Ethology

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Lionfish (*Pterois volitans*) Show Social Attraction to Conspecifics When Selecting Shelters

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ABSTRACT

Group formation in animals can arise from two primary mechanisms: individuals aggregating over resources, or individuals socially benefiting from interacting with conspecifics. Distinguishing between these mechanisms allows us to infer the drivers of group formation, which is of considerable importance for informing management strategies of invasive species. Lionfish (*Pterois volitans*) are a teleost predator native to the Indo-Pacific but invasive in the Western Atlantic Ocean. Lionfish are often observed sheltering in refuges on their own or in groups, with previous research suggesting these groups form due to attraction towards preferred habitats rather than having a social function. Here, we find that lionfish were more likely to shelter with a conspecific rather than choosing to shelter alone. Lionfish were also more likely to shelter with larger conspecifics. Our findings demonstrate that lionfish are socially attracted to one another, which has implications for the control and management strategies of this invasive species.

1 | Introduction

In many species, conspecifics are often observed together, with these groups predominantly forming for two reasons (Krause and Ruxton 2002). First, animals may be attracted to certain environmental conditions or resources, resulting in individuals aggregating together (Krause and Ruxton 2002; Pitcher et al. 1998). In these cases, individuals may not be socially attracted to one another but will compete for resources without holding territories. Alternatively, animals may form social groups to benefit from living with conspecifics. These benefits include increased vigilance, risk dilution, predator confusion and increased foraging efficiency (Krause and Ruxton 2002; Rubenstein 1978). Such benefits of group living outweigh costs like competition, parasite transmission, cannibalism and conspicuousness to predators (Alexander 1974; Rubenstein 1978). In some cases, distinguishing the mechanism behind group formation, and whether these aggregations also provide any social benefits, remains unresolved. For example, *Sphex* wasps, horseflies (*Tabanus sulcifroms*) and other insects form sleeping aggregations which appear to result from individuals converging on a sleeping refuge, despite these species being solitary during the day (Allee 1927). Likewise, *Ophioderma* starfish aggregate due to their negative phototropism but tend not to cluster when shade is abundant (Allee 1927). Behavioural experiments are often needed, therefore, to disentangle the mechanisms behind grouping. Doing so has important implications for understanding the social and ecological drivers of grouping, which can inform effective conservation actions (Blumstein 2010).

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While many animals form social groups for at least some part of their life history, these tendencies can often change depending on species, context and life-history stage. For example, in some fishes such as mackerel (*Scomber* spp.) and herring (*Clupea* spp.), grouping is obligate throughout their life (Pitcher et al. 1998). For other species, grouping is facultative, with individuals selecting if and when they will associate with others (Krause and Ruxton 2002). Nassau groupers (*Epimetheus striatus*), for instance, only form aggregations during breeding periods and are otherwise territorial (Domeier and Colin 1997), and white-saddle goatfish (*Parupeneus porphyreus*) form large daytime shoals, yet will shelter nocturnally in smaller groups or alone (Meyer et al. 2000). Differences in the tendencies to form social groups are driven by the trade-offs between the costs and benefits of group living. For instance, grouping is commonly observed in juvenile fishes when they are more vulnerable to predation (Almany and Webster 2006), but decreases with increasing body size, where the costs of competition between individuals increase (MacPherson 1998). Juvenile bluehead wrasse (*Thalassoma bifasciatum*), for example, either forage solitary or in groups of 2–20 individuals, trading off between the antipredator benefits of grouping (White 2007) with increased competition costs (White and Warner 2007).

In some cases, the benefits of group living can shift depending on individual size and the size of individuals in the groups they are joining. Three-spined sticklebacks (*Gasterosteus aculeatus*), for example, prefer to form groups with similarly sized individuals (Ranta et al. 1992) and even in mixed-species groups, individuals prefer to associate with size-matched heterospecifics (Krause et al. 1996; Quinn et al. 2012). In some cases, individuals may avoid associating with dissimilarly sized conspecifics altogether, owing to the potential risks of cannibalism. Indeed, piscivorous species such as Eurasian perch (*Perca fluviatilis*) and many salmonids form social groups but are also cannibalistic (Andersson et al. 2021; Pereira et al. 2017). Species exhibiting cannibalism, therefore, provide unique systems in which to ask how individuals might change their social preferences depending on the relative size of conspecifics and the risks of cannibalism.

