



Invasive lionfish increase activity and foraging movements at greater local densities

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ABSTRACT: Density-dependent changes in predator foraging behavior due to intraspecific competition for food can have important implications for population dynamics of both the predator and its prey. The Indo-Pacific red lionfish *Pterois volitans* is an invasive predatory reef fish that has reached high population densities and can cause large reductions in small native fishes. To determine whether lionfish behavior or movement varies with local lionfish and/or prey densities, I conducted observations of lionfish on 16 coral patch reefs in The Bahamas. Lionfish foraging activity and movement varied significantly with lionfish density. At higher densities, lionfish exhibited greater activity levels, time away from shelter, and more short-term foraging movements between coral patch reefs and surrounding seagrass habitats. However, these changes were not uniform throughout the day, with differences in activity occurring only at dusk and differences in movement occurring at both dawn and dusk, but not midday. Although some lionfish foraging behaviors varied with prey density, overall lionfish density was more strongly related to differences in lionfish activity patterns. These temporal and spatial changes in lionfish foraging behaviors are consistent with the predicted effects of intraspecific competition and may have important consequences for lionfish removal efforts and native prey populations. Specifically, in areas with higher lionfish densities, prey fishes that are more active at dusk and/or inhabit seagrass beds near coral patch reefs may be more vulnerable to lionfish predation. By culling lionfish, managers may reduce the local foraging movements of lionfish and thus help maintain native fish communities in multiple habitats.

KEY WORDS: Behavior · Coral-reef fishes · Density dependence · Intraspecific competition · Movement · Non-native · Predator–prey interaction · *Pterois volitans*

INTRODUCTION

Local population density can strongly influence individual behavior and demographic rates through a variety of mechanisms. In some species there are benefits to living in groups, including increased access to mates, increased hunting efficiency, and reduced risk of predation (Packer & Rutman 1988, Courchamp et al. 1999, Krause & Ruxton 2002, Gascoigne & Lipcius 2004). However, at high densities, intraspecific competition for food and shelter often causes reductions in individual growth and survival due to increased interference and/or exploitation of resources (Jones 1991, Keddy 2001, Krause & Ruxton 2002, For-

rester 2015). Density-dependent behavioral and demographic changes are not only important to the population dynamics and regulation of a single species (Murdoch 1994, Hixon et al. 2002), but can also influence community-level dynamics and ecosystem processes (Micheli 1997, Clark et al. 2000).

If there is increased competition for food at higher conspecific densities, then predators may alter their foraging behavior in several ways, with subsequent consequences for prey populations. For example, if it takes longer to find and consume prey due to increased resource depletion or interference while foraging at higher densities, some individuals may increase the amount of time spent foraging (Clark & Mangel 1986,

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Shaw et al. 1995, Anholt & Werner 1995, Grand & Dill 1999, Bohlin & Johnsson 2004, White & Warner 2007), which may also be accompanied by an increase in conspecific aggressive encounters (Pintor et al. 2009, Kaspersson et al. 2010). Species that differentially forage over a diel cycle can expand their foraging time by hunting for longer during their typical hunting hours and/or by hunting at more periods of the day (Lawton 1987, Kronfeld-Schor & Dayan 2003, Wasserberg et al. 2006). Hunting at more periods of the day could in turn cause prey species with various diurnal patterns to be differentially susceptible to predation. In addition, predators at higher densities may expand their foraging range, which could enable them to exploit resources that have not yet been depleted and/or escape aggressive interactions in the areas with high densities of conspecifics (Micheli 1997, Forrester et al. 2006, Breed et al. 2013). If predators forage over broader distances, then prey species that inhabit the newly exploited habitats may be consumed.

Changes in foraging behavior as a result of increased local density may be particularly important to the population dynamics of both introduced predators and their native prey. Invasive species often reach higher abundances and individual body sizes in their invaded compared with their native ranges (Sakai et al. 2001, Grosholz & Ruiz 2003), and thus are likely to be strongly affected by intraspecific interactions. Furthermore, many invasive species are both competitively dominant and more abundant than ecologically similar native species in their new locations (Parker et al. 1999, Mack et al. 2000, Mooney & Cleland 2001, Sakai et al. 2001), suggesting that intraspecific rather than interspecific competition will have a larger influence on invasive species. Because invasive predators often cause larger reductions in native prey populations than do native predators (Salo et al. 2007), it is crucial to understand their foraging behavior at different densities and how this behavior in turn influences prey populations.

The Indo-Pacific red lionfish *Pterois volitans* is an invasive predatory reef fish that has reached extremely high abundances in parts of its invaded range (Côté et al. 2013, Albins & Hixon 2013). Since they were first sighted off the coast of Florida in the mid-1980s, lionfish have spread throughout the Caribbean, the Gulf of Mexico, and along the east coast of the Americas (Schofield 2010). Lionfish densities on reefs in their invaded range can be several orders of magnitude higher than in their native range (Green & Côté 2009, Darling et al. 2011, Kulbicki et

al. 2012, McTee & Grubich 2014). At the same time, there is wide variation in lionfish densities within their invaded range, owing in part to differences in the length of time since establishment (Ruttenberg et al. 2012, Dahl & Patterson 2014), removal efforts (Frazer et al. 2012, de León et al. 2013), and abiotic site characteristics including depth and exposure to strong currents and wave surge (Whitfield et al. 2007, Anton et al. 2014). In contrast, invasive lionfish populations are likely unaffected by potential predators (Hackerott et al. 2013, Valdivia et al. 2014, but see Mumby et al. 2011) or interspecific competitors (Albins 2013), especially given that native predators are severely depleted throughout much of the Caribbean (Paddack et al. 2009, Stallings 2009).

