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NOTE

Love thy prickly neighbor? Sea urchin density affects risk assessment in damselfish

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Abstract In coral reef communities, sea urchins and reef fish have a variety of commensal relationships. However, if fish view urchins as a potential form of predator protection, then urchin presence should influence reef fish risk assessment. We investigated whether dusky damselfish (*Stegastes nigricans*) perceive burrowing urchins (*Echinometra mathaei*) as a form of predator protection by asking whether and how urchin presence explains variation in flight initiation distance, the distance a fish fled an approaching threat. We found that when individuals were subjected to a high-risk approach (i.e., one that started relatively close to the fish), and urchin density was high, dusky damselfish tolerated a closer approach than when subjected to high risk with low urchin density. However, when there was low risk and high urchin density, the damselfish fled sooner. We conclude that under high risk, damselfish perceive burrowing urchins as providing added security from approaching threats.

Keywords *Stegastes nigricans* · *Echinometra mathaei* · Risk assessment · Antipredator behavior · Flight initiation distance · Ecology of fear

Introduction

Many individuals acquire protection from predators using the behavior or morphology of other species. Some species even associate with certain heterospecifics to reduce their risk of predation (Srinivasan et al. 2010; Goodale et al. 2017). For example, anemone fish (*Amphiprion chrysopterus*, *A. tricinctus*, *A. frenatus*) share their anemone with cleaner fish (*Labriodes dimidiatus*) and receive cleaning benefits from them (Allen 1972; Arvedlund et al. 2006). Similarly, gobies (*Ctenogobiops feroculus*) and shrimp (*Alpheus djeddenis*) share a burrow constructed by shrimp. It has been observed that shrimp stop burrowing when separated from a goby and that predation on gobies increases rapidly as gobies move away from the burrows (Thompson et al. 2005).

These mutualistic relationships also exist between sea urchins and reef fish. Previous work has found that black sea urchins (*Echinometra lucunter*) act as a predatory refuge for reef fish in the absence of branching coral cover. Both juvenile and mature reef fish hide between and around urchin spines (Nunes et al. 2019). Cryptobenthic fishes (including gobies and blennies) also use sea urchins as refuge from predation (e.g., Patzner and Santos 1992; Patzner 1999). It is possible that burrowing urchins' spines directly provide security as a predator deterrent. Other species of urchins provide habitat structure and complexity in different ways. For instance, burrowing urchins (*Echinometra mathaei*) create crevices in coral by feeding on algae and coral sediment as well as through spinal abrasion

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(McClanahan 1988). It is also possible that burrowing urchins provide indirect security to reef fish through their ability to modify their habitat and create additional escape holes. In Mo'orea, French Polynesia, dusky damselfish, and burrowing urchins coinhabit the same territory and thus are a good system in which to ask whether and how urchins might protect damselfish (Mapstone et al. 2007). While previous research has explored the effect of urchins as a source of refuge, there is little research specifically on the effect of urchin presence on reef fish's perceptions of safety (Nunes et al. 2019).

Predator risk assessment is often measured using flight initiation distance (FID), the distance a subject will allow a threat to approach before escaping (Ydenberg and Dill 1986; Cooper and Blumstein 2015). A modification of the Ydenberg and Dill model suggests that the distance to predator (i.e., starting distance) creates three zones of response based on the costs and benefits of escaping (Blumstein 2003). Thus, the distance at which the experimental threat begins moving toward a subject may reflect the subject's views of relative risk because closer threats would require a higher cost of escape than a more distant threat. The flush early and avoid the rush (FEAR) hypothesis states that animals will flee soon after detecting approaching predators or threats to avoid or minimize the costs of monitoring the threat (Blumstein 2010). Thus, starting distance (SD) typically explains substantial variation in FID and as starting distance to the threat increases, so should FID (Blumstein 2003; Samia and Blumstein 2014).

We asked whether dusky damselfish perceived burrowing urchins as a form of predator protection by examining if the presence of urchins in their territories explained variation in FID. If damselfish view urchins commensally, as a potential form of predator protection, then we expect urchin density to modify damselfish risk assessment, whereby they would tolerate closer approaches in areas with more urchins. We tested this both as a main effect of urchin density and as an interaction with SD.

Methods

We studied flight initiation distance in dusky damselfish on fringing reefs on the north coast of Morea, French Polynesia (details in Supplementary Materials). An observer approached an individual fish slowly ensuring that the subject was not orienting toward them and remained relaxed. Once the observer was about 2.0 m from the subject, and the subject was still relaxed, they pushed a black, 20 cm funnel attached to a 2.0 m pole (marked in cm increments) at 0.25 m/s until the subject fled (Chan et al. 2018). The observer then recorded the extension distance (ED), the distance pole was extended from the observer's body and continued to extend the pole to the initial position of the subject to record starting distance (SD) (Fig. S1). FID was measured as the ED subtracted from the SD (FID = SD–ED). The observer then estimated total fish length (TL).

