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Predator effects on reef fish settlement depend on predator origin and recruit density

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Abstract. During major life-history transitions, animals often experience high mortality rates due to predation, making predator avoidance particularly advantageous during these times. There is mixed evidence from a limited number of studies, however, regarding how predator presence influences settlement of coral-reef fishes and it is unknown how other potentially mediating factors, including predator origin (native vs. nonnative) or interactions among conspecific recruits, mediate the non-consumptive effects of predators on reef fish settlement. During a field experiment in the Caribbean, approximately 52% fewer mahogany snapper (*Lutjanus mahogoni*) recruited to reefs with a native predator (graysby grouper, *Cephalopholis cruentata*) than to predator-free control reefs and reefs with an invasive predator (red lionfish, *Pterois volitans*) regardless of predator diet. These results suggest that snapper recruits do not recognize nonnative lionfish as a threat. However, these effects depended on the density of conspecific recruits, with evidence that competition may limit the response of snapper to even native predators at the highest recruit densities. In contrast, there was no effect of predator presence or conspecific density on the recruitment of bicolor damselfish (*Stegastes partitus*). These context-dependent responses of coral-reef fishes to predators during settlement may influence individual survival and shape subsequent population and community dynamics.

Key words: competition; coral-reef fish; habitat selection; life-history transition; non-consumptive effects; nonnative; predation risk; recruitment.

INTRODUCTION

Predators can have large effects on prey survival through direct consumption, making it beneficial for prey to recognize and defensively respond to predator cues. These defensive strategies of prey lead to non-consumptive effects of predators on prey behavior and morphology (Lima and Dill 1990, Preisser et al. 2005, Peckarsky et al. 2008). For animals with complex life cycles (e.g., amphibians, insects, fishes, marine invertebrates), effective anti-predator strategies are particularly advantageous during major life-history transitions when predators can cause close to 100% mortality (Wilbur 1980, Gosselin and Qian 1997, Almany and Webster 2006). One anti-predator strategy used by a range of taxa is avoiding areas with high predator densities during these transitions (Peckarsky and Dodson 1980, Johnson and Strathmann 1989, Welch et al. 1997, Vail and McCormick 2011). However, avoidance depends on predator recognition and response,

which may not occur when there is a novel predator and/or when there are strong intraspecific interactions (e.g., competition, facilitation). Patterns established during critical life history transitions shape subsequent population dynamics, spatial distributions, and community structure (Wilbur 1980, Jones 1991). As a result, it is essential to understand what factors mediate the non-consumptive effects of predators during these times.

Although prey may have innate predator recognition or rapid learning of cues from nonnative predators (Chivers and Smith 1995), often they either do not respond or respond ineffectively (Polo-Cavia et al. 2010). Whether or not prey respond to a nonnative predator may depend on whether their anti-predator behavior relies on general cues (e.g., presence of injured conspecifics in the area or in the diet of predators) or specific cues (e.g., species-specific predator odor or a combinations of cues) and how similar the novel predator is to native predators (cue similarity hypothesis; Sih et al. 2010).

Along with predator origin and diet, intraspecific interactions can also affect whether and how prey respond to predators (Bolnick and Preisser 2005). At higher conspecific densities, interactions with or cues from conspecifics

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may outweigh any non-consumptive effects of predators. For example, high conspecific densities can weaken effects of predators on spatial distributions through the masking of predator cues by the attractive cues of conspecifics (Ellrich et al. 2015) or via aggressive interactions that force individuals to occupy riskier areas (Holbrook and Schmitt 1997). As there is often high synchrony during critical life-history transitions (Newbold et al. 1994, Sponaugle 2015), intraspecific interactions may be especially important in mediating prey responses during these times.

Coral-reef fishes undergo a major transition from dispersive pelagic larvae to relatively sedentary juveniles (termed “settlement,” measured as “recruitment” by observers some time later). During this time period, small-scale patchiness in predation risk means that even minor changes in settlement location may drastically alter the likelihood of survival (Jones 1991, Connell and Kingsford 1998, Almany and Webster 2006, Hixon 2015). Although it is well established that reef fish larvae can play an active role in determining their settlement location (Leis 2006), there is mixed evidence from a limited number of studies regarding how predator presence affects settlement patterns in the field. Some Pacific damselfishes avoid species-specific predator odors (Vail and McCormick 2011) or predator diet cues (Dixon et al. 2012) during settlement and therefore preferentially settle to areas without predators. However, the only study thus far to examine the non-consumptive effects of predators on settlement in the Atlantic found no evidence of predator avoidance (Almany 2003). Furthermore, it is unknown if nonnative predators influence reef fish settlement or whether conspecific recruit density mediates the effects of predators on settlement habitat (review by Shulman 2015).

