



Don't waste your time: predators avoid prey with conspicuous colors that signal long handling time

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Abstract

Most studies on warning signal theory have focused on aposematic prey, which signal unpalatability through conspicuous signals. Palatable prey that are difficult to capture or process may also use conspicuous signals to advertise unprofitability to predators. Theory predicts that predators should avoid prey with long handling time, especially when other prey with shorter handling times are abundant. However, it is unclear if prey can benefit by signaling longer handling time. In experiments with dough models as prey, we show that chickens can learn to associate colors with increased handling time and avoid such prey when alternative prey are abundant. Overall, our experiment demonstrates that advertising longer handling time to predators can be advantageous to prey when other more profitable prey are abundant.

Keywords Handling time · Antipredatory strategies · Conspicuous colorations

Introduction

An animal's foraging decisions can have direct or indirect fitness consequences (Drent and Daan 1980; Stephens and Krebs 1986) through effects on growth, reproduction and survival (Weimerskirch et al. 2003). In order to maximize fitness, animals need to optimize their diet, use of resource patches and movement between patches (MacArthur and Pianka 1966; Schoener 1969; Cody 1971; Krebs et al. 1974; Werner and Hall 1974; Charnov 1976). A huge body of theoretical and empirical work exists elucidating the optimal choices a predator should make to maximize foraging efficiency (Stephens and Krebs 1986). However, predators need to possess sufficient information regarding the spatial distribution and relative profitability of different prey to make adaptive foraging choices (Kamil 1983; Endler and Rojas 2009), and such information is gathered through experience and learning (Croy and Hughes 1991).

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Prey have also evolved a multitude of strategies to avoid being eaten. Many species possess defenses that make them less profitable to predators, and signal their unprofitability, enabling potential predators to make informed foraging decisions (Barnett et al. 2007; Skelhorn and Rowe 2007; Veselý et al. 2017). Many unpalatable or toxic prey signal their unprofitability through conspicuous warning signals (Ruxton et al. 2004a; Mappes et al. 2005). Salient signals such as conspicuous colors that make prey more perceivable with respect to its environment allow predators to learn quantitative and qualitative information about the preys' toxicity (Speed 2000, 2001; Webb et al. 2008; Barnett et al. 2011, 2014; Skelhorn et al. 2016). Although most work on warning signals is centered on toxic prey, palatable prey with other defenses, e.g. spines or hard protective covering, can also use conspicuous colors to signal their unprofitability (Lev-Yadun 2001, 2016; Ruxton et al. 2004a). Many species use behavioral displays or conspicuous colors to signal to predators at long distances that they have been detected, to prevent pursuit from predators (Hasson 1991; Caro 1995; Zahavi and Zahavi 1997). Nontoxic prey can also use conspicuous colors to signal that they are bitter tasting (Skelhorn and Rowe 2009, 2010), difficult to catch (Hancox and Allen 1991; Pinheiro 1996; Ruxton et al. 2004b; Pinheiro et al. 2016) or too hard and therefore difficult to consume (Wang et al. 2018). In plants, it has been shown that the presence of spines reduces herbivory (Cooper and Owen-Smith 1986; Cooper and Ginnett 1998; Wilson and Kerley 2003) and several plants advertise the presence of spines through conspicuous color patterns (Lev-Yadun 2001, 2009). However, most studies on warning signals have focused on toxicity, and not much is known about what other aspects of the prey's defense predators learn and the tradeoffs that modulate predator decisions.

Handling time, the time required to kill and consume prey, can profoundly influence foraging decisions in predators and thus determine the range of prey items included in the diet (Schoener 1971; Charnov 1976). Studies have indicated that increased handling time can have fitness costs to predators (Sullivan 1988; Lemon 1991). These fitness costs are due to the tradeoff between handling time associated with unprofitable prey and time allocated for other activities such as searching for mates or alternative prey (MacArthur and Pianka 1966; Krebs 1980; Okuyama 2015). Thus, when encounter rates of profitable prey with a short handling time are low, predators should be unselective, but when profitable prey are abundant, predators should selectively avoid prey with longer handling time (Charnov 1976).

