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ORIGINAL ARTICLE

Diet cues alter the development of predator recognition templates in tadpoles

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Abstract

Recognising predators accurately is key to making fine-scale adjustments to behaviour that enhance survival and maximise overall fitness for prey. Prey incorporate information from specific predator features in order to recognise predators and the risk they pose. For olfactory cues, prey can use both predator odour and diet cues to recognise predators. The role of diet cues in predator recognition has only been tested when they provide information about risk and act as an unconditioned stimulus. Thus, it is unclear whether prey use diet cues in the development of more general predator recognition templates. Here, we tested whether diet cues that contain no apparent information about the prey's vulnerability to the predator are used by prey when they learn to recognise predators. We trained predator-naive wood frog tadpoles (*Lithobates sylvaticus*) to recognise the odour of a novel crayfish (*Orconectes virilis*) as risky by pairing tadpole alarm cues with the odour of crayfish fed one of two diets: alfalfa pellets or earthworms (*Lumbricus* sp.). We tested tadpoles from each group for their response to one of the two crayfish diet odour combinations or a water control. Tadpoles displayed antipredator responses to crayfish odour, irrespective of diet. However, their responses were stronger when tadpoles were exposed to crayfish fed the same diet as during training. Such results demonstrate that diet cues play a previously unrecognised but subtle role in predator recognition and suggest that flexibility in prey choice can lead to an advantage for the predator.

Significance statement

Recognising predators and the threat they pose is critical for prey to adjust their behaviour in response to fluctuations in predation risk. There is therefore a need to understand how prey use different cues to develop effective recognition templates that allow for threat-sensitive adjustments to behaviour. Here, we demonstrate that diet cues of predators contribute to the development of predator recognition templates by prey. These results provide new information about how prey develop recognition templates for predators and that, by incorporating diet cues, they are able to adjust their responses to variable risk posed by different predators within a population. Additionally, we suggest that generalist diets may provide unrecognised benefits to predators when switching between prey types.

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Introduction

Many prey are able to adapt and respond to predation risk as it changes in intensity and frequency through time and space (Lima and Bednekoff 1999; Sih et al. 2000). Those individuals that are better able to recognise risky situations and effectively implement the appropriate antipredator response should

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enhance their chances of surviving to reproduce (Helfman 1989; Lima and Bednekoff 1999). The fact that prey are exposed to predators that come and go over time or target specific life stages means that learning about predators and their associated risks is an adaptive response to variability in predation risk (Griffin 2004; Kelley and Magurran 2006). Learning often occurs via associative conditioning, where prey encounter the sight or smell of an unknown predator (conditioned stimulus) paired with a conspecific alarm call or a chemical alarm cue (unconditioned stimulus), both of which elicit a fright response and label the predator a threat (Kelley and Magurran 2006; Ferrari et al. 2010a). By learning about predators, prey are able to adjust their antipredator responses as the risk associated with the predator changes through time (Lima and Bednekoff 1999; Brown et al. 2001). This includes the extinction of responses (forgetting) to predators that are no longer a threat (Ferrari et al. 2010a, 2012).

Acquiring pertinent information is key for prey to develop optimal responses to predators as individuals with more information about variables within their environment will be able to make better-informed decisions about how to manage danger (Dall 2010). Whilst we know much about how prey develop effective responses to risk (Lima and Bednekoff 1999; Sih et al. 2000; Kelley and Magurran 2006; Ferrari et al. 2010a; Brown et al. 2013), less is known about the specific features prey use when learning to recognise predators. A look at the predator recognition literature suggests that not all information available from predators is equal and that different species focus on certain cues whilst ignoring others. For visual features, prey appear to preferentially focus on those that specifically relate to predatory functions, such as the morphology of eyes and their position on the head (Karplus et al. 1982; Beránková et al. 2014), size and shape of the mouth (Karplus et al. 1982), size/shape/silhouette of the body (Engstrom-Ost and Lehtiniemi 2004; Stankowich and Coss 2007; Brown et al. 2011) and posture/orientation (Helfman 1989; Cooper 1998; Schluessel et al. 2014). Experimentally modifying these features can significantly impact antipredator responses of prey, whilst modifying non-functional features has little or no effect (Karplus et al. 1982; Beránková et al. 2014). Furthermore, these features can be used to recognise novel predators that share similar features with a known predator (Griffin et al. 2001; Kullberg and Lind 2002; Stankowich and Coss 2007; Brown et al. 2011). In aquatic systems, olfactory cues are a primary means by which prey recognise predators, and both the predator-specific odour (the odour unique to that species) and diet cues (cues that are emitted as a by-product of digestion) have been shown to play important roles in how prey learn to recognise predators. Generally, the role of these two cues in predator recognition have been considered independently, and it is unclear how the two cue types are used when prey learn to recognise predators.

