

Diet choice in a generalist predator, the invasive lionfish (*Pterois volitans/miles*)

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ABSTRACT

Diet choice in marine species is typically derived from indirect methods such as stomach contents and stable isotope analysis, while choice experiments in controlled laboratory settings are used to infer foraging decisions in the wild. However, these methods are limited in their capacity to make inferences about foraging decisions by predators in variable environments or recreate the array of factors (such as prey traits, predator condition, and environmental conditions) present in natural systems which may interact to affect diet decisions by predators. Recent work has provided evidence for selectivity in the invasive Indo-Pacific lionfish (*Pterois volitans/miles*) despite the predator's apparent opportunistic, generalist feeding behavior. We directly tested diet choice by presenting wild-caught lionfish with multi-species prey assemblages in field enclosures. We offered lionfish equal biomasses of prey species sharing similar prey traits that are both highly abundant on coral reefs and prevalent in the lionfish diet across the invaded range. We then applied compositional analyses to determine relative prey consumption given prey availability. We observed lionfish selectively foraging on prey and manifesting strong consistent preferences for one prey species. Additionally, we observed condition-dependent foraging behavior, as lionfish with higher body conditions were more likely to exhibit selective foraging behavior. Our findings provide direct evidence for diet choice in an invasive generalist species and highlight the importance of preserving the ecological complexity of natural ecosystems in choice experiments, particularly when investigating predator-prey interactions in complex environments.

1. Introduction

Predators transform ecological communities by altering prey behavior (McPeck and Peckarsky, 1998; Peckarsky et al., 1993), shaping food web structure (Carpenter et al., 1987; Paine, 1966; Power, 1990), and affecting prey population and community dynamics (Almany and Webster, 2006; Křivan and Sikder, 1999). Community-level effects depend, in part, on predator foraging behavior, which may vary in response to spatial heterogeneity of prey (Huffaker et al., 1963; Palma et al., 2006), species-specific differences in prey characteristics (Moody et al., 1983; Uiterwaal et al., 2017), the predator's level of satiation (Molles and Pietruszka, 1983; Skutelsky, 1996), and environmental complexity (Crowder and Cooper, 1982). Predators often consume prey

selectively and disproportionately to their relative abundance (Murdoch, 1969), but the extent to which environmental context, e.g., prey availability and habitat complexity, affects selective foraging is not well understood for many predator-prey interactions.

When invasive predators are introduced into a system, they have the capacity to disrupt community assemblages by competing with native predators for resources, altering food webs, and causing significant changes in the reproduction and survival of native species (Elton, 1958; Mack et al., 2000; Sih et al., 2010; Snyder and Evans, 2006). Many of these effects have been documented across the Western Atlantic Ocean, broader Caribbean region, and Gulf of Mexico since the introduction of the invasive Indo-Pacific lionfishes (*Pterois volitans* and *P. miles*; hereafter 'lionfish') in the 1980's (Côté and Maljkovic, 2010; Morris, 2009;

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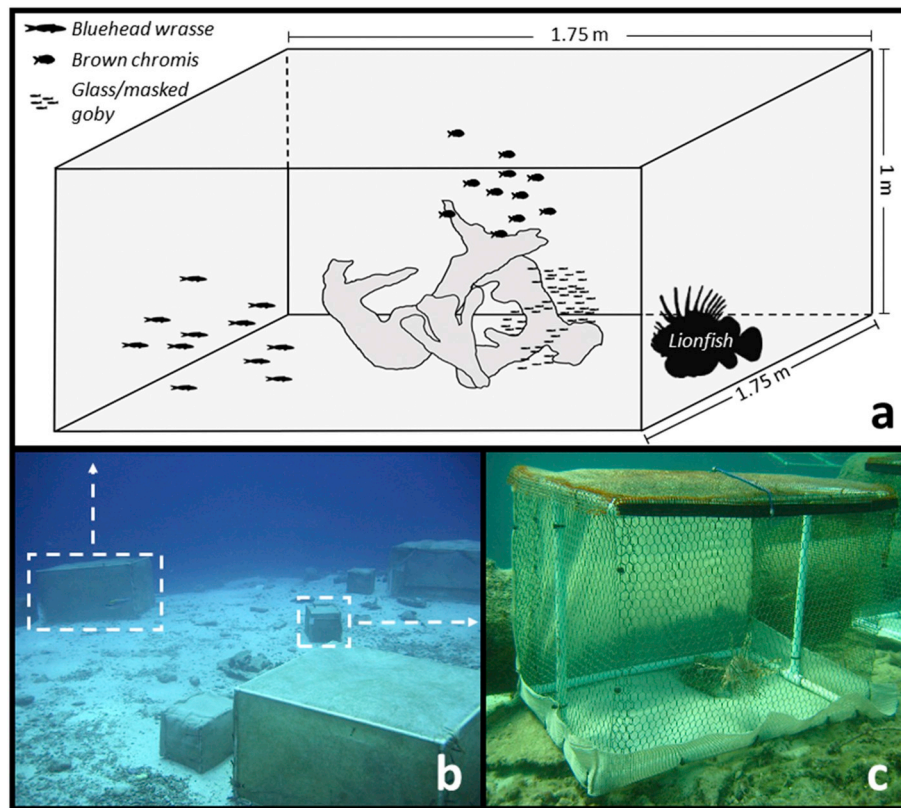


