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Safety Cues Can Give Prey More Valuable Information Than Danger Cues

Barney Luttbeg,[1,*] Maud C. O. Ferrari,[2] Daniel T. Blumstein,[3] and Douglas P. Chivers[4]

1. Department of Integrative Biology, Oklahoma State University, Stillwater, Oklahoma 74078; 2. Department of Veterinary Biomedical Sciences, Western College Veterinary Medicine, University of Saskatchewan, Saskatoon, Saskatchewan S7N 5E2, Canada; 3. Department of Ecology and Evolutionary Biology, University of California, Los Angeles, California 90095; 4. Department of Biology, Collaborative Science Research Building, 112 Science Place, University of Saskatchewan, Saskatoon, Saskatchewan S7N 5E2, Canada

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abstract: The ability of prey to assess predation risk is fundamental to their success. It is routinely assumed that predator cues do not vary in reliability across levels of predation risk. We propose that cues can differ in how precisely they indicate different levels of predation risk. What we call danger cues precisely indicate high risk levels, while safety cues precisely indicate low risk levels. Using optimality modeling, we find that prey fitness is increased when prey pay more attention to safety cues than to danger cues. This fitness advantage is greater when prey need to protect assets, predators are more dangerous, or predation risk increases at an accelerating rate with prey foraging efforts. Each of these conditions lead to prey foraging less when estimated predation risk is higher. Danger cues have less value than safety cues because they give precise information about risk when it is high, but prey behavior varies little when risk is high. Safety cues give precise information about levels of risk where prey behavior varies. These results highlight how our fascination with predators may have biased the way that we study predator-prey interactions and focused too exclusively on cues that clearly indicate the presence of predator rather than cues that clearly indicate their absence.

Keywords: predator-prey interactions, safety, fear, antipredator behavior, risk assessment, Bayesian updating.

Few events are as unforgiving as being eaten by a predator; hence, it is not surprising that prey have evolved an astonishing array of antipredator responses that act to thwart would-be predators (Lima and Dill 1990; Lima 1998; Dall et al. 2005). Predation fundamentally alters prey life histories, morphology, and behavior (Tollrian 1995; Chivers et al. 2001; Brown et al. 2013; Meuthen et al. 2018). Prey decide when and where to forage, eat, live, search for mates, and much more all through the lens of predation risk. Prey face a fundamental trade-off of avoiding predators while trying to perform all of these other tasks. Given that predation varies both spatially and temporally, it follows that prey tend to be adept at assessing current levels of predation risk and adjusting their foraging effort in response (Kats and Dill 1998; Lima and Bednekoff 1999). The success that prey have in balancing the risk of predation with foraging and other tasks depends on how well they can assess current predation risk, the effectiveness of their antipredator responses, and other state-dependent effects, such as hunger level and reproductive state (Luttbeg and Trussell 2013).

There are often many potential sources of information available for prey estimating current levels of predation risk. These cues have been classified along several axes. Cues can be direct, where the prey is detecting something that indicates the presence of the predator, or indirect, where the prey is detecting conditions, such as vegetative cover or illumination (Brown and Kotler 2004), that affect the probability of encountering a predator. Cues can be also classified by whether prey are assessing a cue themselves or using the public information in the behaviors or communications of other prey as indicators of current risk (Fernández-Juricic and Kacelnik 2004; Roth et al. 2008).

One underappreciated aspect of cues indicating the level of predation risk is the way that they differ in their accuracy. It is well accepted that the cues are imperfect because of variance in their production or reception, but an implicit assumption has been that this imperfection is constant across the range of predation risk levels. Cues are assumed to be equally accurate at indicating low and high levels of predation risk. There is little basis for this assumption, and we suggest that the way that prey use different cues to assess and manage predation risk can be better understood if we incorporate this variation.

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[*] Corresponding author; email: luttbeg@okstate.edu.

ORCIDs: Luttbeg, https://orcid.org/0000-0001-5555-8341; Blumstein, https://orcid.org/0000-0001-5793-9244.

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We propose that cues can differ in how accurately they indicate different levels of predation risk. At one end of the spectrum are what we will call "danger cues" that more precisely indicate the probability of a prey being killed by a predator in the near future (predation risk) when it is high. For danger cues, the range of cue values a prey is likely to receive is smallest when predation risk is high and widens as predation risk decreases. It is advantageous for predators to avoid detection by prey, thus, traits like crypsis and ambush hunting modes lead to prey more often failing to detect predators that are present (false negatives) than detecting predators that are not present (false positives). Thus, seeing a predator (a high danger cue) is more informative than not seeing a predator (a low danger cue). We believe that prey seeing predators or smelling kairomones or alarm cues are often danger cues. When a predator is very close and predation risk is high, a prey is likely to receive clear and reliable information about the distance, motivation, and intentions of the predator (Dugatkin and Godin 1992; Etting and Isbell 2014). However, as the predator gets farther away and predation risk is lower, there is a wider range of cue levels that the prey is likely to receive because the distance, motivation, and intentions of the predator might be harder to judge.

At the other end of the spectrum are what we will refer to as safety cues. These are cues that give more precise information about the level of predation risk when predation risk is low. The behaviors of other prey are good candidates for safety cues. Hearing or seeing other prey that share a predator foraging or engaging in conspicuous activities like singing or courtship could be indicative of low predation risk. The intensity of these conspicuous behaviors could vary at the low end of predation risk with them becoming more intense or common as predation risk gets lower. In addition, the types of prey that are active could also indicate the current predation risk. For example, subordinate individuals may return to foraging sooner after a predation risk spike compared with dominant individuals (De Laet 1985). Thus, observing a dominant individual foraging could be a stronger safety cue indicating lower risk than observing subordinate individuals foraging. If moderate predation risk causes conspicuous behaviors to cease, the cue does not provide precise information about risk that is moderate to high because the amount of conspicuous behavior does not vary. This suggests that hearing or seeing other prey act in conspicuous ways could be an example of a safety cue that provides precise information about the level of predation risk when it is low but less precise information when risk is higher. Note that danger and safety cues are giving information about the same quantity (predation risk) but differ in what range of predation risk that information is most precise.

It is important to consider the role of safety cues in shaping the responses of prey to varying predation risk. Studies of the interactions of predators and prey and the resulting population dynamics have focused almost solely on danger cues. The common protocol to measure the nonconsumptive effects of predators is to compare the fitness or performance of prey in the absence and presence of cues produced by predators or by prey being consumed by predators. Ignoring and not including safety cues in the protocols of these studies may be causing prey to never estimate low levels of risk and thus truncating the range of displayed prey behaviors, leading to underestimates of the size of nonconsumptive effects. Likewise, experimentalists should consider what information their control treatments convey to prey. Experiments that manipulate the presence/absence of auditory or olfactory cues sometimes include a control treatment with an apparently nonthreatening smell or sound. However, in some cases perhaps those control treatments could in fact be safety cues, such as when conspecific vocalizations or vocalizations from other potentially vulnerable prey are broadcast (Zanette et al. 2011; Hughes et al. 2014; Suraci et al. 2016). Thus, the observed difference in behavior between the control and danger cue could be the difference between the presence of a safety cue and a danger cue, rather than between an uninformative cue and a danger cue.

