

# Predators use environmental cues to discriminate between prey

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**Abstract** The cognitive processes of predators play a central role in the evolution of prey characters. Numerous studies have shown that vertebrate predators may learn to associate the characteristics of prey (e.g. color) with the cost or benefit of ingesting them, thus forming preferences and aversions for different kinds of prey. Although the distribution and quality of prey types can differ between environmental contexts, which may make it profitable to attack a prey type in some contexts but not in others, the influence of environmental cues in decisions to attack has rarely been addressed. Recent theory suggests that modification of prey preferences by environmental cues such as microhabitat or temperature may influence the evolution of prey characteristics. Here, we show that the environmental foraging context may determine prey choice in great tits (*Parus major*) through learned association between the prey phenotype (appearance and palatability) and a contextual background cue. The same individuals were able to learn and maintain two different sets of food preferences and aversions for use in two different environmental contexts (aviaries with red or blue wooden boards), indicating a role for contextual learning in vertebrate foraging behavior.

**Keywords** Predator psychology · Cognitive ecology · Contextual learning · Associative learning · Prey preferences · Sex difference

## Introduction

Predators encounter prey types of different qualities and must discriminate between them to forage efficiently. Foraging theory predicts that a predator's decision of whether or not to include a prey type in its diet will depend on the availability and profitability of other prey types (Stephens and Krebs 1986). The relative availability of different prey types is determined by the composition of the prey community and the behavior of its member species, which is likely to vary with factors such as temperature, time of day, season and habitat. The profitability of a prey type can also vary between different contexts. For instance, many insect species sequester plant toxins (Bowers 1992; Ruxton et al. 2004), and because toxin content varies widely between plant species the host plant on which an insect prey is encountered can be informative of the prey's unpalatability (Malcolm 1992; Sword 2001). The toxin content of a prey type can also vary seasonally and with habitat type (Moranz and Brower 1998; Fordyce et al. 2005). For instance, queen butterflies (*Danaus gilippus*) have much higher cardenolide concentrations at hydric inland sites than at coastal salt marshes and xeric inland sites (Moranz and Brower 1998). Local variation in toxicity is also found among vertebrate preys that sequester toxins from arthropods (Saporito et al. 2007; Daly et al. 2008).

Since the availability as well as the profitability of prey types may vary between contexts, a predator may benefit from attacking a prey type in some contexts and ignoring it

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in others. If the prey community changes in an unpredictable manner, a predator may resort to environmental tracking and sampling of prey alternatives to adjust its foraging strategies (Stephens and Krebs 1986). However, if the changes are predictably accompanied by contextual cues, the predator may instead learn to pay attention to these cues to forage more efficiently (McLinn and Stephens 2006). Examples of such cues could be substrate or vegetation type, temperature or time of day. Theory predicts that contextual learning may affect the effectiveness of prey defenses and thus the dynamics of predator–prey interactions (Darst 2006; Holen and Johnstone 2006).

The ability to discriminate between preys is often achieved through learning; predators tend to favor profitable prey and to avoid harmful prey as a result of previous experiences with different prey types (Edmunds 1974; Ruxton et al. 2004). Predators are known to use various features of the prey when learning about its quality as food (Ruxton et al. 2004), including visual (Gittleman and Harvey 1980), auditory (Page and Ryan 2005) and olfactory (Woolfson and Rothschild 1990) cues. They may also have innate prey preferences (Ruxton et al. 2004).

Little is known about the extent to which vertebrate predators rely on contextual cues when deciding whether or not to attack prey items. Proximate properties of contextual learning have been extensively studied in experimental psychology (Bouton 1993). Contextual cues are not confined to a particular sensory modality and may be visual, olfactory or temporal. For instance, an operant study showed that pigeons can learn to peck different keys to obtain food depending on contextual light and sound conditions (Thomas et al. 1985). Similarly, rats may use light and sound to find food in a maze that is differently baited in different contexts (Shishimi and Nakajima 2007). The context constitutes any aspect of the training or testing other than the conditioned and unconditioned stimuli, and in this paper “context” refers to this definition, as commonly used in the psychological literature (e.g. Domjan 1998; for contrasting use of the term, see Gamberale-Stille and Tullberg 2001; Bateson et al. 2003). Operant conditioning techniques have also been used to test theories about environmental tracking and cue use (McLinn and Stephens 2006). Experiments using operant techniques have a high degree of empirical rigor, but the extent to which they are informative about foraging behavior is less clear (Fantino and Abarca 1985; Shettleworth 1989; Stephens 2008). To complement earlier work, there is a need for experimental studies of contextual learning in more realistic foraging settings, as well as studies of the use of contextual cues during foraging in the wild.