Fig. 1. (A) Schematic diagram of enclosure dimensions and experimental design. (B) Holding cages were located proximal to enclosures and (C) maintained lionfish in isolation and without food prior to predation trials.

Raymond et al., 2015; Whitfield et al., 2002). As voracious predators, invasive lionfish have the capacity to dramatically alter marine ecosystems; in the Bahamas, for example, by reducing native reef fish biomass and recruitment by 65% and 79%, respectively (Albins and Hixon, 2008; Green et al., 2012), and reducing herbivore diversity, which preceded a phase shift from a coral-dominated mesophotic reef to one dominated by macroalgae (Lesser and Slattery, 2011). The ecological consequences of invasive lionfish are often attributed to their unique predatory strategies (Albins and Lyons, 2012; Black et al., 2014; Green et al., 2011) and broad diet (Côté et al., 2013; Dahl and Patterson, 2014; Morris and Akins, 2009; Peake et al., 2018; Sancho et al., 2018; Valdez-Moreno et al., 2012).

Although lionfish are considered generalist, opportunistic predators (Côté et al., 2013; Côté and Maljkovic, 2010; Layman and Allgeier, 2012; Morris and Akins, 2009; Muñoz et al., 2011), there is mounting evidence suggesting prey discrimination in this species based on prey assemblage variation (Layman and Allgeier, 2012), prey density (Benkwitt, 2016), prey species and body size (Chappell and Smith, 2016; Green and Côté, 2014; Kindinger and Anderson, 2016), as well as prey aggregation behavior and water column position (Green et al., 2019; Green and Côté, 2014). However, these findings have been largely derived from stomach content analysis, laboratory feeding trials, field observations, and null modeling. Unfortunately, these approaches are limited in their capacity to provide the experimental control needed to identify causal relationships while also preserving the ecological complexity of the coral reefs on which lionfish are foraging. An enhanced understanding of diet choice in lionfish could provide insight into the invasibility and impact of lionfish on reefs, as well as improve predictions of how the continued expansion of lionfish populations might affect newly-invaded communities.

We used a manipulative field enclosure experiment to examine diet choice in lionfish presented with multi-species prey assemblages on a spatially-complex reef habitat. We offered lionfish three prey species

that are abundant on Caribbean coral reefs, prominent in stomach content analyses of lionfish across the invaded range, and share both morphological and behavioral similarities. This allowed us to explore whether lionfish exhibit selective foraging behavior even in the presence of abundant and frequently-consumed prey sharing similar traits. In order to quantify individual resource use with resource availability, we offered lionfish prey in a fixed ratio, corresponding to equal biomasses of each prey species. We then used compositional data analysis to determine whether lionfish deviated from non-selective prey consumption (i.e. consumption proportional to prey availability) and, if so, whether selective foraging decisions were consistent across individuals. In addition to determining the strength and direction of selectivity, we assessed if selective foraging behavior in lionfish was condition-dependent.

