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Predator crypsis enhances behaviourally mediated indirect effects on plants by altering bumblebee foraging preferences

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Predators of pollinators can influence pollination services and plant fitness via both consumptive (reducing pollinator density) and non-consumptive (altering pollinator behaviour) effects. However, a better knowledge of the mechanisms underlying behaviourally mediated indirect effects of predators is necessary to properly understand their role in community dynamics. We used the tripartite relationship between bumblebees, predatory crab spiders and flowers to ask whether behaviourally mediated effects are localized to flowers harbouring predators, or whether bees extend their avoidance to entire plant species. In a tightly controlled laboratory environment, bumblebees (*Bombus terrestris*) were exposed to a random mixture of equally rewarding yellow and white artificial flowers, but foraging on yellow flowers was very risky: bees had a 25 per cent chance of receiving a simulated predation attempt by 'robotic' crab spiders. As bees learnt to avoid 'dangerous' flowers, their foraging preferences changed and they began to visit fewer yellow flowers than expected by chance. Bees avoided spider-free yellow flowers as well as dangerous yellow flowers when spiders were more difficult to detect (the colour of yellow spiders was indistinguishable from that of yellow flowers). Therefore, this interaction between bee learning and predator crypsis could lead flower species harbouring cryptic predators to suffer from reduced reproductive success.

Keywords: avoidance learning; *Bombus terrestris*; crab spider; foraging preferences; pollinator behaviour

1. INTRODUCTION

Growing evidence indicates that non-consumptive effects of predators play a significant role in community dynamics (Luttbeg & Kerby 2005; Preisser *et al.* 2005; Schmitz *et al.* 2008). These non-consumptive effects can be even stronger than consumptive effects because they can influence a large proportion of individuals within a prey population, whereas only a small proportion of a population (i.e. those that are eaten) actually suffers directly from predation (Preisser *et al.* 2005). For example, many animals respond to predation risk, usually indicated by the presence of visual or chemical cues, by altering their foraging behaviour to reduce exposure to predators (Lima 1985; Pierce 1988; Gonçalves-Souza *et al.* 2008). Thus, non-consumptive effects of predators usually induce a significant cost to prey via reduced foraging efficiency (Pierce 1988; Verdolin 2006; Heithaus *et al.* 2007). Non-consumptive effects of predators can also have cascading indirect effects on lower levels of organization within complex ecological communities (Schmitz *et al.* 2008). For example, the presence of predators can lead herbivores to shift host plants (Schmitz 2004), which in turn can alter plant diversity and ecosystem function (Schmitz 2003, 2006).

Pollination is an extremely important ecosystem service that has been widely studied in many contexts from individual pollinator behaviour through to complex pollination networks (Memmott 1999; Chittka *et al.*

2004; Olesen *et al.* 2008). Lately, there has been increased interest in the potential impacts of predators on pollination services and plant fitness (Suttle 2003; Dukas 2005; Knight *et al.* 2006). Many predators use the attractiveness of flowers (e.g. lizards: Muñoz & Arroyo 2004; wasps: Dukas 2005; and spiders: Morse 2007), or mimic attractive floral signals themselves (Heiling *et al.* 2006; Bush *et al.* 2008), to lure their prey. Crab spiders (Thomisidae), which are sit-and-wait predators that ambush pollinators on flowers, are perhaps the best studied of these predators (Dukas & Morse 2003; Reader *et al.* 2006; Gonçalves-Souza *et al.* 2008). The ability of some crab spiders to change colour makes them especially intriguing: *Misumena vatia* (Clerck 1757) can change between white and yellow within a few days and can therefore camouflage itself on yellow and white flowers (Chittka 2001; Morse 2007; Insausti & Casas 2008).