In the present paper, we investigate the foraging behavior of great tits (*Parus major*) subjected to changes in prey quality that coincide with changes in a contextual cue. We trained wild-caught birds to search for two visually

distinct prey types in two alternating contexts. In one context, one prey type was palatable and the other unpalatable, while in the other context this was reversed. After training, birds were tested in two experimental trials in which both prey types were palatable in order to isolate the effect of the contextual cue. If environmental context cues are effective in prey choice, we predict that birds in experimental trials will prefer each prey type in the context where it had been palatable during training and thus show reversed preferences and aversions for the two prey types in the two contexts. Alternatively, the birds may only use the visual phenotype and palatability of the prey items as cues to prey discrimination, in which case they will have to relearn the discrimination task each time the palatability of the two prey types changes. If this is the case, we predict that the birds should disregard the contextual cue and be more inclined to track the prey type that had been palatable in the last training trial (Bitterman 1975; Thomas et al. 1984; McLinn and Stephens 2006).

## Methods

### Location and prey items

The experiment was conducted at Konnevesi Research Station in central Finland during February and March 2007. Wild great tits were caught at three locations and were released at their site of capture after the experiment. For details about housing conditions and pre-training to open artificial prey items, see Ihalainen et al. (2007). Permissions for the experiment were obtained from Central Finland Regional Environment Center (KSU-2006-L-249) and the Ethical Committee of the University of Jyväskylä (35/22.5.2006).

The prey items used were small pieces of almond glued between two pieces of paper (9×9 mm) so that the paper covered the entire piece of the almond. Each item either had a black square (prey type 1) or a brown star (prey type 2) of the same size printed on both sides. The marked difference between the symbols was chosen to facilitate discrimination. Both prey types were made in palatable and unpalatable versions. Palatable items contained almond pieces with no additional flavoring. Unpalatable items contained pieces of almond that had been soaked in a chloroquine phosphate solution for 1 h (2 g of chloroquine dissolved in 30 ml of water) and dried completely before being glued to the paper. Chloroquine adds a bitter flavor to the almonds, and such items are usually rejected upon tasting by great tits, while untreated almonds are readily consumed (e.g. Alatalo and Mappes 1996). Great tits do not seem to gain knowledge about the palatability of the almond pieces concealed in prey items without opening them, since birds presented with visually identical items that vary in palatability do not

discriminate between them (Ihalainen et al. 2007; Rowland et al. 2007).

### Aviaries

Trials were conducted in two similar aviaries. They each measured 3.5×3.9×2.3 m (area × height), contained two feeding perches, and had white paper covered by a non-glossy, protective film on the floor. The floor was divided into 8×10 cells, each measuring 30×40 cm. All rows of cells in the grid were separated by wooden boards, but there were no boards separating the columns. To ensure that the aviaries were perceived as different environmental contexts by the birds, the entire boards were painted blue in one aviary and red in the other. There were nine boards per aviary, each measuring 330×7.7 cm and marked with cell coordinates. Observations were made through a one-way mirror.

### Learning experiment

The birds foraged on artificial prey in the aviaries during six training trials (T1–T6) and two subsequent experimental trials (Table 1). They had never experienced the prey or the aviaries before capture; hence, the setting represented a ‘novel world’ (Ihalainen et al. 2007). We used artificial rather than natural cues in this experiment to avoid biased responses caused by previous learning about the cues in the wild. The task presented resembles foraging since prey consumption requires searching on the aviary floor as well as prey handling similar to the opening of a seed. In nature, great tits feed partly on the ground on a diet mainly consisting of seeds and insects (Cramp and Perrins 1993). Thirty-five items of each prey type were available at the start of each trial. Preys were randomly distributed among 76 cells on the aviary floor (maximum of one item per cell) and appeared against a white background. Two cells directly

beneath each feeding perch contained no prey to avoid confusion with the remains of opened prey items. The prey distribution was known to the observer, and the prey types were, in addition, distinguishable from the point of observation in the vast majority of cases. All attacked preys were identified, and we noted the prey type and/or cell coordinate of all attacked items. Not all contact with prey was recorded as attacks. A contact event was recorded as an attack only if it involved opening of a prey item and thus handling or eating of the concealed almond. We noted the timing of attack and the time that passed between the release of a bird into the aviary and its first prey contact (latency). Birds were never trained or tested more than once per day. The eight trials were conducted on consecutive days for 76% of the birds, while the remaining birds experienced a gap day between two of the training trials. No birds experienced a gap day between the ultimate training trial and the first experimental trial or between experimental trials.