2. Materials and methods

2.1. Study site

Curaçao is home to some of the healthiest coral reefs in the southern Caribbean, supporting local fisheries, recreational diving, and tourism. Lionfish were first documented on Curaçaoan reefs in 2009 (Vermeij, 2012), and their population densities have been recorded as high as 127 fish ha⁻¹ (de León et al., 2013). Compared to native population densities of 26 fish ha⁻¹ (Kulbicki et al., 2012), the pervasiveness of lionfish on Curaçaoan reefs demonstrates the potential for this invasive predator to impact local reef communities.

2.2. Enclosure design and placement

We assessed lionfish foraging behavior during predation trials in three artificial enclosures (1.75 × 1.75 × 1 m) constructed with a PVC frame and uncolored mosquito netting to allow water circulation and

ambient light penetration. We selected an enclosure size that would allow all fishes to move freely. We deprived lionfish of food before predation trials inside holding cages (approx. 0.25 m³), constructed with PVC, chicken wire and mosquito netting, to ensure lionfish would engage in predatory behavior during predation trials. We selected holding cage size to allow lionfish to swim, spread their pectoral fins, and otherwise move naturally (Fig. 1). We secured mosquito netting to prevent the passage of additional fish or invertebrates into the enclosures and holding cages.

We placed enclosures approximately 300 m west of the Caribbean Marine Biological Institute (CARMABI). Enclosures were ≥ 6 m apart, in a triangular orientation, and at a depth of 8 to 10 m on a sandy patch proximal to the fringing reef crest in order to reflect the environmental conditions of the neighboring reef inside enclosures. We fitted the enclosures with an artificial reef structure consisting of 4–5 large fragments of dead elkhorn coral (*Acropora palmata*) cleaned of small fish and invertebrates to exclude additional prey items available to lionfish during trials. Structural complexity provided by the elkhorn coral simulated natural conditions with the intent of reproducing more natural prey encounter rates (Crowder and Cooper, 1982) by allowing prey fishes to display natural aggregation and predator avoidance behaviors and for lionfish to engage in natural predatory behavior.

2.3. Prey fish selection

We selected prey fish species for predation trials based on their abundance on Curaçaoan reefs (Fig. S-1; Waitt Institute, 2017), prevalence in the diet of lionfish found in the Caribbean (Côté and Maljkovic, 2010; Green et al., 2011; Rocha et al., 2015), and exhibition of physical features (small, shallow-bodied) and behaviors (demersal, shoaling, non-cleaning) that researchers have previously determined increase risk of predation by lionfish (Green and Côté, 2014). These prey species were the brown chromis (*Chromis multilineata*), the bluehead wrasse (*Thalassoma bifasciatum*) and the masked/glass goby (*Coryphopterus personatus/hyalinus*).

We calculated the average biomass of each prey fish species using the function $W = \alpha L^\beta$, where W is the fish weight (in g) and L is the fish length (in cm; total length for brown chromis and bluehead wrasse and standard length for glass/masked goby, selected for best fit). Length-weight relationship parameters α and β were calculated for each prey fish species using measurements of captured juvenile individuals, as well as records from FishBase as reference (Froese and Pauly, 2016). Length ranges were calculated for each prey fish species utilizing length-weight relationships to ensure predation trials used equal biomasses of prey species that differ in body size (Table S-1).

2.4. Fish collection and husbandry

We collected all prey fishes using hand nets and wall nets. We added prey fish to enclosures at least 12 h before the trial commenced to allow acclimation. We used wall nets to collect initial phase princess parrotfish (*Scarus taeniopterus*), initial phase striped parrotfish (*Scarus iserti*), and four-eye butterflyfish (*Chaetodon capistratus*), approximately the same body size as lionfish used for predation trials, and included these species in predation trials to facilitate acclimation of the experimental fishes to the enclosures (Barlow, 1968).

We collected adult lionfish using hand nets at depths between 5 and 32 m. Once collected, we placed lionfish in the holding cages and deprived them of food for 72 h before the trial commenced. Previous examinations indicate lionfish are able to withstand starvation for several weeks without a significant loss in body condition (Fishelson, 1997), and preliminary assessment of lionfish evacuation rates indicated that 72 h was sufficient time for lionfish to completely empty their stomachs.