Indo-Pacific lionfish (hereafter referred to as lionfish') consist of two closely related fish species (*Pterois miles* and *Pterois volitans*). Lionfish have become invasive in the Western Atlantic Ocean since their introduction in the 1980's (Morris et al. 2008) and *P. miles* have more recently traversed the Suez Canal and invaded the Mediterranean Sea (Turan et al. 2017) where they have rapidly spread north-westwards (Phillips and Kotrschal 2021), with recent sightings as far west as Sicily, Malta and Croatia (Bottacini et al. 2024). While past observations by Fishelson (1975) considered lionfish to be solitary, there are many observations reporting lionfish aggregations (Hunt et al. 2019, Hunt et al. 2020; McTee and Grubich 2014) and lionfish of similar sizes are often observed sharing diurnal refuges (García-Rivas et al. 2017). Whether these groupings are social or result from individuals aggregating on a shared resource (i.e., refuges), however, remains unclear. Indeed, surveys have identified that lionfish aggregate in areas of higher structural complexity, potentially due to more available refugia (Hunt et al. 2019). Moreover, previous choice experiments found no attraction of lionfish to the visual and olfactory cues of conspecifics, with some evidence of lionfish showing aversion towards conspecific olfactory cues in the absence of visual cues (Hunt et al. 2019). While *P. miles* have been observed to form hunting aggregations, initially proposed to involve coordinated hunting (McTee and Grubich 2014), more recent experiments have determined this phenomenon is more likely to involve lionfish aggregating on prey patches (Sarhan and Bshary 2021). Lionfish are also cannibalistic, with visual and genetic gut-content analysis on *P. volitans* in the Gulf of Mexico identifying conspecifics in 26%–42% of individuals' diets (Dahl et al. 2018; Valdez-Moreno et al. 2012). Therefore, smaller individuals may attempt to avoid larger conspecifics altogether. Thus, while evidence suggests lionfish aggregate over resources, further experimental work is needed to determine whether lionfish form social groups.

In this study, we used a behavioral choice experiment to determine whether lionfish displayed social attraction to conspecifics when selecting a shelter as a refuge. Since lionfish can be cannibalistic, we also tested whether the size of a fish already occupying a shelter affected the decision of a focal fish to shelter with that conspecific or not. If lionfish are socially attracted to one another, we expected individuals to be more likely to select a shelter with a conspecific than a shelter without a conspecific. If the risk of cannibalism influences this decision, we predicted the decision to shelter with another conspecific or not would depend on the relative size difference between the pair. In particular, smaller focal fish would be less likely to share a shelter with a larger conspecific, while larger individuals may be more likely to select a shelter with a smaller conspecific.

2 | Methods

2.1 | Experimental Procedure

We caught 6–8 lionfish weekly for 7 weeks ($n = 44$ in total) at Piscadera Bay in Curaçao, Dutch Caribbean (12°07′20.3″ N, 68°58′08.7″ W) between April and May 2023. Fish were captured at dusk by SCUBA divers using clove oil and hand nets. Following capture, lionfish were brought up to a depth of 3 m at an ascent rate of $\leq 1\,\mathrm{m\,min^{-1}}$ with a 3-min stop every 5 m, to reduce the risk of barotrauma to the fish. Lionfish were not fed during the experimental week to control for the effect of hunger on their behaviour. Lionfish are sit-and-wait predators which can withstand food deprivation for > 2 weeks (Fishelson 1997). Lionfish were kept individually in adjacent labelled cages made of PVC and wire mesh (30 × 30 cm) under a jetty ~100 m away from the location of the choice arenas.

Two choice arenas (220 × 60 × 60 cm dimensions) made of PVC pipe and wire mesh were constructed, each consisting of a central choice chamber (120 × 60 × 60 cm) and stimulus chambers (50 × 60 × 40 cm) on either side. The arenas were placed on open sand parallel to the reef crest at a depth of 3.4 and 4.1 m, 10 m apart, respectively. Either side of the central compartment in each choice arena contained a large single-holed cinder building breezeblock, which lined up with another breezeblock in the corresponding stimulus chamber, creating one shelter divided in the middle by 4 mm wire mesh (Figure 1).