Our aim with this article is to investigate how prey fitness is affected when an individual relies on safety versus danger cues when estimating current levels of predation risk to inform their optimal foraging efforts. Using optimality models based on Bayesian updating, we explore how the relative performance of the two cue types depends on the intensity of predation risk, frequency of environmental change, and shape of fitness and predation risk functions.

Methods

We present a model where prey set their foraging efforts depending on their estimate of the current of level of predation risk, their level of previous foraging success, and the time step. These optimal state-dependent foraging efforts are found using a dynamic state variable model. The individual's estimate of the current level of predation risk is a product of Bayesian updating using the information in received safety or danger cues. We then use simulations to measure how average prey fitness varies with how much attention they pay to safety versus danger cues given the optimal foraging effort from the dynamic state variable model and the Bayesian updating of estimates of current predation risk.

We assume that the prey in the model live in an environment with fluctuating predation risk. The level of risk (μ) is a continuous variable ranging from 0 to 1. The model spans 20 time steps. At the beginning of the first time step, the current risk level is randomly drawn from a beta distribution ranging from 0 to 1. For the majority of the results the distribution of risk levels is Beta(hit $= 1$, miss $= 1$), which is a uniform distribution. At the beginning of each subsequent time step, there is a probability that the risk level changes (γ), and when it does a new μ is randomly drawn from the beta distribution of risk levels.

The probability of a prey being killed by a predator is a product of the prey's foraging effort (ε), the current risk level (μ), and the magnitude of the risk posed by predators (κ; all vary from 0 to 1),

$$P(\text{killed}) = \kappa\mu\varepsilon^{\tau}, \tag{1}$$

where τ gives the shape of how the probability of being killed increases with prey foraging effort. The probability of the prey finding food is

$$P(\text{find food}) = \varepsilon. \tag{2}$$

If a prey finds food, x (which is their accumulated foraging success) goes up by 1. We present the model as foraging effort affecting the probability prey find food, but more generally prey are setting the intensity of an activity that affects their fitness (e.g., defending a territory or finding a mate) but also exposes them to predation risk.

At the beginning of each time step, prey set their foraging effort (details below). Whether they get killed by a predator is randomly determined using equation (1). If they survive, whether they find food is randomly determined using equation (2).

We used dynamic state variable modeling to find optimal foraging efforts given every combination of time step, x, and μ. Dynamic state variable models (Clark and Mangel 2000; Houston and McNamara 1999) find optimal state-dependent phenotypes and are typically solved by starting at the fitness an individual achieves at the end of a series of time steps (called the terminal fitness). Then, optimal phenotypes for earlier time periods are found by working backward through time. We used two scenarios to study how prey achieve fitness. The first scenario ("delayed fitness") was used for the majority of our results, while the second ("immediate fitness") was used as a comparison. In the delayed fitness scenario, prey reproduce at the end of the model, and their achieved fitness is x if they are still alive at the terminal time step (T, $t = 20$). Thus, the terminal fitness function is

$$F[T, x, \mu] = x \quad \text{if alive.} \tag{3}$$

Working through backward iteration we found what foraging effort (ε ranging from 0 to 1 at steps of 0.01) produced the maximum expected fitness for a prey given t, x, and μ. The dynamic programming equation for doing this is

$$\begin{aligned} F[t,x,\mu] = {} & \max_{\varepsilon}(1 - P(\text{killed})) \\ & \times \Bigg\{(1-\gamma)[P(\text{find food})F[t+1,x+1,\mu] \\ & \qquad + (1 - P(\text{find food}))F[t+1,x,\mu]] \\ & \quad + \gamma\Bigg[\sum_{z=0}^{100}\text{Beta}(z/100,\text{hit},\text{miss})(P(\text{find food})F[t+1,x+1,z/100] \\ & \qquad + (1 - P(\text{find food}))F[t+1,x,z/100])\Bigg]\Bigg\}. \end{aligned} \tag{4}$$

An individual's expected fitness, which is associated with the level of foraging effort (ε) that gives the maximum expected fitness, is the product of the probability that they are not killed by a predator ($1 - P(\text{killed})$), the probabilities that the environmental state changes (γ) or does not change ($1 - \gamma$), and the probabilities that they find food ($P(\text{find food})$) or not ($1 - P(\text{find food})$). If they are killed by a predator, which occurs $P(\text{killed})$ of the time, their expected fitness is 0 and thus is not included in equation (4). If the environmental state does not change before the next time period ($1 - \gamma$) and they find food ($P(\text{find food})$), their expected fitness is $F[t + 1, x + 1, \mu]$ because time (t) and their foraging success (x) both have increased by 1 and μ has not changed. Alternatively, if they do not find food ($1 - P(\text{find food})$) their expected fitness is $F[t + 1, x, \mu]$, because their foraging success has not increased. If the environmental state does change before the next time period (γ), a new μ is drawn from the beta probability density function with hit and miss both equal 1 for the main results. Expected fitness is found for future values of μ ranging from 0 to 1 at steps of 0.01 weighted by the probability distribution of those new values of μ. The probability of the individual either finding food or not and how that affects expected fitness is done in the same manner as in the first half of the equation.

In the immediate fitness scenario, prey immediately turn their foraging success into fitness at the end of each time step and their expected fitness at the terminal time step is 0. The terminal fitness function is 0 for all state variables. In earlier time steps, prey gain 1 unit of fitness each time they find food, thus expected fitness equals the probability of finding food. As with the delayed fitness scenario, the maximum expected fitness of a prey is found by comparing values produced by foraging efforts (ε) ranging for 0 to 1 at steps of 0.01. This is done with the dynamic programming equation,

$$\begin{aligned} F[t,\mu] = {} & \max_{\varepsilon}(1 - P(\text{killed})) \\ & \times \Bigg\{P(\text{find food}) + (1-\gamma)F[t+1,\mu] \\ & \quad + \gamma\Bigg[\sum_{z=0}^{100}\text{Beta}(z/100,\text{hit},\text{miss})F[t+1,z/100]\Bigg]\Bigg\}. \end{aligned} \tag{5}$$

The prey's foraging effort (ε) is a trade-off between the probability of being killed and fitness gains from finding food. The optimal foraging effort depends on a prey's estimate of μ. We assume that there are two types of cues (safety and danger) available to a prey that differ in what range of μ that they give the most precise information about μ. The danger cue more precisely indicates μ when it is high, while the safety cue more precisely indicates the level of μ when it is low. The probability distributions for cue levels received given μ are

$$\begin{aligned}\Pr(\text{danger cue}|\mu) &= \mathcal{N}(\mu, \theta + (1-\mu)\nu),\\ \Pr(\text{safety cue}|\mu) &= \mathcal{N}(1-\mu, \theta + \mu\nu),\end{aligned} \tag{6}$$

and truncated to range from 0 to 1. Note that for the safety cue the mean cue level is $1-\mu$, thus high safety cues and high danger cues are expected when μ is close to 0 and 1, respectively. The variance in the distributions from which the cues are randomly drawn is composed of θ, which is the baseline variance in cues, and a term, ν, that sets how quickly cue variance increases as μ differs from the level at which the cue most precisely conveys information. The danger cue and safety cue increase in variance as μ is farther from 1 and 0, respectively.