2.5. Experimental design

We added eleven brown chromis, eleven bluehead wrasse, and fifty-five glass/masked goby, corresponding to equal total biomasses of each species, as well as highly mobile dither fish (three parrotfish and three butterflyfish) to each enclosure. The number of prey fish offered to lionfish during predation trials ensured that, were they to exert a strong preference, lionfish could consume the targeted species to satiation. We controlled prey biomass rather than provide equal numbers of each species because of the significant difference in body masses amongst the species (Table S-1), and measurements of consumptive benefit were unavailable for all three prey species.

We conducted predation trials between April and June 2016. Three independent trials started concurrently at 14:15 when an individual lionfish was added to each enclosure. Trials concluded at 20:15 when enclosures were opened and lionfish were removed using a pole spear or hand nets. The trial time was selected on the basis of observed peak foraging activity by lionfish (Green et al., 2011). The trial duration was selected based on preliminary behavioral observations and digestion rate assays, which indicated 6 h as sufficient time for lionfish to exhibit foraging behavior and for researchers to accurately identify lionfish stomach contents.

At the conclusion of a trial, each lionfish was measured (standard length to the nearest cm), weighed (wet weight to the nearest g), and dissected for stomach content analysis of the three focal prey species. Once a trial concluded, we released all dither fish and surviving prey fish from the enclosure, collected new fish for each subsequent trial, and cleaned any algal growth off enclosure walls.

2.6. Statistical analysis

We calculated prey biomass consumed by multiplying the number of each prey fish eaten by the average weight of each prey species. Prior to analyses, we log transformed prey biomass consumed and lionfish wet weight to improve normality and homoscedasticity.

To analyze the proportion of each prey species consumed given the proportion of each prey species available (in accordance with the 11:11:55 ratio), we employed compositional data analysis (CoDA; Aitchison, 1982; Pawlowsky-Glahn and Buccianti, 2011). In particular, we applied a CoDA isometric logratio (ilr) transformation to the data (Egozcue et al., 2003) and, to accommodate for the presence of zero values in the original dataset, we used a Bayesian multiplicative replacement strategy with a square root Dirichlet model (Martín-Fernández et al., 2015b; Palarea-Albaladejo and Martín-Fernández, 2015; Pierotti et al., 2017). This methodology preserves the original ratios between the proportions of prey consumed (that is, the compositional information of the data) (Palarea-Albaladejo and Martín-Fernández, 2015). We used a log-ratio Hotelling's T-squared test to examine differences between the proportion of prey species offered and the proportion of prey species consumed during predation trials (Martín-Fernández et al., 2015a).

To quantify potential divergence from a strategy of non-selective foraging with regard to prey species and their relative numerical representation in enclosures, we created an index of selectivity, normalized to a range of [0,1], and based upon the Aitchison distance (Palarea-Albaladejo et al., 2012; Pawlowsky-Glahn and Buccianti, 2011) between the observed proportions of prey eaten and the expected proportion of prey available (11:11:55) (Pierotti et al., 2017). Aitchison distance between two compositions is defined as the Euclidean distance between the corresponding ilr-transformed vectors. We tested statistical significance of the index of selectivity by calculating a pseudo p -value based on a multinomial distribution with probabilities (p_1, p_2, p_3) equal to the expected proportion of prey available (Egozcue et al., 2015). Index of selectivity values close to zero indicate no deviation in resource use from the distribution of available resources, i.e. with individuals consuming prey in direct proportion to the number of prey

available. Index of selectivity values close to one indicate significant deviations from the expected null of prey consumed in proportion to their abundance, underlying active choice of particular species. Thus, the index of selectivity provides a measure of the strength of selective foraging by lionfish.

We represented index of selectivity values in a ternary diagram to associate indices with prey species offered (Pierotti et al., 2017) and therefore were able to identify the direction of selectivity for each individual lionfish. Together with the compositional index of selectivity, we calculated Ivlev's electivity index (Ivlev, 1961).

Body condition (K) was calculated as $K = W/L^3$, where W is wet weight (g) and L is total length (cm) (Bolger and Connolly, 1989). To determine threshold effects of body condition on index of selectivity, we identified the optimal break point by minimizing the mean squared error. We used a two-sample t -test to determine whether groupings based on body condition had significantly different mean index of selectivity values.

