

Does Cohistory Constrain Information Use? Evidence for Generalized Risk Assessment in Nonnative Prey

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ABSTRACT: Though prey use a variety of information sources to assess predation risk, evolutionary cohistory with a predator could constrain information use, and nonnative prey might fail to recognize risk from a novel predator. Nonnative prey might instead use generalized risk assessment, relying on general alarm signals from injured conspecifics rather than cues from predators. I tested the influence of shared predator-prey history on information use, comparing responses among three native and four nonnative prey species to chemical cues from a native predator and cues from injured conspecific prey. Nonnative prey demonstrated information generalism: (1) responding stronger to alarm cues released by injured conspecific prey than to cues from predators and (2) responding similarly to alarm cues as to cues from predators consuming injured conspecific prey. By contrast, for native prey, multiple information sources were required to elicit the greatest defense. The influence of other sources of chemical information was not predicted by cohistory with the predator: only one nonnative snail responded to the predator; digestion was important for only two native species; the identity of injured prey was important for all prey; and predator and prey cues contributed additively to prey response. Information generalism, hypothesized to be costly in coevolved interactions, could facilitate invasions as a driver of or response to introduction to novel habitats.

Keywords: behavioral plasticity, induced defenses, invasive species, predation cues, predator avoidance, risk assessment.

Introduction

Predation threat recognition is ubiquitous in both plants and animals, and resulting defenses can exert a strong influence on ecological dynamics, community structure, and ecosystem function (Werner and Peacor 2003; Peckarsky et al. 2008; Schmitz et al. 2008). Prey (including plants) commonly respond to a wide range of information modalities in assessing threats, including visual (Blumstein et al.

2000; Cooper 2009), auditory (Moiseff et al. 1978; Lohrey et al. 2009), olfactory/chemical (Hay 2009; Ferrari et al. 2010), and mechanical/tactile cues (e.g., Hazlett and McLay 2000; León et al. 2001; Warkentin 2005). Informative cues can originate from the predator itself (Kats and Dill 1998), from other conspecific or heterospecific prey (Chivers and Smith 1998; Schoeppner and Relyea 2009*b*), or from the interaction between predator and prey (e.g., fecal material, altered prey cues; Jacobsen and Stabell 1999; Agarwala et al. 2003; Schoeppner and Relyea 2009*a*).

The relative value of these signals in risk assessments varies on the basis of two qualities: (1) the quantity of information in the signal and (2) the level of predation risk associated with the information. This is an extension of the threat sensitivity hypothesis, made popular by Helfman (1989), which posited that prey should demonstrate graded responses to risk cues on the basis of the magnitude of threat indicated by any particular cue, optimizing the trade-off between increased probability of survival and increased fitness cost incurred by engaging in defenses. This hypothesis predicts that cues—or cue combinations—indicating a greater probability of predation should elicit a greater magnitude of defense, and it has been well supported empirically (e.g., Schoeppner and Relyea 2008; Hill and Weissburg 2014; Turney and Godin 2014). The amount of information contained in a cue should influence the prey's certainty of predation risk and suggest an appropriate response, and it thus alters the value of the risk information for a given cue. However, the relative value of different cues remains unresolved and most certainly varies across ecological and evolutionary contexts. The majority of experiments on risk assessment are conducted with only one or two species and test a small number of cues, limiting generalization about information use in risk assessments. Moreover, interpreting a lack of response to a given cue is difficult because prey could fail to respond to a cue for multiple reasons: an inability to recognize the cue, an inability to mount the defense, constraints of a fitness trade-off, or because that cue alone (in the individual's or population's history) has not been an accurate predictor of

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predation risk (Carthey and Banks 2014). Disentangling these possibilities presents an ongoing experimental challenge.

One leading assumption is that, in contrast to alarm cues originating from prey, cues originating from predators are more informative because they could indicate the predator's attack strategy, location, and even motivation state (Kats and Dill 1998; Bourdeau 2010a). For this reason, researchers have proposed that cues from injured conspecifics are less useful indicators of risk than cues from predators, and, therefore, it should be costly for prey to respond to general injury cues without additional information indicating which type of defense would maximize the probability of surviving (Sih et al. 2010). Supporting this hypothesis, researchers have noted that prey engage in defenses only when multiple cues are combined (Alexander and Covich 1991; Bourdeau 2010a) or that cues emanating from injured conspecific prey fail to elicit any defense at all (e.g., Slusarczyk 1999; Griffiths and Richardson 2006; Dalesman et al. 2007). A key factor in the information content of an alarm cue is likely to be whether the cue is released actively or passively (Fraker et al. 2009). For instance, vocal alarm signals from birds or prairie dogs contain information about the type and location of predation threats present (Kiriazis and Slobodchikoff 2006; Templeton and Greene 2007).

Evidence of digestion and predator diet could also provide valuable information about risk. Many prey respond stronger to cues from predators fed a conspecific prey than to cues from predators fed a heterospecific prey (Alexander and Covich 1991; Jacobsen and Stabell 2004; Laforsch et al. 2006; Schoeppner and Relyea 2009b). Presumably, information about victim identity provides the responding prey with information about the diet preferences of the predator, and a predator that has the capability and motivation to consume a conspecific should indicate a greater threat. On the other hand, it is less intuitive to predict how prey should respond to digestion per se. Detecting that the predator has digested conspecifics could be more informative than simultaneously detecting a predator along with cues from injured conspecifics, because digestion provides evidence of a causal link between the predator and injured prey cues. But digestion could also indicate lower risk because the predator might be satiated. In the limited number of experiments that have addressed this question explicitly, digestion increased the magnitude of prey response relative to combined cues from predators and injured prey (Jacobsen and Stabell 2004; Schoeppner and Relyea 2009a).

One constraint that can undoubtedly influence the information that prey use to assess risk is the length of evolutionary history the prey shares with the predator (Payne et al. 2004). In species introductions, for example, prey have been exposed to a predator for only a relatively short time and might not have the ability to recognize cues produced by

that predator (Carthey and Banks 2014). Failure to demonstrate any appropriate defense to the novel predation threat could have substantial consequences for the success and impacts of an invasion, whether the prey is the native or the nonnative species in the interaction (Sih et al. 2010). Perhaps the best-known example is the brown tree snake (*Boiga irregularis*) invasion on the island of Guam, which locally extirpated local and endemic prey unfamiliar with a threat from a nocturnal arboreal snake (Fritts and Rodda 1998).