The context (i.e. aviary with red or blue wooden boards) experienced in odd-numbered and even-numbered training trials is referred to as primary and secondary, respectively. Each context was experienced three times during training, in alternating sequence with the other context (Table 1). One prey type was palatable and one was unpalatable in each trial during training. The prey type that was palatable in the primary context was unpalatable in the secondary context and vice versa. Birds had to attack 30 items in each training trial, irrespective of palatability. There were two experimental trials for each bird, one in each context. During the experimental trials, all prey items were palatable in order to isolate the effect of the contextual cue, and birds had to attack ten items before the trial was terminated. Fourteen birds experienced the primary context before the secondary during experimental trials, while 15 birds experienced the secondary context before the primary (Table 1).

**Table 1** The experimental setup

Trial	Palatability B1–B4	B1 (n=4)	B2 (n=3)	B3 (n=3)	B4 (n=4)	Palatability B5–B8	B5 (n=3)	B6 (n=4)	B7 (n=5)	B8 (n=3)
T1	P:■, U:★	Red	Blue	Red	Blue	P:★, U:■	Red	Blue	Red	Blue
T2	P:★, U:■	Blue	Red	Blue	Red	P:■, U:★	Blue	Red	Blue	Red
T3	P:■, U:★	Red	Blue	Red	Blue	P:★, U:■	Red	Blue	Red	Blue
T4	P:★, U:■	Blue	Red	Blue	Red	P:■, U:★	Blue	Red	Blue	Red
T5	P:■, U:★	Red	Blue	Red	Blue	P:★, U:■	Red	Blue	Red	Blue
T6	P:★, U:■	Blue	Red	Blue	Red	P:■, U:★	Blue	Red	Blue	Red
E1	P:■, P:★	Red	Blue	Blue	Red	P:★, P:■	Red	Blue	Blue	Red
E2	P:■, P:★	Blue	Red	Red	Blue	P:★, P:■	Blue	Red	Red	Blue

Each bird was allocated to one of eight blocks (B1–B8) and underwent six training trials (T1–T6) and two experimental trials (E1–E2). In each trial, a bird was presented with prey type 1 (■) and prey type 2 (★) in one of two contexts (red or blue). During training trials, one of the prey types was palatable (P) and the other prey type was unpalatable (U). During experimental trials, both prey types were palatable

## Sample and statistics

Each training trial was completed when the bird had attacked 30 prey items, irrespective of palatability. Twenty-nine birds (12 females and 17 males) completed all six training trials and were included in the experiment. All of these completed the experimental trials. Their training trials lasted  $72 \pm 46$  min, and their experimental trials lasted  $29 \pm 27$  min (mean  $\pm$  SD). Trials in which birds showed signs of exhaustion or distress were terminated for ethical reasons to avoid starvation or injury. Birds that thus did not complete the training were excluded from the experiment and released after having been fed and rested. In total, 21 birds were excluded. Six of the excluded birds (four males, two females) did not approach prey at all during a trial or during pre-training in the home cage. In addition, 14 excluded birds (six males, eight females) did not learn to forage preferentially on the palatable prey type during a prolonged training trial ( $174 \pm 56$  min), but instead foraged preferentially on the unpalatable prey type. Such behavior always resulted in a failure to attack a total of 30 items and hence exclusion for ethical reasons, and it happened most frequently during the second training trial (once during the first training trial, ten times during the second, twice during the third, once during the fourth). Finally, we excluded one male due to a leg injury.