Despite differences in lionfish densities both between and within their native and invaded ranges, how local lionfish density influences their hunting behavior has not yet been examined. Both native and invasive lionfish are primarily crepuscular hunters, with peaks in activity and stomach fullness occurring at dawn or at both dawn and dusk (Fishelson 1975, Morris & Akins 2009, Green et al. 2011, Cure et al. 2012, McTee & Grubich 2014). Invasive lionfish are extremely efficient predators, as they have high prey consumption rates (Albins & Hixon 2008, Côté & Maljkovic 2010) and cause large reductions in the abundance, biomass, and richness of native coral reef fishes (Albins & Hixon 2008, Albins 2013, 2015, Green et al. 2014, Benkwitt 2015). There is evidence that invasive lionfish experience intraspecific competition for food, as lionfish at higher densities on small patch reefs exhibit slower growth (Benkwitt 2013) and have diminishing per-capita effects on prey abundance and biomass (Benkwitt 2015). Given the effect of lionfish density on their individual growth rates, it seems likely that their foraging patterns also change at different local densities.

I conducted observations of lionfish to test the hypothesis that lionfish behavior changes at different lionfish and prey fish densities due to intraspecific competition for food. Specifically, I predicted that if there is intraspecific competition for food, then at higher lionfish densities and/or lower prey fish densities, lionfish will alter their foraging activity by (1) increasing the amount of time spent active and hunting at crepuscular periods and/or (2) increasing the number of periods per day during which they are active and hunting. In addition, I expected that lionfish would change the locations at which they hunt such that they would (3) spend less time sheltering within the reef and (4) increase the distances over which they travel while hunting at higher densities.

MATERIALS AND METHODS

Study sites

This study was conducted between June and August 2012 on coral patch reefs in Rock Sound near Cape Eleuthera, The Bahamas (24° 50' 2.65" N, 76° 16' 6.78" W). Lionfish first arrived at the study site in 2005 and there has been virtually no removal effort in the area, with the exception of isolated lionfish removals for field experiments (Green et al. 2014, Côté et al. 2014). I selected 16 reefs on which lionfish had not been previously manipulated and that were at least 300 m from any reef on which lionfish removals had occurred, which is greater than the maximum distance travelled by the majority of lionfish in the study area (Tamburello & Côté 2015). Reefs were selected to encompass a range of natural lionfish densities (1–16 lionfish reef⁻¹, 0.04–1.01 lionfish m⁻²) and reef sizes (7.88–32.99 m² surface area), and there was no significant correlation between lionfish density and reef size (correlation = -0.11, $t = 0.56$, $p = 0.58$). Reefs were similar to each other in terms of rugosity, benthic community (algae-covered dead coral, live coral, and sponges), and surrounding habitat (sand and seagrass). Lionfish size on the reefs ranged from 6 to 30 cm total length (TL; mean = 18.2 cm), with the majority of lionfish (>90%) between 15 and 25 cm TL.

Lionfish behavior and movement

A pair of divers (observers) visited each reef at 3 times of day: within sunrise + 2 h ('dawn'), >3 h after sunrise and >3 h before sunset ('midday'), and within sunset - 2 h ('dusk'). During the study, sunrise varied between approximately 06:30 and 06:50 h and sunset varied between 19:30 and 20:00 h. Upon arriving at a reef, observers counted the number of lionfish present by conducting lionfish-focused searches, which involved first slowly circling reefs and then swimming over reefs until all areas had been covered. Divers paid particular attention to crevices and overhangs where lionfish are commonly found, and because of the small size of the reefs it was possible to thoroughly search the entire reef area. For each lionfish, observers recorded the size (TL visually estimated to the nearest cm), behavior, and location the moment it was sighted. Behaviors were categorized as resting (sitting on the substrate, not moving), hovering (in the water column oriented parallel to the bottom, but not moving), swimming (actively mov-

ing), or hunting (oriented head down with pectoral fins flared), with the latter 3 categories broadly grouped together as 'active' for some analyses. Similar classifications have been used in previous studies of lionfish behavior (Côté & Maljkovic 2010, Green et al. 2011, Cure et al. 2012). Location was categorized as the microhabitat on which lionfish were observed (e.g. under a ledge, on top of the reef, in the surrounding seagrass) and later divided into 2 major categories: sheltering (hidden under structure) or exposed (on top of reef or in surrounding area).