Finally, we analyzed the relationship between prey biomass consumed, lionfish wet weight and lionfish body condition using a linear regression. We used binary logistic regressions to assess if lionfish standard length or lionfish body condition was associated with prey consumption during predation trials. We compared sex differences in body condition and index of selectivity with two-sample t -tests.

All statistical analyses were conducted using the statistical software R version 3.6.1.

3. Results

We observed twenty lionfish consuming one or more prey fish across twenty-seven predation trials. Lionfish consumed an average of three prey fish (corresponding to 1.14 g biomass), and up to nine prey fish (corresponding to 3.78 g biomass), during predation trials.

Lionfish used in trials ranged from 11.7 to 26.3 cm (mean \pm standard deviation = 16.8 ± 3.7 cm) and 44 to 582 g (mean \pm standard deviation = 173 ± 128 g). There was a significant negative relationship between lionfish body size and prey biomass consumed ($r^2 = 0.208$, $p = 0.044$), and a nonsignificant negative trend between lionfish body condition and prey biomass consumed ($r^2 = 0.134$, $p = 0.112$). We did not find any relationship between lionfish size (Table S-2) or body condition (Table S-3) with no prey consumption by lionfish during predation trials.

Index of selectivity values ranged from 0.06 to 0.95 (Fig. 2), indicating lionfish deviated from a pure generalist strategy of resource consumption proportional to resource availability. This was confirmed with the pseudo- p value, which indicated 65% of the trials resulted in selective foraging behavior that was statistically significant based upon

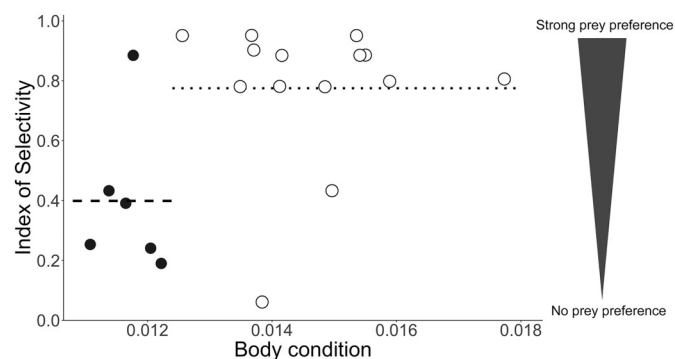


Fig. 2. Relationship between lionfish body condition and index of selectivity. Lionfish with higher body condition had a significantly higher mean index of selectivity than lionfish with lower body condition. Point shape indicates significantly different groups, separated by a body condition value of 0.0124. The dashed and dotted lines represent the mean index of selectivity of lionfish from each group.

an alpha value of 0.05. All statistically significant index values were > 0.78 .

Prey consumption was not proportional to prey availability (Fig. 3; $T_{2,18}^2 = 80.475$, $p < 0.0001$). Lionfish consumed 45% more brown chromis and 48% fewer glass/masked goby than expected from a predator consuming prey in proportion to their abundance. Both the index of selectivity and Ivlev's electivity index confirmed most lionfish exhibited some or strong preference for brown chromis over both bluehead wrasse and glass/masked goby (Fig. 3, Table S-4).

Groups of lionfish with similar index of selectivity values were separated by an optimal threshold body condition value of 0.0124 ($p < 0.01$, Fig. 2). As such, lionfish with a lower body condition had a significantly lower index of selectivity ($t_{18} = 3.119$, $p < 0.01$). There was no significant difference in body condition ($t_{7,8719} = -0.299$, $p = 0.773$) or index of selectivity ($t_{5,545} = 0.407$, $p = 0.699$) between male ($n = 10$) and female ($n = 16$) lionfish. The range of body conditions of lionfish used in this study was reflective of the body conditions of lionfish captured across Curaçao (Ritger et al., 2018).

4. Discussion

This study provides the first experimental, field-based evidence for active prey choice in invasive lionfish, even amongst prey sharing similar behavioral and morphological traits. The majority of individual lionfish demonstrated active selection of prey species, significantly deviating from a pure generalist strategy of foraging in proportion to prey species abundance. In addition, individual lionfish preference was consistently directed towards the same prey species, the brown chromis (*Chromis multilineata*), even in the presence of more abundant prey species sharing traits that make them equally vulnerable to predation by lionfish.