Many palatable prey possess secondary defenses that could potentially prolong handling time (Altwegg et al. 2006; Hammill et al. 2010). In conditions where alternate prey are frequently encountered, signaling long handling time, through conspicuous signals for instance, could be advantageous if predators can associate these signals with unprofitability (Mappes et al. 2005). Here, using captive chickens as predators and edible dough models as prey, we tested the hypothesis that predators can learn to preferentially avoid prey with longer handling time when such prey are associated with a more noticeable salient signal such as conspicuous color.

Materials and methods

Overall design

To test whether birds can associate color with handling time, we designed an experiment where chickens were offered baked and unbaked dough models that resemble small snakes as prey. Each 'prey' consisted of a piece of dough fixed onto a piece of colored paper

slightly wider than the dough piece (Fig. 1). These prey were presented on leaf litter. Our pilot studies with dough pieces suggested that chickens showed no signs of fear and readily consumed both baked and unbaked snake-like dough models (without the underlying colored paper) but took a longer time to consume the baked ones. In the experiment, one group of chickens received both baked and unbaked prey that were coupled with (i.e., fixed onto) brown colored paper ('color-baking unassociated' group), while another group of chickens received the two model types that were coupled with different colors (baked with yellow, unbaked with brown; 'color-baking associated' group). Thus, only the chickens in the color-baking associated group were able to distinguish between the baked and unbaked models based on the paper's color. If chickens learn to associate color with handling time and use this association to avoid unbaked prey, chickens in the color-baking associated group should preferentially feed on the unbaked models, while chickens in the color-baking unassociated group should feed on both model types equally.

Details of prey and predators

We used 26 uniquely identifiable indigenous domestic chickens, maintained in a poultry farm in Vithura, Kerala, India, as predators. We used 2–3 year old male and female chickens maintained in an outdoor pen made of plastic mesh net. The chickens were raised in the poultry farm and fed twice a day (at 8.00 and 16.00 h) with poultry feed and were thus naïve to the dough mixture provided as prey and to natural predators such as snakes. The dough used for the prey was made of wheat flour and brown food color, and shaped to resemble small non-toxic uropeltid snakes (Family Uropeltidae). Indigenous chickens and

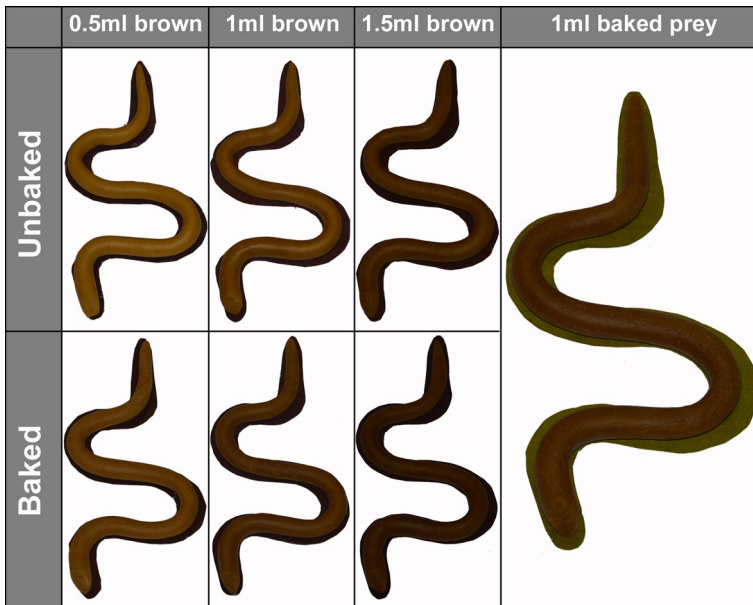


Fig. 1 Images of prey used in the experiments. The dough model and the underlying non-edible colored paper together formed the prey. The rows represent the type of prey (baked/unbaked), and the columns represent the different concentrations of food colors. The last column represents a 1 ml baked model placed on yellow paper used for the color-baking associated group.

wild fowls are regularly known to feed on large uropeltid snakes (Rajendran 1985). Further, these snakes also possess conspicuous colorations on their ventral and lateral side, which they potentially use to advertise their unprofitability associated with long handling time (Cyriac and Kodandaramaiah, unpublished data). Thus, we designed our prey to resemble small uropeltid snakes in shape and size. The dough models were 25 cm long, weighed ca. 18–19 g and were fixed on ‘S’ shaped yellow or brown colored paper (Fig. 1). To manipulate the handling time of the prey, the dough models were either baked in a hot air oven at 80 °C for 60 min or left unbaked at room temperature for the same time (see Supplementary Material, supplementary methods S1.1 for more information). The brown color of the baked models was visually indistinguishable (by the chickens) from that of the unbaked models (see Supplementary Material, supplementary methods S1.2, Table S1).

