



Spatial clustering of trumpetfish shadowing behaviour in the Caribbean Sea revealed by citizen science

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Abstract

The West Atlantic trumpetfish (*Aulostomus maculatus*) performs an unusual hunting strategy, termed shadowing, whereby a trumpetfish swims closely behind or next to another ‘host’ species to facilitate the capture of prey. Despite trumpetfish being observed throughout the Caribbean, observations of this behaviour appear to be concentrated to a handful of localities. Here we assess the degree of geographical clustering of shadowing behaviour throughout the Caribbean Sea, and identify ecological features associated with the likelihood of its occurrence. To do this, we used a citizen science approach by creating and distributing an online survey to target frequent divers across this region. While the vast majority of participants observed trumpetfish on nearly every dive across the Caribbean, using random labelling spatial analyses, we found the frequency of shadowing behaviour was geographically clustered; participants that were within ~ 120 km of each other reported observations of shadowing that were more similar than would be expected by chance. Our survey also highlighted that trumpetfish were more likely to be observed shadowing than observed alone in a particular habitat type, and with particular host species, suggesting potential ecological factors that could drive the uneven distribution of this behaviour. Our results demonstrate that this behavioural hunting strategy is spatially clustered and, more generally, highlight the power of using citizen science to investigate variation in animal behaviour over thousands of square kilometres.

Keywords Animal behaviour · Random labelling · Hunting behaviour · Spatial distribution · Survey

Introduction

The foraging strategies used by predators to acquire prey are diverse, spanning sit-and-wait ambushes (Montgomery and Macdonald 1998; Pembury Smith and Ruxton 2020), pursuits (Wilson et al. 2013), and hunting within groups (Ormond 1980; Packer and Ruttan 1988; DeLoach and Humann 1999; Krause and Ruxton 2002; Lang and Farine 2017). Even within populations, individuals can differ in the strategies they use to hunt their prey. This variation is typically driven by predators adopting strategies that maximise their ability to acquire prey given local ecological

conditions (Giller and McNeill 1981; Flynn and Ritz 1999; Gilmour et al. 2018). For example, the degree of structural complexity in freshwater lakes can mediate a change in hunting strategy adopted by the predatory pike *Esox lucius* (Říha et al. 2021), and the foraging behaviours exhibited by boobies (*Sulidae*) can be accurately predicted by their local oceanographic habitat (Gilmour et al. 2018). Observations of social foraging also appears to be sensitive to the type of habitat, with mixed-species foraging bouts occurring most frequently in habitats with low physical cover (Auster and Lindholm 2008). Mapping variation in the geographical distribution of a given foraging strategy or behaviour, therefore, can highlight differences in the ecological conditions that are responsible for this variation, with important evolutionary and conservation implications. For some systems, however, mapping this variation in the foraging strategies of animals has been more difficult, especially for species that live across large geographical ranges. In particular, collating observations of differences in the hunting behaviour of marine species has been historically limited given that, relative to terrestrial environments, marine environments pose greater

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challenges in terms of logistics, accessibility and equipment (Roy et al. 2012; Cigliano et al. 2015; Gordon et al. 2019; Earp and Liconti 2020).

One marine predatory species that adopts different hunting strategies is the West Atlantic trumpetfish, *Aulostomus maculatus* (hereafter, trumpetfish), a piscivorous fish that is common on coral reefs across the Caribbean (Randall 1967; Kaufman 1976; DeLoach and Humann 1999). One predation strategy exhibited by trumpetfish involves a sit-and-wait approach, with an individual hovering vertically in the water column to strike at prey as they pass below or remerge from their refuge (DeLoach and Humann 1999). While this hunting method appears to be the most common strategy adopted by trumpetfish (DeLoach and Humann 1999), trumpetfish are also observed exhibiting another hunting strategy termed ‘shadowing’ behaviour, ‘riding’ (Ormond 1980; Auster 2008), ‘shadow-stalking’ (Baehr 2007) or ‘aligning’ (Aronson 1983). Shadowing involves a trumpetfish swimming closely above or adjacent to another individual fish, or within a school of fish (hereafter termed ‘hosts’), and appears to facilitate hunting by reducing the trumpetfish’s likelihood of detection by prey, thereby reducing their subsequent striking distance (Eibi-Eibesfeldt 1955; Randall 1968; Kaufman 1976; Ormond 1980; Aronson 1983; Baehr 2007). Trumpetfish have been observed shadowing a variety of host species, including parrotfish (e.g. *Scarus taenipterus*, *Scarus vetula*, *Sparisoma viride*, *Scarus hypselopterus*, *Sparisoma chrysopteron*), groupers (e.g. *Cephalopholis cruentata*, *Epinephelus striatus*), Spanish hogfish (*Bodianus rufus*), tangs (e.g. *Acanthurus coeruleus*, *Acanthurus bahianus*), angelfish (e.g. *Holacanthus ciliaris*) and blue striped grunt (*Haemulon sciurus*) (Collette and Talbot 1972; Baehr 2007), as well as associating with large shoals of fish, particularly tangs but also, creole wrasse (*Clepticus parrae*), sergeant majors (*Abudefduf saxatilis*) and goatfish (e.g. *Mulloidichthys martinicus*, *Pseudupeneus maculatus*) (Randall 1968; Kaufman 1976; Aronson 1983; DeLoach and Humann 1999). Shadowing behaviour may also represent a form of aggressive mimicry, whereby predators adopt the colouration and/or morphology of an associated species to increase access to prey (Ormond 1980; Pembury Smith and Ruxton 2020).