Diet cues are thought to be a distinct set of cues from predator odours. Consequently, they provide independent information through which prey are able to assess predation risk and recognise predators (Chivers and Mirza 2001; Ferrari et al. 2010a). Prey innately respond to a wide range of diet cues that vary in the type information they provide about predation risk (reviewed in Scherer and Smee 2016). For example, some cues are very general in the information they provide and simply label an unknown species as carnivore (Fendt 2006; Ferrero et al. 2011). Other diet cues are more specific, allowing prey to recognise whether a predator has recently eaten a conspecific (Chivers et al. 1996), closely related species (Schoeppner and Relyea 2009) or a prey guild member (Pollock et al. 2003). Whilst these cues provide different types of information, the response they elicit in prey species will depend on their capacity to predict future attacks by predators (Scherer and Smee 2016). Beyond their role as direct indicators of predation risk, diet cues can also be used by prey when learning to recognise novel predator odours (Mathis and Smith 1993; Chivers et al. 1996). Interestingly, diet cues may still influence how prey assess risk even if they contain no innately recognisable information regarding predation risk. For example, lemon damselfish (*Pomacentrus moluccensis*) used diet cues to distinguish between novel predators and non-predators when generalising recognition from a known predator (Mitchell et al. 2015). Irrespective of their actual predatory status, damselfish only recognised novel species that had been fed the same diet as the known predator. This was despite the fact that the diet cues (distantly related fish species and squid) were novel and contained no known information about predation risk. The results suggested that damselfish use both diet cues and predator odours when learning to recognise predators.

If prey also learn about novel diet cues when learning to recognise predators, then to what extent does the presence or absence of those same diet cues alter prey responses during future encounters with those predators? Diet cues have been shown to inhibit recognition of novel predators via generalisation in damselfish when the novel predator was fed a different novel diet from the known predator (Mitchell et al. 2015). It seems unlikely that changes to a known predator's diet should have such dramatic effects on prey antipredator responses during future encounters with the predator. However, diet cues might alter recognition of the predator in a way that allows prey to fine-tune antipredator responses and enhance their chances of survival. Diet cues may also provide a mechanism through which predators are able to mask or manipulate their odours and, therefore, levels of vigilance in their prey. Indeed, it has been suggested that switching between prey types may provide benefits to generalist predators via the manipulation of diet cue-related risk assessment by prey (Lima et al. 2003).

Diet cues clearly influence predator–prey dynamics, yet it is unclear whether they are also used by prey when learning about predators. Here, we tested whether the diet of a predator during a learning event altered antipredator responses during subsequent encounters with the predator when fed a different diet. To do this, we conditioned tadpoles to recognise novel predatory crayfish (*Orconectes virilise*) that had been fed one of two diets (earthworms, *Lumbricus* sp., or alfalfa pellets) by pairing crayfish odour with a tadpole alarm cue. We then tested tadpoles conditioned to one of the two crayfish diet combinations for their behavioural response to one of three odours (crayfish fed earthworms, crayfish fed alfalfa pellets or a water control). We predicted that if tadpoles used both diet cues and kairomones to learn about predators, then they should display a greater response to the odour of the predator fed the learned diet than to the odour of the predator fed the alternative diet. If tadpoles only learn about predator odour, then different predator diet cues will have no effect on the way prey respond to the predator.

Methods

Larval rearing and predator maintenance

Freshly laid egg clutches were collected from local ponds and divided between four 380-L troughs filled with conditioned well water that had been seeded with algae and plankton. This water contained odours from natural ponds, but lacked any predator odours. Once the tadpoles hatched, alfalfa pellets and Tetramin flakes were provided to the tadpoles to supplement the algae present in the pools. Tadpoles were left to develop for 3 weeks, at which point they were removed from the pools, mixed together and randomly assigned to one of twenty 7.4-L pails containing 5 L of conditioned well water and some food (Tetramin flakes and alfalfa pellets).

Crayfish were selected as the novel predator as they are a non-native species that local wood frog population have no experience with (Hanson et al. 1990) and are known to eat tadpoles (Gherardi et al. 2001; Gomez-Mestre and Diaz-Paniagua 2011). Crayfish were fed either earthworms or alfalfa pellets. Diets were chosen to represent two ecologically distinct diets (invertebrates and plant detritus) that are commonly consumed by omnivorous crayfish (Parkyn et al. 2001) and that lacked cues about predation risk to which tadpoles respond innately. Crayfish were housed in individual 10-L aquaria and fed pellets once a day prior to the onset of the experiment protocol.