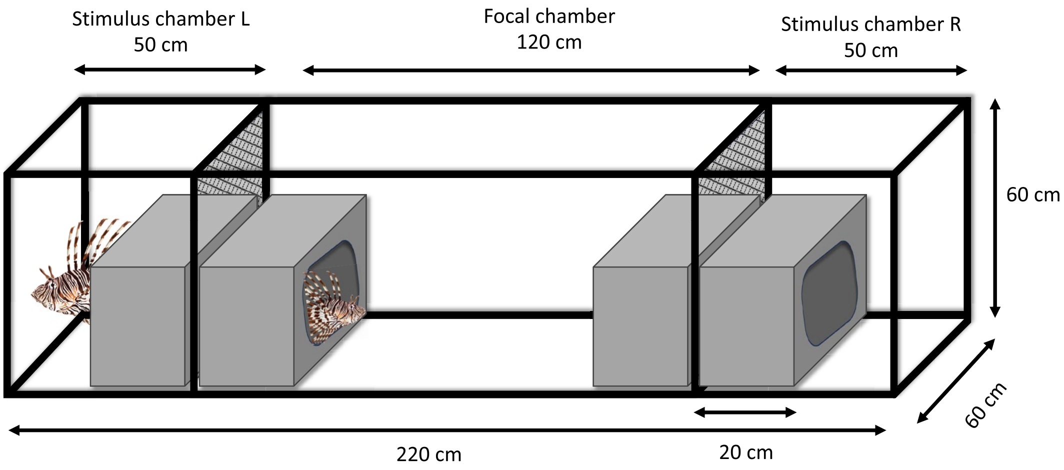

FIGURE 1 | Schematic of one of the two experimental arenas (220 × 60 × 60 cm) consisting of a central focal compartment separated from the left (L) and right (R) flanking stimulus compartments by 4 mm wire mesh dividers. The focal lionfish was placed in the central focal chamber overnight and was tasked with selecting a shelter with or without another lionfish.

For each trial ($n = 44$), a focal fish was placed into the central compartment and a stimulus fish was placed in one of the side stimulus chambers. Stimulus fish were allocated to focal fish based on their approximate size differences such that a range of focal-stimulus size pairings were used (stimulus fish were smaller: $n = 15$ [mean size difference ± SD: 63.0 mm ±36.8], a similar size: $n = 16$ [mean size difference ± SD: 3.6 mm ±26.9] or larger: $n = 13$ [mean size difference ± SD: −74.2 mm ±39.7], than the focal fish, Table S1). Trials were run in both arenas each night for 3–4 nights per week. Fish were first used as a focal fish and then subsequently as a stimulus fish. Lionfish which were caught together (i.e., individuals which were found within 1 m of another individual either in a shelter or exposed on the reef) were not tested together in the same trial. Stimulus fish were never used in the arena in which they had been a focal fish, and the side of the arena (left or right) which held a stimulus fish was alternated between trials. In order to create specific size pairings while avoiding pairing fish which were caught together, some stimulus fish ($n = 3$ individuals) were used more than once. Fish were transported from the holding area to the choice chambers in their individual holding cages by a SCUBA diver and then gently herded into the choice arenas using a rod between 16:30 and 17:00 each evening. The side the focal lionfish had chosen was then recorded between 9:00 and 10:00 the next morning. As lionfish are primarily crepuscular or nocturnal (Green et al. 2011), recording their choice the following morning would have given them an opportunity to explore the arena and select a shelter during the night. If the focal fish was swimming or in the middle of the arena and had not selected a shelter in the morning ($n = 9$ out of 44 trials), the trial was recorded as ‘no choice’. While the relative space inside the hole/sheltering area in the breezeblock would have decreased for larger lionfish, many of the largest lionfish entered and settled in these shelters. One focal fish managed to enter a stimulus chamber and was excluded from analysis ($n = 1$). As lionfish are invasive in the Caribbean and cannot be released, at the end of each week the lionfish were humanely euthanized following Schedule 1 protocol of the Animals (Scientific Procedures) Act 1986 of humane killing for fish (Animal Procedures Committee 2009) by concussion followed by destruction of the brain. They were then photographed with a ruler, and their total length (TL) measured in ImageJ.