Then, 10-min focal observations were conducted on 2 lionfish selected using randomly generated numbers, or a single lionfish when there was only one individual present per reef. During focal observations, a trained observer recorded the behavior of lionfish at 30 s intervals for 10 min using the same categories as above. Simultaneously, a second observer videorecorded the focal lionfish to enable later analyses and confirmation of behaviors and allow divers to keep track of lionfish movement (see next paragraph). The observers also noted any strikes at prey, successful kills, and obviously aggressive interactions (chases, posturing) between lionfish or between lionfish and other species. However, there were very few observed strikes and aggressive interactions by focal lionfish, so those data were not analyzed. The observers maintained a distance of approximately 3 m from focal lionfish, a distance at which divers have no apparent influence on lionfish behavior (Côté & Maljkovic 2010, Green et al. 2011, Cure et al. 2012).

Throughout the entire visit to each reef, divers noted the time when any lionfish departed from or arrived at the reef and its behavior. A lionfish was defined as departing from the reef if it traveled at least 10 m from the reef. A lionfish was considered arriving at a reef if it swam in from the surrounding areas and had not been previously observed at that reef during that observation period. In only 3 instances were divers unsure whether an arriving lionfish was a new individual, as a lionfish was seen departing from the reef and traveled out of sight, and soon after another lionfish of the same size and coloration from the same direction returned. In these cases, it was assumed that these were the same lionfish rather than new individuals. Because the reefs were relatively small and divers had an unobstructed view of the surrounding area, the observers were reasonably confident that they counted all arrivals and departures of lionfish. However, because observers were most likely to miss arrivals and departures on reefs with the highest lionfish densities, if

anything these results likely underestimate the effect of lionfish density on movement.

At the conclusion of the focal observations, the divers re-counted the number of lionfish present while conducting a survey of resident native fishes. Divers recorded the abundance and body size (TL) of all fish 1–15 cm TL, native mesopredators that are ecologically similar to lionfish (e.g. graysby grouper *Cephalopholis cruentata*), and top predators (e.g. Nassau grouper *Epinephelus striatus*) on and within 1 m of the reef. Surveys were conducted by slowly swimming in concentric circles gradually decreasing in size from the reef edge to the center of the reef until the entire reef area was surveyed. By slowly sweeping one hand just above the substrate, divers counted cryptic bottom-dwelling species such as gobies and blennies. Dive lights were used to search for cryptic species in crevices and under ledges.

Statistical analyses

Because multiple observations were conducted on the same reefs and there was evidence of heterogeneity in residuals based on reef, I conducted a series of generalized linear mixed effects models (GLMMs) fit using Gauss–Hermite quadrature with reef as a random effect (Zuur et al. 2009, Bolker et al. 2009). Fixed effects included lionfish density, prey fish density, and time of day. Because there were large fluxes in lionfish density on the reefs at dawn and dusk due to lionfish moving to and from the surrounding habitats (see ‘Results’), I defined lionfish density as the density of lionfish on each reef at midday, which remained relatively constant during each observation period. This measure of lionfish density was significantly positively correlated with the maximum density of lionfish observed on each reef during each of the 3 observation periods (correlation = 0.83, $t = 13.3$, $p < 0.001$), and thus seemed to be an accurate representation of the relative density of lionfish that inhabited each reef throughout the study. Prey density was defined as the density of prey fishes at the time of each visit and was $\log(x + 1)$ transformed. I restricted prey fishes to those ≤ 5 cm TL, which are small enough to be vulnerable to a range of lionfish sizes and encompass the prey sizes most often consumed by all sizes of lionfish (Morris & Akins 2009, Muñoz et al. 2011). Prey density did not significantly vary with time of day (likelihood ratio test $\chi^2 = 2.75$, $p = 0.25$) and there was no significant correlation between lionfish density and prey density (correlation = -0.11 , $t = 0.97$, $p = 0.33$). Because time of day

had the largest influence on lionfish behavior in previous studies (Green et al. 2011, Cure et al. 2012) and to test whether the effect of lionfish or prey fish density on foraging behavior varies at different times of day, I also included interactions between time of day and each of the other explanatory variables as fixed effects. All reefs had similar densities of native mesopredators ($0\text{--}0.05$ fish m^{-2}) and top predators ($0\text{--}0.30$ fish m^{-2}), so I did not include these as explanatory variables in the analyses.

Response variables to test my predictions regarding lionfish behavior were based on observations of all lionfish on the reefs and on focal observations of individual lionfish. From all lionfish, the responses were the proportion of lionfish on each reef that were hunting upon arrival at the reef and the proportion of lionfish on each reef that were active upon arrival at the reef. From focal lionfish, the responses were the proportion of time individual focal lionfish spent hunting and the proportion of time individual focal lionfish spent active. Response variables to test predictions regarding lionfish position and movement were based on all lionfish on the reefs: the proportion of lionfish on each reef that were sheltering during initial observations, the proportion of lionfish arriving at each reef throughout observations, and the proportion of lionfish departing from each reef throughout observations. Because all responses were proportions, I modeled the data following binomial distributions with logit links. I conducted likelihood ratio tests (LRTs) to test for overall significance of fixed effects and Wald Z-tests to test for significance of single parameters (Zuur et al. 2009). All analyses were conducted in R version 3.0.2 (R Core Team 2013) with the associated package lme4 (Bates et al. 2014).