However, nonnative prey are not similarly constrained in their ability to recognize cues generated by injured conspecifics and, indeed, might be more likely than native prey to use those cues to assess risk (the generalized risk assessment hypothesis discussed by Sih et al. [2010]). Generalized risk assessment would mean that cues providing little information about the nature of the threat were relatively more important in generating the total response to the predation threat, and it does not require that the introduced population recognize the novel predator per se. A growing number of studies have addressed whether prey recognize novel predators and/or novel predation threats (for a recent review, see Carthey and Banks 2014), but few have investigated the role of general cues in novel predator-prey interactions (Grason and Miner 2012; Bourdeau et al. 2013).

There are two possible explanations for a possible greater prevalence of information generalism among nonnative species. Information generalism in risk assessment, similar to dietary and habitat generalism, could predispose species to be successful at invading novel habitats. Species that utilize generalized risk assessment might be able to sufficiently reduce biotic resistance to persist on arrival in a novel predation regime and could be characterized as high-risk invaders. Alternatively, the introduction event itself might impose selection for generalized risk assessment if native predators, novel to the invaders, consume all individuals that require information about familiar predators and those that are wary of cues from injured conspecifics survive. Rapid evolution in response to strong selection of biological invasions has been observed in several systems (Strauss et al. 2006; Whitney and Gabler 2008; Nunes et al. 2014). These scenarios are non-mutually exclusive, and their relative importance could have substantial implications for identifying and managing invaders and biocontrol agents.

I tested how information used in risk assessments varies with evolutionary cohistory of predator and prey by assaying behavioral defenses of three species of native and four species of nonnative prey, in response to a single native predator. I hypothesized (table 1) that (1) the shorter evolutionary cohistory with the predator would mean that nonnative prey were less likely than native prey to respond defensively to that predator (i.e., spend more time avoiding than when the predator is absent); (2) native prey would be

Table 1: Hypotheses, predictions, and analyses used to test information use in native and nonnative prey

Hypothesis	Analysis type	Predictions (treatment comparisons)	
		Native prey	Nonnative prey
1. Nonnative prey are less likely to respond to a predator than native prey	Two-way GLMM	Significant effect of predator cues	No effect of predator cues
2. Nonnative prey are more likely to respond to general cues from injured conspecifics than native prey	Two-way GLMM	No effect of injured conspecifics	Significant effect of injured conspecifics
3. Native prey are more likely than nonnative prey to respond synergistically to combined predator and general injured conspecific cues	Two-way GLMM	Positive interaction term	No, or negative interaction term
4. Information generalism is more common in nonnative than native prey	a. Linear contrast	$P > IC$ or $P \approx IC$	$P < IC$
	b. Linear contrast	$P \times IC > IC$	$P \times IC \approx IC$
5. Digestion of prey increases assessment of risk regardless of origin of prey	Linear contrast	$P + IC < P \times IC$	$P + IC < P \times IC$
6. Digestion of conspecific prey increases assessment of risk relative to digestion of heterospecific prey	Linear contrast	$P \times H < P \times IC$	$P \times H < P \times IC$

Note: H, heterospecific prey; IC, injured conspecific; P, predator.

less likely than nonnative prey to respond defensively to general risk cues (passively released injury cues) or would demonstrate a smaller magnitude of response (i.e., spend more time avoiding than when general cues are absent), because such a response carries a fitness advantage only when prey cannot recognize the predator; (3) combining multiple cue types increases the information available to prey nonlinearly only if prey can recognize both cues, and therefore, native prey should be more likely than nonnative prey to show a synergistic response to a combination of predator-released and injured prey cues; (4) information generalism, defined as the greater importance of general cues relative to specific cues in driving the full risk assessment, would be more common in nonnative than native prey. That is, even where prey respond to both general injury cues and cues from the predator itself, the general cues elicit a stronger response in nonnative prey than do the predator cues. In addition, this multispecies, multicue experiment enabled me to test further hypotheses that are related to information use in risk assessment: (5) digestion by the predator increases the perception of risk and (6) digestion of conspecific prey elicits a stronger response than digestion of heterospecific prey. The expectations about the role of evolutionary

cohistory in informing these last two predictions are less clear, but very few multispecies studies have been conducted to address these questions, let alone studies comparing native and nonnative species. Thus, this study afforded an opportunity to investigate interspecific variation in use of information in a more robust way than has previously been attempted.

Methods

To test whether predator-prey cohistory influences risk assessment, I compared information use of chemical cues among seven species of marine snail (three native and four nonnative) in response to a single crab predator (red rock crab, *Cancer productus* Randall) native to coastlines of the northeastern Pacific Ocean. In separate mesocosm experiments, each snail species was exposed to six predation cue treatments (table 2): a control treatment with no added cues, cues from an unfed predator only, cues from injured conspecific prey only, an additive combination of unfed predator and injured conspecific prey cues, a consumptive combination of predator and injured conspecific prey, or a

Table 2: Components of each cue treatment applied to prey species

Treatments	Abbreviation	Predator	Injured conspecifics	Fed
Control	Control	–	–	NA
Predator	P	+	–	No
Injured conspecifics	IC	–	+	NA
Additive combination	$P + IC$	+	+	No
Consumptive combination	$P \times IC$	+	+	IC
General digestion	$P \times H$	+	–	Fish

Note: NA, not applicable (indicates treatments lacking a predator).

general digestive cue treatment in which a bland food was fed to predators. I quantified responses to cues by observing snail avoidance behavior three times per week for multiple weeks (table 3).

The four nonnative snail species (*Ilyanassa obsoleta* Say and *Urosalpinx cinerea* Say from the western Atlantic Ocean; *Ocenebra inornata* Récluz and *Batillaria attramentaria* Sowerby from the western Pacific Ocean; hereafter referred to by genus names) share a similar history in Washington State, having been introduced unintentionally as hitchhikers along with nonnative oysters imported in the 1920s (Wonham and Carlton 2005). The ~100 years since introduction have yielded at most 50 generations in the new habitat for the nonnative species. None of the three native snails (*Littorina sitkana* Philippi, *Nucella lamellosa* Gmelin, and *Alia carinata* Hinds) are known to be invasive elsewhere. However, whether they have been introduced along other coastlines is also not known. The native crab, *C. productus*, is a locally abundant predator in intertidal and subtidal habitats. With strong, crushing claws, *C. productus* is a significant predation threat to snails (Yamada and Boulding 1998) and structures intertidal communities via consumption (Yamada and Boulding 1996).