2.2 | Statistical Analyses

All statistical analyses were performed in R (Version 4.2.2; R Foundation for Statistical Computing, https://www.R-project.org). First, the likelihood of a fish selecting a shelter (1) or not (0) was calculated using a two-tailed binomial test. We then modelled the likelihood of selecting a shelter as a function of focal fish size (TL in mm) using a binomial GLM in the *glmmTMB* package (Brooks et al. 2017) to ask whether the size of the fish influenced their likelihood to select a shelter or not. Of the fish that selected a shelter ($n = 34$), the choice to select a shelter with (1) or without (0) a conspecific was then tested using a two-tailed binomial test. Since we were interested in understanding whether the decision by the focal fish to shelter with a conspecific or not was affected by their relative size difference to the conspecific, we further modelled the choice to shelter with or without a conspecific with focal fish and stimulus fish total lengths (TL) together as an interaction term using a binomial GLM. This interaction term, however, was non-significant and was subsequently dropped from the model, allowing us to test if the size of a conspecific affected a fish's likelihood of choosing a shelter with them, independent of their own size. The significance of factors of interest (e.g., body size) was assessed using the *drop1* function using likelihood ratio tests, comparing models with and without the factor of interest.

3 | Results

Lionfish were more likely to be found in a shelter than freely swimming in the arena at the start of each day (Binomial test: 34/43 selected a shelter, $p < 0.001$), with larger lionfish being less likely to select either of the two shelters than smaller lionfish (Binomial GLM: $\chi^2_1 = 7.48$, $p = 0.006$, Figure 2a). Of the lionfish that did select a shelter, the majority of fish chose to share the shelter with a conspecific rather than occupy a shelter alone (Binomial test: 27/34 selected the shared shelter with a conspecific, $p < 0.001$, Figure 2b).

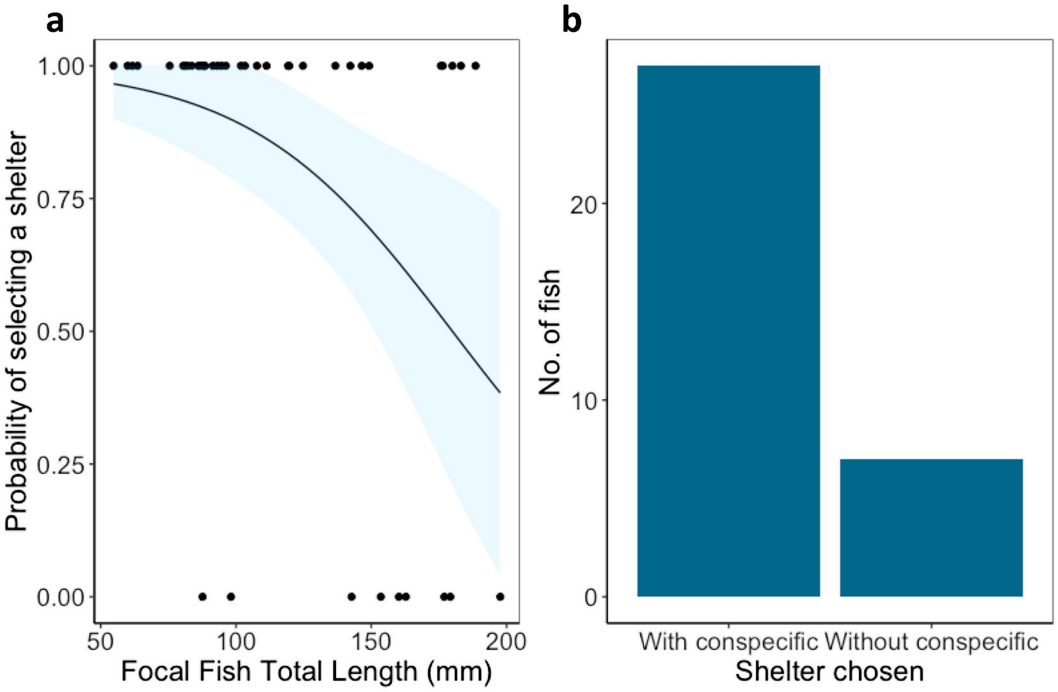

FIGURE 2 | (a) Likelihood of selecting a shelter (1) or not (0) as a function of the size of the focal lionfish (total length in mm). Larger lionfish were less likely to select a shelter than smaller lionfish (Binomial GLM: $\chi^2_1 = 7.48$, $p = 0.006$). (b) Of the fish which selected a shelter, there was a preference for selecting to share a shelter with a conspecific (Binomial test: 27/34 chose the shared shelter, $p < 0.001$). Shaded error bars show 95% confidence intervals.