Habitat and urchin quantification

After recording the FID, hard substrate cover (%) (living and dead coral bommies) was determined by counting the number of occurrences of hard substrate at each individual intercept within a 1.0 × 1.0 m quadrat with 81 equally spaced intercepts centered over the subjects' escape hole. Urchin density was defined as urchins/m^2 of hard substrate and was determined by counting all urchins within the quadrat whether they were on the hard substrate surface or within crevices. Water temperature (in °C) was measured with a thermometer attached to the 2.0 m pole. Rugosity was also measured with a chain (methods in Supplementary Materials) in addition to hard substrate cover, but because rugosity was highly correlated with hard coral substrate (%), we follow Chan et al. (2018) and focus here on hard coral substrate (%).

Statistical analyses

To explain variation in FID, we fitted a linear mixed effects model using lme4 (Bates et al. 2015) and lmerTest package in R (Kuznetsova et al. 2017) with urchin density (mean ± standard deviation: 11.4 ± 8.6 urchins/m^2, range, 0.0–36.4), as our main effect of interest and additional variables included as predictors due to their known effects on damselfish risk assessment (Chan et al. 2018; Chaves et al. 2012). SD (231.4 ± 22.9 cm, range 171.0–291.0 cm) was included as a predictor variable due to the general importance of SD in explaining variation in FID (Blumstein 2003, 2010; Samia and Blumstein 2014). Hard substrate cover (%) (87.7 ± 14.1%, range 27.2–100%), and continuous or isolated coral bommies were included as independent variables based on the damselfish habitat preference for coral bommies (Chaves et al. 2012) and the possibility of more conspecifics living in a continuous coral expanse. Fish size (10.1 ± 1.7 cm, range 5.1–15.2 cm) and water temperature (30.3 ± 0.8 °C, range 29–33 °C) were also included as predictors. Independent variables were all standardized by zero and centering them to permit comparisons among them. Location was included as a random effect. Based on the well-studied relationship between FID and SD (Blumstein 2003), we included the interaction between SD and urchin density to account for factors that may vary as a function of SD (Blumstein et al. 2015) and to determine whether urchin density modified this relationship. We also included the interaction between fish size and hard substrate cover (%) based on the influence of damselfish body size on risk assessment and habitat use (Chan et al. 2018). We calculated Pearson correlation coefficients to test for multicollinearity among independent variables (all $r \leq 0.12$). We calculated the marginal and conditional R^2 for the model using the MuMIn package (Barton 2019). Partial R^2 values for each fixed effect were calculated using the r2glmm package (Jaeger 2017). We tested the assumptions of our model through residual plots, qq-plots, and plots of fitted values and found no evidence to reject assumptions. All models were fitted in R version 3.6.2 (R Core Team 2019).

To help visualize the potential relationship between urchin density and starting distance, we plotted the relationship between FID and SD accounting for urchin density using the package ggplot2 (Wickham 2016). We first calculated the median of urchin densities and then used a median split, whereby values less than the median were categorized as low, and values equal to or above the median were categorized as high (Fig. 1).

Results and discussion

We tested a total of 139 dusky damselfish. After statistically controlling for variation of nonsignificant independent variables (water temperature, continuous or isolated, hard substrate cover (%), fish size, urchin density, Table 1) there was a significant main effect of starting distance (SD) on explaining variation in FID (Estimate ± SE: − 0.532 ± 0.068, $p < 0.001$, Table 1). There was a significant interaction between hard substrate cover (%) and fish size (0.147 ± 0.066, $p = 0.029$, Table 1). The positive estimate for this interaction indicates that FID increased with hard substrate cover (%) and fish size. These results differ from the Chan et al. (2018) study which showed FID decreased as hard coral substrate and size increased. Another study on the impact of structural complexity on a different species of damselfish's FID found lower FIDs as rugosity increased, likely due to the additional refuge available in more complex environments (Quadros et al. 2019). There was also a significant interaction between SD and urchin density (0.016 ± 0.008, $p = 0.043$, Table 1). The interaction between SD and urchin density shows that the effect of urchin presence on whether damselfish tolerate a closer approach is mediated by their perceptions of risk as measured by SD. Therefore, the effect of urchin density on FID depends on whether a damselfish was in a higher risk situation (i.e., small SD), or lower risk situation (i.e., large SD) (Fig. 1).