Previous research has explored defensive responses of *Urosalpinx*, *Nucella*, and *Littorina* to cancrid crab predation cues. All three species respond defensively when they detect *C. productus* preying on conspecific snails (Appleton and Palmer 1988; Yamada et al. 1998; Grason and Miner 2012), but the organismal source of the inducing cue and the response measured has varied. For instance, *N. lamellosa* native to Washington State developed the greatest morphological shell defenses when exposed to cues from *C. productus* consuming conspecific snails—and, to a lesser extent, crabs alone—but did not change shell morphology in response to cues from injured conspecifics (Appleton and Palmer 1988; Bourdeau 2010a). Notably, the proximal cause of the change in shell characteristics might have been starvation due to reduced foraging rates of snails exposed to predation cues; starved *Nucella* produced shells similar to those exposed to cues of crabs fed conspecific snails (Bourdeau 2010b). On the other hand, *L. sitkana*, also native, responded behaviorally to *C. productus* (hiding or climbing out of the water, depending on the population) only when crabs were fed conspecific snails (Yamada et al. 1998). The authors inferred that the snails were therefore responding to alarm cues from injured conspecific snails, though this was not directly tested. Risk responses of *U. cinerea* to coevolved predators have not been examined, but several experiments document the response of nonnative populations to novel predator cues. *Urosalpinx* reduces feeding and increases predator avoidance behavior in response to crabs (*Carcinus maenas*, *C. productus*, and *Romaleon antennarium*) consuming conspecifics, but conflicting evi-

dence exists as to whether snails recognized the crabs themselves or were responding to other chemical information. In one study, *Urosalpinx* did not respond to *R. antennarium* alone (Kimbrow et al. 2009), but a separate study was able to detect avoidance behavior in response to both *R. antennarium* and *C. maenas* (Blum 2012). Additionally, *Urosalpinx* from Washington State spend more time hiding when presented to cues from *C. productus* alone (Grason and Miner 2012).

Collection and Husbandry

Snails were collected by hand from multiple localities in Washington State as they were required for experiments (for collection localities and snail size ranges, see table 3). Nonnative snails were housed in closed-circulating aquaria, while native snails were kept in flow-through seawater tables at Shannon Point Marine Center (SPMC; Anacortes, WA). All snails in holding were exposed to the same source water from the flow-through system at SPMC, which draws from the local beach. While in holding, snails were fed ad lib. on barnacles and bivalves (for predatory snails) or macroalgae and naturally recruiting diatoms (for herbivorous snails) and were not starved before experiments. No snails were directly exposed to cues from *C. productus* while in holding, and snails were not kept in holding for more than 3 weeks before being used in experiments.

Crabs were collected intertidally by hand at SPMC and Shilshole Marina (Seattle, WA) and housed in flow-through sea tables at SPMC. Crabs were fed frozen fish (*Tilapia* sp. or *Pangasius* sp.) or mussels (*Mytilus* spp.) several times weekly. The experiments included both male and female crabs of a broad range of sizes (70–150 mm carapace width), because even young individuals of this species are capable of crushing the shells of all sizes of snails (E. W. Grason, personal observation). Crabs were starved for at least 48 h before experiments to clear the gut.

Mesocosm Experiments

Experiments were conducted in laboratory mesocosms separately for each snail species over multiple years, but all experiments used the same design and equipment. Cue treatments were applied using a coupled, flow-through bin system (fig. A1; figs. A1, A2 are available online). Each coupled bin system was randomly assigned to one of the six cue treatments; eight replicate bin systems were used per cue treatment for a total of 48 bin systems per experiment. Snails on which behavioral observations were made were isolated from cue sources in the downstream bin and were provided with food and a refuge (several pieces of oyster shell) placed at opposing ends of the bin to force a trade-off decision.

Table 3: Experimental details and ecological background for each of seven species of marine snail in behavioral experiments

Species	Native range	Collection locality	Collection habitat	Dates	Snails (no.)	Experiment length (days)	Total observations (no.)	IC used (no.)	Snail length		Crab carapace width		Type of avoidance	
									Mean \pm SD (mm)	<i>n</i>	Mean \pm SD (mm)	<i>n</i>		
Native species:														
<i>Nucella lamellosa</i>	Northeast Pacific	Anacortes, WA (48.509228°, -122.683886°)	Cobble	August 7–September 18, 2013	1	42	18	2	28.4 \pm 4.7	54	109.2 \pm 12.3	27	Mussels (30.9 \pm 3.6 mm, <i>n</i> = 46) Diatoms on slides	Hiding
<i>Littorina sikkana</i>	Northeast Pacific	Anacortes, WA (48.509228°, -122.683886°)	Cobble	October 2–28, 2013	10	26	12	5	10.4 \pm 1.4	103	109.2 \pm 12.3	27	Diatoms on slides	Both
<i>Alia carinata</i>	Northeast Pacific	Case Inlet, WA (47.372406°, -122.816353°)	Eelgrass/mud	June 2–18, 2014	10	16	7	10	8.8 \pm .7	100	102.0 \pm 19.3	32	None/ambient diatoms	Fleeing
Nonnative species:														
<i>Batillaria attramentaria</i>	Western Pacific	Samish Bay, WA (48.577523°, -122.485835°)	Oyster bottom culture beds	May 31–June 12, 2013	10	13	6	5	30.9 \pm 3.4	99	109.2 \pm 12.3	27	None/ambient diatoms	Both
<i>Ilyanassa obsoleta</i>	Western Atlantic	Nemah, WA (46.547293°, -123.899923°)	Mudflat	May 4–23, 2014	3	19	9	3	22.1 \pm 2.1	50	102.0 \pm 19.3	32	Diatoms on slides	Hiding
<i>Ocenebra inornata</i>	Western Pacific	Samish Bay, WA (48.577523°, -122.485835°)	Oyster bottom culture beds	June 21–July 26, 2013	1	36	16	2	29.4 \pm 3.6	109	109.2 \pm 12.3	27	Mussels (33.4 \pm 4.1 mm, <i>n</i> = 27) Oysters (10–25 mm)	Hiding
<i>Urosalpinx cinerea</i> ^a	Western Atlantic	Willapa Bay, WA (46.420718°, -123.933877°)	Oyster hummocks	August 26–September 11, 2009	1	16	8	2	27.3 \pm 3.7	48	108.0 \pm 13.6	36	Oysters (10–25 mm)	Both

Note: In all experiments, each treatment was replicated eight times.