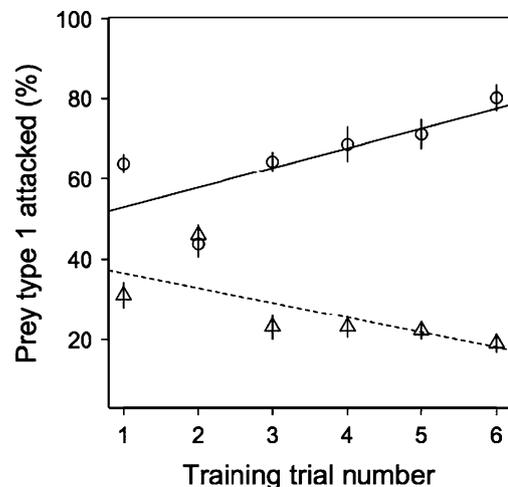
To compare the performance of the same bird over several trials, we used linear mixed-effect models (LMEs) with bird identity as the random effect (Pinheiro and Bates 2000). The LMEs on training data had 174 observations and 29 groups, the LME on data from the experimental trials had 58 observations and 29 groups. To test for the effects of context on prey discrimination, we used the proportion of the prey attacked that was of type 1 as the response. Although prey type 2 was slightly favored over prey type 1, our test of the effect of context was not influenced by the prey type used as response: Since a fixed number of preys was attacked in each trial, the difference in the proportion of prey type 1 taken when type 1 was palatable and unpalatable equals the difference in the proportion of prey type 2 taken when prey type 2 was palatable and unpalatable, respectively. Because the design was also balanced, the prey type used as the response was an arbitrary choice.

Initial models on the effect of context on prey discrimination included the following stimulus variables: palatability of prey type 1 in the corresponding context during training, sex, date, age (for details on aging, see Jenni and Winkler 1994) and trial number, plus interactions between palatability of prey type 1 and trial and sex. The models using data from the experimental trials had two additional stimulus variables: whether the trial was in the primary or secondary context and the order of the primary and secondary context in the experimental sequence, with their interactions with palat-

ability of prey type 1. Models were reduced by backwards elimination and alternative models were compared in likelihood-ratio tests. When models contained a significant interaction, we tested the corresponding main effects in separate models for each level of the interacting factor. Since the approximation of the denominator degrees of freedom in LMEs is debated, we calculated LME  $p$ -values by Markov chain Monte Carlo (mcmc) simulations, generating 10,000 samples from the posterior distribution of the parameters (Baayen et al. 2008).  $F$ -ratios generated from LMEs are denoted  $F_{\text{LME}}$  and have a corresponding  $p$ -value denoted  $p_{\text{mcmc}}$ . Data that were not repeatedly sampled from the same individuals were tested with linear regressions or unpaired  $t$ -tests. All tests were two-tailed and the  $\alpha$ -level was 0.05. Statistical modeling was done with R 2.4.0 using the *lme4* package (R Development Core Team 2006).

## Results

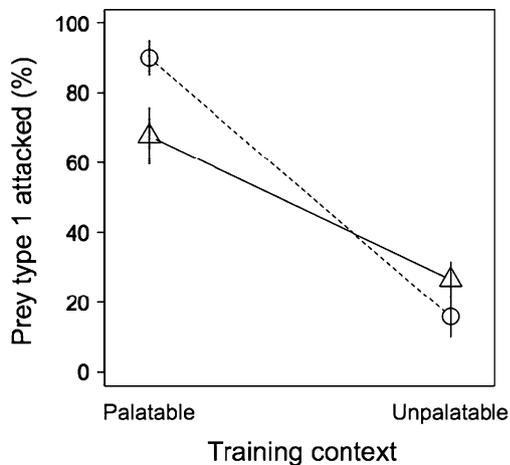
Individual great tits learned to use the contextual cue to switch prey preferences between training trials when the palatability of the prey types switched (Fig. 1). They clearly preferred palatable over unpalatable prey in the first training trial ( $F_{1, 26} = 57.00$ ,  $p < 0.0001$ ). The second training trial was the first time the birds had to switch prey preference. This was a particularly difficult task for them, and they did not attack significantly more palatable than unpalatable prey in this trial ( $F_{1, 26} = 0.65$ ,  $p = 0.43$ ). However, in subsequent training trials, they attacked significantly more



