Journal of Experimental Marine Biology and Ecology 561 (2023) 151871

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

How does damselfish risk assessment vary with increased predator and shoal size?

Emily Burghart [1], Matthew Mar [1], Samuel G. Rivera [1], Caroline Zepecki [1], Daniel T. Blumstein [*]

Department of Ecology and Evolutionary Biology, University of California Los Angeles, Los Angeles, CA 90095, USA

ARTICLE INFO

Keywords:
Risk assessment
Flight initiation distance
Stegastes nigricans
Dusky damselfish
Predator size
Group size

ABSTRACT

Predation is an important factor that influences the behavior of prey species. When approached by a predator, individuals must make escape decisions that may be sensitive to the level of perceived risk. Both predator size and prey group size influence vulnerability and may influence this assessment. If fish perceive larger predators as a greater threat, differences in predator size should reflect differences in their antipredator response. Group size may also influence antipredator response in congregated fish. We investigated the flight initiation distance (FID) of differently sized groups of dusky damselfish (*Stegastes nigricans*) to measure their antipredator response to varying sizes of artificial stimuli. We found no effect of shoal size on FID, indicating that damselfish risk assessment is not influenced by group size. However, we did find that stimulus size interacted with starting distance (SD) to affect FID, with damselfish distinguishing between stimulus sizes at shorter SD but not at longer SD. Adjustment of FID in response to varying stimuli indicates that damselfish risk assessment is plastic, and consequently, antipredator responses may be adaptable in changing ocean ecosystems. Because damselfish are herbivores that feed on algae in coral reefs, understanding factors affecting their assessment of risk is important to understanding the overall ecosystem structure. These behavioral responses could be significant in the context of anthropogenic activities, mainly overfishing, which shifts community composition by disproportionately removing larger top predators.

1. Introduction

The outcome of a prey's interaction with predators depends on their interpretation of information collected from their surroundings (Ydenberg and Dill, 1986). Sensory cues modulate a prey's decisions as they must respond quickly to stimuli with limited information (Leavell and Bernal, 2019), thus effective antipredator responses use any available information to help reduce predation rates and increase fitness (Sih et al., 2010). The threat-sensitivity hypothesis highlights that the intensity of antipredator responses should match the perceived level of threat (Helfman, 1989). Thus, when an individual assesses risk in their immediate environment, their response might be influenced by predator size (Stankowich and Blumstein, 2005) and speed (Cooper et al., 2009), as well as habitat complexity (Cheh et al., 2021; Chan et al., 2019) and the presence of nearby conspecifics (Hager and Helfman, 1991; Lima, 1995).

Predator size may affect risk assessment. In lizards, there is a significant relationship between predator size and flight initiation distance (FID) with larger predators typically eliciting larger FIDs (Samia et al., 2016). Indeed, a meta-analysis found that, in general, an increase in predator body size increases the prey's perceived risk because it emphasizes the difference in size between predator and prey (Stankowich and Blumstein, 2005). A larger predator with the ability to eat larger prey could be considered a greater threat, especially in aquatic systems where most predators consume their prey whole (Scharf et al., 2000; Gill, 2003). Previous studies using models of Atlantic trumpetfish (*Aulostomus maculatus*) to trigger threespot damselfish (*Stegastes planifrons*) found that the same size stimulus prompted a stronger avoidance response in smaller individuals than larger ones (Helfman, 1989). Additionally, bicolor chromis (*Chromis margaritifer)* had graded reductions in excursion distance, and thus increased caution, when presented with larger predator models (Madin et al., 2010). However, other studies show conflicting results regarding the impact of predator size on prey risk assessment in fish. In a controlled experiment on black carp (*Mylopharyngodon piceus*), there was no variation found in the antipredator response to different sizes of a predator species (Tang et al.,

---

[*] Corresponding author.
E-mail address: marmots@ucla.edu (D.T. Blumstein).
[1] Equal authorship

https://doi.org/10.1016/j.jembe.2023.151871
Received 4 April 2022; Received in revised form 28 September 2022; Accepted 11 January 2023
0022-0981/© 2023 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

2017). Thus, both risk assessment and the implications of predator size may vary depending on fish species and their habitats' features, which could lead to different predator avoidance strategies.

There may be a reduction in the perceived threat of predators above a certain size, especially in coral reef habitats. Coral reefs often have high structural complexity, so larger predators may not often be found near the structures where prey are more abundant due to physical obstacles limiting their movement (Chan et al., 2019; Ryer, 1988). Predators also have to consider the costs and benefits of pursuing prey. Prey that are considerably smaller and harder to catch would provide relatively low amounts of energy compared to predation effort and thus would not be targeted as often by larger predators (Turesson et al., 2002; Samia et al., 2016). One study on reef fish found that smaller individuals were willing to forage closer to decoy predators than larger fish, indicating that they perceived less predation risk despite the greater size difference (Catano et al., 2016).

When individuals aggregate with others they may perceive increased safety. Previous meta-analyses on risk assessment found that, in general, shoaling fishes tolerated a closer approach and presumably perceived higher levels of safety when living in groups compared to living alone (Stankowich and Blumstein, 2005; Samia et al., 2019). However, variation in group size itself had no overall effect on FID in fishes (Samia et al., 2019). Despite this, the results of individual studies varied, indicating that "shoal size", here defined as the number of fish in a given area, may have important interactions affecting risk assessment, particularly when analyzed with other factors like predator size and prey body size (Samia et al., 2019).