RESULTS

Lionfish behavior

A total of 95 lionfish were observed at dawn, 126 at midday, and 117 at dusk on and around the 16 coral patch reefs. A significantly higher proportion of lionfish hunted at dawn compared with at dusk and midday, and significantly more lionfish also hunted at dusk compared with at midday (all $z \geq 3.63$, all $p < 0.001$). This effect of time period on the proportion of lionfish hunting on each reef was not modified by lionfish or prey fish density (Lionfish \times Time, Prey \times Time: LRT $\chi^2 = 4.04$, 2.31, $p = 0.13$, 0.32, respectively; see Table S1, Figs. S1 & S2 in the Supplement at

www.int-res.com/articles/suppl/m558p255_supp.pdf). However, the proportion of time that individual focal lionfish spent hunting varied with both time of day and prey density (Prey \times Time LRT $\chi^2 = 16.91$, $p < 0.001$; Fig. 1A, see Table S1 in the Supplement). At dawn and dusk, lionfish spent significantly more time hunting at higher prey densities ($z = 3.09$, 3.38 , $p = 0.002$, 0.0007 , respectively), with the odds of a lionfish hunting increasing by a factor of 2.43 at dawn and 2.58 at dusk for each doubling of prey density (95% CI = 1.60–8.12 and 1.76–8.28, respectively). Regardless of prey density, lionfish spent very little

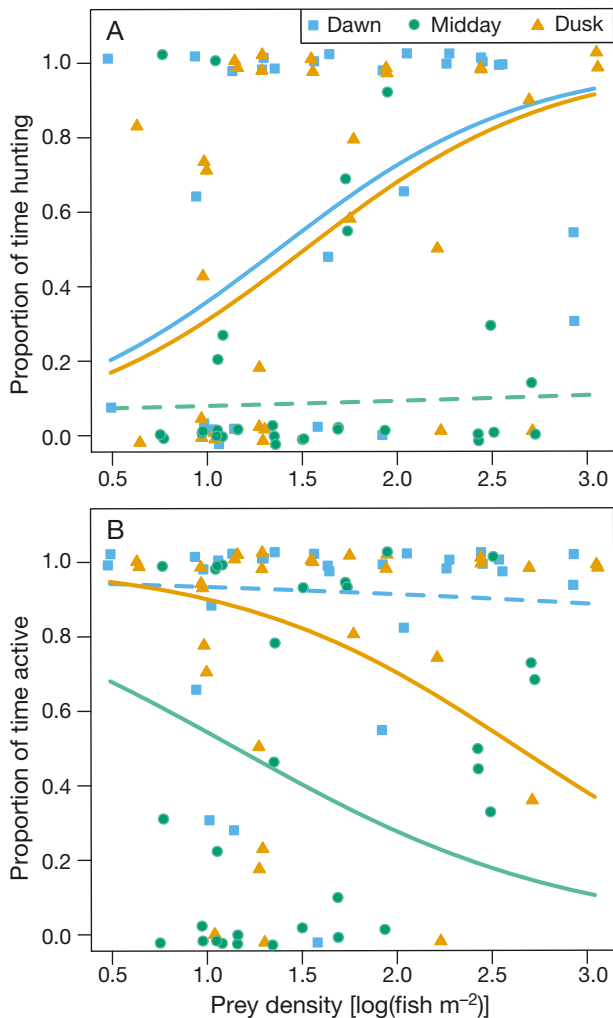


Fig. 1. *Pterois volitans*. Proportion of time individual focal lionfish spent (A) hunting and (B) active (hovering, swimming, or hunting) as a function of prey fish density at dawn, midday, and dusk. Lines are predicted probabilities based on generalized linear mixed effects models. Dashed lines represent slopes that are not significantly different than zero; solid lines represent slopes that are significantly different than zero ($p < 0.05$). Points represent individual lionfish and were randomly jittered to reduce overlap

time hunting in the middle of the day. There was no significant effect of lionfish density on time spent hunting by focal lionfish at any time of day (all $z \leq 1.10$, all $p > 0.27$; see Fig. S1 in the Supplement).

In contrast, the proportion of lionfish active (hovering, swimming, or hunting) varied with both time of day and lionfish density, but not prey density (lionfish \times Time: LRT $\chi^2 = 9.61$, $p = 0.008$; Prey \times Time: LRT $\chi^2 = 0.67$, $p = 0.71$; Fig. 2A, see Table S1, Fig. S2 in the Supplement). Regardless of lionfish density, the majority of lionfish were active at dawn and few were active at midday. At dusk, however, a signifi-