For danger cues, if $\nu = 0$ (fig. 1*a*) the variance in the normal distribution from which the cue level received is drawn is constant (and equals θ) across all levels of risk. However, as ν increases (0.2 and 0.4 in fig. 1*b*, 1*c*), the variances in the distributions from which danger cues are drawn increases as μ gets farther from 1. This models the idea that when risk is high, there is a narrower range of danger cues that can be received by the individual, but as risk gets lower, there is a wider of range of possible danger cues received by the prey (thin lines in fig. 1*b*, 1*c*).

The information that prey gain when they receive a danger cue is contained in the likelihood that the current level of risk is μ given the danger cue received. This is found by taking P(danger cue $|\,\mu$; as seen in fig. 1*a*–1*c*) for each level of μ from 0 to 1. When $\nu = 0$, the shape of the likelihood of the current level of μ given the danger cue received is the same across the range of μ (fig. 1*e*). There is the same amount of information in the cue across the range of danger cue values. If $\nu > 0$, however, then as the observed danger cue goes lower, the likelihood of μ given the observed danger cue becomes more spread out (fig. 1*f*, 1*g*), meaning that a wider range of μ could produce the observed danger cue and that the information in the cue is decreased. The shapes of the likelihoods also change because of the variance in the cues being a function of μ. For example, when $\nu = 0.4$, μ is very likely to be close to 0.9 when the received danger cue is 0.9 (thick line in fig. 1*g*). Conversely, a received danger cue of 0.1 (thin line in fig. 1*g*) is a very good indication that μ is not high, but it does not give precise information about the level of μ.

Safety cues behave the same as danger cues, but in the opposite direction. For the safety cue, if $\nu > 0$ the variance in the normal distribution from which the safety cue is drawn increases as μ gets farther from 0 (fig. 1*d*; note the *X*-axis runs from 1 to 0 for fig. 1*d*). They give precise information about μ when it is low, but less so as μ increases (fig. 1*d*). When $\nu = 0.4$, μ is very likely to be close to 0.1 when the received safety cue is 0.9 (thick line in fig. 1*h*). Conversely, a received safety cue of 0.1 (thin line in fig. 1*h*) is a very good indication that μ is not high, but it does not give precise information about the level of μ. For example, when the other prey cease using conspicuous behavior, this might not indicate to prey the exact level of predation risk but can be a good indication that it is not low.

We want to know how individual fitness is affected by prey using danger versus safety cues. To facilitate this comparison, we assumed that individuals have finite and fixed attention that is divided between the two cue types. α is how much attention the individual pays to the danger cue (between 0 and 1), and $1-\alpha$ is how much attention they pay to the safety cue. During each time step, an individual receives a cue about the risk state of their environment. The probability that they receive a danger cue is α, and if they do not receive the danger cue, they receive the safety cue. Our assumption of finite and fixed attention divided between the two cue types leads to the assumption that α does not affect how effectively individuals forage.

The prey use the information they gain from safety or danger cues to estimate μ using Bayesian updating. At the beginning of the first time step, the individual starts with a weak prior estimate of μ. This prior is in the form of a normal distribution with a mean of 0.5 and a variance of 50. We discretize the probability distribution into steps of 0.01 ranging from 0 up to 1.0. When a cue is received, the likelihoods μ given the cue received (such as shown in fig. 1*d*–1*f*) is used to update the prior estimate of μ to form a posterior estimate of μ.

The foraging effort used by an individual is the average optimal foraging effort (from the dynamic state variable model) for the current time (t) and previous foraging success (x) and across different values of μ weighted by the probabilities of those μ according to the individual's posterior estimate.

Because the state of the environment (μ) is changing over time, it is adaptive for individuals to value new information more than old information by optimally forgetting or discounting older information (McNamara and Houston 1987; Luttbeg and Warner 1999). The probability of the environment changing its state is γ, and when it does change, μ is drawn from an assumed beta distribution

