b). There was no effect of the type of color choice on attack bias. In other words, in the presence of odor chicks showed a similar level of bias against novel colored prey (color choice [a], novel green versus familiar brown) as they did against as aposematically colored prey (color choice [b] novel green versus novel and aposematic yellow).

A separate inspection of the actual crumb numbers consumed (Table 3) can serve to confirm whether observed attack biases in presence of odors are actually due to decreased ingestion of one color and not increased consumption of the other. We test this by comparing the ingestion of crumbs of the reference color (i.e., brown and green respectively) in the presence and absence of any odor. In color choice (a) the mean number of the familiar brown crumbs eaten was around seven for all treatment groups. It appears to be somehow less in the presence of an odor, but the effect is not significant (ANOVA, $F_{1,91} = 0.35$, $p = .71$). In color choice (b) green was the reference color, and significantly less green crumbs were eaten in the presence of odor (ANOVA, $F_{1,89} = 18.76$, $p < .001$).

Table 3
Mean number (± SE) of crumbs eaten in each color choice and odor group of experiment 1 (effect of odor type)

	Pyrazine		Methyl salicylate		Ethyl acetate	
	Present	Absent	Present	Absent	Present	Absent
Color choice (a)						
Brown	6.63 (± 0.60)	7.44 (± 0.27)	7.35 (± 0.32)	7.33 (± 0.36)	7.00 (± 0.36)	7.21 (± 0.39)
Green	4.69 (± 0.79)	7.50 (± 0.22)	5.06 (± 0.70)	6.87 (± 0.61)	5.71 (± 0.71)	7.57 (± 0.33)
Color choice (b)						
Green	4.38 (± 0.51)	6.69 (± 0.45)	6.62 (± 0.68)	7.09 (± 0.53)	3.50 (± 0.69)	6.75 (± 0.47)
Yellow	3.31 (± 0.72)	6.94 (± 0.44)	5.15 (± 0.74)	7.36 (± 0.45)	2.25 (± 0.66)	6.88 (± 0.41)

The test was eight crumbs of one versus eight crumbs of the other color.

Experiment 2: the effect of odor novelty

In experiment 2, prey choice behavior differed significantly amongst the three treatment groups (odor novel; odor familiar; no odor) in the first session (ANOVA on attack biases, $F_{2,55} = 24.58$, $p < .001$). This remained the case in the second session as well (ANOVA, $F_{2,55} = 30.29$, $p < .001$). In both the first and the second experimental session the aversions induced by the presence of ethyl acetate in the odor novel group were much higher than the ones in the odor absent group (Figure 2, $p < .001$ in both sessions, pairwise comparisons with Bonferroni adjustment for multiple comparisons). This replicated our results from experiment 1. Interestingly, the aversions observed in the odor familiar group were close to zero and did not differ from the odor absent group ($p = 1.0$ in both sessions, pairwise comparisons with Bonferroni adjustment for multiple comparisons). Thus, three training exposures to the odor prior to the experiment were sufficient to extinguish the effect of ethyl acetate in triggering biases, at least at the level measurable in our set-up.