Most studies of predation effects on pollination services report density-dependent effects, i.e. reduction of pollinator densities through predation (Dukas 2005; Knight *et al.* 2006). However, there is some evidence that predators can have non-consumptive indirect effects on plant fitness (Louda 1982; Gonçalves-Souza *et al.* 2008). Gonçalves-Souza *et al.* (2008) showed that pollinators tended to avoid flowers that contained visual predator cues (model crab spiders). As a result, flowers bearing model predators became pollen-limited and suffered from poorer seed set and reduced fruit biomass. While this study provides strong evidence of indirect trait-mediated effects of predators on plant reproductive success, it is still largely phenomenological. To gain a better understanding of the role that indirect predator effects play in community

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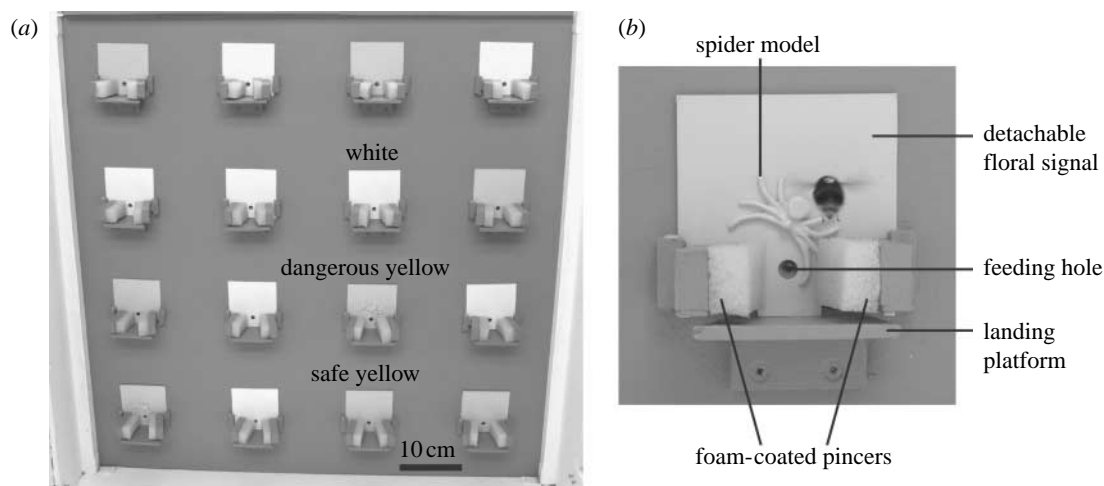
Figure 1. Experimental set-up showing (*a*) the artificial meadow containing yellow and white flowers with two dangerous yellow flowers bearing cryptic (yellow) spiders and (*b*) a close-up view of a single dangerous yellow flower harbouring a cryptic spider. As a bee lands to feed, through the feeding hole, the foam-coated pincers close and capture it for 2 s.

dynamics, we need to focus more on the mechanisms behind the observed effects (Luttbeg & Kerby 2005). Only by taking the complex interaction among flowers, bees and predatory crab spiders into the laboratory under controlled conditions we will be able to start disentangling the factors that characterize this interaction.

One such experiment indicated that avoidance of crab spiders by bumblebees is predominantly a learnt response (Ings & Chittka 2008). Furthermore, by investigating the impact of predator crypsis on predator avoidance learning, another potential indirect effect of predators was discovered: one day after experiencing several failed predation attempts, bees displayed an increased rate of 'false alarms', rejecting more safe flowers when they had previously encountered cryptic predators (Ings & Chittka 2008).

Therefore, our aim here is to determine whether indirect effects of predators on pollinators are just confined to reducing visitation rates to flowers harbouring spiders, or whether the effects of spiders extend further and lead bees to avoid flowers resembling those where they have previously encountered spiders. Furthermore, we examine the interaction between predator crypsis and predator avoidance behaviour. We uncover a trade-off between predator detection and perception of risk that profoundly influences predator avoidance behaviour.

2. MATERIAL AND METHODS

(a) *Predator avoidance learning paradigm*

We constructed a wooden flight arena ($l = 1$ m, $w = 0.72$ m and $h = 0.73$ m), with a UV-transmittent Plexiglas lid, where bumblebees could forage for nectar in an 'artificial meadow' (hereafter 'meadow') containing a mixture of 'safe' and 'dangerous' artificial flowers (full details are given in Ings & Chittka 2008). The meadow consisted of 16 artificial flowers, with detachable floral signals (7×7 cm acrylic, 1 mm thick, painted white or yellow) and artificial feeders, arranged in a 4×4 vertical grid on a grey background (figure 1*a*). Food (50% (v/v) sucrose solution; hereafter 'nectar') was accessed through a hole in the arena wall 10 mm above a wooden landing platform (40×60 mm). The platform was flanked by two foam-coated pincers ($35 \times 10 \times 20$ mm wooden blocks with their inside surfaces coated with $35 \times 10 \times 20$ mm white