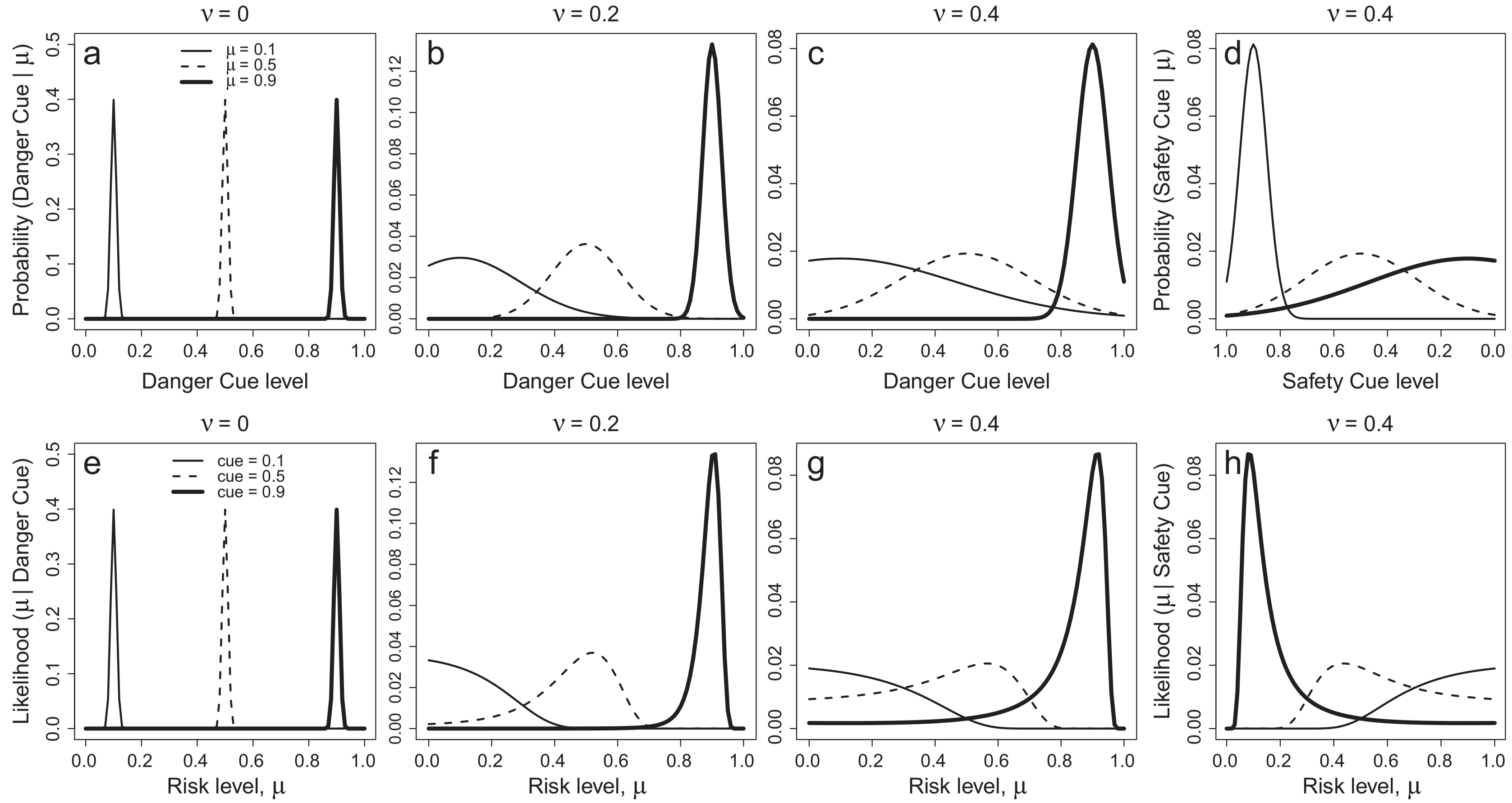

Figure 1: Probabilities of cues received given risk levels and likelihoods of risk levels given cues received. Probability distribution of the danger cues received with $\theta = 0.01$ and $\nu = 0$ (*a*), $\nu = 0.2$ (*b*), and $\nu = 0.4$ (*c*), and safety cues received with $\theta = 0.01$ and $\nu = 0.4$ (*d*) all given different true risk levels (μ). The likelihoods of μ with $\theta = 0.01$ and $\nu = 0$ (*e*), $\nu = 0.2$ (*f*), and $\nu = 0.4$ (*g*) given different danger cues received and with $\theta = 0.01$ and $\nu = 0.4$ (*h*) all different safety cues received.

of risk levels. Thus, for each time step (excluding the first) after an individual has updated their estimate of μ on the basis of the cue received and employed a foraging effort on the basis of their estimate of μ, the individual optimally forgets previous information with their new estimate being the weighted average of their previous estimate weighted by $(1 - \gamma)$ and the assumed beta distribution of risk levels (μ) weighted by γ. This was done by multiplying the height of each discrete bin of μ by $(1 - \gamma)$ and redistributing the removed bin heights on the basis of the assumed beta distribution.

We explore how the relative fitness achieved by using danger and safety cues depend on how their precisions (ν) vary with μ, the magnitude of the risk posed by the predator (κ), the shape of how the probability of being killed increases with prey foraging effort (τ), the distribution of risk levels, and the type of fitness function. Code for the model was written in the R programming language (ver. 3.6.0; R Core Team 2017), and the code has been deposited in the Dryad Digital Repository (Luttbeg et al. 2019; https://doi.org/10.5061/dryad.m60f221). For each manipulation of these parameters, we did 10,000 replicates of individuals paying different levels of attention to the two cue types ($\alpha = 0, 0.25, 0.5, 0.75$, and 1). We report the average achieved fitness and the relative fitness, which was calculated by dividing average fitness values by the average fitness achieved by individuals paying attention only to safety cues ($\alpha = 0$).

Results

When $\nu = 0$, there is no difference in information from safety and danger cues (eq. [6]) and thus how much attention is paid to the two cue types had no effect on prey fitness (fig. 2*a*, 2*b*). As ν was increased, the average fitness for both cue types decreased because information in the cues was decreased over parts of their ranges, but the loss of fitness was greater for the danger cue. The relative fitness for individuals paying more attention to the danger cue (higher α) decreased as ν increased. As the two cue types became less precise at indicating μ at one end of the μ spectrum, it became more advantageous for prey to pay attention to the safety cue over the danger cue.

We look at the optimal foraging efforts found by the dynamic state variable model to understand why using safety cues confers higher fitness than using danger cues. Optimal foraging efforts depend on x, t, and μ. For $t = 10$, when μ is estimated by the prey to be >0.4, the optimal prey foraging effort is 0 (hiding) for all displayed levels of x (fig. 2*c*). Therefore, the danger cue is providing precise information about a range of μ where foraging efforts do not vary much. In comparison, the safety cue provides precise information about lower values of μ, where a prey's optimal foraging effort can vary dramatically. When x is low, the value of μ at which optimal foraging efforts changes from 1 to 0 shifts to the right as t increases, but for moderate to high levels of x, it is largely unchanged by t. Thus, the danger cue provides more valuable information than the safety cue only when t is high and x is low.

The advantage of safety cues over danger cues increases as the intensity of predation risk (κ) increases. The relative fitness that prey achieved decreased as their attention to the danger cue increased, and the rate of the decrease was greater when predators posed a higher risk (higher κ) to prey (fig. 3*a*).

In many circumstances, how often varying environments change their states can affect optimal prey responses (Lima and Bednekoff 1999; Gabriel et al. 2005). However, we found that the relative fitness of different levels of attention (α) to the danger cue was not affected by the probability that the environmental state changed (γ; fig. 3*b*).

The shape of how predation risk changes with the intensity of foraging effort (τ in eq. [1]) affected relative fitness from attention to the two cue types. Increasing τ above 1 causes P(killed) to increase at an accelerating rate as ε increases and decreases the P(killed) over the range of ε between 0 and 1, which leads to higher optimal foraging efforts when predation risk is estimated to be low. When $\tau = 2.0$, prey use the maximum foraging effort ($\varepsilon = 1$) over a broader range of estimated μ, and this reduced the fitness advantage of safety cues over danger cues (fig. 3*c*). Decreasing τ below 1 causes P(killed) to increase at an decelerating rate as ε increases and increases P(killed) over the range of ε between 0 and 1, which favors less intense foraging when estimated predation risk is low. When $\tau = 0.5$, the region in which optimal foraging efforts vary is shifted to lower values of μ, and this increases the advantage of safety cues over danger cues (fig. 3*c*).

We varied the distribution of risk levels to see how the relative performances of safety and danger cues were affected by the relative frequencies of low and high risk levels. We looked at scenarios when high levels of predation risk (μ) were more common (Beta(2, 1)) and less common (Beta(1, 2)) than a uniform distribution (fig. 4*a*). Relative fitness achieved when an individual paid more attention to the danger cue was increased when high risk levels were more common and decreased when high risk levels were less common (fig. 4*b*).

When prey immediately convert their foraging effort into fitness ("immediate fitness," eq. [5]), individuals paying attention to the safety cue achieved higher average fitness than those using the danger cue, but the advantage was severely reduced (fig. 5*a*, 5*b*). Asset protection is the principle that individuals should take less risk when they have more assets (like future reproductive value) to lose (Ludwig and Rowe 1990; Clark 1994). When individuals