Acclimatization phase

In the first phase of the experiment, the chickens were introduced into a corridor that opened into the experimental arena consisting of a 100 cm cubical cardboard structure. Black paper lined the inner walls and floor of the experimental arena and corridor. Each chicken underwent one training session per day for five consecutive days. Each session lasted 2 min during which period the chicken could explore the arena and feed on small oval pieces of unbaked brown dough randomly scattered into the arena before introducing the chickens. Chickens were starved for at least one hour before starting the trials. The dough pieces were kept moist and fresh, unlike the snake models that were either baked or left unbaked at room temperature for an hour. On the third session, the dough pieces were scattered on leaf litter, such that the chickens had to search for the dough.

Learning phase

After the acclimatization sessions, in the learning phase, we introduced each chicken to either a baked or an unbaked prey placed in the center of the arena on leaf litter along with small dough pieces scattered randomly in the arena. We randomly assigned 13 chickens each to the color-baking associated and color-baking unassociated treatments. We randomly presented each chicken with either a baked or an unbaked prey in the center of the arena on leaf litter along with 25 small dough pieces scattered across the arena. The small dough pieces represent ‘other available prey’ under natural conditions and together weighed ca. 20 g, slightly more than the snake model. All chickens were starved for at least one hour prior to the start of the learning phase. The chickens in the color-baking unassociated group received both baked and unbaked models on brown underlying paper, while chickens in the color-baking associated group received the baked model on yellow underlying paper and the unbaked on brown underlying paper (Fig. 1). To reduce the effect of chickens learning luminance (total reflectance) cues of the baked and unbaked models, we prepared both baked and unbaked dough models with three concentrations (0.5 ml, 1.0 ml and 1.5 ml) of brown food color which produced three degrees of luminance. For each chicken, we recorded the attack latency (time from start of the trial to the first attack on the model) and the handling time (time from the first attack till the model was completely eaten). Each chicken received five baked and five unbaked prey in random order over the 10 learning sessions (one session per day) during which we expected the birds to learn that both prey types presented on either of the colored paper (yellow/brown) were edible. The order of the chickens and the food color concentration of the models were also randomized.

We used small pieces of unbaked dough in the acclimatization phase and as alternate prey in the learning phase, to ensure that the total nutritional value of the snake models and the alternate prey were equal. Although using small pieces of unbaked dough in the acclimatization phase may lead to chickens becoming familiarized with the unbaked snake prey more than with the baked prey, our intention in the learning phase was to allow the chickens to learn by the end of 10 learning sessions that all prey types (baked/unbaked models on yellow/brown paper) were equally edible.

Choice test

After the chickens had gone through the learning phase, we carried out four two-choice trials for each chicken (one trial per day) where the chicken simultaneously received a baked and an unbaked prey placed 20 cm apart at the center of the arena. We also ensured that both models were placed at approximately the same distance from the center of the arena. As in the learning phase, the baked prey had yellow underlying paper and the unbaked brown underlying paper for the color-baked associated group, while both baked and unbaked prey had brown underlying paper for the color-baked unassociated group. The prey was placed on the leaf litter without the additional smaller pieces of dough in the arena. The position (left or right) of the models and the order of the chickens for each trial were randomized. As in the learning phase, chickens were placed in the corridor, allowed to enter the arena and attack the models. We recorded the model that was attacked first and attack latency for both models.