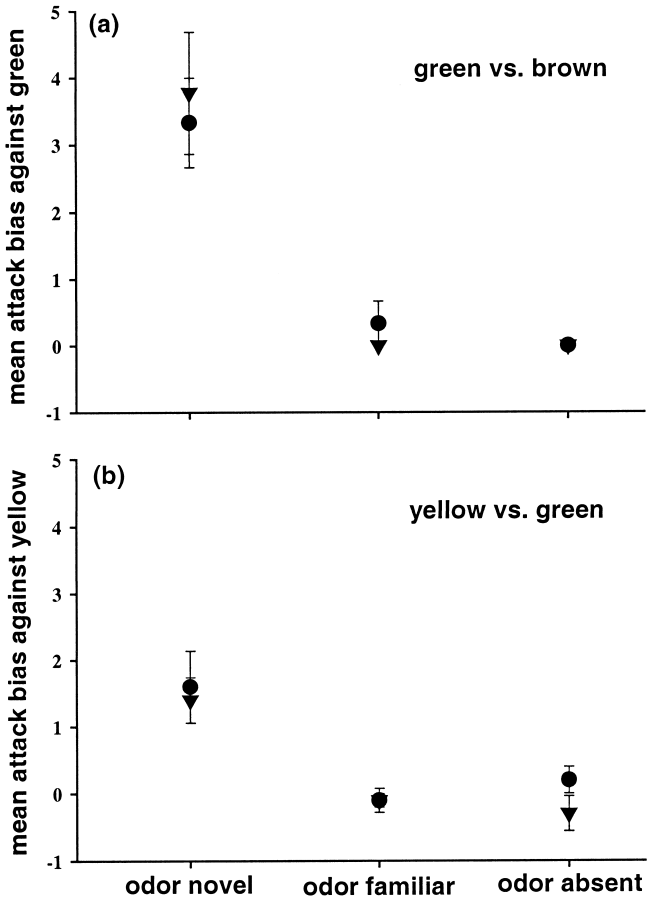

Figure 2
(a) Mean attack bias (± SE) of 5-day old birds against the novel color in the presence of ethyl acetate as novel or familiar odor, or in its absence ($n = 9$ in all groups). (b) Mean attack bias against the specific color yellow in the choice experiment of yellow in the presence of ethyl acetate as novel or familiar odor, or in its absence ($n = 10$ in all groups). Color choices as in Figure 1. Circles, first session; triangles, second session.

In this experiment, there was also an effect of color choice offered (ANOVA, $F_{1,56} = 4.27$, $p = .044$), and a two-way interaction between color choice offered and odor treatment (ANOVA, $F_{2,55} = 3.22$, $p = .048$). Ethyl acetate triggered smaller biases against novel yellow (when the other color was novel green) than against novel green (when the other color was familiar brown). The results were similar in the second session (ANOVA: color choice, $F_{1,56} = 8.07$, $p = .006$; color × odor interaction, $F_{2,55} = 7.54$, $p = .01$).

A separate analysis on the crumb colors in this experiment with only ethyl acetate (Table 4) confirms the presumed direction in which the odor presence affects ingestion. Here, in the presence of the novel odor in color choice (a) less brown crumbs are eaten than in its absence (trial one: ANOVA, $F_{1,17} = 5.54$, $p = .032$). The direction is similar, but not significant for the ingestion of green crumbs in color choice (b) (trial one: ANOVA, $F_{1,19} = 1.10$, $p = .31$). There is no increased consumption of any of the colors in the odor novel group from trial one to trial two (one-way ANOVAs, all differences ns).

DISCUSSION

Our experiments provide three main findings. First, we demonstrate that not only pyrazine, but also a plant odor without known association with aposematic defenses (methyl salycilate) and a purely artificial compound (ethyl acetate) can induce innate aversions against novel and typically aposematically colored (yellow) food. This argues that predators may have quite general responses to odors that may be exploited by insects in the name of defense, and argues against the view that aversive reactions of predators are solely the result of specifically evolved responses to the odors of unpalatable prey.

In addition, our second experiment demonstrates that novelty is an essential prerequisite for prey to benefit from this multimodal interaction. In our choice experiment, familiar colors are not obviously avoided in the presence of even novel odors, and both novel and aposematic colors are not obviously avoided when the odor present is familiar (although it always remains possible that weak aversions are not detected by our procedures). As shown for pyrazine (Rowe and Guilford,

Table 4
Mean number (± standard error) of crumbs eaten in each treatment group of experiment 2 (effect of odor novelty)

	Ethyl acetate, trial 1			Ethyl acetate, trial 2		
	Familiar	Novel	Absent	Familiar	Novel	Absent
Color choice (a)						
Brown	7.56 (± 0.34)	6.44 (± 0.60)	7.89 (± 0.11)	7.56 (± 0.44)	6.22 (± 0.68)	8.00 (± 0.00)
Green	7.22 (± 0.66)	3.11 (± 0.82)	7.89 (± 0.11)	7.56 (± 0.44)	2.44 (± 0.94)	8.00 (± 0.00)
Color choice (b)						
Green	6.00 (± 0.84)	4.20 (± 0.81)	5.50 (± 0.93)	5.80 (± 1.08)	4.10 (± 1.02)	5.10 (± 1.00)
Yellow	6.10 (± 0.84)	2.60 (± 0.88)	5.40 (± 1.05)	5.90 (± 1.10)	2.80 (± 0.93)	5.30 (± 1.02)

The test was eight crumbs of one versus eight crumbs of the other color.