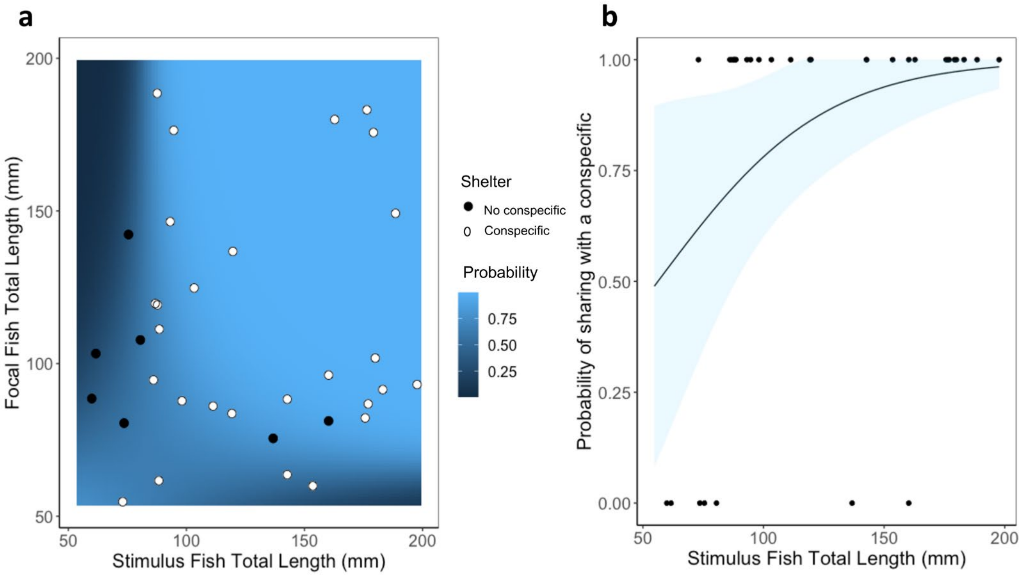

FIGURE 3 | (a) Outcome of a focal lionfish sheltering with (white points) or without (black points) a conspecific as a function of the stimulus fish and focal fish size. The heat in the plot represents the probability of fish sharing a shelter or not derived from the model prediction of the non-significant interaction between the focal fish size and the stimulus fish size (Binomial GLM: $\chi^2_1 = 3.57$, $p = 0.059$). There was no evidence that smaller focal fish avoided larger stimulus fish. (b) The choice to share a shelter with a conspecific was affected by the total length (TL) of the stimulus fish (Binomial GLM: $\chi^2_1 = 5.40$, $p = 0.020$) but not the focal fish size (Binomial GLM: $\chi^2_1 = 1.07$, $p = 0.300$), with fish preferring to shelter with larger conspecifics. Shaded error bars show 95% confidence intervals.

There was a non-significant interaction between the size of the focal fish and the size of the stimulus fish on the likelihood of the focal fish sharing a shelter with the stimulus fish (Binomial GLM: $\chi^2_1 = 3.57$, $p = 0.059$, Figure 3a), with no evidence that focal fish actively avoided larger stimulus fish than themselves. Instead, there was evidence that the likelihood of sharing a shelter with a conspecific increased as a function of the stimulus fish's total length (Binomial GLM: $\chi^2_1 = 5.40$, $p = 0.020$,

Figure 3b). There was no evidence that the size of the focal fish affected whether it would shelter with a conspecific or not (Binomial GLM: $\chi^2_1 = 1.07$, $p = 0.300$).

4 | Discussion

Larger lionfish were less likely to shelter than smaller lionfish, with the likelihood of a lionfish being observed swimming outside the shelter increasing with fish size. Of the lionfish that did select a shelter, fish were more likely to choose a shelter with a conspecific than without a conspecific. At the size ranges tested, there was no evidence that smaller lionfish avoided lionfish larger than themselves. Instead, lionfish were more likely to share a shelter with a conspecific as the size of that conspecific increased. Overall, despite previous studies suggesting that lionfish do not form social groups, these results suggest that lionfish shelter with conspecifics due to social attraction.