^a Data reproduced from Grason and Miner (2012).

I applied cue treatments upstream of the snails. In treatments that included crabs, a single crab was enclosed in the upstream bin and fed or starved as appropriate for the treatment (table 2). To generate cues of injured conspecifics that were not consumed by predators (IC and P + IC treatments), conspecific snails were lightly crushed, sufficiently to inflict shell and tissue injury but not to liquefy snails. Injured snails were then wrapped in a mesh pouch, which was attached to the inflow of the downstream bin, so that cues from injured snails were thoroughly dispersed throughout the downstream bins, but crabs (upstream) were prevented from detecting those same cues. In treatments where crabs were fed conspecific snails, the snails provided to the crab were first injured in the same manner as above before being added to the upstream bin with the crab. The bland diet for crabs consisted of frozen fish fillet (*Tilapia* sp. or *Pangasius* sp.) similar in mass to the snail body tissue used for injury cues (IC, P + IC, and P × IC treatments).

Behavioral observations and reapplication of cue treatments occurred three times per week, with the observations taking place before reapplication of cue treatments to minimize the effect of the disturbance on the behavior of the organisms. On those days, crabs were fed diets appropriate for the treatment, and injured conspecific pouches were replaced. In order to avoid the overaccumulation of cues, I removed crab waste and shell debris from all bins with crabs at least twice weekly. Flow rates were maintained in the system at approximately 2 L min⁻¹.

I assessed responses to risk cue treatments by observing the proportion of time snails in the downstream bin were engaged in predator avoidance behavior. Snails typically avoid predator encounters in two ways, either by hiding or by attempting to crawl out of the water (e.g., Haddock 1980; Alexander and Covich 1991; Turner et al. 1999). During observations, the location of each snail was categorized as flight (emersion), hiding (under or behind the refuge or behind other structures in the bin), or neither (feeding or crawling in any open area of the bin). *Batillaria* commonly buries in response to predators (Wells 2013); in that experiment, I added a layer of clean play sand to the bin at a depth of approximately 1.5 cm. *Batillaria* that were partially or fully buried in the sand were considered to be hiding. Another snail species (*Littorina*) would often climb onto the underside of the lid of the bin and fall off when I removed the lid to record observations. Such snails could be found oriented on the bottom of the bin with their operculum facing upward and were also considered to be attempting to flee via emersion.

The number of snails in each replicate downstream bin was consistent for each species—that is, within each experiment—but varied among species to partially account for variations in natural density (table 3). Thus, the whelk species, which occur in relatively lower densities, were isolated

as individual snails in each replicate downstream bin. By contrast, groups of 10 *Alia* were placed in each replicate downstream bin for that experiment, because that species occurs in densities × 100 greater in situ (E. W. Grason, personal observation).

Analysis

It is unlikely that all species of marine snail have evolved the same types of avoidance behaviors, because ecological contexts and shell morphology likely make different types of behavioral defenses (such as emersion and refuge use) more or less valuable to each species or population. I am aware of no published information documenting effect of behavioral defenses on survivorship in the presence of predators for these species. To avoid biasing the interpretation of behavior on the basis of a prior expectation of what is believed to be adaptive, I calculated predator avoidance behavior separately for each snail species.

Avoidance behavior was defined as the location metric (hiding, fleeing, or the sum of both, as indicated in table 3) that yielded the largest effect size for the full information treatment (predators eating conspecifics; P × IC). Effect size was calculated as the odds ratio of the response to the P × IC treatment (predators consuming injured conspecific prey) relative to the control (no cues). For example, avoidance behavior for *Alia* was defined as the number of snails fleeing in each bin on a given day, because the location metric that maximized the difference between the P × IC and control treatments was flight only. By contrast, the location metric for which the greatest effect size of the P × IC treatment was observable for *Littorina* was the sum of snails fleeing and hiding. The metric that yielded the greatest effect size was used for avoidance for all comparisons for that species.

To test hypotheses about influence of evolutionary cohistory of predator and prey on information use, I compared the proportion of time prey spent avoiding between native and nonnative species (table 1). Separate binomial generalized linear mixed effects models (GLMMs) of avoidance were constructed for each species, where the response variable was the number of snails avoiding in each bin on a given observation day, with the total number of snails in the observation bin (table 3) as the number of trials. Thus, the odds ratio for the logit link function was calculated as the ratio each day of the number of snails avoiding to the number of snails not avoiding. The GLMMs also included replicate bin as a randomly varying intercept to account for the repeated measures structure of multiple observation days within each experiment (table 3). A two-factor implementation of this model—using the control, the crab only, injured conspecifics only, and the additive combination (P + IC as the true factorial combination of the two cues) treatments—tested the separate and combined effects of

the main constituent cues (table 1; hypotheses 1–3). I further used linear contrasts to address additional a priori questions about the importance of digestion and the relative influence of constituent cues (table 1; hypotheses 4–6).

Because the experiments were conducted separately for each species, I used meta-analysis to test for differences between native and nonnative species as a group. Effect size was calculated for each species for each hypothesis test as the parameter estimate from the GLMM described above (tables A1–A7; tables A1–A8 are available online) divided by the estimated standard error from the model. Thus, replication for the meta-analysis comparison was three native and four nonnative species. The difference between native and nonnative species was then tested for each hypothesis with *t*-tests (natives, $n = 3$; nonnatives, $n = 4$). This approach has the benefit of incorporating the variation in estimates (standard error) and random effects into effect sizes.