The strength of diet choice was condition-dependent in lionfish, as evidenced by the relationship between lionfish body condition and the compositional index of selectivity (Fig. 2). Lionfish with body conditions below 0.0124 were more likely to be non-selective foragers, while lionfish with body conditions above 0.0124 were highly selective foragers. Lionfish in better condition presumably had the energetic flexibility to actively choose amongst prey types (Lambert and Dutil, 1997), while those in poorer condition were more likely to consume the easiest (or more frequently encountered) prey in an attempt to rapidly recover (though with suboptimal prey choices). Furthermore, the negative relationship between lionfish body size and prey biomass consumed suggests the impact of food deprivation on lionfish foraging behavior is size-dependent. Although larger organisms have higher energetic requirements (Schmidt-Nielsen, 1984), larger individuals generally have a greater ability to fast than smaller individuals (e.g., Calder, 1974; Schulz and Bowen, 2005), which often leads to variable foraging behavior amongst conspecifics (Milinski and Heller, 1978; Molles and Pietruszka, 1983). With a greater body mass, larger lionfish are able to withstand food deprivation longer than smaller lionfish (Fishelson, 1997), and our results suggest physiological state may be playing an important role in the foraging behavior of smaller, potentially hungrier, individuals. However, lionfish are very resilient to starvation (Fishelson, 1997) and so further experiments are needed to understand these relationships.

Lionfish strongly targeted brown chromis disproportionately to their relative abundance (Fig. 3), even though the three prey species were present in equal biomass during predation trials and all three prey species are often heavily consumed by lionfish across the invaded range (Peake et al., 2018). Variation in selective foraging did exist amongst individuals, as few lionfish consumed primarily bluehead wrasse and one individual consumed only glass/masked goby. Overall, however, our results demonstrate that our population of lionfish strongly preferred brown chromis over all other prey species. Consumption of abundant, small, planktivorous, shoaling glass/masked gobies was infrequent, suggesting differences in prey species biomass per foraging

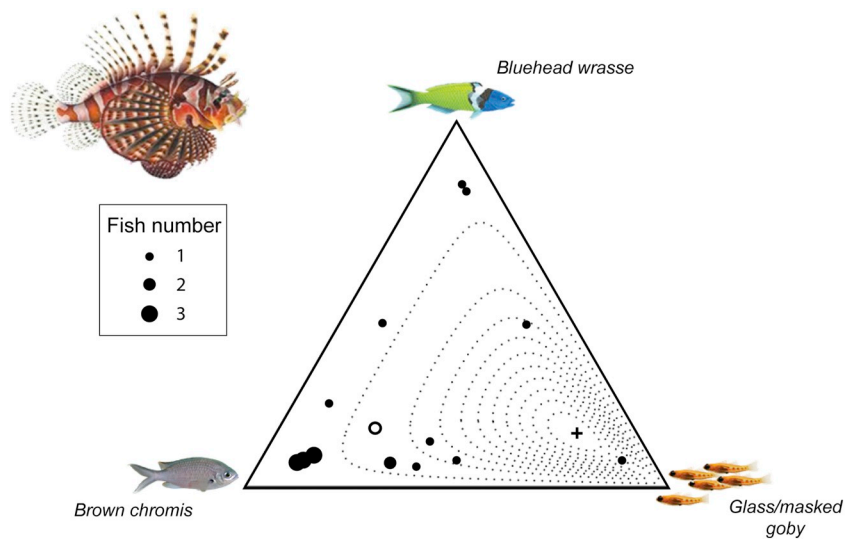


Fig. 3. Ternary diagram showing index of selectivity values from predation trials. Most lionfish exhibited some or strong preference for brown chromis. Each point in the ternary diagram represents the index of selectivity of an individual lionfish. The size of each point indicates the number of lionfish sharing an index of selectivity. Disproportionate consumption of prey shifts a point away from the + symbol, representing prey consumption proportional to prey availability (in accordance with the 11:11:55 ratio of prey offered), towards a corner representing the targeted prey species. The O symbol represents the geometric mean of lionfish prey consumption across all predation trials. The dashed contour lines depict the index of selectivity at 0.1 increments.

event played a role in lionfish prey choice. And yet, although brown chromis and bluehead wrasse shared similar biomass values (Table S-1), lionfish targeted brown chromis over bluehead wrasse.