Larger lionfish were less likely to select a shelter than smaller lionfish. Smaller fishes face a higher risk of predation due to the gape limitation of many coral reef predators (Dunic and Baum 2017). Moreover, larger lionfish possess greater defenses against predation, in the form of larger venomous spines compared to smaller individuals (García-Rivas et al. 2018; Morris Jr and Whitfield 2009). Sheltering in refugia is typically thought to be a response used to avoid threats (Lima and Dill 1990), and therefore larger lionfish may be less likely to shelter owing to a reduced perception of risk. Indeed, as lionfish grow, they become more active during the day, making larger maximum movements between patch reefs, while smaller lionfish tend to explore in low-light conditions (Benkwitt 2016; García-Rivas et al. 2018). Another possibility for larger fish being less likely to shelter could be due to shifts in habitat preferences as lionfish grow. During their lifetimes, lionfish display an ontogenetic niche shift: smaller lionfish primarily consume invertebrates and utilize inshore areas such as seagrass beds, mangroves and sheltered reefs, while larger lionfish are piscivorous and inhabit deeper reef environments (Alexander et al. 2012; García-Rivas et al. 2018; Morris and Akins 2009). Smaller lionfish may, therefore, be more likely to select a shelter in a sandy area, where the experimental arenas were located, and larger lionfish instead may have been attempting to move to deeper habitats.

Through observational and experimental approaches, previous studies have concluded that lionfish aggregate over resources rather than forming through social attraction (Hunt et al. 2019). Indeed, there was previously no evidence of lionfish being socially attracted to the visual or olfactory cues of conspecifics (Hunt et al. 2019). Here we find, however, evidence for social attraction in lionfish when controlling for available habitat structure. Indeed, individuals showed a strong preference for sharing a shelter with a conspecific rather than sheltering alone. Differences in experimental conditions between our study and previous ones could reflect these discrepancies. First, the length of time fish were given to move towards or away from a conspecific was different between studies. In our study, lionfish were given the entire evening to interact through the mesh and acclimate to the choice chamber before selecting their shelter, while in previous studies, fish were given 10 min to make this decision. Allowing the lionfish the entire evening to acclimate to the experimental arena and assess the two shelters and stimulus conspecific may have led to different behavioral outcomes in experiments. For example, the absence of social attraction in previous studies, and even the aversion to olfactory cues of conspecifics, may be an initial reaction of the lionfish to unfamiliar individuals or conditions. Indeed, some fish can recognize individuals through visual or olfactory cues, preferring to associate with familiar individuals (Kohda et al. 2015; Wang and Takeuchi 2017). If familiarity between lionfish could be established over the course of an evening, this longer exposure time to conspecifics may have increased the likelihood of fish choosing to shelter together.

Differences in the social attraction of lionfish between studies may also be due to differences in the local threat levels faced by the experimental fish used. Indeed, areas with elevated mortality risk could drive differences in lionfish social attraction. Natural predation on lionfish in their invaded range has rarely been observed, with only a few reports of lionfish being consumed by species such as large-bodied groupers (Dahl et al. 2018; Maljković et al. 2008). Moreover, there is no relationship between the abundances of lionfish and native predators in The Bahamas, Cuba, and on the Mesoamerican Barrier Reef between Belize and Mexico (Hackerott et al. 2013). Further, in areas where lionfish abundance and grouper abundance are negatively correlated, this is thought to be due to competition between predators rather than intraguild predation (Mumby et al. 2011). Therefore, it is unlikely that differences in sociability are caused by variation in natural predation between the sources of lionfish used in Hunt et al. (2019) (Honduras) and this study (Curaçao). Human hunters, however, represent a major source of mortality for lionfish (Andradi-Brown et al. 2017). In Curaçao, there are higher reported numbers of lionfish hunters than in Honduras (Holmes, Matchette and Herbert-Read in prep). Differences in recreational lionfish hunting pressure between these areas, therefore, may affect whether lionfish adopt anti-predator behaviours such as grouping. Indeed, there is evidence from other areas that lionfish hunting has shaped the population structure and behaviour of lionfish. For example, targeted removals of larger individuals have altered the size composition of lionfish populations (Frazer et al. 2012), and in areas where lionfish are hunted, individuals tend to be found deeper within shelters and are less active on reefs compared to areas where human hunting does not occur (Côté et al. 2014). There is the potential, therefore, that areas with increased human hunting could be shaping lionfish anti-predator social behaviour.