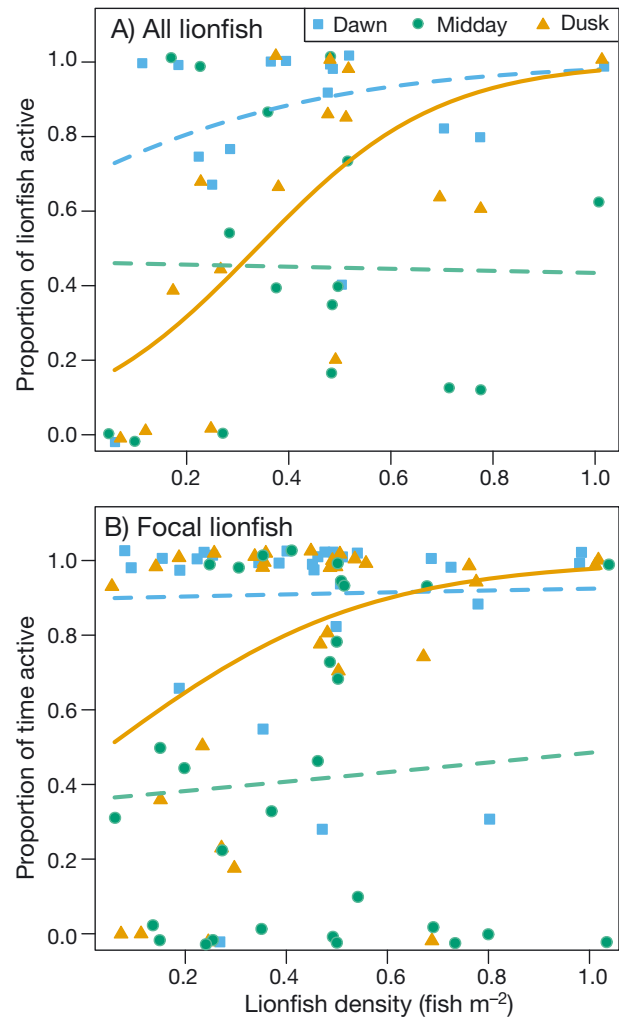


Fig. 2. *Pterois volitans*. (A) Proportion of lionfish that were active (hovering, swimming, or hunting) upon arrival at the reef and (B) proportion of time individual focal lionfish spent active as a function of lionfish density at dawn, midday, and dusk. Lines are predicted probabilities based on generalized linear mixed effects models. Dashed lines represent slopes that are not significantly different than zero; solid lines represent slopes that are significantly different than zero ($p < 0.05$). Points represent reefs (A) and individual lionfish (B) and were randomly jittered to reduce overlap

cantly higher proportion of lionfish were active at higher lionfish densities, with the odds of a lionfish being active increasing by a factor of 1.78 for each increase in lionfish density by 0.1 fish m^{-2} (95% CI = 1.21–2.61; $z = 2.93$, $p = 0.003$). Similar to these reef-level patterns, individual focal lionfish spent significantly more time active at dusk at higher lionfish densities ($z = 2.14$, $p = 0.032$, 95% CI = 1.03–2.07; Fig. 2B). The amount of time individual lionfish were active at dusk and midday also varied significantly with prey density (Fig. 1B), with the odds of being active decreasing by 37.8% for each doubling of prey density on a reef at dusk (95% CI = 19.3–73.7%, $z = 2.85$, $p = 0.004$) and 42.3% at midday (95% CI = 19.7–90.5%, $z = 2.22$, $p = 0.027$). These activity patterns were primarily driven by hunting and hovering behavior, as no lionfish were observed swimming upon arrival at the reef and focal lionfish spent an average of 1.6% of their time swimming, compared with 46.3% spent hunting and 21.1% spent hovering.

Lionfish movement

The position of lionfish varied significantly with both lionfish density and time of day, but not with prey density (Lionfish \times Time: LRT $\chi^2 = 14.59$, $p < 0.001$; Prey \times Time: LRT $\chi^2 = 0.88$, $p = 0.64$; Fig. 3A, see Table S1, Fig. S3 in the Supplement). At dusk, for each increase in lionfish density by $0.1 \text{ lionfish m}^{-2}$, the odds of a lionfish sheltering decreased by a factor of 0.58 (95% CI = 0.39–0.87, $z = 2.63$, $p = 0.009$). The majority of lionfish were exposed at dawn and the majority of lionfish sheltered at midday across all lionfish and prey densities.

Likewise, lionfish exhibited predictable movements between coral patch reefs and surrounding seagrass and sand habitats that varied with lionfish density and time of day, but not with prey density (Lionfish \times Time: LRT $\chi^2 \geq 8.13$, $p < 0.017$; Prey \times Time: LRT $\chi^2 \leq 4.15$, $p > 0.13$; Fig. 3B,C, see Table S1, Fig. S3 in the Supplement). At dawn, a higher proportion of lionfish arrived from the surrounding areas at reefs with greater lionfish densities ($z = 2.06$, $p = 0.039$; Fig. 3B). For each increase in lionfish density by 0.1 fish m^{-2} , there was an increase in the odds of a lionfish arriving at the reefs by a factor of 1.42 (95% CI = 1.02–1.99). At midday, there was very little lionfish movement, regardless of lionfish density. At dusk, a pattern opposite to that at dawn was observed, with a significantly higher proportion of lionfish departing from the reefs at higher lionfish densities ($z = 2.96$, $p = 0.003$; Fig. 3C). For each additional $0.1 \text{ lionfish m}^{-2}$ on