**Fig. 1** Discrimination learning during training. Twenty-nine great tits went through six training trials. Each bird experienced that the palatability of prey types 1 and 2 alternated in consecutive trials, in sequence with a contextual cue. Shown are the percentages of the total number of attacked prey that was of type 1 in trials where prey type 1 was palatable (circles, solid best fit line) and in trials where it was unpalatable (triangles, dashed best fit line). Points and bars indicate means  $\pm 1$  SE, respectively

palatable than unpalatable prey (T3:  $F_{1, 26}=91.24$ ,  $p<0.0001$ ; T4:  $F_{1, 26}=64.81$ ,  $p<0.0001$ ; T5:  $F_{1, 26}=123.93$ ,  $p<0.0001$ ; T6:  $F_{1, 26}=199.84$ ,  $p<0.0001$ ). Training resulted in learning, since the difference in the proportions of attacked prey that was palatable and unpalatable generally increased as training progressed ( $F_{LME}=27.22$ ,  $p_{mcmc}<0.0001$ ; Fig. 1). During training, there was no difference between males and females in the proportions of attacked prey that was palatable and unpalatable ( $F_{LME}=0.29$ ,  $p_{mcmc}=0.57$ ). The change across training trials in the difference between the proportions of attacked prey that was palatable and unpalatable did not differ between the sexes (i.e. the three-way interaction between sex, palatability of prey type 1 and training trial number;  $F_{LME}=0.65$ ,  $p_{mcmc}=0.79$ ). There was no difference between the sexes in latency to attack the first prey item in the first training trial (unpaired  $t_{27}=1.04$ ,  $p=0.31$ ) or in the time spent completing the first training trial once feeding had started ( $t_{27}=1.53$ ,  $p=0.14$ ).

During the subsequent experimental trials, in which both prey types were palatable, great tits still preferred prey type 1 over prey type 2 in the context where prey type 1 had been palatable during training and preferred prey type 2 over prey type 1 in the other context (males:  $F_{LME}=33.65$ ,  $p_{mcmc}<0.0001$ ; females:  $F_{LME}=118.10$ ,  $p_{mcmc}<0.0001$ ; primary context:  $F_{1, 26}=8.38$ ,  $p=0.008$ ; secondary context:  $F_{1, 26}=169.04$ ,  $p<0.0001$ ; Fig. 2). This demonstrates that the great tits were able to use the information given by the environmental context in prey discrimination. Both males and females clearly used the environmental context cue during experimental trials, but



**Fig. 2** Use of the contextual cue during experimental trials. Both prey types were palatable during the experimental trials. Great tits avoided attacking a given prey type in the context where it had been unpalatable during training but preferred it in the context where it had been palatable. The preferences are expressed as the mean  $\pm$  SE percent of prey type 1 attacked in the context where it had been palatable versus the context it had been unpalatable during training. Female (circles, dashed line,  $n=12$ ) and male (triangles, solid line,  $n=17$ ) prey choice is shown separately

female behavior was more strongly determined by it ( $F_{LME}=9.11$ ,  $p_{mcmc}=0.01$ ; Fig. 2). The great tits performed better during experimental trials in the secondary than the primary context ( $F_{LME}=13.72$ ,  $p_{mcmc}=0.0002$ ). However, there was no significant difference in performance between great tits that experienced the primary context before the secondary in experimental trials and those that experienced the secondary first ( $F_{LME}=0.30$ ,  $p_{mcmc}=0.48$ ). This shows that the birds did not use the temporal sequence of the changing stimuli during training as a cue for prey discrimination. The birds attacked similar proportions of the prey type that was palatable according to the contextual cue in the first and in the second experimental trial ( $F_{LME}=0.01$ ,  $p_{mcmc}=0.88$ ). This shows that the birds during experimental trials were not tracking the prey type that had been palatable during the ultimate training trial.

## Discussion

This study supports the hypothesis that predators can use environmental context cues in prey discrimination. The palatability of the two prey types was reversed between contexts during training, and we hypothesized that the birds could avoid overconsumption of unpalatable prey either by paying attention to the contextual cue or by relearning the discrimination task each time the palatability switched and the preferred prey type turned unpalatable. In the experimental trials, in which both prey types were palatable, individual birds reversed their preferences and aversions for the two prey types according to the contextual cue, clearly preferring the prey type that had been palatable in the given context during training. It is therefore clear that foraging behavior had become strongly influenced by the contextual cue. There was no evidence for resource tracking of the prey type that had been palatable in the ultimate training trial, since birds attacked similar proportions of the prey type that was palatable according to the contextual cue in the first and in the second experimental trial.

Resource tracking of the prey type that had been palatable in the previous training trial was prominent during early training. In the second training trial, the birds attacked a similar proportion of palatable and unpalatable prey. The first preference reversal (which happened in the second training trial) seemed to be a particularly salient learning experience, since the birds later generally performed better during experiments in their secondary than their primary context. Perhaps the contextual learning was enhanced by the unpleasant experience of attacking so many unpalatable prey items during the second training trial. As training progressed, the birds got better at associating the palatability of the prey types to the contextual cue, and resource tracking waned.