Because lionfish are cannibalistic (Dahl et al. 2018), and in general, larger conspecifics represent a greater competitive threat (Mitchem et al. 2019), we predicted smaller lionfish would avoid larger lionfish. Instead, we found no evidence of an aversion of smaller lionfish to shelter with larger individuals. It is possible that the smaller individuals in our study were beyond the gape-limit of the largest lionfish in our study and/or the mesh barrier separating individuals afforded them a level of protection reducing their perceived risk. However, many piscivorous fishes can consume prey items up to more than half of their body size depending on the species (Dunic and Baum 2017), and lionfish less than ~198 mm in length are cannibalistic (Dahl et al. 2018). While in our study there were only 10 cases where the focal fish was approximately half the size of the stimulus fish, in eight out of these cases, the focal fish chose to shelter with the stimulus fish. Much like European minnows (*Phoxinus phoxinus*) that inspect predatory pike (*Esox lucius*) (Murphy and Pitcher 1997), smaller lionfish may choose to remain close to larger individuals to have information about their location and level of threat instead of actively avoiding them. Conversely, larger lionfish in our study may not represent a threat owing to a reduced motivation to feed. Overall, however, there was no evidence that lionfish avoided sheltering with larger conspecifics as would be predicted if avoiding cannibalism.

Instead, we observed a preference for individuals to select shelters with larger individuals. Given larger individuals are typically perceived as having higher reproductive potential (Basolo 2004), this preference could also be due to reproductive opportunities. However, this is unlikely to be the case in our study, since many of the smaller lionfish in our study were not of reproductive size. Indeed, histological studies on lionfish in Bermuda showed the smallest reproductively active individual was 189 mm in length (Eddy et al. 2019), with the largest individual in our study being ~198 mm. In the wild, despite aggregations consisting of similarly sized individuals (García-Rivas et al. 2017), aggregating individuals do not differ in gonadosomatic index when compared to solitary individuals (Hunt et al. 2019). Grouping for reproductive opportunities in lionfish, therefore, seems unlikely. Instead, the observation that lionfish were more likely to select a shelter with larger conspecifics may be due to larger lionfish being more salient or easier to detect.

In summary, we find that lionfish show social attraction when selecting diurnal shelters and prefer to shelter with larger individuals regardless of their own body size. Our findings have implications for conservation efforts such as the targeted removal of lionfish from reefs. For instance, one promising method for the removal of invasive lionfish from reefs is using the Gitting's Trap (Gittings et al. 2017; Harris et al. 2020). This method relies on lionfish being attracted to the trap, which then closes to catch fish before retrieval. While the cues that are used by lionfish to detect and identify conspecifics remain unknown, given that lionfish are attracted to conspecifics, this information could enhance the attractiveness and therefore efficacy of lionfish traps.

Author Contributions

Roxanne B. Holmes: conceptualization, investigation, writing – original draft, methodology, validation, visualization, writing – review and editing, formal analysis, project administration, data curation. **Nadia M. Hamilton:** investigation, conceptualization, methodology, writing – review and editing. **Katie Dunkley:** formal analysis, writing – review and editing. **James E. Herbert-Read:** conceptualization, methodology, supervision, formal analysis, writing – original draft, funding acquisition, writing – review and editing, visualization.

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Ethics Statement

All procedures were approved by the University of Cambridge Animal Welfare and Ethical Review Body (UBS reference number: OS2022/14). Daily, captive lionfish were examined for signs of stress (e.g., injuries, changes in skin and eye appearance, unusual ventilation rate or posture). Animals did not show any of these signs during the experiment. Lionfish were transported to and from the experimental arena in their individual housing cages to reduce any stress associated with handling and were not netted again after their initial capture, being gently herded between the experimental arena and the holding cages for trials.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The raw data and R scripts that support the findings of this study are available as Supporting Information.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.