Cue production

The crushed tadpole cues were prepared by first euthanizing tadpoles with a rapid blow to the head (UCACS protocol 2015031), pulverising their bodies with a mortar and pestle, and filtering and diluting the solution in 20 mL of water. The solution was then used shortly after preparation during conditioning. For the conditioning phase, crushed tadpole cues were produced at a concentration of three tadpoles per 20 mL.

To produce the crayfish odours, four crayfish (two per diet) were kept in individual 3.5-L pails containing 2 L of conditioned well water and fed equal amounts of either alfalfa pellets or earthworms every day for 4 days prior to making the cues for conditioning. Crayfish are able to clear their foregut within 9 h (Loya-Javellana et al. 1995), suggesting that crayfish would have completely evacuated their guts over the 4 days and removed any residual diet cues from previous diets. One hour after the final feeding, crayfish were moved to a clean pail containing 1 L of water and were left for 24 h. Prior to conditioning or testing, equal amounts of water were removed from each of the four crayfish pails and the water from crayfish fed the same diet was mixed together for our stock solution.

Experimental protocol

Tadpoles were left to acclimate in pails (15 tadpoles per pail) for 24 h prior to the conditioning phase. Pails were assigned to one of two conditioning treatments for the conditioning phase, which consisted of an exposure to 20 mL of crushed tadpole cues paired with either 20 mL of worm-fed crayfish odour or 20 mL of alfalfa-fed crayfish odour. Tadpoles were then left undisturbed for 1 h (between ~1600 and 1700 hours), after which, each pail received a complete water change. To demonstrate that learning has occurred, a conditioning control is normally required (a false or pseudo-group). However, we have published numerous papers demonstrating that this population do not innately recognise natural or invasive predators, but learn to recognise predators using the protocol described (Ferrari et al. 2010b, 2012; Chivers and Ferrari 2013, 2014; Ferrari and Chivers 2013; Chivers et al. 2015). To reduce the number of tadpoles used, we excluded the conditioning control group in this instance. A total of 149 tadpoles were conditioned.

The day following conditioning, tadpoles from both conditioning treatments were tested for their response to one of three odours: worm-fed crayfish odour, alfalfa-fed crayfish odour or a water control (this produced six test groups; two conditioning treatments × three test odours). Individual tadpoles were placed into 0.5-L cups and left to acclimate for an hour prior to testing. Behavioural observations were conducted during a 4-min pre- and a 4-min post-stimulus injection observation. Following the pre-stimulus observation, 5 mL of one randomly assigned odour was carefully injected on the side of the cup and the post-stimulus observation began immediately. Each tadpole was exposed to one cue only. The observer was blind to both conditioning treatment and the

testing odour ($n = 16–28$ tadpoles per test group). During observations, tadpole activity (number of times they crossed the midline of the cup) was measured. Activity levels are a well-established measure of antipredator behaviour in larval amphibians as they reduce activity in response to predation cues (Ferrari et al. 2009, 2010a).

Statistical analysis

We used a two-way repeated measures analysis of variance (ANOVA) to test the effects of conditioning (crayfish fed worms vs. crayfish fed alfalfa pellets) and test odour (crayfish fed worms vs. crayfish fed alfalfa pellets vs. water) on the activity of tadpoles through time (pre- and post-behavioural observations as repeated measures). As tadpoles were conditioned in groups within each pail, we included pail as a nested factor to account for the lack of independence amongst the tadpoles from the same conditioning group.