As a result of the different number of snails in each downstream bin (table 3), the duration of each experiment differed; experiments in which multiple snails were included in each replicate bin provided greater resolution on effects of treatments more quickly and were concluded earlier to avoid sacrificing snails unnecessarily. Longer experiments could be associated with either decreased effect size (if prey habituate to cues or hunger drives them to forage in spite of risk) or increased effect size (if small changes in behavior are durable and effect size accumulates over time). To address the concern that experiment duration confounded differences in effect size observed between native and nonnative snails, I regressed the effect size for each hypothesis against the duration of the experiment (fig. A2; table A1). I did not find evidence that length of experiment was associated with a trend in effect sizes for any of the hypotheses tested in the meta-analysis. Because only one effect size per hypothesis can be estimated per species (i.e., per experiment), it is not possible with this data to replicate experimental duration independently for this analysis. A stronger test of the effect of duration on effect size would include replicated experiments of differing lengths.

Data for analyses and figures are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.86sk5> (Grason 2017). All analyses were conducted in R (R Development Core Team 2013) using the lme4 package (Bates et al. 2015).

Results

The magnitude of responses to consumptive cues of predation varied greatly among species (fig. 1), and observations supported only a subset of my predictions about the role of evolutionary cohistory in risk assessment. Native and nonnative prey did not differ significantly in their response to cues from an unfed predator (fig. 2; hypothesis 1, *t*-test: $t =$

-0.302 , $P > .10$). Though all prey species showed a trend toward increasing time avoiding in the predator-only treatment relative to the control, the magnitude of this increase was significant for only one nonnative species, *Urosalpinx* (fig. 1d; table A5).

Nonnative prey responded defensively to general cues from injured conspecifics more frequently—and at a greater magnitude—than native prey (fig. 2; hypothesis 2, *t*-test: $t = 3.206$, $P = .024$). Two of the three native species did not increase avoidance when they were exposed to cues emanating from injured conspecifics, and the third (*Littorina*) responded in the opposite direction as would be expected for a defensive response (fig. 1f; table A2); that is, they spent less time avoiding when they detected cues of injured conspecifics than when those cues were absent.

Contrary to my prediction, native and nonnative prey did not differ on the basis of how they responded to combined constituent risk cues (fig. 2; hypothesis 3, *t*-test: $t = -2.352$, $P = .065$). None of the seven prey species tested had a significant interaction between the predator and injured conspecific cues relative to the combined cue treatment ($P + IC$). One nonnative species (*Urosalpinx*) showed a trend toward an antagonistic response to the combination treatment (fig. 2), but the interaction term of the two-way GLMM was not distinguishable from 0 (table A5).

Nonnative species diverged from native species in that the former demonstrated information generalism; avoidance behavior by all nonnative prey assayed was driven primarily by general cues from injured conspecifics, which were the most important source of information in their risk assessment. Information generalism was not shown by any of the native species. Two pieces of evidence support this inference. First, for nonnative prey species, cues from injured conspecifics provoked a greater defensive response than cues from the predator itself (fig. 2; hypothesis 4a, *t*-test: $t = -3.646$, $P = .015$). By contrast, prey that shared an evolutionary history with the predator (natives) either showed greater avoidance to cues from the predator (P) than to cues from injured conspecific cues (*Littorina* and *Alia*; tables A3, A4, respectively) or responded similarly to the two component cues (*Nucella*; table A2). As a group, nonnatives spent more time than natives avoiding predators when they detected cues from injured conspecifics alone compared with when they detected cues from the predator alone. Second, for all nonnative prey (and only for nonnative prey), avoidance in response to chemical cues from injured conspecific prey (IC) was statistically indistinguishable from avoidance in response to the full predation cue ($P \times IC$; fig. 2; hypothesis 4b, *t*-test: $t = -3.206$, $P = .024$). Cues from injured conspecifics alone were sufficient to elicit the maximum increase in avoidance observed (tables A5–A8). Conversely, all native prey in the consumptive predation treatment ($P \times IC$) spent more time avoiding

