Ontogenetic shifts in perceptions of safety along structural complexity gradients in a territorial damselfish.
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Yinny Chan†, Sara Lo†, Alyssa Quan†, and Daniel T. Blumstein*

Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, USA

*Address correspondence to Daniel T. Blumstein. E-mail: marmots@ucla.edu

†These authors contributed equally to this work.

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Abstract

Age and body size can influence predation risk and hence habitat use. Many species undergo ontogenetic shifts in habitat use as individuals grow larger and have different age-specific predation pressures. On coral reefs, a number of fish species are more tolerant of threats in structurally complex habitats that contain more refuges than in less structurally complex habitats. However, we do not know how risk perception varies with age, and whether age interacts with habitat complexity. Adults and juveniles, because of their size, may face different risks in structurally simple versus complex habitats. We used flight initiation distance as a metric to analyze perceptions of risk in a species of damselfish Stegastes nigricans. All else being equal, fish fleeing at greater distances are inferred to perceive higher risk. We targeted juvenile and adult damselfish to assess whether there are ontogenetic shifts in perceptions of safety in relation to structural complexity, inferred based on percent coral cover and rugosity. We found that adult damselfish tolerated closer approach in more complex habitats as measured by percent coral cover, but not rugosity, whereas juvenile fish always allowed closer approach than adult fish regardless of complexity. This ontogenetic shift in habitat use may result from juvenile fish taking bigger risks to maximize growth, whereas older animals, who are closer to their maximum body size, can afford to take fewer risks and protect their assets.

Key words: Stegastes nigricans, habitat complexity, risk assessment, ontogenetic shifts, antipredator behavior, flight initiation distance.

Habitats influence the behavior and distribution of prey in that they vary in the degree to which they provide refuges from predators and other required resources (Crowder and Cooper 1982). More structurally complex habitats provide greater shelter for prey and lead to higher species abundance and diversity due to reduced predation risk (Gratwicke and Speight 2005). In young mammals with limited mobility such as white-tailed deer fawns Odocoileus virginianus, neonate fallow deer Dama dama, and North American porcupines Erethizon dorsatum, having suitable shelter has a major impact on survival (Grovenburg et al. 2012; Kjellander et al. 2012; Mabille and Berteaux 2014). Habitat structural complexity is particularly important for predator avoidance in aquatic systems (Hixon and Beets 1993; Lehtiniemi 2005). Aquatic species tend to avoid high predation risk areas that have scarce protective cover (Dill 1987), though intermediate cover may allow more efficient foraging and higher growth rates (Crowder and Cooper 1982). On coral reefs, habitat complexity influences the behavior and distribution of reef fish that depend on coral for protection, resources, or reproduction (Komyakova et al. 2013). For instance, juvenile Australasian snappers Pagrus auratus choose more structurally complex habitats in the presence of a predatory threat over less complex habitats (Ross et al. 2008). Two labrid fish species, Brazilian wrasse Halichoeres

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**Materials and Methods**

**Study site and subjects**

We measured the FID of dusky damselfish at 2 fringing reef sites with abundant damselfish next to the Ta’ahiamanu Public Beach (17° 29' S, 149° 51' W) and next to Maharepa (17° 29' S, 149° 48' W) in Mo’orea, French Polynesia from 20 January to 3 February 2018. All experiments were conducted between 07:00 h and 16:00 h every other day and thus avoided dawn and dusk. These fringing reefs have experienced shifts in algal communities from dominant algal turf to dominant foliose macroalgae, as well as declining live coral cover (mainly Acropora spp. and Porites lobata) since 2010 after perturbations from a crown-of-thorns sea star Acanthaster planci outbreak (Adam et al. 2011; Han et al. 2016). Damselfish defend individual, non-overlapping territories that form colonies with adjacent territories occupying the same reef structure (Williams 1978; Karino and Nakazono 1993). These territories consist of both live and dead coral (Gochfeld 2010) covered with filamentous algae which damselfish farm and feed (Hata and Kato 2004). Dusky damselfish are ideal for these experiments because they were abundant at our Mo’orean study site, and because they pugnaciously territorial (Hata and Kato 2002), we could avoid resampling individuals by moving to a different coral structure after collecting data on an individual. We targeted individuals that were <4.0 cm and those >8.5 cm long to allow us to focus on the differences in risk assessment between younger and older individuals. We categorized each subject into size classes “small” (presumably younger damselfish) and “large” (presumably older damselfish).