Analyses

All analyses were carried out in R 3.3.2 (R Core Team 2016). To check if chickens showed any preference towards the two prey types, we calculated the mean attack latency for each chicken across learning trials for the baked and unbaked and carried out a non-parametric Wilcoxon signed-rank test. Since our experimental design involved repeated trials on the same chicken, we used linear mixed effect models (LMM) or generalized linear mixed models (GLMM) for our analyses using the R package *lme4* (Bates et al. 2015). We first tested for differences in attack latency and handling time between the baked and unbaked models measured during the learning phase. Since attack latency and handling time were non-normally distributed, we log-transformed the data making the residuals to be normally distributed. We fit LMMs with handling time as the dependent variable, prey type (baked/unbaked) as a fixed factor and chicken ID as a random factor (Supplementary Material, Table S2). We compared this model with a null model where handling time was not dependent on prey type using the Type II Wald Chi-square tests. To test if attack latencies varied across trials and prey type for the two treatments, we compared LMMs with log-transformed attack latencies as the dependent variable and prey type and/or trials as fixed factors along with chicken ID as a random factor. As an alternate approach, we used mixed-effect cox models to test for differences in attack latency between the baked and unbaked models in the package *coxme* (Therneau 2018). Since the latency to first attack represents the risk of attack or hazard, we used a mixed effect cox model that allows fitting a time-to-hazard response variable along with fixed and random factors as the explanatory variables. We fit mixed effect cox models with attack latency as the response variable, prey type (baked/unbaked) and experimental group (color-baking associated/color-baking unassociated groups) as fixed factors, and chicken ID and trial as random factors. We compared

the fit of these models to a null model. To check whether there was a difference between the color-baking associated and color-baking unassociated groups in terms of preference for the unbaked model (model first attacked) in the choice tests, we fit a generalized linear mixed model where the first attack was predicted by an interaction between prey type (baked/unbaked) and experimental group (color-baking associated/color-baking unassociated groups) with a binomial logit link function along with individual chicken, trial, model concentration and side of the model as random factors. We compared this model with a null model where the first attacks were not predicted by experimental group and prey type. Further, we used GLMM to test the effect of experimental group and prey type on the attack latency of the first attack of chickens in the choice tests.

Model comparisons were done using Δ Akaike Information Criterion (Δ AIC) values (Supplementary Material, Table S2, S3). We considered Δ AIC between 2 and 10 as moderate support and Δ AIC > 10 as strong support against a model (Burnham and Anderson 2002). We performed post hoc tests with Tukey contrasts to test for homogeneity across groups using the R package *multcompv*. 1.4-8 (Hothorn et al. 2008).

Results

In the learning phase, the handling time of chickens differed significantly with model type (Type II Wald Chi-square tests: $\chi^2 = 65.63$, $df = 1$, $P < 0.0001$) and was higher for the baked (mean = 35.90 ± 14.46 s) than for the unbaked models (mean = 21.41 ± 17.19 s) (Supplementary Material, Table S2, Fig. S1). There was no significant difference in the mean attack latency across learning trial between the baked and unbaked prey for each chicken in the color-baking unassociated group (Wilcoxon Signed-Rank Test: $V = 59$, $N = 13$, $P = 0.3757$) and the color-baking associated group (Wilcoxon Signed-Rank Test: $V = 53$, $N = 13$, $P = 0.6355$). In the first learning session, chickens had longer attack latencies towards the baked prey as compared to the unbaked prey in both the color-baking associated and the color-baking unassociated groups (Fig. 2). However, this difference reduced markedly in subsequent learning sessions and there was no significant difference between the attack latency for the baked and unbaked prey in both treatments (Fig. 2; Supplementary Material, Table S2), suggesting no avoidance of the underlying colored paper. Fitting different mixed-effect cox models also indicated that the null model where prey type and experimental group did not explain attack latency was significantly better than a model with an interaction between experimental group and prey type (Δ AIC = 2.73, $\chi^2 = 8.7319$, $df = 3$, $P = 0.0331$) and a model with only prey type (Δ AIC = 2.15, $\chi^2 = 4.1496$, $df = 1$, $P = 0.0416$) as explanatory variable (Supplementary Material, Table S2). The GLMM analysis on the first choices of the chickens indicated that the model with an interaction between the experimental group (color-baking associated /color-baking unassociated groups) and prey type (baked/unbaked) was significantly better than the model with only experimental group as the predictor variable (Δ AIC = 6.53, $\chi^2 = 10.53$, $df = 2$, $P = 0.005$) or the null model (Δ AIC = 4.53, $\chi^2 = 10.53$, $df = 3$, $P = 0.01$). In the color-baking associated group, where baked prey had underlying yellow paper, chickens preferentially attacked the unbaked prey first (estimate = 1.2969, $Z = 3.11$, $P = 0.01$) (Fig. 2). However, in the color-baking unassociated group, where both baked and unbaked prey had underlying brown paper, chickens were equally likely to first attack either the baked or the unbaked prey (estimate = 0.23, $Z = 0.58$, $P = 0.94$) (Fig. 2). The GLMM on attack