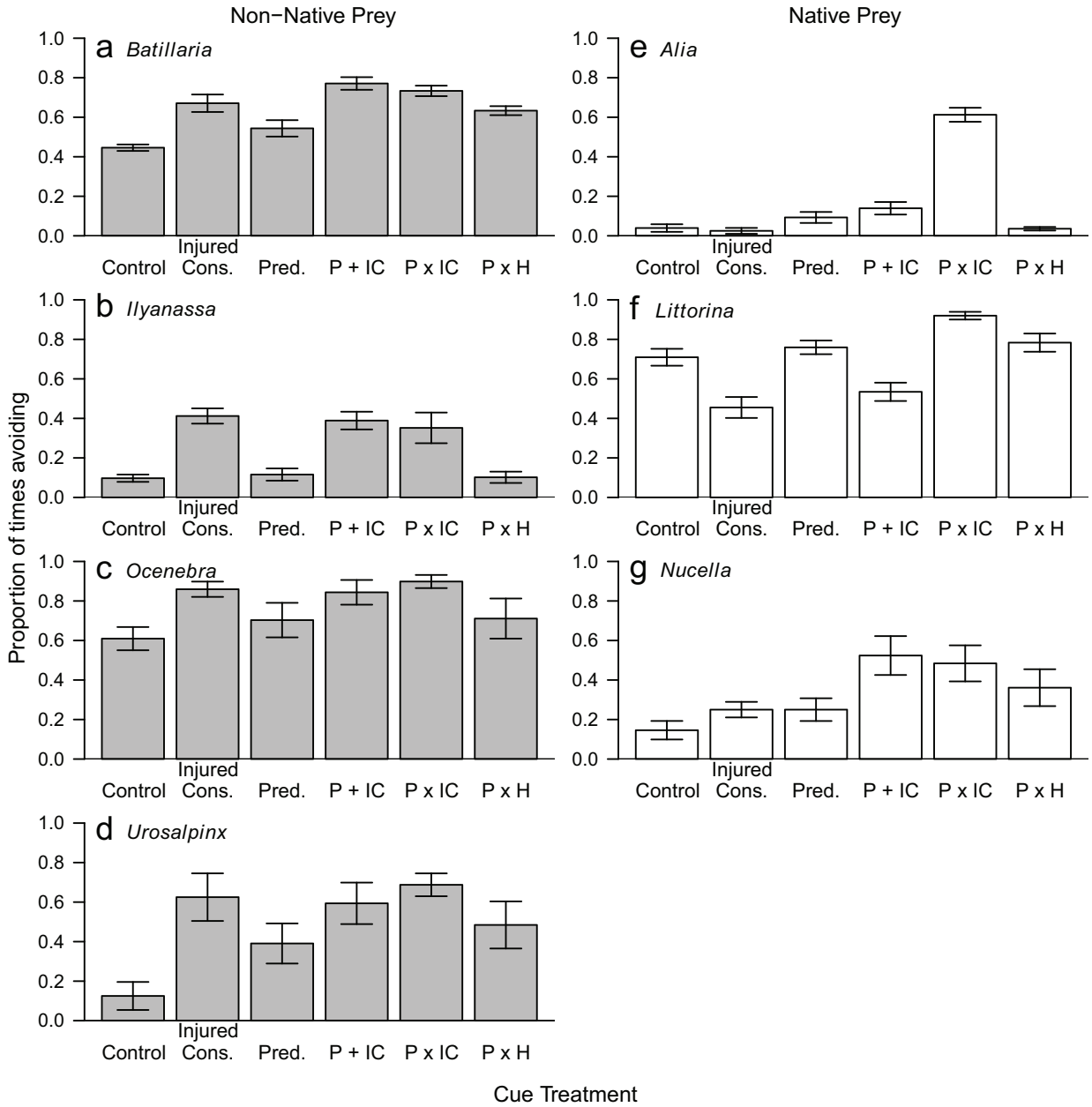


Figure 1: Proportion of times prey were observed to be avoiding (fleeing, hiding, or the sum of both) for four nonnative (a–d; filled bars) and three native (e–g; open bars) snail species in response to cues from a novel native predatory crab, *Cancer productus*. a, *Urosalpinx cinerea*. b, *Ocenebra inornata*. c, *Batillaria attramentaria*. d, *Ilyanassa obsoleta*. e, *Nucella lamellosa*. f, *Littorina sitakana*. g, *Alia carinata*. H, heterospecific prey; IC, injured conspecific; P, predator.

than they did in the injured conspecific cue treatment (IC; tables A2–A4).

Digestion of conspecific prey (P + IC vs. P × IC) increased avoidance behavior for only two species (*Littorina* and *Alia*), both native, but the difference between native and nonnative prey in terms of the importance of digestion was not significant (fig. 2; hypothesis 5, *t*-test: $t = -2.162$,

$P = .083$). For *Littorina*, the avoidance response reversed direction in response to digestion; this species spent less time avoiding when predator and injured conspecific cues were additively combined (P + IC) compared with the control treatment, but it spent more time avoiding than the control when crabs digested conspecifics (P × IC; fig. 1f). While digestion itself was not always important to risk assessment,

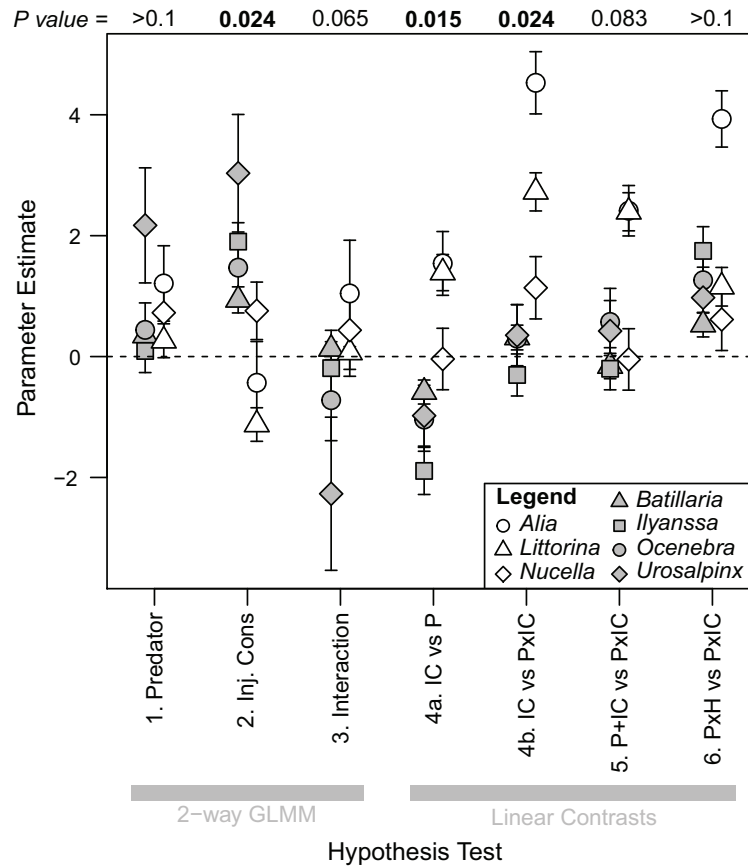


Figure 2: Parameter estimates (\pm estimated standard error) for generalized linear mixed effects models (GLMMs) of hypothesis tests. Filled symbols are nonnative species, and open symbols are native species; native and nonnative points are jittered slightly for visibility. Bold *P* values indicate a significant difference between native and nonnative species for that test. For linear contrasts, a positive parameter estimate indicates that the second treatment listed generates greater avoidance behavior; that is, *Alia* avoids more in response to predators consuming conspecifics ($P \times IC$) than to cues from injured conspecifics alone (IC), while *Ilyanassa* avoids more in response to cues from injured conspecifics (IC) than to cues from an unfed predator (P).

the identity of prey being digested was generally important to the prey tested, and prey spent more time engaging in avoidance behavior when they detected predators consuming conspecifics than when predators were fed a bland heterospecific prey. The magnitude of increase in avoidance in response to predator diet was similar between native and nonnative prey, and there was no statistical difference in effect size of the contrast between the $P \times H$ and $P \times IC$ treatments between native and nonnative prey (fig. 2; hypothesis 6, *t*-test: $t = -0.924$, $P > .10$).

Discussion

I observed that native and nonnative prey diverged in their use of general cues in assessing risk from a native predator and that information generalism was a shared trait among only the nonnative snails assayed here. While all species of prey demonstrated avoidance behavior in response to

chemical cues from a native predator attacking, consuming, and digesting prey (fig. 1), nonnative prey employed a generalized risk assessment strategy based primarily on strong responses to general alarm cues from injured conspecifics. Conversely, alarm cues from injured conspecific prey did not cause native prey to increase their avoidance behavior, and those species required multiple sources of information to engage in the greatest magnitude of observed defensive behavior. Patterns of response to the predator by itself and the importance of digestion were variable among prey species independent of evolutionary cohistory with the predator, indicating that some aspects of risk assessment might be more important in novel predator-prey interactions than others. The only source of information that increased avoidance for every single species was victim identity.