Risk dilution may increase an individual's perception of safety as group size increases (Ydenberg and Dill, 1986; Beauchamp, 2014) and may play a role in affecting fish escape decisions (Samia et al., 2019). Risk dilution refers to the idea that an individual's chance of being targeted by a predator decreases as group size increases because there are more potential targets for a predator to choose from (Beauchamp, 2014). For example, when bluntnose minnows (*Pimephales notatus*) are in the presence of a predator, their individual feeding rate is higher and less time is allocated towards vigilance when in larger shoals, suggesting that minnows associate a larger shoal size with a lower predation risk (Morgan, 1988). Also, reef fish in a group are less likely to flee from an approaching threat when more of their neighbors are within view, indicating that they are aware of conspecifics when making escape decisions (Hein et al., 2018).

Group size effects may also be explained by the "many eyes hypothesis" which states that larger groups have improved detection range due to more individuals keeping watch against predators (Lima, 1995; Cooper and Blumstein, 2015; Samia et al., 2019). This idea could help explain variation in FID, a common metric used to estimate risk assessment. However, while risk dilution would indicate increased perceived safety and decreased FID, the "many eyes hypothesis" would indicate increased FID since the fish can detect a predator from farther away as a group and flee sooner (Stankowich and Blumstein, 2005).

Not all social groups function in the same ways and individuals will have varying levels of interaction with their conspecific neighbors. While members of some groups communicate risk with each other (Treves, 2000; Beauchamp, 2014), other groups may consist of individuals who merely respond to the behavior of others and act mainly to ensure their own safety (Oliveira et al., 1998; Beauchamp, 2014; Goulart and Young, 2013; Gil and Hein, 2017; Hein et al., 2018). These individual interests are especially important to consider when working with territorial species which can compete for resources within their colony. For example, elevated mortality rates in *Dascyllus flavicaudus* and *D. trimaculatus* damselfish have been observed as population density increases due to competition for shelter, with individuals driving their neighbors out into higher-risk areas to secure refuge for themselves (Holbrook and Schmitt, 2002).

Dusky damselfish (*Stegastes nigricans*) and their habitat make an ideal system in which to study the impacts of group size and predator size on antipredator behavior for multiple reasons. Primarily, due to varying environmental complexity, there is variation in the number of conspecifics a given individual is surrounded by (Karino, 1995). Additionally, within colonies, damselfish maintain neighboring territories which often include a patch of algae that they farm individually and protect from both conspecifics and heterospecifics (Karino, 1995; Hata and Kato, 2004). This site-tenacity helps avoid resampling of unmarked individuals. Also, damselfish abundance on coral reefs makes them relatively easy to observe (Feeney et al., 2021) and ensures they are naturally exposed to different predators of varying sizes.

We studied dusky damselfish risk assessment in relation to group size and predator size, using FID as a proxy of threat perception. We hypothesized that a physically larger stimulus would prompt a longer FID because of the greater perceived threat of a potential predator. We also hypothesized that group size would interact with stimulus size to allow for a closer approach due to the effects of risk dilution.

2. Methods

2.1. Study site and species

We measured the FID of dusky damselfish at two fringing reef sites, one adjacent to Ta'ahiamanu public beach (17° 29′ S 149° 51′ W) and the other at Maharepa (17° 29′ S 149° 48′ W) in Moorea, French Polynesia. Experiments took place every other day between 15 and 25 January 2022. Each of our study sites had abundant damselfish which we studied in shallow water (< 2 m) using snorkels.

Previous studies noted that dusky damselfish either maintain nonoverlapping solitary or clustered territories, varying with coral patch size (Karino, 1995). These contiguous territories often appear on bommies, which are structures of coral that are distinct from each other and the surrounding reef (Chan et al., 2019). Since damselfish territories are generally separated from one another this allows us to avoid resampling since we are sampling different areas of the reef.

2.2. Measuring FID

Four observers worked together to collect data. For each sample, the first observer snorkeled through the reef to locate an appropriate, unsampled area. This individual then identified an experimental subject to flush, maintained a distance of >2 m away (a distance from which damselfish appear to behave naturally), and for a period of ca. 90 s, counted the number of conspecifics within a 1 m radius around the focal subject.

Each trial consisted of pushing one of three different sized stimuli towards the focal subject. The small (6.35 cm diameter), medium (12.7 cm diameter), and large (25.4 cm diameter) stimulus sizes were cycled through, being changed between each trial in random order. During the flush, the flusher pushed a 2.0 m pole with the stimuli affixed at the end towards the focal subject at a constant rate of 0.08 m/s (following Chan et al., 2019). In order to standardize flushing speed, the flushers practiced sliding the pole at a specified rate (25 cm/3 s) to train themselves to a consistent speed underwater. Once the fish fled, as indicated by rapid, sudden movement away from the stimulus, the flusher stopped extension. The pole was marked at every cm and the flusher noted the distance they pushed the pole as the extension distance (ED). The starting distance (SD) was measured by extending the pole from the observer's position to the original position of the target fish and recording the distance. Each of these values, as well as the depth of the focal subject prior to fleeing, were recorded immediately following measurement. From starting distance and extension distance, FID was calculated as the difference between the two (SD - ED).