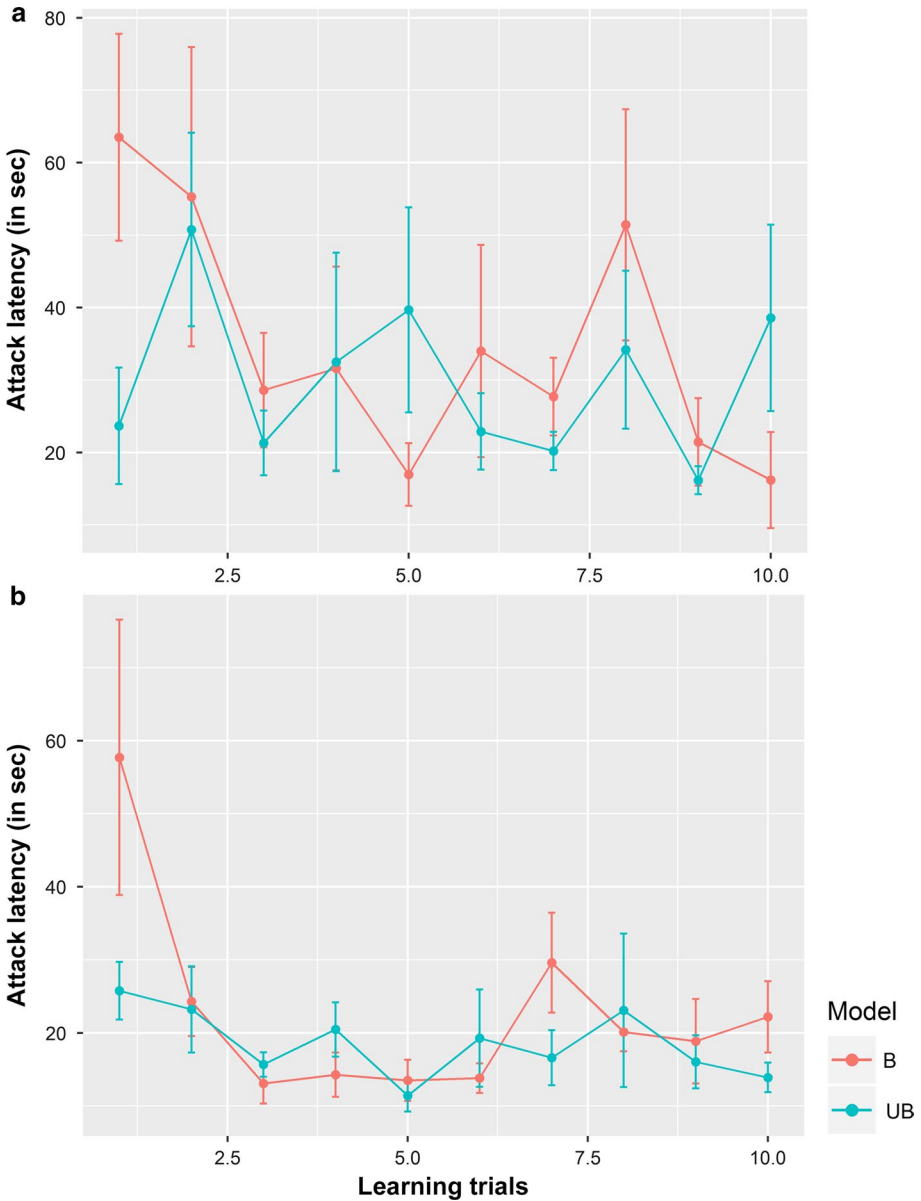


Fig. 2 Difference in attack latency between the baked (B) and unbaked (UB) dough models during the 10 learning sessions in the learning phase. **a** Attack latency in the color-baking associated group. **b** Attack latency in the color-baking unassociated group.