Due to a significant interaction between conditioning, test odour and time, we split the analysis by conditioning treatment and ran two one-way repeated measures ANOVAs testing for the effects of test odour on activity levels through time, with pail included as a nested factor. Paired t tests with a Bonferroni correction were used to explore significant effects of cue. Data met parametric assumptions.
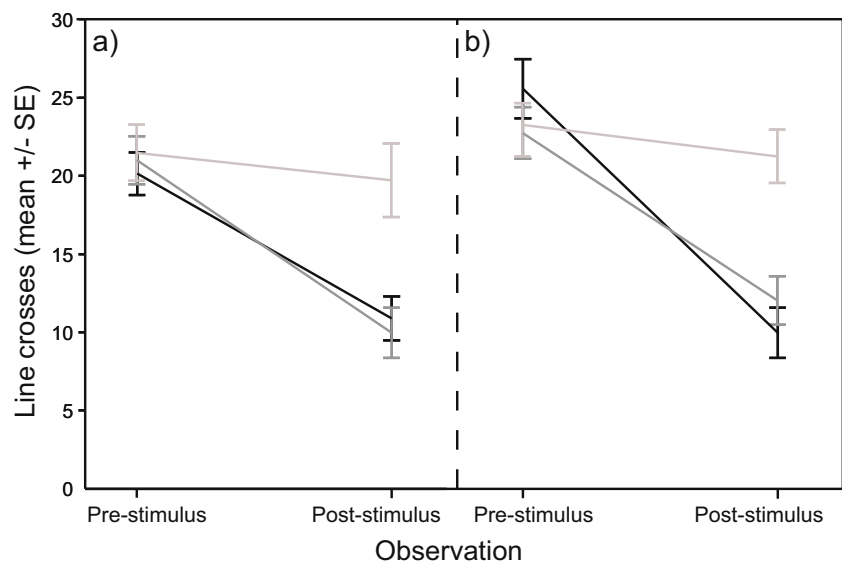
Results

The behaviours of tadpoles were affected by an interaction between conditioning and test odour and time ($F_{2,129} = 3.225$, $p < 0.05$; Supplementary Table 1). Further analysis showed that the test odour had a significant effect

on the activity levels of tadpole conditioned with crayfish fed earthworms (one-way repeated measures ANOVA: $F_{2,61} = 16.6$, $p < 0.0001$) and tadpoles conditioned with crayfish fed alfalfa pellets ($F_{2,68} = 8.05$, $p < 0.001$). Tadpoles from both conditioning groups showed a greater reduction in activity (~45–60 %) after being exposed to either of the crayfish odours compared to tadpoles exposed to water (<10 % reduction, all $p < 0.005$; Fig. 1). The interactions stem from the fact that tadpoles conditioned with crayfish fed earthworms showed a greater reduction in activity when exposed to crayfish fed earthworm odour compared to crayfish fed alfalfa pellets ($F_{1,46} = 5.13$, $p < 0.05$), whilst tadpoles conditioned with crayfish fed alfalfa pellets showed a different pattern, displaying similar reduction in activity to both odours ($F_{1,45} = 0.64$, $p = 0.43$).

Discussion

Recognising predators and the risk they pose is a fundamental prerequisite for effective predator evasion. Here, we demonstrate that prey use both predator odour and diet cues when learning to recognise predators and show that changes in a predator's diet can alter how prey respond to predators during future encounters, even when the diets appear to contain no relevant information to the prey about predation risk. Tadpoles displayed a strong antipredator response (reduction in activity) when exposed to either crayfish odour, irrespective of the crayfish diet cues experienced during conditioning. Tadpoles did not respond to the water controls. Importantly, tadpoles showed a greater reduction in activity (~20 %) to odours of crayfish fed the known diet (i.e. the one they were conditioned to recognise) compared to the odours from crayfish fed the

Fig. 1 Mean activity (±SE) of wood frog (*Lithobates sylvaticus*) tadpoles before and after exposure to the odour of crayfish (*Orconectes virilis*) fed alfalfa pellets (*black bars*), crayfish fed earthworms, (*Lumbricus* sp.; *dark grey bars*) or a water control (*light grey bars*). Tadpoles were initially conditioned to recognise crayfish as a predator by pairing injured tadpole cues with odour from crayfish fed either alfalfa (**a**) pellets or earthworms (**b**)

alternative diet; however, the differences in response to cray-fish diet cues were only significant for tadpoles conditioned with crayfish fed earthworms. These results suggest that tad-poles incorporate information from diet cues when learning about novel predators. Furthermore, the results suggest that prey may be able to obtain pertinent information about the current threat posed by a predator and that prey use such cues to refine their antipredator responses.