Damselfish at our study sites varied in size, so the flusher was trained to visually identify subject size ranges. This was accomplished using reference cards of varying lengths which the observer would view from 2 m away underwater, the approximate distance of the observer from the subject for each trial. This training was repeated until the flusher could estimate sizes accurately and consistently. Ultimately, we sampled a range of damselfish sizes (6–16 cm) during our trials. While a flush was occurring, other observers remained several meters away from the focal damselfish. One recorded data, one carried materials and alternate stimulus treatments, and one quantified benthic habitat composition after the flush.

2.3. Measuring habitat conditions and substrate composition

In addition to FID, we collected data on the physical characteristics of each area where a fish was flushed. Following a flush, one observer measured the substrate composition using a 1.0 × 1.0 m quadrat with a grid containing 81 intercept points (Cheh et al., 2021). This quadrant was placed over the substrate closest to the focal subject's starting location. At each intercept point, the type of benthos was recorded and tallied. Possible benthos included "sand", "rubble", "hard substratum", "live coral", and "macroalgae" (Chan et al., 2019). Rubble was considered to be broken pieces of coral or rock, while hard substratum referred to standing dead coral structures. Points were marked as live coral if coral was found at that point and were marked macroalgae if algae larger than algal turf was growing there. From these measurements, we calculated the proportion of each substrate type and calculated the sum of the proportion of coral cover and hard substratum in the grid. We recorded the temperature with an underwater pool thermometer and noted the Beaufort scale.

2.4. Statistical analysis

We explained variance in FID by fitting a general linear model that tested a series of main effects and interactions using the lm() command in R version 4.2.1 (R Core Team, 2018). In addition, we used the packages emmeans v1.7.2 (Lenth, 2022), ggplot2 v3.3.3 (Wickham, 2016), patchwork v1.1.1 (Pedersen, 2020), performance v0.8.0 (Lüdecke et al., 2021a, 2021b), rsq v2.2 (Zhang, 2021), and see v0.6.8 (Lüdecke et al., 2021a, 2021b). Throughout our analyses, we set our alpha to 0.05. We visually explored the distribution of our data with histograms and determined that there was no need for data transformations before fitting the model and running the analyses. Additionally, we calculated a correlation array between numerical independent variables to test for multicollinearity and found none (all values ≤ 0.355).

Our model included the following main effects: treatment size, because existing meta-analyses indicated that larger predator body size may increase perceived risk by prey (Stankowich and Blumstein, 2005); observer, to account for any methodological variation between flushers; starting distance, because of its importance in explaining FID variation (Blumstein, 2003; Harbour et al., 2019; Cooper and Frederick, 2007); shoal size, which is thought to influence vigilance and perceived safety (Magurran et al., 1987; Turesson et al., 2002; Stankowich and Blumstein, 2005); fish size, which has been shown to influence risk assessment (Magurran et al., 1987; Turesson et al., 2002; Stankowich and Blumstein, 2005); and the proportion of live coral and hard substrate, because previous studies indicated that FID may decrease in environments with higher structural complexity (Quadros et al., 2019; Chan et al., 2019). We also included interactions between starting distance and treatment, treatment and shoal size, treatment and fish size, and proportion of live coral and hard substratum and treatment. We calculated partial R^2 values using the rsq package to estimate the variation explained by each variable in the model.

In addition, we investigated the effects of location, Beaufort scale, fish depth, and contiguous vs. bommie landscape on FID. We sequentially added these variables one at a time into the original model and found that none were significant (location, $p = 0.266$; Beaufort scale, $p = 0.957$; fish depth, $p = 0.830$; contiguous vs. bommie landscape, $p = 0.903$). Thus, we present the results of the original model mentioned above.

We calculated estimated marginal means to test for the differences between treatments and calculated estimated marginal means of linear trends to explore significant interactions with treatment. To visualize the effect of a significant interaction on FID, we used the package ggplot2 to plot SD by FID by treatment (Fig. 1). We evaluated assumptions of the linear model using the package performance. The plots of fitted values for linearity and homogeneity were flat and horizontal, QQ plots were straight, and residuals were approximately normal.

3. Results

We performed FID experiments on a total of 147 dusky damselfish (Fig. 1a) in groups of varying sizes (Fig. 1b). We restricted our dataset to 130 experimental trials by excluding trials run during relatively intense weather conditions, as determined by a Beaufort Scale rating > 2, which included excessive wind and wave action that may have reduced our control over our sampling procedure. Additionally, due to limitations on our ability to precisely run experimental trials at long starting distances, data points with SD > 2.0 m were removed. Data points with SD < 1.1 m were also removed to ensure treatments were tested within similar ranges since short SD measurements were tested disproportionately more often with the small stimulus.

Our final dataset consisted of 130 trials with the following characteristics: shoal size index (mean ± standard deviation: 5.0 ± 2.8), starting distance (163.0 ± 20.5 cm), fish size (10.9 ± 1.8 cm), and proportion of live coral and hard substratum (0.79 ± 0.17). After controlling for the contribution of independent variables, we found a significant main effect of the observer ($p = 0.001$) and a significant interaction between starting distance and treatment ($p < 0.001$) (Table 1).

When starting distance was small, the larger stimulus elicited a longer FID ($p < 0.001$), whereas at higher starting distances, there was no discrimination between stimuli in FID response (Fig. 2). The observer differences can be accounted for by the significant difference in SD displayed by the observers, with one observer's SD measurements being consistently larger ($p < 0.001$). However, there was not a significant difference in FID between the observers ($p = 0.32$) and the differences in SD were not in the shorter range where the main significant interaction was observed, indicating that observer effects did not significantly impact our results. The final model significantly ($p < 0.001$) explained 20.43% of the variation in FID (Table 1).