Although all three prey species offered to lionfish in our experiment share similar behavioral and morphological characteristics that increase their susceptibility to predation (Green and Côté, 2014), increased vulnerability of brown chromis to predation by lionfish could be attributed to additional, unmeasured prey traits such as prey mobility (Eubanks and Denno, 2000). For example, bluehead wrasse swim in a rapid, more continuous motion over a longer duration than brown chromis. Although glass/masked goby move in very short, rapid bursts in closely-knit shoals, which may increase its ease of capture, lionfish did not target them during predation trials. This suggests that energy investment per predation attempt might not make it profitable for lionfish to hunt individual gobies unless, perhaps, when their densities are particularly high, which might account for their abundance in the stomach contents of lionfish captured around the same reefs (Ritger et al., 2018).

Lionfish consumptive patterns may furthermore be a reflection of local prey assemblages. Differences in local prey availability and prey assemblage variation have been suggested as drivers of prey consumption patterns (Côté and Maljkovic, 2010; Jud and Layman, 2012; Layman and Allgeier, 2012; Muñoz et al., 2011). Although we controlled for community differences in focal prey abundance during predation trials by using prey species that are highly abundant on local reefs (Fig. S-1) and highly preferred by lionfish across the invaded range (Peake et al., 2018), the distribution of prey fish inside enclosures was not an exact reflection of Curaçaoan reef fish communities. Field surveys identified planktivores such as brown chromis, bluehead wrasse, and glass/masked goby comprising nearly half the total fish biomass (Sandin et al., 2008) and over half of the density of fishes on Curaçaoan reefs (Fig. S-1). However, brown chromis and glass/masked goby are far more abundant than bluehead wrasse on Curaçaoan reefs (Fig. S-1). Additionally, the overall biomass of brown chromis on Curaçaoan reefs is significantly higher than both glass/masked goby and bluehead wrasse (Fig. S-1). The difference in consumption rates of brown chromis and bluehead wrasse during our predation trials may be due to lionfish encountering brown chromis on local reefs more frequently, creating a search image (Lewis, 1986) and thus targeting brown chromis more often. However, selective foraging may also vary temporally and spatially with differences in local prey availability and fluctuations in predator condition (Gilinsky, 1984). In fact, considerable variation in lionfish diet has been recorded across the invaded range (Peake et al., 2018), likely due to regional differences in reef community structure and prey availability. Additional studies are needed to assess whether the strength of diet choice found by our study

represents a more general pattern of selective foraging or a more localized pattern dependent on community assemblages around Curaçao.

Despite the vast literature on lionfish diet in the invaded range (Benkwitt, 2016; Côté and Maljkovic, 2010; Green et al., 2011), this represents the first study to provide direct evidence for diet choice in this invasive mesopredator. Selective foraging behavior might not necessarily be reflected in dietary studies of invasive lionfish because stomach content analyses offer only a snapshot of a predator's diet at a single point in time. Moreover, foraging strategies can shift with declines in the availability of preferred prey or predator condition (Murdoch, 1969; Vance, 1978), levels of structural complexity of the substrate (Crowder and Cooper, 1982), underwater light conditions (Hobson et al., 1981; Munz and McFarland, 1973), and environmental disturbance (Ratsimbazafy, 2007; Wen et al., 2016). Unfortunately, results uncovering such complexities are not often documented because tracking lionfish behavior in situ is a labor-intensive process and it is often difficult to tease apart multi-level interactions on complex coral reefs. Likewise, measuring foraging behavior of lionfish in captivity creates an artificial environment for both the predator and the prey by altering environmental and chemical cues important to predator-prey interactions in aquatic systems (Chivers and Smith, 1998). Laboratory manipulations can also elevate predator consumption rates (Breen and Metaxas, 2008) by increasing the risk of predation for prey species that may not have been so easily captured by the predator in the natural environment (Marsh-Hunkin et al., 2013). By allowing experimenters to control biotic variables without excluding abiotic forces, experimental enclosures in a semi-natural environment can provide a useful tool to gain insight into the factors influencing complex predator-prey interactions.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jembe.2020.151311>.

Declaration of Competing Interest

None

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