1999), after just a few exposures with ethyl acetate, all biases are apparently lost.

Finally, it would appear that odors trigger similar degrees of aversion against both a novel color (with the effect of familiarity controlled for) and a specific, aposematic color per se (with the effect of novelty controlled for).

It remains to be explained, then, why some odors, like pyrazines, are more commonly used in warning displays than others. Odors differ in their intensity and volatility, and perhaps a physiological threshold might limit the efficiency of certain compounds. This is an interesting parallel to warning colors, where intensity could be interpreted as the brightness aspect of color; to what extent such signal properties can be generalized, however, remains to be investigated. The widespread use of pyrazines might be best explained by their great efficiency (high volatility, low olfactory threshold) paired with low costs of production (relatively simple molecular structure, occurrence in many food plants). Alternatively, some odors might be more memorable in avoidance learning than others (Roper and Marples, 1997b; Woolfson and Rothschild, 1990).

These differences in odor intensity might also explain why aversions elicited by artificial odors have escaped attention. Marples and Roper (1996) tested pairs of naïve chicks for their latency to eat novel colored food and water, but did not find any effect of vanilla and thiazole. Only odors naturally associated with chemical defense (two different types of pyrazine and almond) seemed to have an effect. It could well be that the concentration of the two artificial odors in this case was not high enough to elicit an aversive response.

Several ''properties'' of aposematic coloration have been discussed and separately shown to increase unconditioned aversions in naive predators: (1) novelty (Jones, 1986; Mappes and Alatalo, 1997; Marples and Roper, 1996), (2) intrinsic color/pattern (Mastrota and Mench, 1995; Roper and Cook 1989; Schuler and Hesse, 1985; Sillèn Tullberg, 1985; Smith, 1975), (3) contrast with background, or conspicuousness (Roper and Redston, 1987), and (4) gregariousness (Gamberale and Tullberg, 1996, 1998). Our experimental design aimed on eliciting, separating and comparing the effects of novelty and specific (aposematic) coloration within a single experiment. Prey items were all presented on the same background and gregariousness is unlikely to have had any effect as crumbs were presented individually, and at most two might have been visible to a chick at any one time. In our experimental model of innate aversions triggered by odors, there are clearly aversive effects due to both visual and olfactory aspects of the prey. Novelty seems to play its own and important role in how aposematic prey decreases initial attack rate. Prey benefit from looking novel and also by being a specific, aposematic color. The way in which these properties interact with each other remains to be resolved, but it seems reasonable to assume that both in concert are more efficient, perhaps producing higher aversions together than singly.

Although novel coloration alone has been shown to be aversive in several other studies with naive chicks (see above, also Roper and Marples, 1997a), in our choice experiment chicks did not appear to avoid novel colored prey when odor was absent (see also Rowe and Guilford, 1996, 1999). One possible explanation for this difference is that in our experiments birds were offered only single prey at each encounter. The presentation of multiple prey (Roper and Marples, 1997a), simultaneous rather than sequential choice, or the measurement of latencies might reveal weaker color neophobia effects. Furthermore, our birds while kept separate from any potentially biasing stimuli received extensive training from day 1 of their life and were well familiar with testing arena and experimental task. Therefore, they might not react to stimuli that they would have been alerted to had the experimental apparatus or procedure been less familiar to them. This argument is on the same line as the one made above about novelty of odor as an additional stimulus. Thus, it is still possible that certain aversive responses remain hidden in our experiments and inferences of ''no difference'' must be made with this in mind. This underlines the strength of effects where differences actually are observed.

These findings have considerable significance for the functional understanding of warning signals. Without the necessity to invoke aversion learning, multimodal warning signals can apparently exploit innate predispositions, similar to the way that startle displays are proposed to function (Sargent, 1990; Schlenoff, 1985). To date, the facilitation of avoidance learning has been the favored explanation of the adaptive significance of aposematic displays. Our findings advocate the additional prominent role of innate aversions.

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