4. Discussion

The size of a potential predator is a factor considered in damselfish risk assessment, but only under certain conditions. After controlling for other significant variables, we found that damselfish tolerated a closer approach from smaller visual stimuli than larger stimuli at shorter starting distances, with their FID varying significantly between treatment sizes. However, at longer starting distances, FID did not vary between treatment sizes. These results indicate that damselfish modified their antipredator responses to stimulus size in high threat (shorter SD) situations, but not in lower threat (longer SD) situations. A potential explanation as to why a larger stimulus elicited greater antipredatory responses, albeit within a particular range of SDs, is that larger size is associated with a predator's greater ability to consume prey (Scharf et al., 2000; Gill, 2003). The perception of larger predators being a greater threat aligns with the positive correlation between predator size and successful capture rate of prey (Fuiman and Magurran, 1994). Under high risk (i.e., shorter SD), larger predators were considered more threatening.

While we had hypothesized that larger predators in structurally complex environments would be perceived as less threatening, our results do not support this idea. However, the complexity of coral reef habitats may help explain the interaction we observed with starting

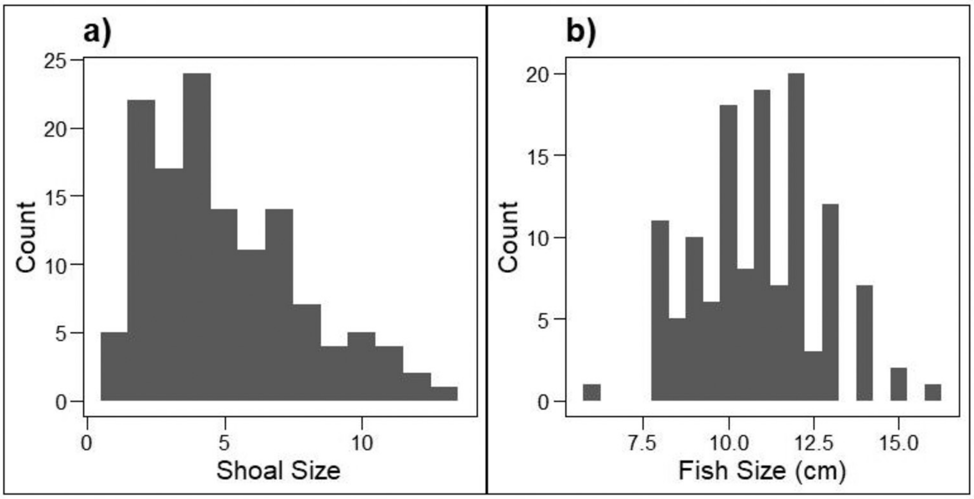

Fig. 1. a) Histogram showing the distribution of shoal sizes observed during trials; b) Histogram showing the distribution of focal fish sizes sampled.

Table 1
Results of general linear model to explain variation in damselfish flight initiation distance (FID) (model $p < 0.001$, adjusted $R^2 = 0.204$).

Variable	F	p	Partial R^2
Starting Distance	9.587	0.002	<0.001
Treatment	2.632	0.076	0.112
Shoal Size	2.014	0.159	<0.001
Fish Size	0.725	0.396	0
Proportion of Coral and Hard Substratum	0.016	0.899	0
Observer	7.902	0.006	0.089
Starting Distance*Treatment	9.230	<0.001	0.126
Treatment*Shoal Size	0.292	0.747	0.009
Treatment*Fish Size	0.060	0.942	0.009
Treatment*Proportion of Coral and Hard Substratum	1.729	0.182	0.029

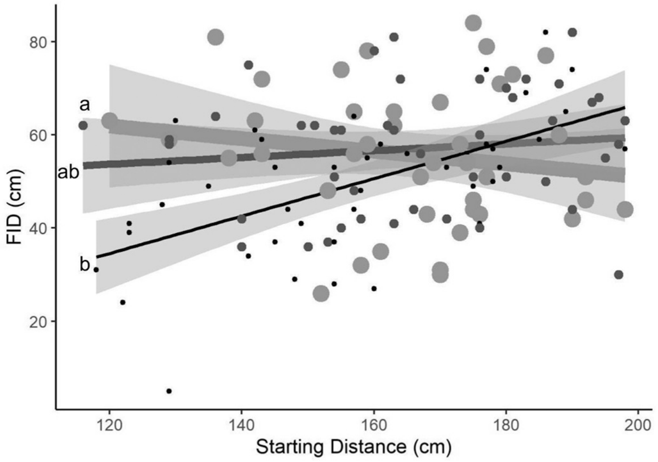

Fig. 2. Interaction plot of FID and starting distance comparing the relationships of the three different treatment sizes. The different circle sizes and shades correspond to different stimuli sizes. The large, light gray circles and trendline represent the large stimulus, the moderately sized, dark gray circles and trendline represent the mid-size stimulus, and the small, black circles and trendline represent the small stimulus. The gray bars surrounding the trendlines are 95% confidence intervals. Letters on the left side of each trendline represent significant differences between slopes.

distance. Structural complexity could limit the prey's detection range, making it difficult to distinguish between the sizes of far-off predators. However, during our study, starting distances were never longer than 2 m, making it unlikely that the damselfishes' visual abilities explained the pattern of results. Additionally, predators may have greater difficulty locating prey at farther distances on a reef where coral structures may obscure their view or allow prey to blend into their surroundings, compared to predators in a pelagic environment. If so, distant predators may be perceived as less of a threat.