Two field experiments were conducted to investigate how predator origin, predator diet, and conspecific density influence the non-consumptive effects of predators on reef-fish settlement. In the first experiment, I manipulated the presence and identity of prior resident fishes and measured daily recruitment to small patch reefs (*Effects of predator origin*). If coral-reef fishes recognize cues from a native but not invasive predator, then reefs with caged native predators will experience lower recruitment compared to reefs with caged invasive predators and control reefs with no predators. In the second experiment, the diet of resident predators was manipulated to test the hypothesis that reef fishes respond to predator diet cues rather than to the identity of the predator (*Effects of predator diet*). If reef fishes respond to predator diet cues, then recruitment will be lower to reefs with predators fed conspecifics than to reefs with predators fed heterospecifics and control reefs with no predators, regardless of predator origin. Finally, for both experiments it was predicted that if intraspecific interactions among settling reef fishes modify their response to predators, then there will be the lowest proportional recruitment to reefs with predators at low recruit

densities. At higher recruit densities, however, intraspecific interactions may weaken the effects of predators leading to a more even distribution of recruits among control and predator reefs.

METHODS

Study site and species

This study was conducted off the leeward coast of Bonaire, Dutch Caribbean (12°9'13.01" N, 68°16'42.79" W), an oceanic island that is surrounded by a continuous fringing reef. Red lionfish (*Pterois volitans*), first sighted in Bonaire in 2009 (Schofield 2010), were used as the invasive predator for all experiments. Lionfish consume a wide range of native fishes, with recruit-sized fishes being particularly vulnerable to lionfish predation (Albins and Hixon 2008). Graysby grouper (*Cephalopholis cruentata*) and French grunt (*Haemulon flavolineatum*) were used as native species for comparison with invasive lionfish. Graysby grouper are ecologically similar to lionfish and also consume a high proportion of small recruit fishes (Randall 1967, Stallings 2008) whereas French grunt consume primarily small crustaceans (Randall 1967).

In order to measure recruitment to reefs that differ only in the presence of predators, 15 standardized reefs were constructed halfway between the shore and the coral-reef crest on an approximately 55 m wide and 5 m deep sand flat. Each reef measured 80 × 60 × 15 cm, and consisted of dead coral rubble placed inside of stainless steel wire baskets. The reefs were placed in three groups (statistical blocks) separated by approximately 17 m, with each block containing five reefs spaced approximately 3 m apart (Appendix S1; Vail and McCormick 2011).

Effects of predator origin

Each reef within each block was randomly assigned one of the following treatments: invasive piscivore (red lionfish; mean total length [TL] ± SEM: 155 ± 10 mm), native piscivore (graysby grouper; TL: 131 ± 10 mm), native invertivore (French grunt; TL: 148 ± 19 mm), empty cage (no predator), and empty control (no cage and no predator). Each predator was housed in individual hardware-cloth cages (150 mm diameter × 300 mm length, 10 mm mesh) such that recruiting coral-reef fish were exposed to chemical and some visual cues from the predator, but the predator could not consume recruits. Each treatment or empty-cage reef had two cages placed on opposite sides of the reef and dye tests confirmed that water from cages reached the adjacent reef. Predators were collected between 1 and 3 d prior to the experiment from nearby reefs by SCUBA divers using handnets. All piscivores were fed bicolor damselfish (*Stegastes partitus*) daily and the same individuals were used throughout the entire experiment. Invertivores were fed freeze-dried bloodworms and mysid shrimp daily, but often refused

food and therefore were replaced halfway through the experiment with new individuals.