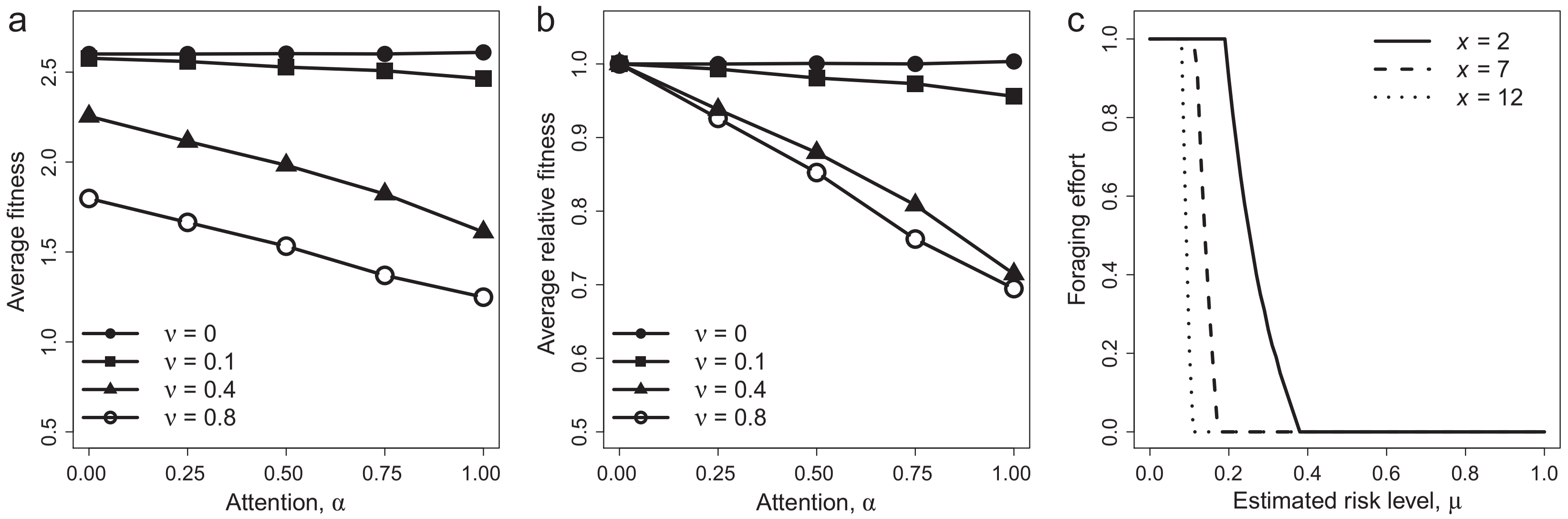

Figure 2: The effect of ν on the fitness and relative fitness of individuals paying different levels of attention to the two cue types, and optimal foraging efforts for prey. We varied the variance term, ν, with $\theta = 0.01$, $\kappa = 0.75$, $\tau = 1$, and $\gamma = 0.2$ and show average fitness achieved (*a*) and average relative fitness achieved (*b*). Optimal foraging efforts (*c*) from the dynamic state variable model for different levels of μ and x given $t = 10$, $\kappa = 0.75$, $\tau = 1$, and $\gamma = 0.2$.

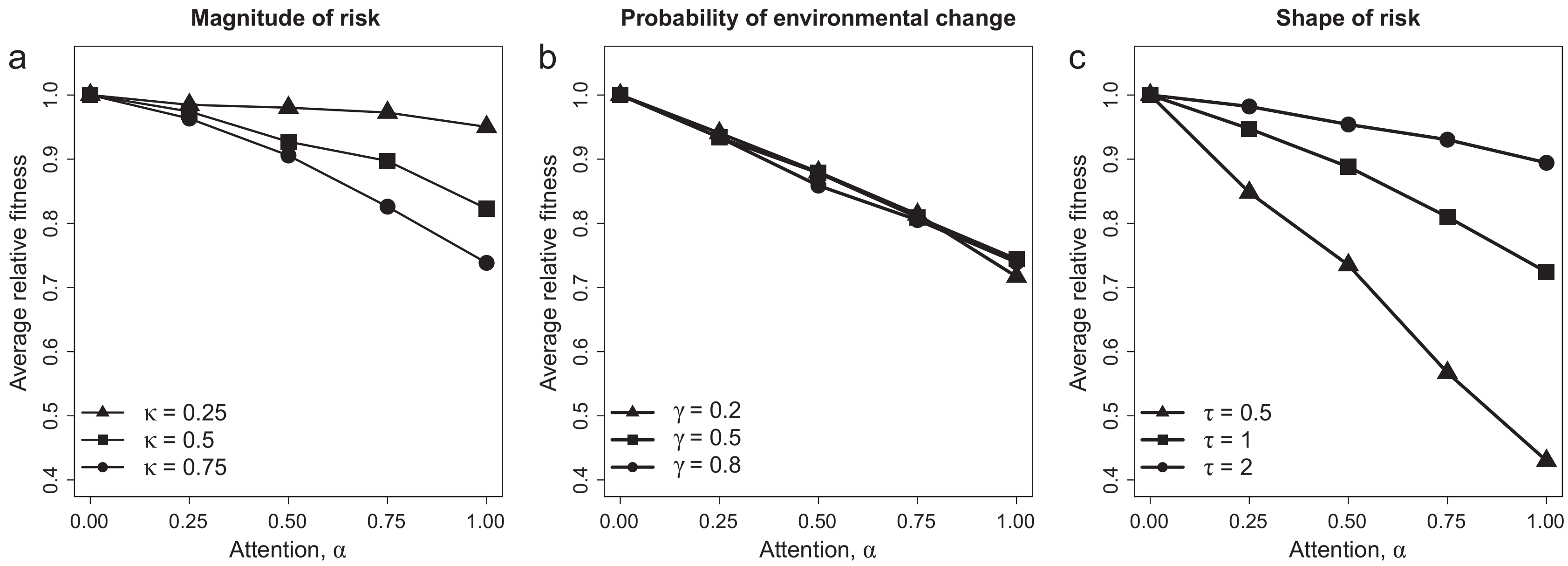

Figure 3: The effects of magnitude of predation risk, probability of environmental change, and shape of the predation risk curve on the relative fitness of individuals paying different levels of attention to the two cue types. We varied (*a*) the magnitude of predation risk (κ) with $\theta = 0.01$, $\nu = 0.4$, $\tau = 1$, and $\gamma = 0.2$; (*b*) the probability of the environmental state changing (γ) with $\theta = 0.01$, $\nu = 0.4$, $\tau = 1$, and $\kappa = 0.75$; and the (*c*) shape of how predation risk changed (τ) as foraging effort increased with $\theta = 0.01$, $\nu = 0.4$, $\gamma = 0.2$, and $\kappa = 0.75$.

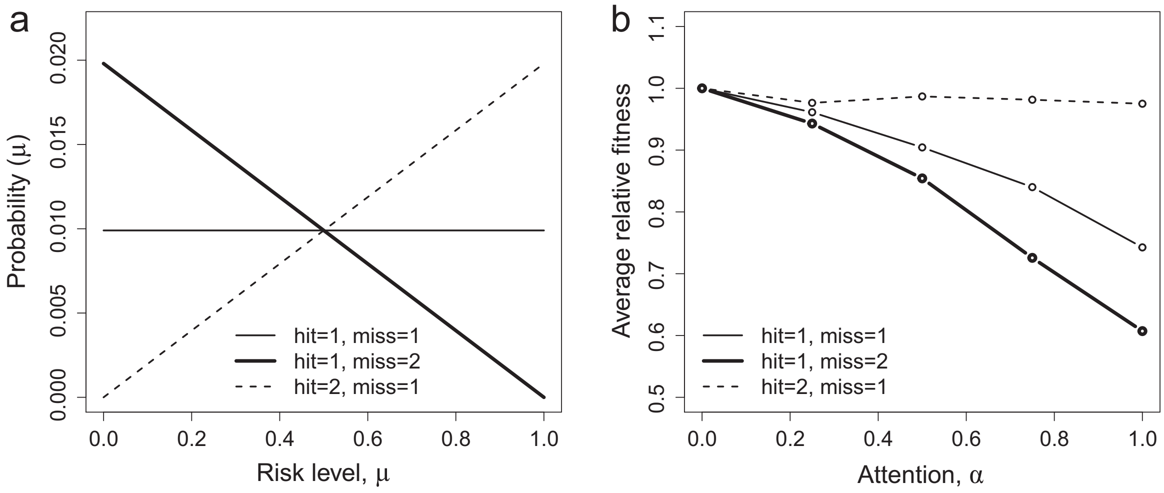

Figure 4: Beta distributions of the probabilities of risk levels and its effect on the relative fitness of individuals paying different levels of attention to the two cue types. Beta distributions of risk levels (*a*) and the resulting average relative fitness levels achieved for different levels of attention paid to the two cue types (*b*) with $\theta = 0.01$, $\nu = 0.4$, $\kappa = 0.75$, $\tau = 1$, and $\gamma = 0.2$.