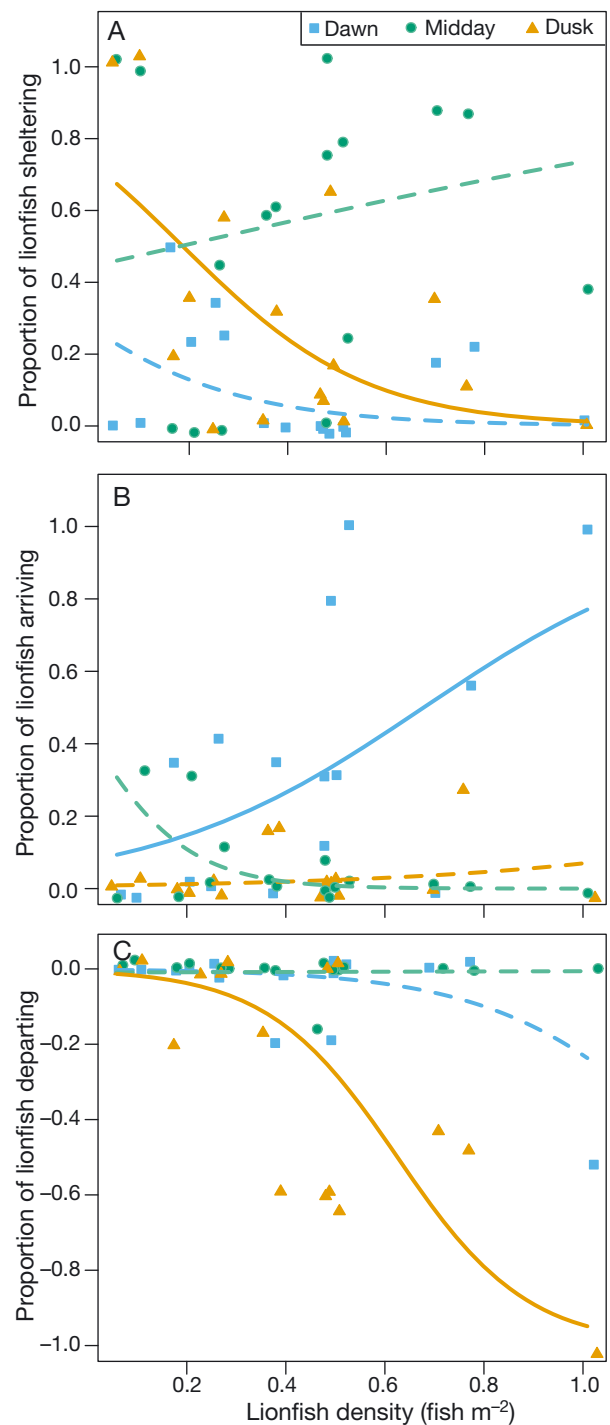


Fig. 3. *Pterois volitans*. (A) Proportion of lionfish that were sheltering upon arrival at the reef, (B) proportion of new lionfish that arrived at each reef, and (C) proportion of lionfish that departed from each reef as a function of lionfish density at dawn, midday, and dusk. Lines are predicted probabilities based on generalized linear mixed effects models. Dashed lines represent slopes that are not significantly different than zero; solid lines represent slopes that are significantly different than zero ($p < 0.05$). Points represent reefs and were randomly jittered to reduce overlap

a reef, the odds of a lionfish departing from the reef at dusk increased by a factor of 2.57 (95% CI = 1.75–4.79). Approximately 50% of the lionfish that departed from a reef returned to the same reef within the observation period. Larger lionfish exhibited more movements between coral patch reefs and the surrounding habitats, whereas no lionfish less than 15 cm TL was ever observed arriving at or departing from the reefs (Fig. 4).

DISCUSSION

There were significant differences in lionfish foraging activity and movement at different local densities that were consistent with the predicted effects of intraspecific competition. At higher densities, lionfish exhibited greater activity levels, time away from shelter, and more short-term movements between coral patch reefs and surrounding habitats. However, these changes with density were not consistent throughout the day, with the greatest differences in behavior occurring at dusk. Although prey density was associated with changes in some foraging behaviors by individual lionfish, overall it appears that lionfish density was more important in explaining activity patterns. These spatial and temporal changes in behavior may, in turn, change which prey individuals and species are most susceptible to lionfish predation.

Similar to prior studies in both their native and invaded ranges, I observed high levels of lionfish activity at dawn and dusk but very little activity

during the middle of the day (Green et al. 2011, Cure et al. 2012, McTee & Grubich 2014). Despite this overall consistency in diel activity patterns, there is still considerable variation in lionfish activity levels among locations within both their native and invaded ranges due in part to local differences in habitat, current strength, and prey availability (Cure et al. 2012). The differences in behavior on reefs with varying lionfish densities in the present study, combined with the wide range of lionfish population density both within and between oceans (Green & Côté 2009, Darling et al. 2011, Kulbicki et al. 2012), suggest that local lionfish density may also help explain some of the site-specific variation in hunting behavior.