The first experiment ran from 17 July through 1 August 2014, encompassing 15 nights around the new moon. To measure settlement, a pair of divers counted and removed all fish from each reef every morning beginning within an hour of sunrise. Conducting surveys every morning minimized the amount of time after settlement (which typically occurs at night), and consequently is assumed to reduce the influence of post-settlement processes on the distribution of recruits (Vail and McCormick 2011, Dixon et al. 2012, Sponaugle 2015). Newly settled recruits were easily distinguishable from older immigrants by their small size (<1–3 cm TL, depending on species) and coloration patterns. Divers returned approximately 2 h before sunset and again counted and removed all fish from each reef. Very few fish were observed during afternoon censuses, indicating that there was almost no net recruitment or immigration during the day and that the morning removals were effective. Divers randomized treatments within blocks daily by moving treatment cages to avoid any confounding influence of differences among reefs. Because all prior residents were removed and treatments were rotated daily, each block within each day was considered an independent replicate.

Effects of predator diet

To determine whether the diet of native or invasive predators affects settlement, the experiment described above was repeated using different treatments. Each reef within each block was randomly assigned one of the following treatments: native piscivore (graysby grouper; TL 149 ± 5.2 mm [mean \pm SEM]) fed bicolor damselfish (*S. partitus*) recruits, native piscivore (graysby grouper; TL 149 ± 6.8 mm) fed mahogany snapper (*Lutjanus mahogoni*) recruits, invasive piscivore (red lionfish; TL: 144 ± 4.0 mm) fed bicolor damselfish recruits, invasive piscivore (red lionfish; TL 157 ± 3.6 mm) fed mahogany snapper recruits, and empty cage control. Recruits of these two reef fishes were chosen as feed for the predators because they were the most abundant recruits to the reefs during the first experiment (Appendix S2: Table S1). All predators were starved for at least 24 h and then fed their assigned diet treatment beginning at least 24 h before the start of the experiment. All predators were fed every morning and the same individuals were used for the entire experiment. This experiment ran from 18 August through 28 August 2014, encompassing 10 nights around the new moon.

Statistical analysis

Statistical analyses focused on the two most abundant species of recruits during both experiments, bicolor damselfish (hereafter “damselfish”) and mahogany snapper (hereafter “snapper”; Appendix S2: Tables S1 and S2). For analysis, sampling days with extremely low

recruitment were excluded, during which the number of recruits to any block was less than the number of reefs (<5 individuals per species). Thus, the number of sampling days in July was 14 for damselfish and 6 for snapper, and the number of days in August was 7 for both species. In addition, there were 4 d in the first experiment that had extremely high recruitment of damselfish and 2 d during the second experiment with extremely high recruitment of snapper relative to any other day in either experiment (Appendix S2: Fig. S1). To facilitate comparisons between the first and second experiments, statistical analyses were conducted both including and excluding these extreme days. The exclusion of these days did not change the results for damselfish, therefore results including all days are reported. However, for snapper the inclusion of these days influenced some analyses, so results both including and excluding these 2 d are reported.

Daily counts of recruits were converted into the proportion of individuals on each reef out of the total number of recruits for that species to any reef within each block. Because the response variable was a proportion and there was evidence of overdispersion, generalized linear models using a quasibinomial family and logit link function were run, which weights each proportion based on sample size. To determine whether the effects of predator treatment varied with recruit density, for each experiment an effect of treatment \times conspecific recruit density (total per night) was tested. When the interaction term was significant, post-hoc pairwise comparison tests were conducted that account for multiple comparisons by controlling the false discovery rate using the package multcomp (Hothorn et al. 2008). When the interaction term was not significant, it was removed from the model and an effect of predator treatment across all recruit densities was tested. Post-hoc tests were conducted as above.

RESULTS

Effects of predator origin

The effect of predator treatment on recruitment of snapper did not depend on conspecific density (Treatment \times Density $\chi^2 = 2.25$, $P = 0.69$). Overall, recruitment of snapper was highest to invasive piscivore, empty cage, and empty control reefs, with intermediate levels of recruitment to native invertivore reefs and lowest levels of recruitment to reefs with native piscivores (Treatment $\chi^2 = 15.78$, $P = 0.003$; Fig. 1a; Appendix S3: Table S1). There were 52.6% more snapper recruits on reefs with the invasive piscivore compared to reefs with the native piscivore, with the odds of a snapper recruiting to a reef with the invasive piscivore an estimated 3.67 times the odds of a snapper recruiting to a reef with the native piscivore (95% CI 2.43–5.55).

There was approximately equal recruitment of damselfish to all reefs regardless of predator treatment and conspecific density (Treatment \times Density $\chi^2 = 2.44$, $P = 0.65$; Treatment $\chi^2 = 3.79$, $P = 0.43$; Fig. 1b).

