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Dear enemy effects in the stoplight parrotfish, *Sparisoma viride*

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Territories are areas where individuals or groups maintain priority access to resources through social interaction and arise when the benefits of priority access exceed the costs of establishment and defense (Brown, 1964; Kaufmann, 1983). The aggressiveness of territory defense may vary depending on the identity of the territorial intruder, leading to neighbor–stranger dynamics (Christensen & Radford, 2018). The dear enemy effect is a phenomenon in which territory holders act less aggressively with neighbors than strangers (Fisher, 1954), and has been observed in many animal taxa (e.g., Briefer et al., 2008; Jaeger, 1981; Leiser & Itzkowitz, 1999). This strategy is thought to arise from differences in the relative threat of neighbors and strangers (Temeles, 1994). Once territorial boundaries are established, neighboring territory holders should pose little threat to one another relative to nonterritorial intruders that may attempt to evict them to gain access to territories and their associated benefits.

Parrotfishes are protogynous hermaphrodites that transition from female (initial phase) to male (terminal phase). In the stoplight parrotfish, *Sparisoma viride*, males defend daily foraging areas as stable intraspecific territories containing harems of females (Manning & McCoy, 2023a; van Rooij, Kroon, et al., 1996). Territory size in *S. viride* is positively correlated with harem size (Mumby & Wabnitz, 2002; Smith et al., 2023), and haremic females share substantial space with territorial males (Manning et al., 2022). Mating success is higher in territorial males (van Rooij, Kroon, et al., 1996), and female defense may be the primary function of territoriality (Smith et al., 2023). However, prior work has postulated that food resources may also be defended by territorial *S. viride* (van Rooij, de Jong, et al., 1996; van Rooij, Kroon, et al., 1996). Indeed, these functions may be related. Territorial males have greater access to high-yield food resources relative to nonterritorial males (Bruggemann et al., 1994), which may help to offset the cost of territory defense (reduced body condition; van Rooij et al., 1995). Territorial contests (hereafter, interactions) typically consist of displays (e.g., charges and fin erections; Video S1) and/or escalated chases (Video S2). Prior observations of territorial contests in *S. viride* suggested that dear enemy effects could mediate

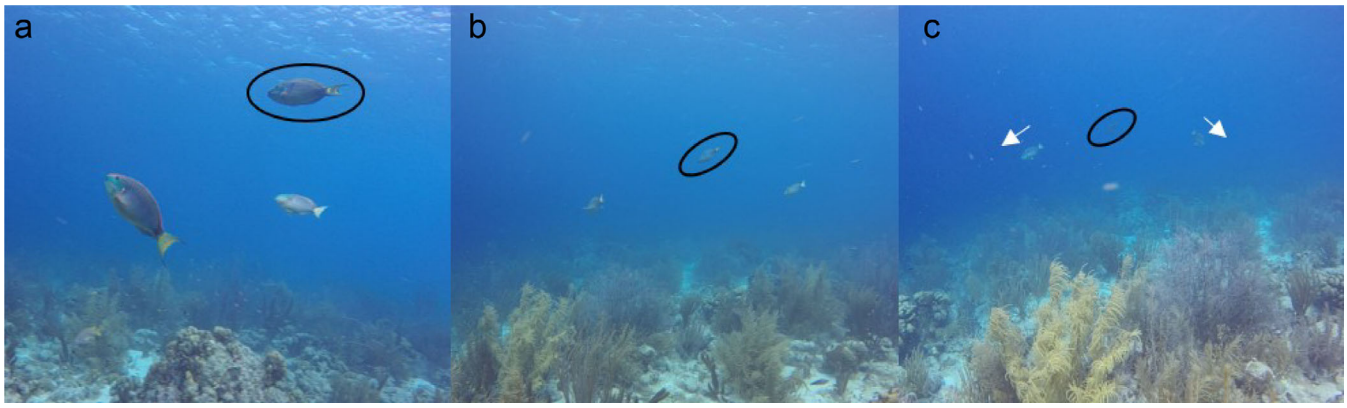

FIGURE 1 Two neighboring territorial male *Sparisoma viride* chased a nonterritorial "floater" (circled) along their shared territory boundary at a fringing reef in Bonaire (a, b). The territory holders eventually split off and returned to their respective territories (white arrows) without interacting with one another (c), and the floater continued to swim away down the reef. January 22, 2019. Credit: Joshua C. Manning.

territorial interactions in this species (Figure 1). Thus, we investigated dear enemy effects in *S. viride*. Consistent with our prior observations and dear enemy recognition, we hypothesized that interactions between territory holders and neighbors would be less frequent, shorter, and less aggressive than interactions with nonterritorial "floaters." Neighboring territory holders should pose less threat to one another than floaters that may attempt to evict them and/or spawn with their harems. However, the strength of this relationship may depend on the degree to which food resources are defended. In the event that food resources are also defended, a neighbor's attempt to annex a portion of an owner's territory constitutes a potential loss of resources and should elicit increased aggression, moderating the strength of dear enemy effects.