Damselfish must consider the costs of fleeing in addition to the costs of vigilance when responding to a potential threat. The flush early and avoid the rush (FEAR) hypothesis predicts that prey will flee soon after detecting a predator to minimize the costs of continual vigilance (Blumstein, 2010); thus, starting distance should be positively correlated with FID (Samia et al., 2013). However, our results are largely inconsistent with the FEAR hypothesis because only our small treatment size demonstrated a clear positive correlation between SD and FID, while the medium and large treatments had essentially no relationship between SD and FID (Fig. 1).

Prior studies have found that most, but not all, species follow the FEAR hypothesis (Samia et al., 2013). Importantly, we lack a general understanding of what situations prey do not follow the FEAR hypothesis in, as well as why certain species do not exhibit FEAR effects (Samia et al., 2013; Samia and Blumstein, 2015). FEAR has been most intensively studied in terrestrial species, while little work has gone into understanding FEAR responses in fish (Samia et al., 2013; Samia and Blumstein, 2015; Chen et al., 2020).

The environmental context and the level of threat an individual perceives can influence FID, potentially altering whether or not a FEAR response is observed (Chen et al., 2020). In birds, different perch heights associated with different levels of safety explained variation in FID, demonstrating how the risk perceived in a situation can be impacted by an individual's surroundings (Chen et al., 2020). Skinks in areas with less human activity had longer FIDs, indicating that human activity influenced the background levels of risk perceived (McGowan et al., 2014).

The significant interaction between SD and treatment size we report illustrates how varying levels of background risk influence how damselfish react to predatory stimuli. Other studies on prey fish have found that variations in background risk, as detected by olfactory cues, act in conjunction with immediate risk factors to determine antipredator responses (Brown et al., 2006). Different starting distances, and by extension different risk levels, significantly influenced the way damselfish responded in predatory situations. Thus, variations in background risk may help explain differences in FEAR effects (Brown et al., 2006; Chivers et al., 2014).

The different relationships between SD and FID as a function of stimulus size may result from damselfish's different risk assessment strategies for each size. On one hand, when a damselfish encounters smaller stimuli, the stimulus's diameter may not be a clear indicator of threat level. For example, an approaching predatory eel may have a similar size appearance to a non-threatening fish. In this case, a damselfish may base its risk assessment on the total duration or speed of the small stimuli's approach, which would produce a positive correlation between SD and FID (Cooper et al., 2009). On the other hand, a larger stimulus may be identified as a predator based on size alone, reducing the strength of the relationship between SD and FID as seen in Fig. 1. For a territorial species, such as damselfish, this conditional strategy may be more beneficial compared to the FEAR hypothesis strategy.

We failed to detect a significant effect of shoal size on risk assessment. Past research has found mixed results regarding the importance of shoal size in fish risk assessment, with some finding that larger shoals tend to have a lower FID in response to predators (Morgan and Godin, 1985; Samia et al., 2019) while others found no significant effect of shoal size (Januchowski-Hartley et al., 2011; Samia et al., 2019). Because individual studies within these meta-analyses had indicated shoal size effects, we decided to reexamine shoal size in relation to other size-related effects. However, our findings support the hypothesis that shoal size is not a significant factor involved in predation risk assessment (Samia et al., 2019), at least in this species of damselfish. Threat-reduction benefits from group living might be group size-independent, with fish only perceiving a difference in safety between shoals and solitary life (Helfman and Winkelman, 1997; Samia et al., 2019). Alternatively, the type of "shoal" could be a greater contributor to the antipredator benefits of grouping; damselfish live in territorial colonies rather than aggregating in more ephemeral shoals (Hata and Kato, 2004; Murray, 1978). Thus, they may not perceive a significant increase in safety because they are not dynamically forming groups for protection.

Another explanation for the lack of shoal size effect is the greater abundance of shelter in benthic habitats like coral reefs (Quadros et al., 2019). In a more complex habitat, the protection that damselfish perceive due to refuge availability may outweigh the benefit of reduced risk in a larger group. Meanwhile, in more open habitats where shelter is scarce, it is possible that prey rely more on shoals to reduce risk (Queiroz and Magurran, 2005). Additionally, in complex habitats where hiding is the primary method of predator avoidance, forming larger shoals could make individuals more conspicuous and detectable to predators (Lehtinirmi, 2005; Samia et al., 2019).

Structural complexity could also impair a damselfish's ability to detect conspecific cues, making them unreliable indicators of risk, while also lessening the benefits of group vigilance. The "many eyes" hypothesis relies on the assumption that individuals monitor other members of their group to decide on their own levels of vigilance and antipredator response (Roberts, 1996; Lima, 1995). On territories with complex protruding structures and rounded bommies, damselfish may not be able to monitor each other consistently enough to perceive any increased safety from group vigilance. Although damselfish do have to watch their neighbors to maintain their territories, it may be difficult to split their focus between vigilance and territory defense.