immediately convert x into fitness, they have no assets to protect because x is immediately spent. Resulting optimal prey foraging efforts are less cautious with nonzero foraging efforts being used for higher estimated μ (fig. 5*c* compared with fig. 2*c*), which increases the usefulness of the danger cue. As individuals get closer to the end of the model, they become even less cautious. In general, the safety cue is valuable precise information during earlier time steps of the model and by the danger cue during later time steps; thus, neither cue type does substantially better than the other.

Discussion

Prey are exposed to a myriad of cues that potentially give them information about the current state of their environment (Ferrari et al. 2010). What cues individuals should pay attention to depends on their costs, timeliness, precision, and redundancies. We tested how much attention prey should pay to two types of cues that differ in the levels of predation risk that they most precisely indicate. We found that prey consistently achieved higher fitness when they paid more attention to safety cues that give more precise information about low levels of predation risk than to danger cues that give more precise information about high levels of predation risk. Past research has focused mostly on how cues that indicate the current presence of predators affect prey phenotypes and resulting trophic dynamics (Polis and Holt 1992; Schmitz et al. 1997; Relyea 2003; Preisser et al. 2005). We believe that our results highlight that prey should also modify their phenotypes on the basis of cues that indicate that predation risk is currently low and that the addition of this perspective might alter predictions and understanding of ecological dynamics.

We found that, in general, individuals achieved higher fitness when all of their attention was on the safety cue. The advantage of the safety cue increased as the two cue types became less precise (higher ν) at indicating predation risk (μ) at one end of the μ spectrum. Prey fitness was decreased more by the danger cue being poor at precisely indicating low levels of risk than by the safety cue being poor at precisely indicating high levels of risk. We also found that the advantage of the safety cue was larger when predators posed a higher risk (higher κ) and when the shape of how ε affects P(killed) increased predation risk. We found that the relative performance of the two cue types was not affected by the probability of environmental change but was affected by the distribution of environmental states. And finally, switching from individuals achieving fitness only if they survived to the end of the model duration to them achieving fitness immediately after foraging success greatly reduced the advantage of safety cues over danger cues. While most species likely experience a delay in achieving fitness, longer delays should generally increase asset protection and make prey behavior more risk averse, with the caveat that asset protection increases with more assets and thus depends on the rate of asset accumulation. We predict that, in general, species with longer delays in reproduction are likely to more strongly pay attention to safety cues over danger cues.

These results are caused by the cost of being killed by a predator heavily outweighing the benefits from foraging

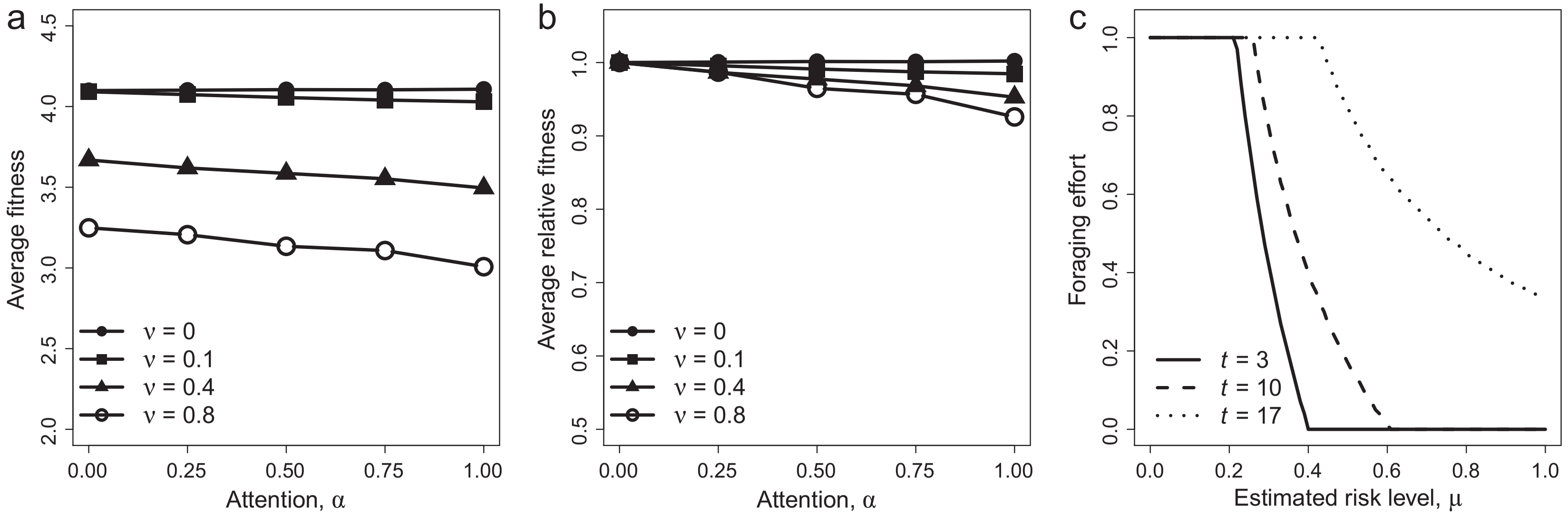

Figure 5: Given immediate fitness, the effect of ν on the fitness and relative fitness of individuals paying different levels of attention to the two cue types, and optimal foraging efforts. We varied the variance term, ν, with $\theta = 0.01$, $\kappa = 0.75$, $\tau = 1$, and $\gamma = 0.2$, and show average fitness achieved (*a*) and average relative fitness achieved (*b*). Optimal foraging efforts (*c*) from the dynamic state variable model for different levels of μ and t given $\kappa = 0.75$, $\tau = 1$, and $\gamma = 0.2$.

success (Bouskila and Blumstein 1992) and how that shapes the value of information. Optimal prey behaviors when making trade-offs between the risk of predation and the benefits of foraging are generally risk averse (Johnson et al. 2013). Thus, there can be a wide range of estimated predation risk that lead to prey not foraging. The value of information received from a cue can be measured as the difference in the expected fitness of individuals with and without the information (Stephens 1989). When a prey already estimates that predation risk is high, a danger cue that gives the prey a more precise estimate of predation risk will have no value because it does not alter their behavior. In comparison, the information in a safety cue will often have value when it precisely indicates lower levels of predation risk because information about the exact level of low μ often leads to changes in prey behavior.