**Measuring FID**

By snorkeling in shallow water (<2.0 m), 3 observers worked together to collect the FID and habitat complexity measurements. We located an appropriate area without a predator present and identified a suitable subject. One observer approached the focal subject whereas the other observers remained >3.0 m away. All individual damselfish were oriented towards us at the start of the experiment, and all were in immediate vicinity of shelter during approach. Once approximately 2.0 m from the subject (2.16 ± 0.15 m) the first observer pushed, at 0.5 m/s, a black, 18-cm-diameter funnel attached to a 2.0 m pole (marked in cm increments) towards the subject until the subject fled. A second observer then swam up and held the looming object in place whereas the first observer measured the FID, given by the distance from the end of the object to the initial
location of the fish. We also measured the extension distance (ED), the distance that the pole was extended from the first observer’s body, from which we calculated the starting distance, the distance between the funnel and the subject at the start of the experiment by adding ED and FID. We defined flight as the instance at which an alerted damselfish darted away from the looming object. Similar to Nunes et al. (2015), we recorded the actions of the fish immediately after it fled as “flee to hole” if the fish sought shelter in a hole or under a structure, “swim away” if the fish swam away from the looming object without retreating to shelter, or “return” if the fish returned less than 5 s after fleeing. The first observer estimated fish size by measuring the distance between protruding structures on the coral that the fish passed. We also recorded the number of conspecifics on the same coral structure during the FID trial and the depth of the fish (all depths were between 0.2 m and 1.4 m and the effect of depth was not analyzed further). Water temperature varied within 8°F during our study.

Quantifying habitat complexity
After completing an FID trial, we measured rugosity and percent coral cover. We measured rugosity along 4 radiating directions 90° apart, centered at the subject’s initial position. For each measurement, we draped a weighted fine-link chain along the benthic topography and measured the length of the chain adhering to the benthos across a 1.0 linear meter (Risk 1972). We calculated the total rugosity as the sum of the 4 surface distances, with terrain becoming flatter as total rugosity approached 4.0 m.

One observer measured percent coral cover by centering a 1.0 m × 1.0 m gridded quad with 81 equally-spaced intercepts over the subject’s initial position. At each of the intercepts, we tallied the number of occurrences of each type of benthos in the following mutually exclusive categories: macroalgae, sand, rubble, live coral, and hard substratum. We defined “macroalgae” as any visible algae that had a holdfast and was not algal turf (Bruno et al. 2009), and “rubble” as benthos that consisted of broken down pieces of coral fragments or rock that were larger than sand particles (Rasser and Riegl 2002). We defined “live coral” as living coral structure that could provide refuge, and “hard substratum” as dead reef structure, typically covered in algal turf, that could provide refuge and was not rubble nor covered by macroalgae. For our analyses we summed the intercepts over live coral and hard substratum to represent the total amount of coral in which fish could presumably shelter.

Statistical analyses
We explained variation in log 10 transformed FID by fitting a traditional general linear model in SPSS version 24 (IBM Corp 2016). Our independent variables included size classes small (mean ± SD: 2.62 ± 0.60 cm; n = 38) and large (10.5 ± 0.95 cm; n = 31), for which 95% confidence intervals did not overlap, as well as starting distance (216.51 ± 15.01 cm; range 191–249 cm), number of conspecifics (2.29 ± 2.26 individuals per structure; range 0–10 individuals), water temperature (mean 84.1°F; range 82°F–90°F), total rugosity, percent cover of live coral and hard substratum combined, and the interaction between size and rugosity as well as the interaction between size and percent live coral and hard substratum cover. We report adjusted R² values and set our alpha to 0.05. Variances between these groups were homogenous (Levene’s test of equality of error variances, P = 0.097), and residuals from our analysis appeared normal. To determine whether escape strategy varied by size, we created a size by escape behavior frequency contingency table and tested it with a Chi-square test.