We observed 10 territorial male *S. viride* at two fringing coral reef sites in Bonaire ($n = 5$ site^{-1}) for 45 min each and recorded the duration, level of aggression (display/chase), and relationship of the interacting fish (neighbor/floater) for all territorial interactions between the focal, territory holder, and intruding males (Appendix S1: Section S1). We found no differences in the number or duration of interactions between focal males and intruding neighbors or floaters (Appendix S1: Figure S1, Tables S1 and S2). However, focal males were more likely to engage in escalated chases with intruding floaters than neighbors (Figure 2a; $\chi^2 = 5.03$, $df = 1$, $p = 0.02$; Appendix S1: Table S3). In fact, 27 of 28 interactions between territory holders and floaters involved chases, while only 14 of 22 interactions with neighbors involved chases.

Dear enemy effects are often context dependent. Aggression toward neighbors may increase in the presence of females (Leiser, 2003), when mates are fertile (Moser-Purdy et al., 2017), or when neighbors are displaced (Husak & Fox, 2003). In some species, the dear enemy effect is a reciprocal tit-for-tat relationship between neighbors, which is stabilized, in part, by retaliation against cheaters (i.e., increased aggression and/or vigilance; Olendorf et al., 2004; Sogawa & Kohda, 2018). Five of the 14 observed escalated interactions between neighboring male *S. viride* began after the focal fish chased an intruding female *S. viride* out of its own territory and into its neighbor's, eliciting aggressive retaliation by the neighbor. However, retaliation generally ended when neighbors retreated to their respective territories. Additionally, we observed 16 instances in which neighboring males were actively foraging or swimming in their respective territories within a few meters (usually <10 m) of one another with no obvious signs of aggression. We only observed one instance in which an apparent floater was nearby without eliciting an aggressive response from the focal fish. These noninteractions provide further evidence of the more passive treatment of territory-holding neighbors relative to floaters, and the observed behavior is suggestive of a tit-for-tat relationship in this species.

Game theory predicts that escalated contests among neighbors should be uncommon because payoffs are small compared with the cost of escalation (Maynard Smith & Parker, 1976). Territory holders already have priority access to territories and the resources within (i.e., mates and food). Regardless, we might still predict increased aggression among neighbors if the abundance of food resources differs among territories, increasing the risk that neighbors may try to annex portions of neighboring territories (Temeles, 1994). The cover of epilithic turfs and crustose coralline algae (primary foraging