Our results support this interpretation. When predators posed a higher threat (higher κ) and when the shape of how foraging effort (ε) affects P(killed) increased overall predation risk, a broader range of high estimated predation risk caused the prey to stop foraging. This increased the circumstances in which precise information from danger cues about high levels of predation risk had no value and thus increased the relative superiority of the safety cue. In addition, changing from delayed fitness to immediate fitness decreased the range of predation risk that caused foraging to cease and thus decreased the advantage that safety cues had over danger cues.

A danger cue would be superior to a safety cue if the danger cue were more likely to alter prey behavior than the safety cue. For example, a danger cue would be more valuable than a safety cue if prey used the maximum foraging effort across a broad range of low predation risk levels and decreased their foraging efforts at high predation risk levels. This could occur if the fitness benefits of foraging success greatly exceed the potential costs of predation, such as when starvation is probable or when prey need to achieve a threshold level of foraging success to mature and reproduce (Lima and Bednekoff 1999) and food is scarce.

The relative performances of individuals relying on safety and danger cues did not depend on how often the environment changed (γ), but rather on the distribution of environmental states. The two cue types do not fundamentally differ in how quickly they can indicate to a prey that the environment has changed, thus γ did not affect the relative performance of the two cue types. We have seen that relying on safety cues tends to produce higher fitness because it is giving precise information in the range of low risk levels where prey are more likely to alter their behavior. Thus, when those low risk levels occur less often than high risk levels, the relative superiority of safety cues is reduced. When a cue type is superior in one range of environmental states, increasing the occurrence of states in that range increases the relative fitness of using the cue.

There are several examples of prey responding to what might be safety cues. Many involve prey using the behaviors of other prey to indicate the reduction of predation risk. Hughes et al. (2014) found that the crab consumption of clams was reduced by exposure to sounds from predatory fish compared with a silent control, but clam consumption was increased by exposure to the sound of foraging snapping shrimp compared with the silent control. Thus, the sound of foraging shrimp is perhaps a safety cue for crabs, indicating low predation risk. Similarly, female crested anoles (*Anolis cristatellus*) displayed at higher rates when exposed to the calls of bananaquits (*Coereba flaveola*)—who are not their predator but who may share predators and potentially are a competitor—compared with silence (Huang et al. 2011). Laboratory rats reduced their movements when the sound of another moving rat stopped and resumed movement when the sound of movement resumed (Pereira et al. 2012). Safety cues are not restricted to the acoustic domain. Seeing other active prey may facilitate safety recognition. For instance, house finches (*Haemorhous mexicanus*) were quicker to resume feeding when other birds were observed feeding (Roth et al. 2008). Chemical cues can also be used as environmental indicators of safety. Lactating dogs release a dog appeasing pheromone (DAP). Adult dogs exposed to DAP display reduced barking amplitude (dB) and frequency and exhibit less fear (Tod et al. 2005).

Other potential safety cues indicate that the predator's motivation or ability to capture prey is currently reduced. For example, larval California newts (*Taricha torosa*) recognize the chemical defenses (tetrodotoxin) of cannibalistic adults as a threat. However, cannibalistic adults prefer to feed on earthworms, and injured earthworms release an amino acid (arginine) that when detected by larval newts indicates safe locations despite the presence of the feeding cannibals (Ferrer and Zimmer 2007). In a tritrophic system, the presence of larger predators can cause avoidance by smaller predators (Ramesh et al. 2017); thus, cues indicating the presence of larger predators could serve as safety cues for prey that suffer higher predation risk from the smaller predators. For example, in Tasmania, introduced feral cats (*Felis catus*) are a medium-sized predator for many smaller mammals, including swamp rats (*Rattus lutreolus*). Cats were detected less frequently at traps that were scented with scat from the larger Tasmanian devil (*Sarcophilus harrisii*). Swamp rats tended to be caught less often at traps that were scented with cat scat but more often at traps scented with Tasmanian devil scat (Lazenby and Dickman 2013). This would be an example of a safety cue if the presence of the scent of a Tasmanian devil gives the prey precise information about low levels of risk because of cats being displaced, but the absence of the Tasmanian devil cue gives less precise information about high levels of risk when cats might be more present.

We defined safety and danger cues by how their precision varied with μ. However, there have been few studies that have quantified how the correlation of cues with μ change as μ varies. There is some evidence that olfactory cues might match our definition of danger cues. Olfactory cues are high near their source and then decline to a point where their concentration does not change much as the distance to the source increases (Webster and Weissburg 2001). Thus, close to the source, where predation risk is high, changes in concentration are detectable and could give precise information about distance to the source. But farther from the source, the olfactory cue changes little or is undetectable and thus gives little precise information about distance to the source. We are unaware of any equivalent data on safety cues but believe that the activity levels other prey, number of active prey, and what prey are being active changes little when a predator is nearby but do change as the predator gets farther away. This would be a safety cue if the activity levels of other prey give more precise information about predation risk when it is lower.

Safety cues could have large effects on prey physiology and trophic dynamics. How efficiently prey convert energy into growth and reproduction is affected by variation in predation risk and uncertainty. The growth efficiency of the dog whelk (*Nucella lapillus*) is lower when exposed to varying predation risk in comparison with the constant absence or presence of predation risk (Trussell at al. 2011). The presence of safety cues during periods of low risk might reduce the uncertainty experienced by prey and consequently reduce the stresses of living in a varying environment. This might have consequences for the respiration rates and endocrinology of prey and thus growth efficiencies. The risk of predation has been shown to have large effects on trophic dynamics (Peacor and Werner 2001). The presence of cues that reliably indicate current levels of predation risk in a timely manner are needed for nonconsumptive effects to occur (Luttbeg and Trussell 2013). The presence of safety cues could increase these nonconsumptive effects by making periods of high and low risk more detectable. However, safety cues could also allow prey to more immediately resume their foraging after predation risk has declined, which could reduce the size of nonconsumptive effects. We found that prey fitness was increased by attention to safety cues, indicating that they consume more resources when they use the safety cues, and therefore trait-mediated effects are probably reduced. This might be particularly important for how trait- and density-mediated effects have been measured.

The fear of being captured and killed by a predator conjures up considerable emotions for most people. Perhaps it is not surprising that predation research has concentrated on understanding and measuring predation risk. Recently, we have seen some effort directed toward understanding how prey recognize safety, in the context of both nonpredators and safe locations (Ferrari and Chivers 2011; Chivers et al. 2014). We hope that this empirical work combined with this modeling will turn the tables on this risk paradigm and cause people to consider the role of safety in driving not only prey behavior but also morphology and life history.

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Literature Cited

Bouskila, A., and D. T. Blumstein. 1992. Rules of thumb for predation hazard assessment: predictions from a dynamic model. American Naturalist 139:161–176.

Brown, G. E., M. C. O. Ferrari, C. K. Elvidge, I. Ramnarine, and D. P. Chivers. 2013. Phenotypically plastic neophobia: a response to variable predation risk. Proceedings of the Royal Society B 280:20122712.

Brown, J. S., and B. P. Kotler. 2004. Hazardous duty pay and the foraging cost of predation. Ecology Letters 7:999–1014.