Results
Overall, we flushed 69 damselfish; 38 small and 31 large (mean ± SD: FID small 18.24 ± 11.58 cm; FID large 54.26 ± 16.53 cm). After controlling for other potentially important independent variables (Table 1), there was no significant interaction between size and total rugosity (616.13 ± 87.01 cm; P = 0.332; Table 1), but there was a significant interaction between size and percent cover of live coral and hard substratum (71.03 ± 15.94%; P = 0.026; Table 1). The estimate for the interaction of percent coral and hard substratum cover and size category was negative, indicating a decreasing FID as size and coral and hard substratum cover increased for large fish (Figure 1). There was no significant effect on the FID of small fish as size and coral and hard substratum cover increased (Figure 1). This model (P < 0.001) significantly explained 64.4% of the variation in FID. Small and large damselfish did not employ categorically different escape strategies (P = 0.423; Table 2). In our contingency table, one data point was removed as it did not have an escape response recorded.

Discussion
Damselfish have ontogenetic shifts in their perceptions of risk. We found that larger damselfish increased their FID as percent coral and hard substratum cover decreased, indicating that they perceived higher risks in habitats with presumably fewer refuges. Smaller damselfish did not significantly modify FID as a function of percent coral and hard substratum cover; however, they consistently had significantly shorter FIDs than adults. This indicates that damselfish do not adjust their choice of habitat according to their individual size; rather, there is an ontogenetic shift in perceptions of risk that explains differences in antipredator behavior. These results suggest either that young fish perceived a lower risk of predation along these habitat gradients or that they were willing to take greater risks. Thus, it appears that as damselfish grow, habitat complexity influences their assessments of risk. There are at least 2, non-mutually exclusive, hypotheses that may explain these observed patterns.

First, juvenile fish may not have the experience to recognize certain predator cues and engage in appropriate antipredator behavior (Kelley and Magurran 2003). Many species of fish require experience to recognize predatory olfactory and visual cues (Karplus et al. 2006, Mitchell et al. 2011). However, learning may be rapid; in environments with novel predators, predator-naive juvenile damselfish learned to respond quickly to predatory threats and survived better (Mitchell et al. 2011; Ferrari et al. 2014). This shows that although adult fish may have more developed predator recognition and antipredator responses, juvenile fish can also rapidly learn, so it is unlikely that our ca. 2.6 cm long fish, which already have shown that they can survive in a predator rich environment, were entirely predator-naive.

Second, the asset protection principle predicts that the larger the reproductive asset, the more important it is to protect (Clark 1994). Juvenile damselfish accepted higher risks in the presence of a predator, whereas adult fish decreased foraging behavior and hid for longer periods (Lomstedt and McCormick 2011). This may be because adult fish have greater reproductive value since juveniles have not yet reached sexual maturity. In S. nigricans, the largest 25% of individuals in a colony reproduce (Karino and Nakazono 1993). Thus, large adult fish may generally be more wary as a way to maximize
their reproductive output, whereas juveniles take greater foraging risks so that they can have a chance to reproduce when mature. Therefore, as fish mature they have a greater need for refuges, indicated by an ontogenetic shift in their perceptions of security provided by varying coral cover.