Our results show that great tits' prey preferences and aversions were fully reversed from one context to the other, documenting an active association between the context and the prey appearance and palatability as experienced during training. Individual birds clearly learned and maintained different sets of prey preferences and aversions for use in different environmental contexts. Our findings are in line with current knowledge in experimental psychology, which suggests that the associations between conditioned and unconditioned stimuli may be hierarchically controlled by other cues (Pearce and Bouton 2001). It has previously been shown that context may influence prey preferences in invertebrates. In one study, spiders learned to avoid distasteful prey in one context but did not retain the learned association in another context (Skow and Jakob 2006). This is in contrast to our findings, where the birds at first clearly generalized across contexts: The association between prey type and palatability that was acquired in the first training trial was transferred to the different context of the second training trial, as made evident by the birds' difficulties in switching preferences. Bees have also been shown to use contextual cues when making foraging decisions (Gould 1987; Collett and Kelber 1988). In a study of color vision, worker bumblebees were trained in two alternating light conditions to forage on artificial flowers containing rewarding and aversive solutions (Lotto and Chittka 2005). Yellow flowers were rewarding and blue flowers aversive in one context, while blue flowers were rewarding and yellow ones aversive in the other. During test trials, the flowers were non-rewarding, and the preference for flower color was controlled by the contextual cue.

McLinn and Stephens (2006) tested hand-raised blue jays (*Cyanocitta cristata*) in an operant chamber to investigate whether foragers should pay attention to environmental cues or perform environmental tracking under environmental uncertainty. In each trial, the birds chose between pecking two differently colored keys to obtain a reward (or not) after first having observed a third signal key. The probability by which a certain key color was rewarding was interpreted as the degree of environmental certainty, while the probability by which a third signal key was of the same color as the rewarding key was interpreted as the reliability of an environmental cue. The birds paid attention to the cue when it was reliable and the environmental certainty was low but ignored it as environmental certainty increased (McLinn and Stephens 2006). The use of the same color in the signal key and one of the response keys makes the interpretation of them as representing an environmental cue and a prey type slightly problematic. In our experiment, the contextual cue did not overlap as much with the prey items but was more firmly placed in the background. Moreover, we believe that our study contributes a somewhat more natural foraging setting, in which wild birds foraged on artificial prey items in a fashion that resembled their foraging behavior in the wild.

Some great tits were excluded from our experiment for ethical reasons, mainly during early training. The majority of excluded birds did not approach novel prey or did not switch preference between trials. Note that the inclusion criterion (i.e. to attack 30 prey items, irrespective of palatability) in no way required the birds to use the contextual cue. Perhaps the experimental approach adopted here masked an ability to solve the task at hand among some birds. More extensive pre-training to approach and open artificial prey and/or less distasteful unpalatable prey during training may have resulted in a fewer exclusions.

We found an unexpected sex difference in the use of contextual cues during experimental trials. Additional work is needed to verify this finding. A higher fraction of females than males were excluded from the experiment for ethical reasons, and if the tendency to perform behavior leading to exclusion is positively correlated with low performance in experimental trials such exclusions could potentially have introduced a bias regarding sex differences. Previous studies in the same laboratory with discrimination tasks that do not involve the use of environmental cues have not revealed any sex difference in prey choice (J. Mappes, unpublished data). A recent study showed that individual variation in reaction to aposematic prey is associated with personality type in great tits (Exnerova et al. 2010). Future work aimed at explaining individual variation in the use of contextual cues should therefore also control for personality traits.

We conclude that great tits can learn to use environmental cues in prey discrimination. Moreover, we have shown that they are able to maintain different sets of preferences and aversions for the same prey types for use in different environments. Great tits are generalist predators that use a range of microhabitats and experience variations in the abundance of prey types (Hinde 1952; Perrins 1979). Such properties may favor behavioral flexibility of the kind shown in this study. Although vertebrate predators are likely to experience variation in the availability and/or profitability of prey, and we have shown that great tits are able to use contextual cues that are informative of such variation in an experimental foraging-like setting, we do not yet know the extent to which predators rely on contextual cues when foraging in nature. Hence, more research is needed to better understand the functional significance of contextual learning in foraging ecology.

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**Conflicts of interest** The authors declare no conflict of interest.

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