Chivers, D. P., J. M. Kiesecker, A. Marco, J. Devito, M. T. Anderson, and A. R. Blaustein. 2001. Predator-induced life history changes in amphibians: egg predation induces hatching. Oikos 92:135–142.

Chivers, D. P., M. I. McCormick, M. D. Mitchell, R. A. Ramasamy, and M. C. O. Ferrari. 2014. Background level of risk influences learning of predators and non-predator by coral reef damselfish. Proceedings of the Royal Society B 281:20140355.

Clark, C. W. 1994. Antipredator behavior and the asset-protection principle. Behavioral Ecology 5:159–170.

Clark, C. W., and M. Mangel. 2000. Dynamic state variable models in ecology: methods and applications. Oxford University Press, New York.

Dall, S. R., L. A. Giraldeau, O. Olsson, J. M. McNamara, and D. W. Stephens. 2005. Information and its use by animals in evolutionary ecology. Trends in Ecology and Evolution 20:187–193.

De Laet, J. F. 1985. Dominance and anti-predator behaviour of great tits *Parus major*: a field study. Ibis 127:372–377.

Dugatkin, L. A., and J. G. J. Godin. 1992. Prey approaching predators: a cost-benefit perspective. Annales Zoologici Fennici 29:233–252.

Etting, S. F., and L. A. Isbell. 2014. Rhesus macaques (*Macaca mulatta*) use posture to assess level of threat from snakes. Ethology 120:1177–1184.

Fernández-Juricic, E., and A. Kacelnik. 2004. Information transfer and gain in flocks: the effects of quality and quantity of social information at different neighbour distances. Behavioral Ecology and Sociobiology 55:502–511.

Ferrari, M. C. O., and D. P. Chivers. 2011. Learning about nonpredators and safe places: the forgotten elements of risk assessment. Animal Cognition 14:309–316.

Ferrari, M. C. O., B. D. Wisenden, and D. P. Chivers. 2010. Chemical ecology of predator-prey interactions in aquatic ecosystems: a review and prospectus. Canadian Journal of Zoology 88:698–724.

Ferrer, R. P., and R. K. Zimmer. 2007. The scent of danger: arginine as an olfactory cue of reduced predation risk. Journal of Experimental Biology 210:1768–1775.

Gabriel, W., B. Luttbeg, A. Sih, and R. Tollrian. 2005. Environment tolerance, heterogeneity and the evolution of reversible plastic responses. American Naturalist 166:339–353.

Houston, A. I., and J. M. McNamara. 1999. Models of adaptive behaviour: an approach based on state. Cambridge University Press, Cambridge.

Huang, B., K. Lubarsky, T. Teng, and D. T. Blumstein. 2011. Take only pictures, leave only . . . fear? the effects of photography on the Western Indian anole *Anolis cristatellus*. Current Zoology 57:77–82.

Hughes, R. A., D. A. Mann, and D. L. Kimbro. 2014. Predatory fish sounds can alter crab foraging behaviour and influence bivalve abundance. Proceedings of the Royal Society B 281:20140715.

Kats, L. B., and L. M. Dill. 1998. The scent of death: chemosensory assessment of predation by prey animals. Ecoscience 5:361–394.

Johnson, D. D. P., D. T. Blumstein, J. H. Fowler, and M. G. Haselton. 2013. The evolution of error: error management, cognitive constraints, and adaptive decision-making biases. Trends in Ecology and Evolution 28:474–481.

Lazenby, B. T., and C. R. Dickman. 2013. Patterns of detection and capture are associated with cohabiting predators and prey. PLoS ONE 8:e59846.

Lima, S. L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Advances in the Study of Behavior 27:215–290.

Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. American Naturalist 153:649–659.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Ludwig, D., and L. Rowe. 1990. Life-history strategies for energy gain and predator avoidance under time constraints. American Naturalist 135:686–707.

Luttbeg, B., M. C. O. Ferrari, D. T. Blumstein, and D. P. Chivers. 2019. Data from: Safety cues can give prey more valuable information than danger cues. American Naturalist, Dryad Digital Repository, https://doi.org/10.5061/dryad.m60f221.

Luttbeg, B., and G. C. Trussell. 2013. How the informational environment shapes how prey estimate predation risk and the resulting indirect effects of predators. American Naturalist 181:182–194.

Luttbeg, B., and R. R. Warner. 1999. Reproductive decision-making by female peacock wrasses: flexible versus fixed behavioral rules in variable environments. Behavioral Ecology 10:666–674.

McNamara, J. M., and A. I. Houston. 1987. Memory and the efficient use of information. Journal of Theoretical Biology 125:385–395.

Meuthen, D., S. A. Baldauf, T. C. Bakker, and T. Thünken. 2018. Neglected patterns of variation in phenotypic plasticity: age-and sex-specific antipredator plasticity in a cichlid fish. American Naturalist 191:475–490.

Peacor, S. D., and E. E. Werner. 2001. The contribution of trait-mediated indirect effects to the net effects of a predator. Proceedings of the National Academy of Sciences of the USA 98: 3904–3908.

Pereira, A. G., A. Cruz, S. Q. Lima, and M. A. Molta. 2012. Silence resulting from the cessation of movement signals danger. Current Biology 22:R627–R628.

Polis, G. A., and R. D. Holt. 1992. Intraguild predation: the dynamics of complex trophic interactions. Trends in Ecology and Evolution 7:151–154.

Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to death? the effects of intimidation and consumption in predator-prey interactions. Ecology 86:501–509.

Ramesh, T., R. Kalle, and C. T. Downs. 2017. Staying safe from top predators: patterns of co-occurrence and inter-predator interactions. Behavioral Ecology and Sociobiology 71:41.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Relyea, R. A. 2003. Predators come and predators go: the reversibility of predator-induced traits. Ecology 84:1840–1848.

Roth, T. C., J. G. Cox, and S. L. Lima. 2008. The use and transfer of information about predation risk in flocks of wintering finches. Ethology 114:1218–1226.

Schmitz, O. J., A. P. Beckerman, and K. M. O'Brien. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. Ecology 78:1388–1399.

Stephens, D. W. 1989. Variance and the value of information. American Naturalist 134:128–140.

Suraci, J. P., M. Clinchy, L. M. Dill, D. Roberts, and L. Y. Zanette. 2016. Fear of large carnivores causes a trophic cascade. Nature Communications 7:10698.

Tod, E., D. Brander, and N. Waran. 2005. Efficacy of dog appeasing pheromone in reducing stress and fear related behaviour in shelter dogs. Applied Animal Behaviour Science 93:295–308.

Tollrian, R. 1995. Predator-induced morphological defenses: costs, life history shifts, and maternal effects in *Daphnia pulex*. Ecology 76:1691–1705.

Trussell, G. C., C. M. Matassa, and B. Luttbeg. 2011. The effects of variable predation risk on foraging and growth: less risk is not necessarily better. Ecology 92:1799–1806.

Webster, D. R., and M. J. Weissburg. 2001. Chemosensory guidance cues in a turbulent chemical odor plume. Limnology and Oceanography 46:1034–1047.

Zanette, L. Y., A. F. White, M. C. Allen, and M. Clinchy. 2011. Perceived predation risk reduces the number of offspring songbirds produce per year. Science 334:1398–1401.

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