foam) that could be rapidly closed by remotely controlled solenoids. Wooden parts were painted with the same grey paint as the wall. All flowers contained nectar rewards, but bees attempting to feed from dangerous flowers were subjected to a simulated predation attempt by a crab spider: bees were captured and held by the sponge-coated pincers for a fixed duration of 2 s before being released. Dangerous flowers were also fitted with life-sized crab spider (*M. vatia*) models ($l = 12$ mm; made from Gedeo Crystal resin) placed on the floral signal above the feeding hole (figure 1*b*). The spider models were painted with the same yellow and white paints as the flowers. A quantitative model of bee colour vision showed that bees could not discriminate between the colour of yellow spiders and yellow flowers, but they could easily detect white spiders on yellow flowers (Ings & Chittka 2008).

During the experiments, a constant flow (1.85 ± 0.3 µl min^{-1}) of nectar was supplied to each flower and dispensed from the tips of three 26G syringe needles (BD Microlance Drogheda, Ireland; 0.45×13 mm) using KD200 syringe pumps (KD Scientific, Holliston, USA). This flow rate was chosen to mimic the overall nectar availability of a larger natural flower patch such that bees would be able to continue foraging in the meadow until they filled their crops. A maximum droplet volume of 4.70 ± 0.3 µl could be reached before it fell into a 'waste pot' (not accessible to bees); the reward droplet was subsequently replenished. This prevented the food supply in unvisited dangerous flowers becoming substantially more plentiful than that in safe flowers.

(b) *Pre-training*

Before avoidance training, all bees were subjected to a pre-training phase to ensure they had associated the yellow flowers with rewards. During this phase, the bees were allowed to forage individually in the meadow containing only 16 safe yellow flowers (no spiders) for a minimum of 100 visits. A visit consisted of a bee landing on a flower and either attempting to feed or inspecting and leaving the flower.

(c) *Avoidance training*

During training, the meadow consisted of a random mixture of eight white and eight yellow flowers (both equally rewarding). Two randomly selected yellow flowers harboured spiders and were therefore dangerous, i.e. bees would

Table 1. Summary of individual avoidance learning curves fitted using the state-space smoothing algorithm (Smith *et al.* 2004). (The threshold choice (mean $\pm$ 1 s.e.m.) is the choice at which there is a reasonable certainty (above 0.95) that the bee is choosing yellow less than chance for the remainder of the experiment. The percentage of bees is the proportion of bees in each treatment that cross the threshold.)

flower type	threshold choice		percentage of bees	
	cryptic	conspicuous	cryptic	conspicuous
all yellow	102.0 ± 19.5	111.0 ± 19.3	43.75 ($n=7$)	31.25 ($n=5$)
dangerous yellow	70.8 ± 13.5	84.0 ± 10.1	56.25 ($n=9$)	43.75 ($n=7$)
safe yellow	128.3 ± 17.4	113.5 ± 17.7	37.50 ($n=6$)	25.00 ($n=4$)

be trapped for 2 s if they landed and attempted to feed (bees that landed briefly but left before attempting to feed were not trapped). Thus, bees that had previously been trained to forage on yellow flowers would have a 25 per cent chance of receiving a simulated predation attempt if they continued to forage on yellow flowers only. No spiders were present on the white flowers.

Two groups of bumblebees (16 bees in each) from a single colony (*Bombus terrestris dalmatinus* Dalla Torre, obtained from Syngenta Bioline Bees, Weert, The Netherlands) were exposed to predation risk from either cryptic (yellow spider on yellow flower) or conspicuous (white spider on yellow flower) artificial crab spiders. We used these colour pairs since we have previously established that bumblebees are able to detect and learn to avoid both combinations (Ings & Chittka 2008).

All bees were tested individually and were allowed to forage for a minimum of 200 flower visits. As this took several foraging bouts (i.e. the bees filled their crops and returned to the nest), the flower positions were randomized between each bout to eliminate the possibility of bees learning the positions of dangerous flowers. This ensured the bees could rely only on visual predator cues.