We also found no significant effect of our measure of habitat complexity on risk assessment, even though past studies focusing on structural complexity have found it to help explain variation in FID (Chan et al., 2019; Cheh et al., 2021). The minimal effect we observed might be due to territorial damselfish generally having a specified refuge to flee to since they do not travel far from their individual territories. Damselfish may only consider the availability of their predetermined refuge, rather than the overall amount of habitat complexity surrounding them. It is also possible that the range of structural complexity we observed was not wide enough to detect a difference in risk assessment. The lack of structural complexity effects could also be explained by the size of our stimuli relative to damselfish refuges. Our treatment sizes were all large enough that they would not have been able to pursue the fish into the coral structure, so even as habitat complexity varied, the safety that fish perceived by having a refuge where a predator could not follow would remain consistent.

With the recent loss of larger top predators due to overfishing, the community composition of coral reef systems has shifted drastically (Demartini and Smith, 2015). Damselfish and other reef prey species may also shift their antipredator responses over time to better respond to the predators they encounter most often (Brown et al., 2006). These changes to the levels of risk they tolerate before fleeing could allow them to focus more on foraging and territory defense, significantly impacting their role in coral reef ecosystems. Plasticity allows damselfish to increase expected fitness by adapting to certain conditions, and dynamically adapt risk assessment (Beaty et al., 2016). Within the scope of our study, we found that damselfish dynamically assessed potential predators according to size under high risk situations. There may be a limit to the plasticity we observed because we assumed that our experiments simulated real predator-prey interactions. Understanding the true nature of plasticity and its consequences is needed to better understand the impact of modified predator populations on coral reef ecosystem persistence.

Author statement

All authors conceived and designed the study which was conducted by the first four authors. DTB guided the analyses that were conducted by the first four authors. DTB guided the writing, which was conducted by the first four authors. All authors edited and approved the publication of this paper.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We thank the Gump Research Station staff for logistical support, and Connor Philson for field assistance and comments. The UCLA Department of Ecology and Evolutionary Biology provided partial financial support. Damselfish were studied under permits from the Government of French Polynesia and animal use protocols issued by UCLA.

References

Beaty, L.E., Wormington, J.D., Kensinger, B.J., Bayley, K.N., Goeppner, S.R., Gustafson, K.D., Luttbeg, B., 2016. Shaped by the past, acting in the present: transgenerational plasticity of anti-predatory traits. Oikos. 125, 1570–1576. https://doi.org/10.1111/oik.03114.

Beauchamp, G., 2014. Social Predation: How Group Living Benefits Predators and Prey. Elsevier/Academic Press, Waltham, MA.

Blumstein, D.T., 2003. Flight-initiation distance in birds is dependent on intruder starting distance. J. Wildl. Manag. 67, 582–587 https://doi.org/3802692.

Blumstein, D.T., 2010. Flush early and avoid the rush: a general rule of antipredator behavior? Behav. Ecol. 21, 440–442. https://doi.org/10.1093/beheco/arq030.

Brown, G.E., Rive, A.C., Ferrari, M.C.O., Chivers, D.P., 2006. The dynamic nature of antipredator behavior: prey fish integrate threat-sensitive antipredator responses within background levels of predation risk. Behav. Ecol. Sociobiol. 61, 9–16. https://doi.org/10.1007/s00265-006-0232-y.

Catano, L.B., Rojas, M.C., Malossi, R.J., Peters, J.R., Heithaus, M.R., Fourqurean, J.W., Burkepile, D.E., 2016. Reefscapes of fear: predation risk and reef heterogeneity interact to shape herbivore foraging behaviour. J. Anim. Ecol. 85, 146–156. http://www.jstor.org/stable/24701615.

Chan, Y., Lo, A., Quan, A., Blumstein, D.T., 2019. Ontogenetic shifts in perceptions of safety along structural complexity gradients in a territorial damselfish. Curr. Zool. 65, 183–188. https://doi.org/10.1093/cz/zoy091.

Cheh, A., Fadaee, N., Kalhori, P., Williams, D.M., Anchieta, J., Nunes, C., Blumstein, D.T., 2021. Love thy prickly neighbor? Sea urchin density affects risk assessment in damselfish. Coral Reefs 40, 21–25. https://doi.org/10.1007/s00338-020-02035-0.

Chen, X., Xie, W., Shuai, L., 2020. Flush early and avoid the rush? It may depend on where you stand. Ethology. 126, 987–992. https://doi.org/10.1111/eth.13073.

Chivers, D.P., McCormick, M.I., Mitchell, M.D., Ramasamy, R.A., Ferrari, M.C.O., 2014. Background level of risk determines how prey categorize predators and non-predators. Proc. R. Soc. B Biol. Sci. 281, 20140355. https://doi.org/10.1098/rspb.2014.0355.

Cooper, W.E., Blumstein, D.T., 2015. Part I - overview and behaviors preceding and following initiation of escape. In: Cooper, W.E., Blumstein, D.T. (Eds.), Escaping from Predators: An Integrative View of Escape Decisions. Cambridge University Press, pp. 1–15.

Cooper, W.E., Frederick, W.G., 2007. Optimal flight initiation distance. J. Theor. Biol. 244, 59–67. https://doi.org/10.1016/j.jtbi.2006.07.011.

Cooper, W.E., Hawlena, D., Pérez-Mellado, V., 2009. Interactive effect of starting distance and approach speed on escape behavior challenges theory. Behav. Ecol. 20, 542–546. https://doi.org/10.1093/beheco/arp029.