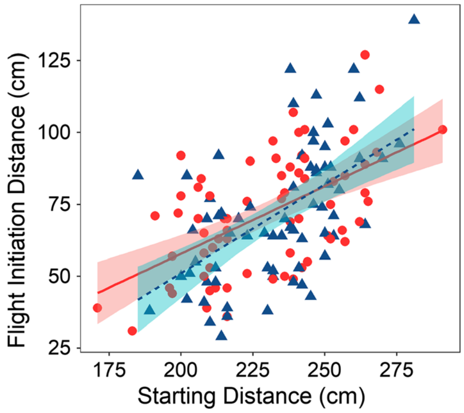

Fig. 1 The effect of urchin density (determined by median split) on flight initiation distance as a function of starting distance (higher risk is seen at smaller starting distances, while lower risk is seen at higher starting distances). Low urchin densities (< 10 urchins/m^2) are illustrated with red circles and the solid line, while high urchin densities (≥ 10 urchins/m^2) are illustrated with blue triangles and the dashed line

These findings suggest that risk perception in the dusky damselfish is influenced by urchin density, but that this influence depends on context. We found that damselfish in areas of high urchin density, when exposed to lower risk simulated predator approaches, fled at greater distances than individuals living in areas of low urchin density. As simulated predation risk increased, damselfish tolerated a closer approach when they were also in an area of higher urchin density. This implies damselfish risk assessment shifted as a function of both urchin density and risk intensity. Accounting for both fixed and random effects, this model explained 37.2% of the variation in FID. If we look at just the fixed effects, 36.2% of the variation was explained, suggesting that the random effect of location had a minimal influence on FID.

Urchin spines likely pose a risk to predators and deter them from following prey into crevices occupied by urchins, thus urchins may provide security to damselfish by deterring predators from pursuit. In this case we would expect damselfish to tolerate closer approaches when they are found in areas with increasing urchin density. Our results supported this idea, but only under situations with high predation risk. Redlip blennies (*Ophioblennius trinitatis*) are another species who tolerated closer approaches when living with more sea urchins, underscoring the importance of urchins for security for some species (Nunes et al. 2019). However, the effect of predation risk level was not assessed in that study. Urchins may also provide security indirectly to damselfish by creating refuges. As bioeroders, urchins create crevices in the coral bommies the damselfish inhabit (McClanahan 1988; Mapstone et al. 2007). Bommies with high urchin density would, over time, develop more escape holes. It has also been shown that structural complexity in coral reefs is positively

Table 1 Results of general linear model (± SE) to explain variation in damselfish flight initiation distance (FID) (model $p < 0.001$, adjusted $R^2 = 0.362$)

Source	Estimate	SE	p	Partial R^2
Intercept	70.13	2.136	< 0.001	
Starting distance (SD) (cm)	**0.532**	**0.068**	**< 0.001**	**0.304**
Temperature (°C)	−2.754	2.064	0.186	0.013
Continuous or isolated	7.047	5.037	0.164	0.014
Hard substrate cover (%)	−0.058	0.122	0.635	0.043
Fish size (cm)	1.377	0.945	0.149	0.016
Urchin density	0.080	0.189	0.671	0.042
Starting distance (cm) * Urchin density	**0.016**	**0.008**	**0.043**	**0.031**
Hard substrate cover (%) * fish size (cm)	**0.147**	**0.067**	**0.029**	**0.034**

[*] Bold indicates significant ($p < 0.05$) effects

correlated to fish biomass and density, indicating that increased complexity is beneficial for reef fish (Graham and Nash 2013). This increased availability of refuges can help explain why damselfish tolerate closer approaches with high urchin density under high-risk situations. Future research could untangle the direct versus indirect nature of the predator protection provided by urchins to damselfish.

Antipredator behavior can have cascading effects and influence the structure of communities and even ecosystems (Madin et al. 2011, 2019). Damselfish are considered key species in reef environments (Chaves et al. 2012), increasing algal biomass, productivity (Brawley and Adey 1977), and species diversity (Sammarco 1983). However, time and energy invested in antipredator behavior could come at the expense of algal farming. Behavioral changes caused by predation could have consequences that can alter the performance of coral reef ecosystems (Benevides et al. 2019). Our results suggest that variation in urchin density and risk intensity may have an impact on dusky damselfish antipredator behavior. Thus, this relationship is only beneficial to damselfish when relative risk of a simulated predatory encounter is high. From this study and others, we see that interspecies interactions clearly affect antipredator behavior.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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