(d) *Statistics*
Individual learning curves were fitted to the binary choices (yellow or white) that bees made during each visit of the training phase. We used the state-space smoothing algorithm of Smith *et al.* (2004) to calculate the probability of a bee choosing a yellow (safe or dangerous) flower at each of its 200 choices. This algorithm also calculates the choice at which there is a reasonable certainty (above 0.95) that the bee is choosing yellow flowers less frequently than by chance for the remainder of the experiment. We took chance levels of selecting safe or dangerous yellow flowers to be the probability of selecting yellow if bees foraged at random and did not respond to the presence of spiders on yellow flowers. Thus we used 0.5 (8/16) as the chance probability of choosing any yellow flower, 0.125 (2/16) for a dangerous flower and 0.375 (6/16) for a safe yellow flower (no spider). These are the most conservative estimates because bees were pre-trained to forage on yellow flowers and *B. terrestris* has no differential preference for white over yellow (Chittka *et al.* 2004).

We used paired *t*-tests to determine whether the probability of choosing yellow flowers calculated by the algorithm differed from chance levels at the outset (choice zero) and end (last 30 choices) of the training phase.

3. RESULTS
(a) *Avoidance of yellow flowers*
Bumblebees modified their foraging preferences after experiencing simulated predation attempts on yellow flowers. The probability of choosing yellow flowers fell significantly below that expected by chance (0.5) for 37.5 per cent of bees tested ($n=12$; table 1). Furthermore, when viewed at the population level, the probability of a yellow flower receiving a visit by a bee fell below the chance level of 0.5 after 70–88 (cryptic = 70, conspicuous = 88) flower choices (figure 2a). By the last 30 choices (out of 200), the probability of choosing a yellow flower was significantly below the chance level of 0.5 for bees encountering either cryptic or conspicuous spiders (figure 2a; cryptic = 0.258 ± 0.031 (mean $\pm$ 1 s.e.m.), paired *t*-test, $t=-8.802$, $p<0.001$, d.f. = 15; conspicuous = 0.344 ± 0.054, $t=-2.904$, $p=0.011$, d.f. = 15). The overall avoidance of yellow flowers was stronger, although not significantly so (figure 2a; $F_{1,30}=1.947$, $p=0.173$), for bees encountering cryptic spiders.

(b) *Avoidance of dangerous flowers*
At the beginning of the training phase, the probability of bees choosing dangerous flowers was significantly lower than would be expected by chance alone (figure 2b; cryptic: paired *t*-test, $t=-2.57$, $p=0.021$, d.f. = 15; conspicuous: $t=-8.557$, $p<0.001$, d.f. = 14). After receiving an average of three simulated predation attempts (cryptic: 3.4 ± 0.4; conspicuous: 2.9 ± 0.5), the probability of visiting dangerous flowers fell even further below the chance level (figure 2b) to 0.020 ± 0.005 for bees in the cryptic spider group and 0.023 ± 0.006 for bees in the conspicuous spider group.