latencies also indicated that the model with interaction between experimental group and prey type (baked/unbaked) was significantly better than both a model with only experimental group as the predictor variable ($\Delta AIC = 106.1, P < 0.0001$) and the null model where attack latency was not determined by experimental group or prey type ($\Delta AIC = 105.3, P < 0.0001$). The best fit model indicated that prey type (estimate = -0.6913 ,

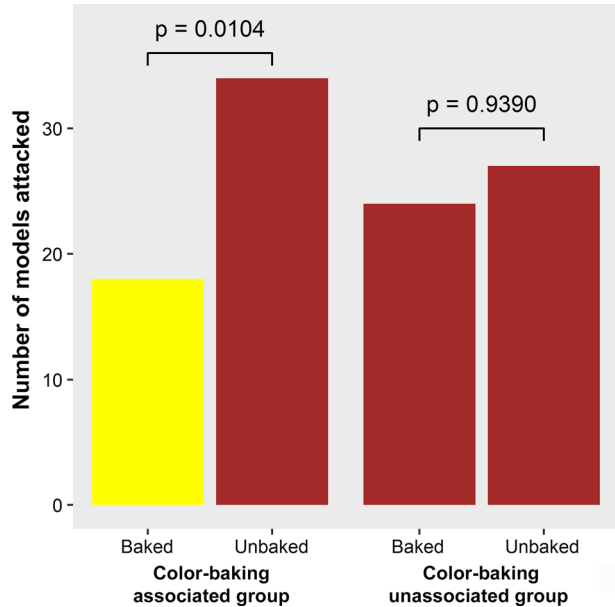
$t = -1.995$, $P = 0.05$) and the interaction between experimental group and prey type (estimate = -1.20 , $t = -2.61$, $P = 0.01$) significantly influenced attack latency.

Discussion

Our captive bird experiment demonstrates that birds can learn to preferentially avoid models with increased handling time when associated with conspicuous colors. However, we only test how advertising longer handling time can be advantageous when alternate prey are abundant, and how abundance of other profitable prey can determine predators decisions needs further evaluation. We also acknowledge that other factors such as taste, odour and nutrient value could potentially influence differential preference between the baked and unbaked prey. Although chickens have fewer taste buds than mammals, studies have indicated that chickens are sensitive to taste stimuli (Gentle 1971; Rowland et al. 2015; Liu et al. 2018; Niknafs and Roura 2018). It has been shown that birds that have ingested bitter-tasting chemicals show aversive responses such as shaking of the head, vomiting, whipping of the beak or tongue/beak movement (Gentle 1971; Ganchrow et al. 1990; Rowland et al. 2015). However, our chickens showed no aversive response towards the baked or unbaked prey. Further, in the learning phase, chickens received prey (baked/unbaked) along with small unbaked dough pieces (alternative prey). Thus, if chickens had a taste preference for unbaked dough, we would expect the time to attack the baked dough would be longer since chickens would consume the preferred unbaked dough first. However, we find no significant difference in the attack latencies between baked and unbaked prey in the learning phase, which would not be expected if chickens preferred the taste of one model over the other. Birds are also known to have a keen sense of smell (Amo et al. 2008; Caro et al. 2015; Leclaire et al. 2017a, b). If the preference towards unbaked prey in our experiments was due to odour cues, we would expect chickens to discriminate the prey based on odour and prefer the unbaked models even when the prey is not associated with any visual cues. However, we find that there was no such preference for any specific prey type in the color-baking unassociated group (Fig. 3) suggesting that discrimination of the baked and unbaked models was based on visual cues. Also, it has been shown that heat treatment of wheat grains at 70 °C or 100 °C does not decrease apparent metabolizable energy, and only heating above 85 °C can affect digestibility (O'Neill 2008). The prey used in our experiment were made of wheat dough with the unbaked prey left at room temperature and the baked prey treated at 80 °C, and are thus not likely to differ in overall nutritional quality. Given these reasons, we consider it highly unlikely that the preferential avoidance of the baked models in the color-baking associated group is influenced by taste or differences in nutritional quality, but is rather influenced by the difference in handling time between the baked and unbaked prey.