Exploitative competition for food is the likely cause of reduced growth rates in juvenile lionfish at higher densities (Benkwitt 2013, 2015). However, if exploitative competition for food was the main driver of changes in lionfish foraging behavior, then lionfish should exhibit greater hunting, activity, and movement at lower prey densities regardless of lionfish density, which was not the case in this study. Instead, individual lionfish spent more time hunting but less time active at higher prey densities, which suggests that they may spend less time searching for prey at higher prey densities (Anholt & Werner 1995, Lubin & Henschel 1996, Harding et al. 2007). In contrast, the proportion of lionfish on each reef that were hunting, active, sheltering, and moving did not vary with prey density. A possible explanation is that the species composition of prey has a larger influence on lionfish foraging behavior than total prey density. Lionfish exhibit diet preferences for certain prey characteristics, with small, solitary, bottom-dwelling fishes most susceptible to lionfish predation (Green & Côté 2014). Therefore, teasing apart the influence of overall prey density compared with densities of preferred prey may further clarify the role of exploitative competition in affecting the foraging behavior of lionfish.

In contrast, many aspects of lionfish activity changed at increased lionfish densities, which suggests that interference competition is the main form of competition among lionfish and is driving the changes in lionfish foraging behavior. However, aggressive interactions between lionfish are rare (Cure et al. 2012), and I likewise observed few apparent aggressive encounters between lionfish at any density. Instead, lionfish may interfere with each other's foraging efficiency in ways other than direct aggression (Krause & Ruxton 2002). For example, in several instances I observed one lionfish strike at a prey fish, and immediately thereafter several others swam to

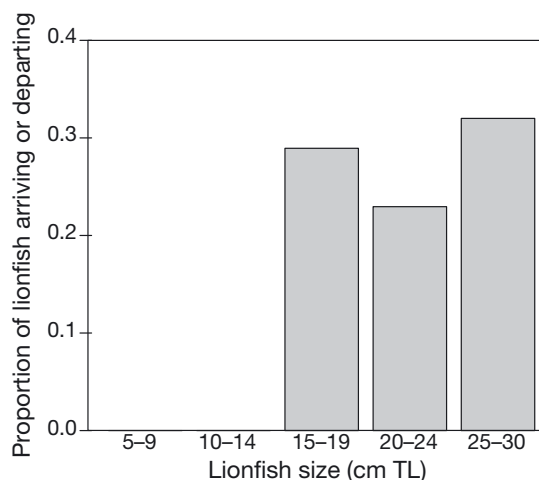


Fig. 4. *Pterois volitans*. Proportion of lionfish within each size class that arrived at, or departed from, the reefs. Sample sizes (number of lionfish) in each size class (from smallest to largest): 7, 10, 235, 61, and 25

the same location. Even without being aggressive, the presence of these other lionfish could potentially decrease the foraging efficiency of some individuals. In addition, perceived competition, in the form of mirrors or competitors in separate tanks, causes changes in the foraging activity and behavior of many other species (Barnard et al. 1983, Dill & Fraser 1984, Nonacs & Calabi 1992), further suggesting that even without direct aggressive encounters, conspecifics could have a significant effect on lionfish foraging behavior.

Escaping intraspecific competition is a major driver of density-dependent movement in many coral-reef fishes (Abesamis & Russ 2005, Grüss et al. 2011, Green et al. 2015), and a tagging study of lionfish conducted over the course of several months also found greater movement among patch reefs at higher lionfish densities (Tamburello & Côté 2015). The crepuscular movements observed in the present study, however, appeared to be short-term foraging excursions given that approximately half of the lionfish returned to the same reef within the observation period, and lionfish in this system cause reductions in prey fish populations in the areas surrounding coral patch reefs up to at least 30 m from the nearest reef (Benkwitt 2016). Many other families of coral-reef fishes, including grunts (Haemulidae) and snapper (Lutjanidae), exhibit similar crepuscular movements between coral patch reefs and seagrass beds. These fishes leave their daytime reef shelters and forage in the surrounding seagrass at night, with important consequences for prey populations as well as community structure and nutrient transfer (Nagelkerken 2009, Ogden et al. 2014). Several species of scorpionfish (Scorpaenidae), which are in the same family as lionfish, also leave their shelter in the evening, forage at night, and return to the same shelter in the morning (Harmelin-Vivien & Bouchon 1976).

The effects of intraspecific competition are often asymmetric, such that smaller, subordinate individuals in a population are most affected (Jones 1991, Peckarsky & Cowan 1991, Davey et al. 2005, Nilsson 2006, Ward et al. 2006, Samhuri et al. 2009). If this is the case, then only certain individuals may change their foraging locations and behavior at higher levels of competition (Webster 2004, Breed et al. 2013). In the present study, the behaviors of randomly selected individual lionfish were fairly consistent with the initial behaviors of all lionfish on the reefs, which suggests that the effects of competition may be equally experienced by all individuals. However, no focal observations were conducted on lionfish less than 13 cm TL, so there may be differences in the