DeMartini, E.E., Smith, J.E., 2015. Effects of fishing on the fishes and habitat of coral reefs. In: Mora, C. (Ed.), Ecology of Fishes on Coral Reefs. Cambridge University Press, pp. 135–144. https://doi.org/10.1017/CBO9781316105412.016.

Feeney, W.E., Bertucci, F., Gairin, E., Siu, G., Waqalevu, V., Antoine, M., de Loma, T.L., Planes, S., Galzin, R., Lecchini, D., 2021. Long term relationship between farming damselfish, predators, competitors and benthic habitat on coral reefs of Moorea Island. Sci. Rep. 11, 14548. https://doi.org/10.1038/s41598-021-94010-0.

Fuiman, A., Magurran, A., 1994. Development of predator defences in fishes. Rev. Fish Biol. Fish. 4, 145–183. https://doi.org/10.1098/rspb.1987.0004.

Gil, M.A., Hein, A.M., 2017. Social interactions among grazing reef fish drive material flux in a coral reef ecosystem. PNAS. 114, 4703–4708. https://doi.org/10.1073/pnas.1615652114.

Gill, A., 2003. The dynamics of prey choice in fish: the importance of prey size and satiation. J. Fish Biol. 63, 105–116. https://doi.org/10.1111/j.1095-8649.2003.00214.x.

Goulart, V.D.L.R., Young, R.J., 2013. Selfish behaviour as an antipredator response in schooling fish? Anim. Behav. 86, 443–450. https://doi.org/10.1016/j.anbehav.2013.05.041.

Hager, M.C., Helfman, G.S., 1991. Safety in numbers: shoal size choice by minnows under predatory threat. Behav. Ecol. Sociobiol. 29, 271–276. https://doi.org/10.1007/BF00163984.

Harbour, D., Henson, E., Boers, C., Truman, D., Fernando, C., Guay, P.J., Weston, M.A., 2019. Flight initiation distance in lepidopterans is species-specific and positively related to starting distance. J. Asia Pac. Entomol. 22, 41–43. https://doi.org/10.1016/j.aspen.2018.11.015.

Hata, H., Kato, M., 2004. Monoculture and mixed-species algal farms on a coral reef are maintained through intensive and extensive management by damselfishes. J. Exp. Mar. Biol. Ecol. 313, 285–296.

Hein, A.M., Gil, M.A., Twomey, C.R., Couzin, I.D., Levin, S.A., 2018. Conserved behavioral circuits govern high-speed decision-making in wild fish shoals. Proc. Natl. Acad. Sci. 115 (48), 12224–12228. https://doi.org/10.1073/pnas.1809140115.

Helfman, G.S., 1989. Threat-sensitive predator avoidance in damselfish-trumpetfish interactions. Behav. Ecol. Sociobiol. 24, 47–58. https://doi.org/10.1007/BF00300117.

Helfman, G.S., Winkelman, D.L., 1997. Threat sensitivity in bicolor damselfish: effects of sociality and body size. Ethology. 103, 369–383. https://doi.org/10.1111/j.1439-0310.1997.tb00153.x.

Holbrook, S.J., Schmitt, R.J., 2002. Competition for shelter space causes density-dependent predation mortality in damselfishes. Ecol. 83, 2855–2868. https://doi.org/10.1890/0012-9658(2002)083[2855:CFSSCD]2.0.CO;2.

Januchowski-Hartley, F.A., Graham, N.A.J., Feary, D.A., Morove, T., Cinner, J.E., 2011. Fear of fishers: human predation explains behavioral changes in coral reef fishes. PLoS One 6, e22761. https://doi.org/10.1371/journal.pone.0022761.

Karino, K., 1995. Male-male competition and female mate choice through courtship display in the territorial damselfish *Stegastes nigricans*. Ethology. 100, 126–138. https://doi.org/10.1111/j.1439-0310.1995.tb00320.x.

Leavell, B.C., Bernal, X.E., 2019. The cognitive ecology of stimulus ambiguity: a predator–prey perspective. Trends Ecol. Evol. 34, 1048–1060. https://doi.org/10.1016/j.tree.2019.07.004.

Lehtinirmi, M., 2005. Swim or hide: predator cues cause species specific reactions in young fish larvae. J. Fish Biol. 66, 1285–1299. https://doi.org/10.1111/j.0022-1112.2005.00681.x.

Lenth, R.V., 2022. Emmeans: estimated marginal means, aka least-squares means. In: R package version 1.7.2. https://CRAN.R-project.org/package=emmeans.

Lima, S.L., 1995. Back to the basics of anti-predatory vigilance: the group-size effect. Anim. Behav. 49, 11–20. https://doi.org/10.1016/0003-3472(95)80149-9.

Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P., Makowski, D., 2021a. Performance: an R package for assessment, comparison and testing of statistical models. J. Open Source Software. 6, 3139. https://doi.org/10.21105/joss.03139.

Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P., Wiernik, B.M., Makowski, D., 2021b. See: an R package for visualizing statistical models. J. Open Source Software 3393. https://doi.org/10.21105/joss.03393. Version 0.6.8. 6.

Madin, E.M.P., Gaines, S.D., Warner, R.R., 2010. Field evidence for pervasive indirect effects of fishing. Ecology. 91, 3563–3571. https://doi.org/10.1890/09-2174.1.

Magurran, A.E., Pitcher, T.J., Dodd, J.M., 1987. Provenance, shoal size and the sociobiology of predator-evasion behaviour in minnow shoals. Proc. R. Soc. B Biol. Sci. 229, 439–465. https://doi.org/10.1098/rspb.1987.0004.