Theory predicts that predators maximize their fitness by optimizing their foraging decisions depending on the profitability of prey, by assessing the cost and benefit of attacking the prey (Krebs et al. 1974; Werner and Hall 1974; Charnov 1976; Mappes et al. 2005). Theoretical models and experimental evidence suggest that when profitable prey are encountered at high rates, predators should preferentially avoid unprofitable prey with longer handling time (Charnov 1976; Krebs et al. 1977) as in our experiments. Although it is intuitive that advertising handling time should be advantageous to the prey under such conditions, no study to our knowledge has specifically tested if predators can learn to avoid prey that honestly signal long handling time.

Fig. 3 Results of the choice tests. The bars represent the number of first attacks on the baked and unbaked dough models by domestic chickens from the color-baking associated and color-baking unassociated groups in the choice tests. The color of the bars indicates the color of the paper on which the models were placed (brown or yellow). *P* values are indicated on the top of the bars and obtained from Tukeys post hoc tests.



Although results from some studies suggest that predators associate large prey size with long handling time and hence avoid larger prey (Werner and Hall 1974; Bence and Murdoch 1986; Creswell and Mclay 1990; Cooper Jr and Anderson 2006), these studies do not control for factors such as morphological defenses associated with larger size (Whitman and Vincent 2008; Stevison et al. 2016) that could influence predator choice. On the contrary, we control for the size and mass of prey in our captive chicken experiment and provide clear evidence supporting the idea that predators can learn the relative handling time of prey when advertised using conspicuous colors. Recently Wang et al. (2018) showed that *Pachyrhynchus* weevils from Taiwan advertised their hardness to lizard predators through blue spots on their elytra. Increased hardness could also manifest as increased handling time. However, it was noted that the lizards spat out weevils soon after attacks and that the average hardness of the weevils was higher than the average bite force of the lizards (Wang et al. 2018). Although we manipulated the hardness of the snake models in our experiment, both the baked and unbaked models were easily consumed and differed only in the time required to be completely consumed (Supplementary Material, Fig. S1).

Warning signal theory has so far been centered on aposematic animals that signal toxicity (Stevens and Ruxton 2012; Rowe et al. 2017), or on spiny plants (Lev-Yadun 2001, 2009, 2016; Ruxton et al. 2004a). Although aposematism is widespread in the animal kingdom (Poulton 1890; Cott 1940; Ruxton et al. 2004a; Caro and Ruxton 2019), such a strategy does not represent the whole range of defenses that make prey unprofitable to predators. More recently, studies have suggested that prey with traits apart from toxicity, such as distastefulness, hardness and even physical structures such as spines or thorns, can benefit from advertising their unprofitability through conspicuous signals (Rojas et al. 2017; Wang et al. 2018; Winters Anne et al. 2018; Rojas et al. 2019; Caro and Ruxton 2019). Our study highlights how evolving defenses that increase the handling time of predators and signaling long handling time can itself be advantageous when alternate prey are abundant. Given that predators tend to optimize foraging efficiency depending on their internal state and

external environment (Barnett et al. 2007, 2011, 2014; Skelhorn and Rowe 2007; Endler and Rojas 2009; Halpin et al. 2013, 2014), our understanding of what makes a prey unprofitable under specific circumstances is still limited. Thus, future studies should be directed towards addressing how predators rank the profitability of different prey and under what scenarios prey benefit from advertising unprofitability.

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Author's contribution VPC conceived the study, designed and carried out the experiment, and analyzed the data; UK provided materials; VPC and UK wrote the paper and gave final approval.

Availability of data and materials All data generated or analyzed during this study are included in this published article (and its supplementary information files).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical statement All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The experimental protocol was approved by the Institutional Animal Ethics Committee of Indian Institute of Science Education and Research Thiruvananthapuram.

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