Multiple species comparisons in similar predator-prey interactions are a critical first step in identifying how in-

formation use might be constrained by ecology or evolution and where varying contexts can select for divergent strategies. These experiments were conducted on wild-collected snails, admitting the possibility that prior individual experience with risk cues could have influenced responses observed in the laboratory. This was partially controlled for by collecting multiple snail species from the same locality and by the observation that crab presence was not appreciably different across those localities (E. W. Grason, personal observation). However, the influence of prior individual experience with predators as well as the role of trade-offs between behavioral and morphological defenses (e.g., Bourdeau 2013) cannot be ruled out here. In addition, for the species that responded to general cues from injured conspecific prey, the relevant factor might be ambient predation or injury rates of prey at the field collection locality. Future studies could explicitly incorporate the effect of individual and population-level experience on behavioral responses to predation threats, because previous studies have observed that these can influence the presence and magnitude of defenses in snails, particularly in direct-developing or dispersal-limited species (Yamada et al. 1998; Trussell 2000; Turner et al. 2006).

Generalized Risk Assessment in Nonnative Snails

This meta-analysis of behavior of prey from a broad phylogenetic background—and replicated geographic origin—stands as the strongest support to date for general information use by nonnative species (Sih et al. 2010). Evidence for generalized risk assessment by nonnative snails is found in the relative importance of chemical cues originating from injured conspecifics. Alarm cues, though hypothesized to be uninformative about the nature of the threat, were both necessary and alone sufficient to explain the greatest magnitude of avoidance behavior observed for any of the nonnative species.

These experiments suggest that information generalism in risk assessment—similar to dietary and habitat generalism—could be associated with invasion success. However, they do not enable me to distinguish between two possible explanations for this association: whether information generalism predisposes a species to successfully invade or whether the process of invasion selects for this trait via rapid evolution. Regarding the latter, rapid evolution in response to invasions has been observed on much shorter timescales than these introductions (Whitney and Gabler 2008), yet nothing is known about the variation present in the founding populations or the strength of selective pressure. The only evidence that can be brought to bear is the response of other populations (both native and nonnative) of these invasive snails to general information. I am aware of no published studies testing defensive responses

to cues from native predators in the native range, but studies on two species' responses to nonnative predators do exist. *Ilyanassa* has been observed to spend more time hiding when exposed to chemicals from crushed conspecifics but not cues from *Carcinus maenas* L., itself introduced to the native range of *Ilyanassa* (Atema and Stenzler 1977), and no treatment of the full predation cue was tested for comparison. An observed response to injured conspecifics alone is not sufficient evidence for generalized risk assessment; rather, that response must be compared with the magnitude of responses to other predation cues. Thus, while Atema and Stenzler (1977) made it clear that *Ilyanassa* did respond to general risk cues, it did not fully test for generalized risk assessment. *Batillaria*, in a separate invasive population in California, apparently do demonstrate generalized risk assessment. Snails in experiments hid similarly in response to cues from injured conspecifics and cues of nonnative *C. maenas* consuming conspecifics but not to cues from the crab itself (Wells 2013). Thus, more information is required to assess strength of evidence for the explanations of information generalism: rapid evolution or invasion as a filter.

Regardless of the origin of this trait, generalized risk assessment could result in what has been referred to as level 4 naiveté (Carthey and Banks 2014), where prey respond appropriately and effectively to a novel predation threat but incur excess nonlethal effects because they overinvest in defense. Indeed, I have observed that for nearly all species, increased avoidance was correlated with significantly reduced feeding rates (E. W. Grason, unpublished data). If reduced feeding carries sufficient cost and does not improve survival compared with a more specific risk recognition strategy (requiring predator cues), relative influence of general cues in risk assessments might decrease over time, and generalized risk assessment could disappear entirely in introduced populations, unless other factors maintain this trait.

In addition, there are two important caveats in evaluating support for the role of information generalism in biological invasions. First, although the native species of prey assayed here are not known to be invasive elsewhere, an additional test of this hypothesis would include known failed invaders, which would be expected to require combined cues or respond stronger to cues from predators than cues from injured conspecific prey. Second, information generalism could extend beyond responses to injured conspecifics. Increased support for the importance of this trait in invasions would be found if nonnatives behave defensively in response to cues from a wider range of injured heterospecific prey than natives.

Responses to the Predator

Contrary to my prediction, response to native predator cues was not explained by whether the prey was also na-

tive. In spite of the expectation that predator cues should be accurate and informative indicators of predation risk, none of the native prey species increased avoidance in response to cues from *Cancer productus*. Further, though it would seem less likely that nonnative prey rather than native prey would have evolved the ability to detect the native predator, the only prey species that did respond to *C. productus* was nonnative.

Regarding the latter observation, apparent recognition of native *C. productus* by the nonnative *Urosalpinx* echoes other observations of nonnaive nonnative species (Pearl et al. 2003; Freeman and Byers 2006). However, the basis for the recognition ability observed here remains uncertain. Several potential, non-mutually exclusive explanations exist: (1) rapid adaptation in the <50 generations since introduction (Freeman and Byers 2006), (2) associative learning (Hazlett et al. 2002; Ferrari et al. 2008), and (3) recognition via similarities to coevolved predators of the same archetype in the native habitat (Carthey and Banks 2014). Crabs of the genus *Cancer* overlap in geographic range with native populations of all the nonnative species, though it is unknown whether the source populations for the invasions occurred within those ranges. There is evidence that *Urosalpinx* from another part of the nonnative range are able to recognize several species of crab with which it shares no—or a very short—evolutionary history (*Romaleon antennarium* Stimpson and *Carcinus maenas*), lending support for the importance of archetypes for that species (Blum 2012; but see Kimbro et al. 2009). However, additional explorations of behavior of *Urosalpinx* from the native range as well as naive, laboratory-reared individuals are necessary to determine support for any of these mechanisms. Neophobia, an aversion to any novel sensory stimulus, is an unlikely explanation because crabs are present at sites where *Urosalpinx* was collected, and thus snails used in the experiment have most certainly been exposed to those cues.