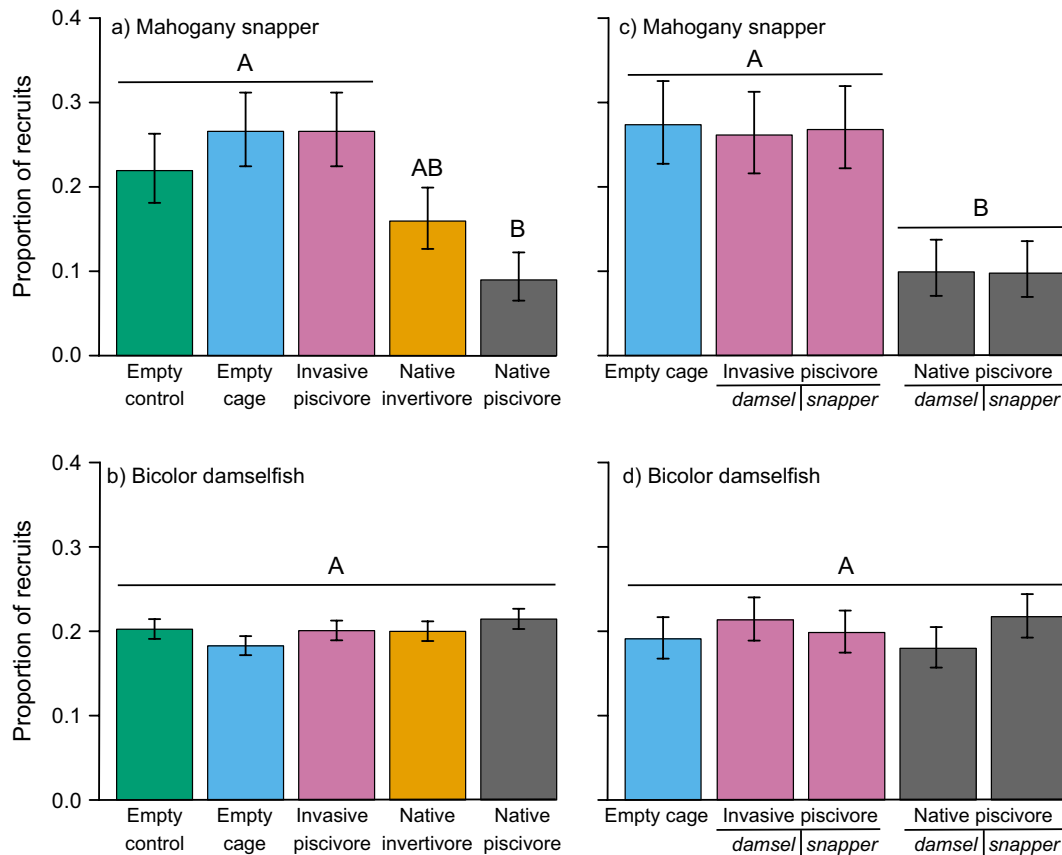


FIG. 1. Proportional recruitment (number of recruits per reef/total number of recruits per block) of mahogany snapper and bicolor damselfish to reefs with different predator treatments (a, b) in July 2014 testing for the effects of predator origin and (c, d) in August 2014 testing for the effects of predator diet. (a, b) All piscivores were fed bicolor damselfish and invertivores were fed mysid shrimp and bloodworms and (c, d) piscivores were fed either bicolor damselfish (“damsel”) or mahogany snapper (“snapper”). Bars represent means and standard errors estimated from generalized linear models. (a, c) Snapper recruitment was different among treatments in both experiments ($P < 0.01$). (b, d) Damselfish recruitment did not differ among treatments in either experiment ($P > 0.48$). Letters above bars indicate groups that differ ($P < 0.05$) based on post-hoc tests. Sample sizes: (a) 18 (3 reefs per treatment for 6 nights), (b) 42 (3 reefs per treatment for 14 nights), (c) 15 (3 reefs per treatment for 5 nights), and (d) 21 (3 reefs per treatment for 7 nights).