behavior of the smallest individuals that were not captured in the present study. In terms of movement, larger lionfish were more likely to travel between patch reefs and the surrounding habitats, with smaller lionfish (<15 cm TL) never departing from their home reefs. Similarly, previous studies of lionfish movement have found high site fidelity of small lionfish over the course of several months (Jud & Layman 2012, Benkwitt 2013, Tamburello & Côté 2015), although some larger lionfish also have high site fidelity (Akins et al. 2014). This apparent discrepancy may be caused by factors besides competition. Smaller individuals may remain closer to shelter as an adaptive response to predation (Lima & Dill 1990), although there are few documented predators of lionfish in either their native or invaded range (Bernadsky & Goulet 1991, Maljković et al. 2008). Smaller lionfish may also be more affected by strong ocean currents, and therefore remain sheltered on coral patch reefs because they are unable to swim into open areas. Finally, smaller lionfish consume different prey than larger lionfish, as there is an ontogenetic shift from a primarily invertebrate-based to a fish-based diet by the time lionfish reach approximately 20 cm TL (Morris & Akins 2009, Muñoz et al. 2011). Consequently, smaller individuals may not need to forage over broader distances because their preferred food may not be depleted near reefs. This seems likely given that the majority of lionfish were between 15 and 25 cm TL, with only a few smaller individuals on each reef. Therefore, the majority of competition for food likely occurred between individuals in larger size classes.

Although intraspecific competition is a likely explanation for increased activity and movement of lionfish at higher densities, there are several other non-mutually exclusive possibilities. First, at higher densities there may be more opportunities to engage in group hunting behavior, which has been shown to increase per-capita consumption rates of lionfish in the Indo-Pacific (Kendall 1990, Lönnstedt et al. 2014). If invasive lionfish also have increased hunting success when in groups, then there may be an advantage to being more active and increasing their foraging movements at higher densities. Lionfish may also spend less time sheltering and undergo more foraging movements at higher densities due to differences in the perceived risk of being attacked by larger predators. Even when a prey species is not subject to direct predation, it may still modify its behavior in response to predators, so departing from the relatively safe shelter of the reefs in groups may provide 'safety in numbers' for lionfish (Creel &

Christianson 2008). Finally, some activity and movement into the surrounding seagrass may be related to spawning behavior, which likely occurs at night. On one occasion, I observed apparent courtship behavior similar to that described by Fishelson (1975) and Green et al. (2011). Three lionfish (between 19 and 28 cm TL) rapidly departed the reef, and once 20 m away in the open sand and seagrass they swam in circles around each other for approximately 2 min. Two lionfish then returned to the reef while the remaining lionfish continued swimming rapidly away from the reef for at least 200 m. The fact that lionfish can spawn up to every 4 d (Morris 2009) suggests another explanation for why larger lionfish departed the reefs on a regular basis, especially when there were higher local densities of mature adults.

Overall, the observed behavioral differences among invasive lionfish at different densities may have implications for native prey populations. There was a peak in feeding and activity at dawn regardless of lionfish density, but at dusk lionfish were more active only at higher densities. This observation suggests that native prey species that are primarily active at dusk will be affected only in areas with high lionfish densities. At both dawn and dusk, there was increased movement to and from habitats surrounding patch reefs at higher lionfish densities. Given that lionfish deplete prey populations in the habitats surrounding coral patch reefs (Benkwitt 2016), lionfish at higher densities may be causing greater reductions in a wider range of prey species, potentially including juveniles of commercially and ecologically important fishes that use seagrass beds as nursery grounds (Nagelkerken 2009, Ogden et al. 2014). In contrast, lionfish were almost always resting during the middle of the day regardless of lionfish density, which suggests that strictly diurnal fishes may be relatively safe from lionfish predation when these prey fishes are most active. In addition to increasing their time spent foraging and their foraging movements, many fishes shift to feeding on less preferred prey at higher densities (Coates 1980, Dill 1983, Holbrook & Schmitt 1992, Schindler et al. 1997, Svanbäck & Persson 2004, Agashe & Bolnick 2010). There is currently no evidence that lionfish have different isotopic diet signatures at sites with high compared with low lionfish densities (J. Curtis unpubl. data), but if they do alter their diets at higher densities, then there may be even more consequences for prey populations.

Future studies should be conducted to determine the extent to which these results apply to other locations with different lionfish densities and habitat characteristics. Densities of lionfish observed here

(mean = 3763 lionfish per hectare) are comparable to the maximum reported densities from small artificial structures in the Gulf of Mexico (3850 lionfish per hectare; Dahl & Patterson 2014), but higher than those observed on larger patch and continuous reefs in many parts of the invaded range (mean ~3–640 lionfish per hectare; McTee & Grubich 2014). Based on these differences, the effects of lionfish density on patch reefs where lionfish are concentrated within small, isolated areas may be diluted when scaled up to continuous reefs. However, even on larger reefs, lionfish often aggregate in small groups around structures during the day, and there is some evidence that on large patch reefs (100–1200 m²) lionfish similarly move over a broader area including the surrounding sand while foraging during crepuscular times (A. C. D. Davis unpubl. obs.).

The main method of managing lionfish populations is through manual removal by divers, which is a time- and labor-intensive process. However, removals can significantly reduce local lionfish abundances (Frazer et al. 2012, de León et al. 2013) and even partial removals can help maintain native prey populations on coral patch reefs (Green et al. 2014). Given that at higher densities lionfish also have increased activity levels at dusk and movements at both dawn and dusk, removals on patch reefs may be most efficient during midday when lionfish are aggregated on the reefs. Furthermore, removals may have more benefits than previously documented. By keeping lionfish densities low, managers may reduce the local foraging movements of lionfish and thus help maintain native fish communities in multiple habitats.

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