Perhaps more surprising than the fact that the one nonnative prey species did increase avoidance in response to a novel native crab predator was the observation that native snails did not change their defensive behavior in the presence of that same predator. The failure to respond to a given cue or combination of cues admits multiple possibilities: (1) an inability to recognize the cue, (2) a low probability of risk associated with that cue, (3) a constrained fitness trade-off, or (4) an inability to mount a defense. Because all snails increased avoidance in response to at least one of the cue treatments, the last possibility can be ruled out. Support for the third possibility would be observed if prey had reduced their avoidance behavior during longer experiments, because they needed to emerge in order to feed (i.e., the life vs. lunch hypothesis). However, longer experiments were not associated with a reduction in avoidance behavior (fig. A2; table A1). These experiments did

not, however, enable me to distinguish between the first two explanations. While it seems unlikely that native snails would not have evolved the ability to detect a coevolved predator if that cue indicated risk, particularly because this crab is a known predation threat at the collection localities for all three native species, it is also possible that selection has acted on the chemical cues released by the crab to reduce their detectability by prey (Havel 1987).

It is worth noting that I measured only one type of antipredator response—avoidance behavior—and it is possible that prey were indeed responding to the predator cues but via an unquantified metric. Different types of antipredator defenses, behavior, morphology, and life history are likely variably valuable in different contexts and therefore might be differentially responsive to various information sources and cue modalities. Moreover, organisms can trade-off investment among different types of defense. Prey that have invested in thicker shells might not need to reduce their time foraging in the open if their shell is an effective defense (Rundle and Brönmark 2001). All prey assayed in this study were collected from areas where crabs are known to be common; thus, all prey had prior environmental exposure to crab cues, which reduces the possibility that inference about whether natives and nonnatives differ in this regard is confounded by previous exposure to the predator, though an additional test for response to predator cues could use laboratory-reared naive prey.

Responses to Multiple Cues and Digestion of Prey

Numerous previous studies have separately argued for the importance and universality of either responses to predator cues (e.g., Kats and Dill 1998) or responses to alarm signals (e.g., Chivers and Smith 1998), but studies rarely test both and their combination. Responses to combined or multiple cues are not always linear (Bourdeau 2010a; Grason and Miner 2012), meaning that inference from partial treatment combinations can lead to erroneous conclusions. Previous research concluded that because *Littorina sitkana* did not respond defensively to cues from *C. productus* but did defend when conspecifics were fed to crabs, the defense was driven by alarm cues from conspecifics (Behrens Yamada 1989). I have shown that this is not the case, because avoidance behavior decreased when *Littorina* was exposed to injured conspecific cues, regardless of whether a crab was present, indicating that digestion of conspecifics is also required to reverse the response to injured conspecifics. This reduction of avoidance in response to injured conspecifics is somewhat perplexing but robust across multiple experiments (E. W. Grason, unpublished data), and it underscores the fact that multiple selective pressures are likely operating on intra- and interspecific signals.

My prediction that increased information content of combined cues should increase risk perception nonlinearly (synergistically) for native prey—but additively for nonnative prey—was not supported. To the contrary, all species responded additively to the combined cue treatment (nonsignificant interaction), including all of the nonnative snails that failed to recognize the predator. This is perhaps not surprising if those prey species are truly unable to recognize the predator, in which case only an additive response would be expected. The predominance of additive interactions observed here suggests that additivity might be the null expectation in response to combined information sources, even where both constituent cues also elicit a response.

Though, as a group, natives did not differ from nonnative prey in terms of the importance of digestion per se to risk assessment, chemical cues related to ingestion, digestion, and/or excretion of conspecific prey were clearly influential for two native species, *Alia* and *Littorina*. This suggests that for these species at least, those chemicals likely contribute to increased certainty of risk in terms of either probability of predation or information content of the cues. For *Littorina*, the reversal of direction of avoidance behavior relative to the control suggests that digestion provides categorically different information from general cues, though the nature of that information remains unknown. *Alia* shows a trend toward increased avoidance in response to the additive predation cue (P + IC), but digestion substantially increases the magnitude of avoidance. This can be explained if crabs are often in the environment along with injury cues unrelated to the crab but not often associated with a predation threat. The presence of crabs young enough to be interested in small *Alia*, however, would be indicated by digestion, which might increase the value of digestive cues.

Additional explanations for the two failed predictions regarding differences between natives and nonnatives (hypotheses 1 and 3) warrant consideration. Nonnative and native prey might demonstrate similar behavior either because the nonnatives behave as I would expect natives to behave or because natives behave as I would expect nonnatives to behave. Regarding the former, selection over ~50 generations could have resulted in rapid evolution among nonnative prey, such that their response patterns are no longer distinguishable from native prey. However, in both cases, observations failed to support the predictions because native snails behaved as I expected nonnative snails to: none of the snails—native or nonnative—increased avoidance in response to the predator cues alone (hypothesis 1), and cues combined to influence avoidance additively in all prey species (hypothesis 3). Thus, it is possible that these are responses constrained by factors other than evolutionary cohistory, such as ecology, physiology, or experimental design.

Conclusions

This study underscores the value of multicue, multispecies experiments to informing the theoretical framework on how the influence of risk information can change within and among species, over time, and across contexts (Hoverman et al. 2005). A subset of the response patterns that I observed related to general information originating from injured conspecifics were distinct between native and nonnative prey, suggesting that shared evolutionary history of predator and prey could place a constraint on the use of general information. By contrast, the cues for which responses varied irrespective of status as native or nonnative might be those for which selection depends on ecological or evolutionary contexts not explored here. These offer a promising avenue for future research into which factors influence whether responses to the predator, responses to alarm cues, and the importance of digestion are relatively more or less valuable in risk assessments.

I found strong support for the hypothesis that nonnative prey use risk assessment cues thought to be maladaptive in coevolved interactions (Sih et al. 2010), potentially reducing the negative effects of naiveté. These results also suggest that this trait might play a role in facilitating biological invasions. The impact of generalized risk assessment—relative to other patterns of information use—on community dynamics remains an open and inviting question. Nevertheless, understanding how prey use information to assess predation risk is critical to precisely characterizing the selective forces operating on predator-prey arms races. Biological invasions offer an excellent opportunity to investigate these questions because selection can be strong in novel interactions and community perturbations are often readily apparent.

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