(c) *Avoidance of safe yellow flowers*
The probability of a bee choosing safe yellow flowers (i.e. those without spiders) fell steadily during the training phase (figure 2c). However, the level of avoidance differed between the two spider visibility treatments. Only four bees (out of 16) in the conspicuous spider treatment (table 1) visited fewer yellow flowers than expected by chance by the end of the training phase. Furthermore, overall visitation rates to safe yellow flowers were close to chance levels throughout the training phase, and by the last 30 choices the probability of a bee visiting a safe yellow flower (0.330 ± 0.052) was not significantly below 0.375 (paired *t*-test, $t=-0.851$, $p=0.408$, d.f. = 15). By contrast, six bees (out of 16) encountering cryptic spiders (table 1) avoided yellow flowers (with or without spiders) by the end of the training phase (figure 2c). Overall, bees in the cryptic spider treatment consistently visited fewer safe yellow flowers as training progressed, and the probability of a safe yellow flower being visited fell below the chance threshold of 0.375 after 131 choices
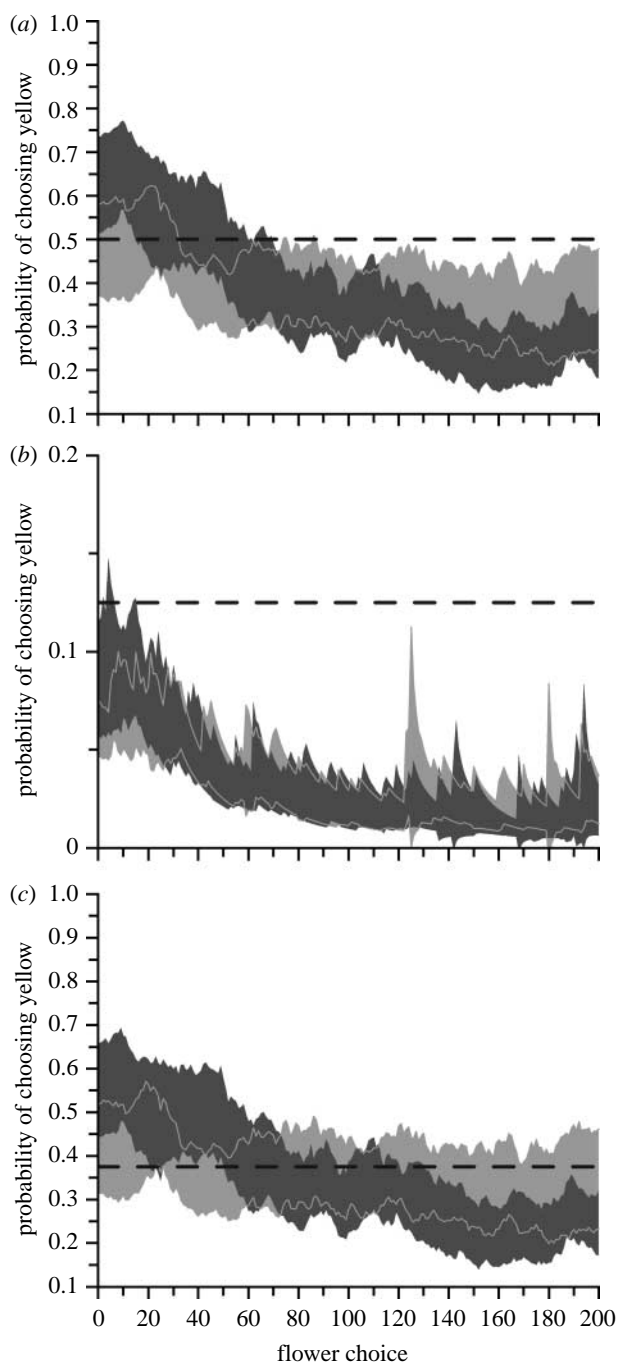
Figure 2. Probability of (*a*) any yellow flower receiving a visit, (*b*) a dangerous yellow flower (with a spider) receiving a visit and (*c*) a safe yellow flower (no spider) receiving a visit. Filled areas represent 95% CI (based on individual values calculated for each bee using the state-space smoothing algorithm of Smith *et al.* 2004) for the probability of a bee choosing a yellow flower. The dark grey area represents bees ($n = 16$) in the cryptic spider (yellow) treatment and the light grey area represents bees ($n = 16$) in the conspicuous spider (white) treatment. Where overlap between the areas occurs, the upper and lower 95% CI for bees in the conspicuous spider treatment are shown by light grey lines. The probability of a yellow flower being visited, assuming flowers are chosen at random, is shown by the dashed line.

(figure 2*c*). The probability of choosing a yellow flower continued to fall and remained significantly below 0.375 (0.244 ± 0.031) for the last 30 flower choices of the training phase (paired *t*-test, $t = -4.223$, $p = 0.001$, d.f. $= 15$).

4. DISCUSSION

In this study, we experimentally demonstrate that bees' experience of simulated predation attempts by crab spiders led them not only to avoid flowers harbouring spiders, but also to generalize their adverse experience to flowers of the same species that do not harbour spiders. At a population level, these combined effects ultimately led to a significant reduction in visitation rates to flower species that harbour crab spiders.

(a) *Avoidance of yellow flowers*

Most bees responded to pre-training on yellow flowers by visiting more yellow flowers than white flowers at the beginning of the training phase. However, as bees gained experience of the equally rewarding white flowers, coupled with receiving simulated predation attempts at 25 per cent of the yellow flowers, they started to shift their foraging preference towards white flowers (figure 2*a*).