In many species of fish, group size has been found to influence antipredator behavior (Larson and McCormick 2005; Brown et al. 2006). We used the number of conspecific damselfish in a colony as a reference for group size. However, we found that the number of conspecifics on the same structure did not have a significant effect on damselfish FID. Previous studies have also shown that size of the subject and starting distance have an influence on FID (Catano et al. 2015; Cooper and Blumstein 2015; Nunes et al. 2015), however in our study neither of these were significant. Variation in temperature also did not have a significant effect. For *S. nigricans*, it seems that it is coral and hard substratum cover, rather than other environmental factors, which has a profound influence on perceptions of security.

Although neither total rugosity nor percent cover of coral and hard substratum had any significant direct effect on FID, the interaction between percent cover and body size was significant whereas the interaction between rugosity and body size was not. This is notable because in several species of labrid fishes, variation in rugosity explained variation in their FIDs (Nunes et al. 2015). There are 2 possible explanations for this result. First, the 4 lines we measured for rugosity may have extended too far from an individual’s territory to accurately characterize the focal subject’s territory. However, previous studies on dusky damselfish have shown that the radius of an individual’s territory, centered at a core algal mat, ranges from 0.55 to 2.80 m (Jan et al. 2003), which encompasses our rugosity measurements of 1.0 m. Indeed, we saw individual fish move >1 m from their territory. Second, percent cover of live and dead coral may be a more accurate measurement of the amount of crevices, and hence refuges, available than rugosity. Percent cover of live and dead coral measures the total substrate available for shelter while rugosity, measured with a chain, can produce the same value for structures with different amounts of protection (Nunes et al. 2015). Shorter coral structures with many holes may have the same rugosity as a taller coral structure with few holes, leading to different fish FIDs for the same rugosity estimate. However, rugosity has been shown

**Figure 1.** Effect of percent live coral and hard substratum cover on FID of dusky damselfish. Small damselfish and large damselfish are represented by orange circles and blue diamonds, respectively. Damselfish photographs modified from http://fishbase.org.

**Table 1.** Results of a general linear model to explain variation in FID

| Source                                      | Estimates | P     | Partial η² |
|---------------------------------------------|-----------|-------|------------|
| Corrected Model                             |           | <0.001| 0.685      |
| Intercept                                   | 3.826     | 0.011 | 0.103      |
| Size (large)                                | 0.759     | 0.174 | 0.031      |
| Starting distance (cm)                       | 0.003     | 0.244 | 0.023      |
| Temperature (°F)                            | −0.031    | 0.067 | 0.055      |
| Number of conspecifics                      | −0.017    | 0.168 | 0.031      |
| Total rugosity                              | −0.001    | 0.065 | 0.056      |
| Percent live coral and hard substratum cover| 0.003     | 0.326 | 0.016      |
| Size (large) × Percent live coral and hard substratum cover | −0.009 | 0.026 | 0.080 |
| Size (large) × Total rugosity               | 0.001     | 0.332 | 0.016      |

**Table 2.** Contingency table of the frequency of large and small damselfish that responded in each escape behavior category

|                | Small | Large |
|----------------|-------|-------|
| Flee to hole   | 25    | 24    |
| Swim away      | 8     | 4     |
| Return         | 5     | 2     |
to correlate with habitat complexity and thus shelter and FID in previous studies (Luckhurst and Luckhurst 1978; Ménard et al. 2012; Nunes et al. 2015).

We have identified the importance of structural complexity on ontogenetic shifts in predator risk assessment. Adult damselfish seemingly perceive greater risk from predators because they are protecting their reproductive assets, whereas juveniles are expected to take greater risks in order to maintain high foraging and growth rates. However, some studies show that flexibility in growth rate, which may include slow growth in certain environments, can help individuals survive (Gagliano and McCormick 2007; Gagliano et al. 2007). In the future, understanding how variation in growth rate influences risk perception in juveniles would be valuable. In addition, quantifying the availability of specific refugia in coral crevasses that are available to each fish, and further differentiating between morphologically distinct coral species would help examine ontogenetic shifts in predator risk assessment along a more fine-scale and precise structural complexity gradient.

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