An outstanding question regarding the shadowing behaviour of trumpetfish relates to the geographical distribution and incidence of this behaviour across the Caribbean. Observations of shadowing behaviour within the Caribbean appear to be concentrated to a few islands, namely Bonaire (Aronson 1983; Baehr 2007; Auster 2008), Jamaica, and Union Island of Saint Vincent and the Grenadines (Kaufman 1976), despite trumpetfish being found throughout this region (Frances and Guerrero 2014; Luna and Bailly 2020). We do not know therefore whether these localities represent genuine increased incidences of this behaviour in the Caribbean,

or whether the prevalence of shadowing behaviour is evenly distributed across the Caribbean. We are also yet to identify the ecological conditions that are associated with this behaviour. If shadowing behaviour is used to reduce detection by prey (Kaufman 1976), shadowing behaviour should be more likely to occur in habitat types with less physical cover, such as within habitats with patchy reef or reef flats. Equally, given that shadowing involves using the physical presence of another fish to avoid detection, and different species are likely to offer different levels of concealment, there may be differences in how often shadowing behaviour is observed with different host species.

To assess the degree of geographical clustering of shadowing behaviour across the Caribbean, and to identify ecological features that may increase the likelihood of shadowing behaviour, we adopted a common citizen science approach. We created and distributed an online survey to dive shops throughout the Caribbean Sea and the Gulf of Mexico, with specific questions related to trumpetfish and their shadowing behaviour. The use of citizen science in this manner provides a cost-effective means of collecting and analysing extensive data sets across vast spatial and temporal scales (Bonney et al. 2009; Frigerio et al. 2018; Gordon et al. 2019; Earp and Liconti 2020). The utility of such approaches has increased in recent years with the advancement and accessibility of portable technologies (e.g. smartphones and digital cameras; Frigerio et al. 2018; Buchholz et al. 2019; Earp and Liconti 2020) and the advent of (social) media platforms, whereby communication and the sharing of graphical content is both instant and global (Nelson and Fijn 2013; Ballance 2018; Tiralongo et al. 2019; Germanov et al. 2019). In addition, the increased popularity and commercialisation of scuba diving in certain geographic areas offers the opportunity to expand the use of citizen science to investigate the prevalence of specific underwater behaviours (Roy et al. 2012; Cigliano et al. 2015; Gordon et al. 2019; Earp and Liconti 2020). Reflective of prior observations, we predicted that shadowing behaviour would be spatially clustered in the Caribbean. We also predict that observations of shadowing behaviour should be more likely in habitat types with less physical cover and there would be differences in how often shadowing behaviour was observed with different host species.

Methods

Survey recipients, design and distribution

The targeted audience for this survey were staff at, and regular users of, dive shops across the Caribbean. In this way, we aimed to capture the observations of experienced divers that are diving most frequently at a given dive location in

the Caribbean. Participants were asked to answer questions concerning their observations of trumpetfish within 20 km of their dive shop. The overall geographical region of interest reflected the expected distribution of trumpetfish, derived from the data collated by FishBase (Luna and Bailly 2020), and included all coastlines of the Gulf of Mexico and all islands within the Caribbean Sea. The process of searching the region of interest involved sequentially scanning coastlines in Google Maps (Google; Mountain View, CA, USA; <https://www.google.com/maps>) with the search term “dive shop”. Dive shops were included on the candidate list if they had a website which had either a public email address or an online contact form. This amounted to a list of 545 candidate dive shops in total. Some coastlines did not return any positive search results for “dive shop”, namely regions of South Mexico, West Honduras, Nicaragua, Colombia and South Cuba. The corresponding geographical coordinates (latitude and longitude) for each dive shop was identified (using what3words; London, UK; <https://www.what3words.com/aboutus>). If a dive shop only had an online contact form, a direct weblink for the survey was included as the message. We used Survey Monkey (Survey Monkey; San Mateo, CA, USA; <https://www.surveymonkey.com>) to create and distribute the survey via email. The survey was distributed to the candidate list in July 2020 and was followed by three weekly reminder emails. The survey was then closed in August 2020 giving divers at each dive shop 4 weeks to respond. The divers who received the survey and respond on behalf of a given dive shop are hereafter referred to as the ‘participants’ of the survey. All procedures were approved by the University of Cambridge Psychology Research Ethics Committee (PRE.2020.080).

The survey, entitled “Trumpetfish Survey”, contained three key parts: the introduction (Supplementary Appendix 1.1), the participant information statement (PIS; Supplementary Appendix 1.2) and the question body (for the full list see Supplementary Appendix 1.3). There were 20 questions in total, which we estimated would take participants no longer than 5 min to complete.