There was considerable variation in the responses of individual bees and not all bees avoided yellow flowers by the end of the training phase (table 1). The mechanisms behind such variation are still poorly understood, but avoidance learning performance does not appear to be related to body size or age (Ings & Chittka 2008). Perhaps this variation reflects differences in individual risk sensitivity thresholds (Brown *et al.* 2006; Smee & Weissburg 2006). However, from a plant's perspective, the most important observation is that yellow flowers received fewer visits by a population of pollinators when some of these flowers harboured artificial predators (see also Dukas & Morse 2003; Robertson & Maguire 2005; Gonçalves-Souza *et al.* 2008). Are bees just responding to the presence of spiders on particular flowers (Gonçalves-Souza *et al.* 2008) or do they learn to avoid the risky flower species? We can address these questions by dissecting the overall avoidance of yellow flowers into two components: avoidance of dangerous flowers and avoidance of safe yellow flowers.

(b) *Avoidance of dangerous flowers*

The probability of a visiting a dangerous yellow flower was significantly below the conservative chance level of 0.125 for both treatment groups at the beginning of the training phase. While this could be taken to suggest the presence of an innate avoidance of spider shapes (e.g. Dukas 2001; Reader *et al.* 2006; Gonçalves-Souza *et al.* 2008), it is just as likely to reflect bees' continued search for what is familiar, i.e. yellow flowers without spiders. However, bees visited at least one dangerous flower and received a simulated predation attempt. Consequently, avoidance of flowers harbouring spiders was strongly reinforced and the probability of visiting a dangerous flower fell during training (figure 2*b*). But are bees just avoiding the dangerous flowers?

We know that bees are capable of detecting and avoiding flowers harbouring either conspicuous or cryptic spiders in a patch of yellow flowers (Ings & Chittka 2008). However, 24 hours after experiencing a simulated predation attempt, bees appeared to generalize their perception of danger to all yellow flowers in the patch. So it is possible that bees in the current study, where they had an alternative safe foraging option (white flowers), started to avoid all yellow flowers.

(c) *Avoidance of safe yellow flowers*

Bees in the conspicuous spider treatment continued to visit yellow flowers at the level expected by chance, i.e. 0.375 (6 out of 16 flowers), during the entire training phase (figure 2c). We can therefore conclude that they are just avoiding flowers harbouring spiders (e.g. as in Gonçalves-Souza *et al.* 2008). By contrast, bees encountering cryptic spiders started to avoid safe yellow flowers towards the end of the training phase (figure 2c). This suggests that bees are generalizing their perception of risk from flowers with spider models to all flowers that resemble the dangerous ones, i.e. yellow flowers.

Bumblebees can accurately detect and avoid cryptic spiders, but there appears to be a trade-off between foraging preferences and predation risk because detecting cryptic spiders comes with an increased foraging cost, i.e. longer inspection times (Ings & Chittka 2008). Such a trade-off between foraging efficiency and predation risk made sense when all flowers were yellow (Ings & Chittka 2008). However, in our current study, bees had the option of foraging from safe, equally rewarding white flowers. Therefore, bees appear to be making a functional decision to give up yellow flowers and concentrate on the alternative safe flower species rather than risk mistakenly landing on a dangerous flower.

5. CONCLUSIONS

By rigorous experimental examination of predator avoidance learning in bumblebees, we provide evidence that indirect effects of sit-and-wait predators are not confined to the individual flowers where they hide (e.g. Gonçalves-Souza *et al.* 2008), but can extend to an entire population of flowers with similar appearance (typically of the same species). In particular, we found that even though bumblebees are able to accurately detect and avoid cryptic spiders (Ings & Chittka 2008), they chose to avoid all flowers resembling those that harboured cryptic spiders when alternative safe flower species were available. This did not occur when the spiders were highly conspicuous. Furthermore, learnt predator avoidance is maintained well (at least 24 hours: Ings & Chittka 2008) compared with appetitive learning (Keasar *et al.* 1996). Therefore, our results suggest that the behaviourally mediated indirect effects of cryptic predators could impact on plant reproductive success more severely than conspicuous predators (Gonçalves-Souza *et al.* 2008) by greatly reducing visitation rates to flower species harbouring the predators (e.g. see Suttle 2003).

Our study clearly demonstrates that the magnitude of indirect effects is dictated by a complex interaction among preys' experience of predators and failed predation attempts, their ability to detect and discriminate predator cues, and their learning and memory capabilities. Ultimately, this interaction results in a trade-off between the costs of avoiding local predator cues and the benefits of foraging in a patch containing predators, which can have cascading effects on lower trophic levels.

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