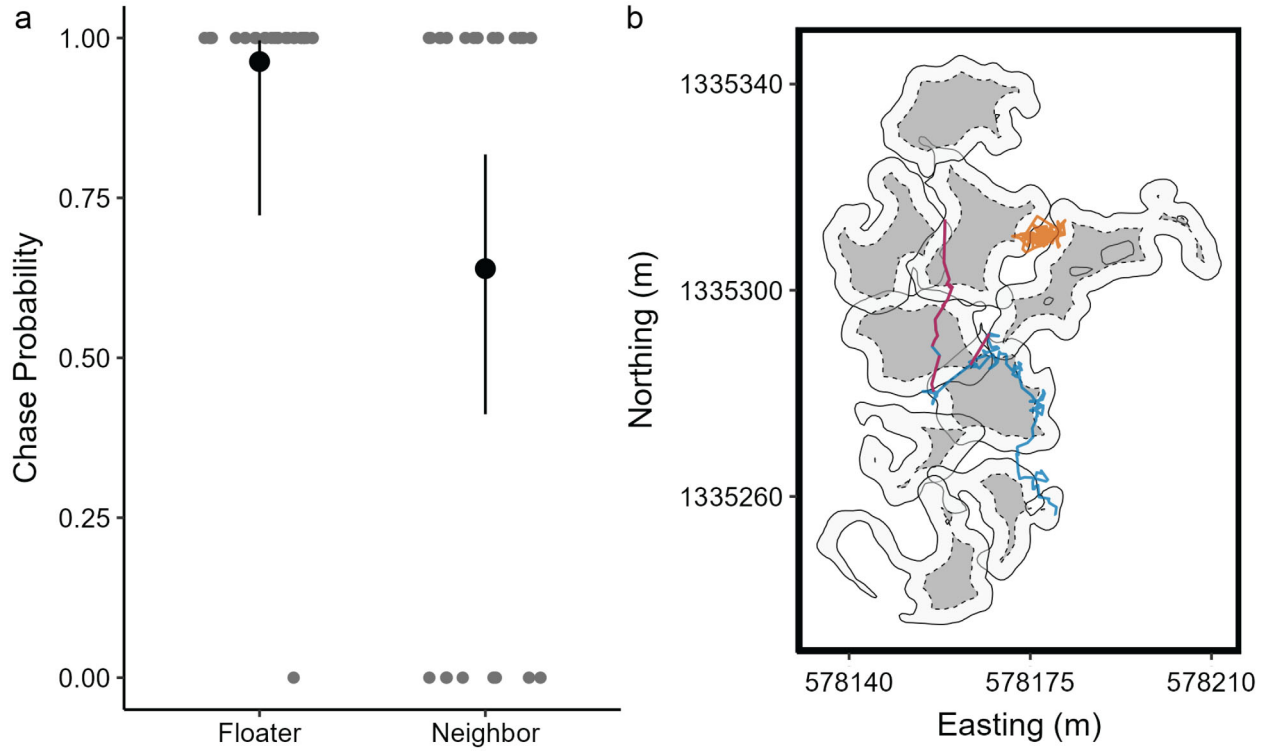

FIGURE 2 (a) The marginal mean (±95% asymptotic CIs) probabilities of territory holders chasing floaters and neighbors extracted from the fitted generalized linear mixed model (large black points and error bars). The raw data are also displayed (small gray points). (b) The home ranges (i.e., territories; solid black polygons) of nine male *Sparisoma viride* at Invisibles fringing reef in Bonaire. Buffer zones, defined as the areas within 2.95 m (Manning et al., 2022) of the 95% home range contours for each individual, are indicated by dashed lines. The two floater tracks are indicated by solid lines. Individual 1 is in orange, while Individual 2 is in blue (not being chased by a territory holder) and maroon (being chased by a territory holder). We removed holes (areas with no estimated probability of use) within home ranges to simplify.

substrate; Manning & McCoy, 2023b) did not differ among territories, but did differ among reef sites ($F = 4.99$, df $= 1$, $p = 0.03$; Appendix S1: Section S2 and Table S4). However, there were no differences in the number, duration, or aggressiveness of interactions between *S. viride* between sites (Appendix S1: Tables S1–S3). As such, it seems unlikely that food-related payoff asymmetries influenced *S. viride* interactions and that female defense may be more important. We observed 4.1 ± 0.5 (mean ± SE, range = 2–7) female *S. viride* (>~10 cm fork length) in our focal territories, which is similar to densities of haremic individuals reported in prior studies (Mumby & Wabnitz, 2002; Smith et al., 2023; van Rooij, Kroon, et al., 1996). While it is possible that the relative difference in neighboring harem sizes may affect territorial contests, our data were insufficient to investigate these effects. Future work investigating the role of the harem in mediating territorial interactions will better elucidate the mechanisms stabilizing the dear enemy relationship in *S. viride*.

We mapped the territories of *S. viride* at both sites and opportunistically tracked two floaters at one site (Appendix S1: Section S3). Upon visualizing the movement of these floaters, it became apparent that they remained within the buffer zones of territories unless chased by territory holders, using these areas as spatial refugia from aggression (Figure 2b). One floater remained in the buffer zone for the entire 20-min GPS track, despite multiple approaches by a territorial male. Whenever the territorial male approached, the floater stopped foraging and sheltered within reef structure and gorgonians until the territorial male left. It is possible that floaters use territory boundaries to search for preferable territory locations in a manner analogous to birds prospecting for breeding sites (Reed et al., 1999), and familiarity with territory boundaries can increase their chances of filling vacancies (Bruinzeel & van de Pol, 2004).

Territoriality plays an important role in regulating animal populations, including by determining the upper limits of population size and buffering population responses to variations in resource availability (Packard & Mech, 1980; Wood et al., 2012). The importance of floaters for population regulation depends upon fecundity, the relationship between reproductive success and territory size, and the costs of territory defense (López-Sepulcre &

Kokko, 2005). Floaters can reduce equilibrium population sizes if they strongly influence the cost of territory defense (López-Sepulcre & Kokko, 2005). The prevalence of territoriality in parrotfishes (Manning & McCoy, 2023a), the ease with which territorial behavior and social structure can be observed, and their importance to coral reef ecosystems make parrotfishes an excellent study system for future work investigating neighbor–stranger dynamics and the importance of territoriality for population regulation. Parrotfishes are important grazers on coral reefs, contributing to successional dynamics in the reef benthos (Clements et al., 2017) and to bioerosion and sediment production/reworking (Bonaldo et al., 2014). An improved understanding of the mechanisms underlying territoriality in parrotfishes, including neighbor–stranger dynamics, will elucidate processes contributing to population regulation and provide insights into how socially mediated space use may affect the delivery of their ecological functions in an ecosystem that is rapidly being altered by human activity.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Manning, 2024) are available in Zenodo at https://doi.org/10.5281/zenodo.11406492.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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