Effects of predator diet

Across the range of recruit densities observed in the first experiment (<10.0 individuals \cdot m $^{-2}$ \cdot night $^{-1}$), the effect of predator and diet treatment on recruitment did not depend on the density of snapper (Treatment \times Density $\chi^2 = 1.73$, $P = 0.78$). Regardless of piscivore diet, snapper recruitment to invasive piscivore and empty cage control reefs was higher than recruitment to native piscivore reefs (Treatment $\chi^2 = 19.1$, $P < 0.001$; post hoc, all $Z \geq 2.39$, all $P < 0.028$; Fig. 1c; Appendix S3: Table S2). Similar to the first experiment, the odds of a snapper recruiting to the invasive piscivore reefs compared to native piscivore reefs were an estimated 2.83 times higher (95% CI 2.15–3.73) and there were 52.4% more snapper recruits to invasive piscivore reefs compared to native piscivore reefs.

However, when two nights with extremely high recruitment of snapper (15.69 and 28.61 individuals/m 2) were included, there was an interactive effect of predator treatment and density (Treatment \times Density $\chi^2 = 28.00$,

$P < 0.001$; Fig. 2; Appendix S3: Table S3). As conspecific density increased, proportional recruitment to reefs with native predators increased such that at the highest recruit densities there was approximately equal recruitment of snapper to all reefs regardless of predator treatment.

Once again, damselfish recruitment was approximately equal to all reefs (Treatment \times Density $\chi^2 = 4.75$, $P = 0.31$; Treatment $\chi^2 = 1.56$, $P = 0.82$; Fig. 1d).

DISCUSSION

Predation is a key process that influences coral-reef fish communities immediately following settlement (Jones 1991, Hixon 2015), yet there are large gaps in our understanding of the factors that mediate the non-consumptive effects of predators on this transitional life stage. In this study, mahogany snapper had lower recruitment to reefs with caged native piscivores than to reefs with caged invasive predators, and these effects did not depend on

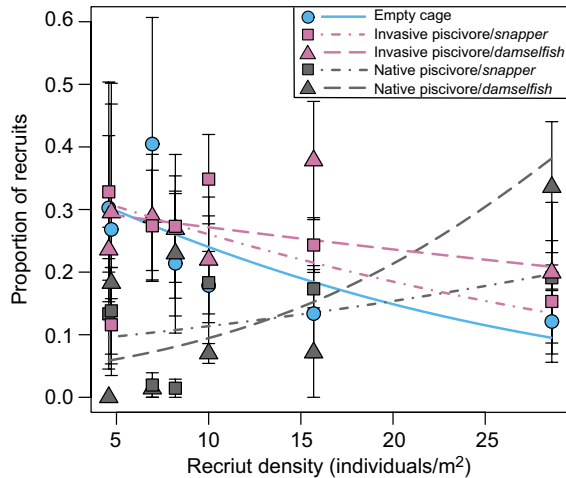


FIG. 2. Proportional recruitment (number of recruits per reef/total number of recruits per block) of mahogany snapper to reefs with different predator treatments as a function of conspecific recruit density (total number of recruits per night) during August 2014 (*Effects of predator diet*). Points and error bars represent means and standard errors ($n = 3$ reefs per treatment per night). Curves show fitted regression lines from a generalized linear model. Recruitment varied with both recruit density and predator treatment (Density \times Treatment interaction, $P < 0.01$).

the prior diet of the predators. These results suggest that snapper recruits may be particularly vulnerable to predation by nonnative predators. In addition, the density of conspecific recruits modified the effects of predator presence on recruitment in a manner suggesting that at extremely high densities intraspecific competition among recruits also influences the distribution of settlers on reefs. In contrast, recruitment of bicolor damselfish was unaffected by predator presence or recruit density, highlighting the importance of interspecific variability in the processes that influence settlement.

There is a clear selective advantage for dispersing organisms to avoid habitats with predators due to high predation rates on new juveniles (Gosselin and Qian 1997, Almany and Webster 2006). Although this predator avoidance has long been documented for many aquatic insects and marine invertebrates (Peckarsky and Dodson 1980, Johnson and Strathmann 1989, Welch et al. 1997, Binckley and Resetarits 2005), for coral-reef fishes the limited field evidence is mixed (Almany 2003, Vail and McCormick 2011, Dixon et al. 2012). Thus, this study provides the first demonstration that any Atlantic reef fish has lower recruitment to areas with native predators compared to control areas with no predators. However, there were also 52% fewer snapper recruits to reefs with a native predator compared to reefs with an invasive predator. Consequently, prey species including snapper may be experiencing a “double whammy,” as they are more likely to settle to reefs with invasive lionfish compared to reefs with native predators, and once there, they are more susceptible to predation because lionfish have higher

consumption rates than native predators (Albins 2013). Evidence for similar maladaptive habitat selection as a result of human-caused environmental change is growing, with exotic species now recognized as the most important cause of such “ecological traps” (Robertson et al. 2013).