Studies have demonstrated that prey can learn to recognise almost any novel odour as a risk, including ecologically irrel-evant odours, when paired with a chemical alarm cue (Leduc et al. 2007; Ferrari et al. 2010a). We might have expected prey to incorporate diet cues into the characteristics of a predator signature they learn. However, rather than using all available cues, prey may be predisposed to use cues that directly pro-vide information about predation risk (Karplus et al. 1982; Beránková et al. 2014). These studies suggest that prey have undergone selection to only use cues that enhance decision-making about predation risk and ignore cues that do not offer relevant information. The presence of conspecifics in diet cues clearly provides information about predation risk (Chivers and Mirza 2001), but as shown here and in a previous study (Mitchell et al. 2015), diet cues still affect how prey respond to predators, even when diet cues contain no predation risk cues that are innately recognised by prey. This suggests that in the absence of direct predation cues, diet cues provide ecolog-ically relevant information about risk. The information from such diet cues may allow prey to adjust responses based on intraspecific variation in the level of risk posed by predators (Scherer and Smee 2016). Many species that are considered generalist predators actually comprised individual specialist predators that only target a subset of prey species consumed by the population as a whole (Bolnick et al. 2003). For exam-ple, sea otters (*Enhydra lutris*) show intraspecific diet prefer-ences that are maintained along matrilines (Estes et al. 2003). Similarly, wolf spiders (*Hogna helluo*) show a greater prefer-ence for the odour of prey that it has recently consumed (Persons and Rypstra 2000). Such preferences for certain prey can last for several months (Bryan and Larkin 1972) and sug-gest that the risk of being attacked by a given predator within the population may not be equal amongst predators with dif-ferent diet preferences. Altering antipredator behaviours in response to changes in predator diets represents an adaptive response to predator foraging strategies and provides a fitness benefit to the prey. The influence of diet cues on the antipred-ator responses of prey should, therefore, be directly dependant on the frequency with which predators switch between differ-ent prey types. For example, diet cues may have a large effect on prey responses to predators if predators show strong pref-erences for specific prey and only occasionally switch be-tween different prey species. Conversely, diet cues may have little effect on antipredator responses if predators frequently/opportunistically switch between different prey species.

From the predators' perspective, the presence of diet cues might have a negative impact on optimal foraging strategies and capture success rate. To counter this, predators should de-velop behaviours/mechanisms that minimise detection or ma-nipulate the information available from diet cues. For example, by manipulating their diet cues, predators may gain significant advantage during interactions with prey, where the outcome of predation events can be determined by a few milliseconds dif-ference in prey responses (Domenici 2010; Domenici et al. 2011). In fact, optimal foraging models that include responsive prey show that switching between different prey allows gener-alist predators to reduce prey vigilance and increase foraging success to the point where they outperform specialist predators (Lima et al. 2003). Lima et al. (2003) suggested that altering information from diet cues might be a primary means through which predators could manage prey vigilance. In support of this idea, Northern pike (*Esox lucius*) have been shown to selective-ly defecate away from their foraging sites in order to avoid detection by prey (Brown et al. 1995). Studies have also shown that certain predators may be able to prevent prey from recognising them through olfactory cues, but as yet, it is un-known how they are able to do so (Lonnstedt and McCormick 2013; Resetarits and Binckley 2013).

The fact that alterations to diet cues reduced antipredator responses but did not prevent recognition suggests that recog-nition is based primarily on predator kairomones and the diet cues add secondary information that modifies responses along a generalised gradient, as suggested by Mitchell et al. (2015). Understanding how diet cues alter antipredator responses may depend on how predators process the metabolites of their prey. If the diet directly alters the predators' odour, then prey will learn diet cues and kairomones as a single cue. In subsequent encounters, responses will depend on the prey's ability to gen-eralise recognition from a known odour to a similar odour. Alternatively, diet cues may be independent of predator kairomones, simply passing through the digestive system without altering the predators' odour. The fact that prey are able to recognise heterospecific alarm cues learnt by detecting them in the diet of predators suggests that such cues may pass through the digestive system unchanged (Mirza and Chivers 2003). In this instance, diet cues and predator odours may act as independent conditioned stimuli and provide independent information about risk.

A long-standing assumption about chemical cues is that they are harder to manipulate than visual cues and, thus, pro-vide reliable information (Munoz and Blumstein 2012). Yet, there is a growing number of studies suggesting that both predators and prey alter the chemical cues that they release to avoid detection or even camouflage themselves simply by altering their diets (Fishlyn and Phillips 1980; Ruxton 2009; Resetarits and Binckley 2013; Brooker et al. 2014). Such findings suggest it may not be as hard as previously thought to manipulate chemical cues and that such modifications may

significantly alter the dynamics of predator–prey interactions. Certainly, pike appear to actively manipulate prey behaviour by defecating away from their prey (Brown et al. 1995), but it is unclear whether both predators and prey actively manipulate the chemical composition diet cues to deceive others. Further work is needed to understand the extent to which both predators and prey can deceive each other by manipulating different components of their chemical cues.

Compliance with ethical standards All work was done in accordance with the University of Saskatchewan animal care protocol 2015031. Care was taken to minimise handling stress in tadpoles and crayfish during the experiment. All animals were housed in low densities and fed daily. Following the completion of the experiment, all tadpoles were returned to the ponds from which they were collected.

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