McGowan, M.M., Patel, P.D., Stroh, J.D., Blumstein, D.T., 2014. The effect of human presence and human activity on risk assessment and flight initiation distance in skinks. Ethology. 120, 1081–1089. https://doi.org/10.1111/eth.12281.

Morgan, M.J., 1988. The influence of hunger, shoal size and predator presence on foraging in bluntnose minnows. Anim. Behav. 36, 1317–1322. https://doi.org/10.1016/S0003-3472(88)80200-8.

Morgan, M.J., Godin, J.J., 1985. Antipredator benefits of schooling behaviour in a cyprinodontid fish, the banded killifish (*Fundulus diaphanus*). Z. Tierpsychol. 70, 236–246. https://doi.org/10.1111/j.1439-0310.1985.tb00515.x.

Murray, I., 1978. Group organization of a territorial damselfish, *Eupomacentrus planifrons*. Behav. 65, 125–137. https://doi.org/10.1163/156853978X00233.

Oliveira, R.F., McGregor, P.K., Latruffe, C., 1998. Know thine enemy: fighting fish gather information from observing conspecific interactions. Proc. R. Soc. B Biol. Sci. 265, 1045–1049. https://doi.org/10.1098/rspb.1998.0397.

Pedersen, T.L., 2020. Patchwork: The Composer of Plots. R package version 1.1.1. https://CRAN.R-project.org/package=patchwork.

Quadros, A., Barros, L.S.F., Blumstein, D.T., Meira, V.H., José, Anchieta C., Nunes, C., 2019. Structural complexity but not territory sizes influences flight initiation distance in a damselfish. Mar. Biol. 166, 65. https://doi.org/10.1007/s00227-019-3508-2.

Queiroz, H., Magurran, A.E., 2005. Safety in numbers? Shoaling behavior of the Amazonian red-bellied piranha. Biol. Lett. 1, 155–157. https://doi.org/10.1098/rsbl.2004.0267.

R Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Roberts, G., 1996. Why individual vigilance declines as group size increases. Anim. Behav. 51, 1077–1086. https://doi.org/10.1006/anbe.1996.0109.

Ryer, C., 1988. Pipefish foraging: effects of fish size, prey size and altered habitat complexity. Mar. Ecol. Prog. 48, 37–45. https://doi.org/10.3354/meps048037.

Samia, D.S.M., Blumstein, D.T., 2015. Birds flush early and avoid the rush: an interspecific study. PLoS One 10, e0119906. https://doi.org/10.1371/journal.pone.0119906.

Samia, D.S.M., Nomura, F., Blumstein, D.T., 2013. Do animals generally flush early and avoid the rush? A meta-analysis. Biol. Lett. 9, 20130016. https://doi.org/10.1098/rsbl.2013.0016.

Samia, D.S.M., Blumstein, D.T., Stankowich, T., Cooper Jr., W.E., 2016. Fifty years of chasing lizards: new insights advance optimal escape theory. Biol. Rev. 91, 349–366. https://doi.org/10.1111/brv.12173.

Samia, D.S.M., Bessa, E., Blumstein, D.T., Nunes, J.A.C.C., Azzurro, E., Morroni, L., Sbragaglia, V., Januchowski-Hartley, F.A., Geffroy, B., 2019. A meta-analysis of fish behavioural reaction to underwater human presence. Fish Fish. 20, 817–829. https://doi.org/10.1111/faf.12378.

Scharf, F., Juanes, F., Rountree, R., 2000. Predator size-prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Mar. Ecol. Prog. 208, 229–248. https://doi.org/10.3354/meps208229.

Sih, A., Bolnick, D., Luttbeg, B., Orrock, J., Peacor, S., Pintor, L., Preisser, E., Rehage, J., Vonesh, J., 2010. Predator-prey naïveté, antipredator behavior, and the ecology of predator invasions. Oikos. 119, 610–621. https://doi.org/10.1111/j.1600-0706.2009.18039.x.

Stankowich, T., Blumstein, D.T., 2005. Fear in animals: a meta-analysis and review of risk assessment. Proc. R. Soc. B Biol. Sci. 272, 2627–2634. https://doi.org/10.1098/rspb.2005.3251.

Tang, Z., Huang, Q., Wu, H., Kuang, L., Fu, S.J., 2017. The behavioral response of prey fish to predators: the role of predator size. PeerJ. 5, e3222 https://doi.org/10.7717/peerj.3222.

Treves, A., 2000. Theory and method in studies of vigilance and aggregation. Anim. Behav. 60, 711–722. https://doi.org/10.1006/anbe.2000.1528.

Turesson, H., Persson, A., Brönmark, C., 2002. Prey size selection in piscivorous pikeperch (*Stizostedion Lucioperca*) includes active prey choice. Ecol. Freshw. Fish 11, 223–233. https://doi.org/10.1034/j.1600-0633.2002.00019.x.

Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis Version 3.3.3. Springer-Verlag, New York.

Ydenberg, R., Dill, M., 1986. The economics of fleeing from predators. In: Advances in the Study of Behavior, 16, pp. 229–249. https://doi.org/10.1016/S0065-3454(08)60192-8.

Zhang, D., 2021. Rsq: R-squared and related measures. In: R Package Version 2.2. https://CRAN.R-project.org/package=rsq.