The cues that snapper recruits use to identify predators likely explain why they did not avoid invasive lionfish. Native prey species are less likely to recognize and respond to invasive predators when they are dissimilar from their native predators (Cox and Lima 2006, Sih et al. 2010). Lionfish represent a novel predator archetype, as they are visually, chemically, and behaviorally different from other predators, especially in their invasive Atlantic range (Anton et al. 2016), but also in their native Pacific (Lönngstedt and McCormick 2013). Furthermore, native species are more likely to recognize and respond to nonnative predators when they rely on general cues, including conspecifics in the diets of predators (Sih et al. 2010, Nunes et al. 2013). Thus, the fact that snapper recruitment did not depend on the prior diet of any predator, combined with the novelty of lionfish, likely explains why lionfish did not elicit an anti-predator response. Future studies should examine whether recruits develop a response to this invasive predator over time via evolution and/or plasticity in anti-predator responses, as has occurred in a range of other species (reviewed in Strauss et al. 2006, Berthon 2015).

At the highest recruit densities there was no apparent effect of predator treatment on recruitment of snapper. This result suggests that at high densities there may be increased competition for resources in the preferred habitats, resulting in a more even distribution of recruits consistent with the predictions of an ideal free distribution (Fretwell and Lucas 1969). Although the observed patterns were primarily driven by two nights with extremely high densities of recruits, the strong intraspecific competition for shelter space and food among early post-settlement reef fishes (Jones 1991, Forrester 2015) suggests that these processes also occur during settlement. Furthermore, the only other studies to investigate the interactive effects of predation risk and conspecific density on decisions during dispersal found a significant effect on an aquatic insect and marine invertebrate (Baines et al. 2014, Ellrich et al. 2015). Therefore, these interactive effects should be better incorporated into investigations of larval behavior and settlement patterns across multiple taxa.

Unlike mahogany snapper, bicolor damselfish were not affected by predator presence at any density, perhaps due to interspecific differences in behavior and larval sensory abilities. Bicolor damselfish are more social and aggressive than mahogany snapper (Robertson et al. 1988), so perhaps intraspecific interactions across all recruit densities are more important than predator cues for recruitment of bicolor damselfish. In addition, bicolor damselfish settle at a smaller size than mahogany snapper (Robertson et al. 1988; C. E. Benkwitt, *personal observation*). Because size is often correlated with

development of sensory systems (Victor 1991), bicolor damselfish may be less equipped to recognize cues from predators at settlement. Instead, recruits of bicolor damselfish may cope with predator presence in other ways, including spending more time hiding in the reef than mahogany snapper (C. E. Benkwitt, *personal observation*). Regardless of the mechanism, species-specific differences in anti-predator responses are important because they can alter community interactions. In this case, mahogany snapper consume recruits of other species of the same cohort within the first few days following settlement (Shulman et al. 1983), and can therefore have a large influence on the distribution and survival of other coral-reef fish recruits. Recognizing interspecific differences in the response of recruits to predators is also important because thus far almost all studies have been conducted using Pacific damselfishes (but see Almany 2003), yet these results are likely not generalizable across families or oceans.

Despite the high mortality rates due to predation during critical life-history transitions, the factors that influence the non-consumptive effects of predators during these times are relatively understudied compared to other life stages (but see Binckley and Resetarits 2005, Davenport et al. 2014, Ellrich et al. 2015). Understanding the context-dependent differences in the response of various prey species to predators can provide insights into the factors that determine individual survival, which in turn affects which individuals enter the adult population and shapes subsequent population and community structure. This knowledge is even more important given the rapid pace of global change across all ecosystems. Local populations of many species are in decline, which may alter the intensity of intraspecific interactions and how these mediate anti-predator responses. At the same time, human-caused predator introductions are increasing worldwide, so determining whether prey species respond to nonnative predators and whether their responses rely on general or specific cues can help predict their susceptibility to novel predators.

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