Most of the questions utilised a five-point frequency scale as a response—a commonly used Likert-type scale (Vagias 2006; Robinson 2014)—including never, rarely, sometimes, often, and always. While this scale included a neutral response of “sometimes”, we also included an “I don’t know” answer to allow participants to opt out of a question. Participants were informed that their responses to the questions should relate to observations of trumpetfish within 20 km of their dive shop. The first three questions addressed (i) the dive shop that the participant most frequently visited (typed response), (ii) how often the participant went diving (‘dive frequency’; three-point) and (iii) how often the participant observe trumpetfish on their dives (‘trumpetfish frequency’; five-point). The remaining questions addressed

the frequency that participants observed shadowing by trumpetfish overall (‘shadowing frequency’; five-point), the shadowing of specific host fish groups (each five-point), and observations of the habitats where trumpetfish were seen to be alone (i.e. not shadowing) or shadowing. Each of the ten host fish groups were chosen based on documented events of them having been either shadowed by trumpetfish or been associated with trumpetfish foraging behaviour in the literature. Questions concerning the habitat types and host fish were accompanied by reference images.

To be included within the subsequent analyses, participants had to have fully answered the first three questions; for example, participants that named multiple dive shops (in Q1) were removed. If multiple participants named the same dive shop as their primary location, then these survey responses were collated, and a (rounded) mean response for each question was recorded. This accounted for potential non-independent answers from within the same dive shop. In this way, for the analyses, each ‘participant’ (dive shop) represented a unique and independent observation.

Testing for clustering of trumpetfish shadowing behaviour

We first quantified whether there was evidence for spatial clustering of shadowing behaviour across the Caribbean, using a combination of pair correlation functions (PCFs) and random labelling analyses (RLAs). To do this, each participant’ location (i.e. dive shop location) were assigned to one of two states; (i) shadowing behaviour was frequently observed at that location (often and always responses) or (ii) shadowing was infrequently observed at that location (never or rarely responses). Responses that shadowing behaviour was “sometimes” observed were excluded from the analyses due to their ambiguity (as is commonly done for Likert-type scale responses) (Johns 2005). The spatial distributions of the different states can be described using PCFs, which describe how the density of points change as a function of distance from each point averaged out over the population (Illian et al. 2008). Quantifying whether the prevalence of shadowing behaviour is clustered or dispersed is implemented by calculating the PCF for each of the behavioural states (frequent or infrequent shadowing behaviour), and then comparing these PCFs to null expectation PCFs that would be expected given just the locations of the dive shops (Wiegand and Moloney 2013). To generate the null expectations, we used random labelling analyses, following the methods of Mitchell and Harris (2020). For each behavioural state, we generated null expectation envelopes of the spatial distribution (PCF) of the participants using 999 Monte Carlo simulations, whereby the state of the participant coordinates was randomly changed, while

the geographical positions of the sample sites were held constant (Pélissier and Goreaud 2001; Raventós et al. 2010). If the observed PCF of each behavioural state is greater than the null expectation PCF envelopes, then the behaviour is more clustered than expected; likewise, if the observed PCF is lower than the null expectation PCF envelopes, then the behaviour is more segregated or spaced out than expected. We used Diggle's goodness-of-fit test (Diggle 2002) to test for significance of this clustering, which represents the total squared deviation between the observed pattern and the simulated pattern across the studied distances (Diggle 2002; Diggle et al. 2005). If the observed PCF fell outside of the RLA generated Monte Carlo envelopes and had a $p_d < 0.05$, then the distributions of each behavioural state were found to be significantly different from the null expectation. RLAs were performed in Programita (Wiegand and Moloney 2004, 2013; Wiegand et al. 2006; Raventós et al. 2010).

Correlates of shadowing behaviour with ecological variables

To establish whether participants were more likely to observe trumpetfish to be shadowing, rather than alone, in particular habitats, for each participant we created a shadowing likelihood score for each habitat as follows: 'often observed shadowing behaviour in that habitat' (1 or 0) minus 'often observed trumpetfish that were alone in that habitat' (1 or 0). Therefore, if shadowing behaviour was more, less, or equally likely to be observed in a given habitat compared to trumpetfish being alone, this scored 1, -1 and 0 respectively. The shadowing likelihood scores (ordinal dependent variable) were then analysed using cumulative link mixed models (function `clmm` in the `ordinal` package) (Christensen 2019), which included habitat as a nominal fixed effect and participant ID as random effect.

Finally, we asked which host fishes trumpetfish were often observed to be shadowing (i.e. shadowing frequency; ordinal dependent variable). Shadowing frequency was also analysed using cumulative link mixed models, with host as a nominal fixed effect and participant ID as random effect.

We used the `emmeans` function from the `emmeans` package (Lenth et al. 2020) to compute the pairwise differences between each habitat, in terms of frequent observations and the shadowing likelihood scores, as well as the shadowing frequency of each host species. The most similar habitat types and host fish, respectively, were then assigned into equivalent groups using the `cld` function (Lenth et al. 2020). All analyses were performed in R v. 3.3.2 (R Foundation for Statistical Computing, <https://www.R-project.org>). Geographical maps were generated from the 'world' dataset

provided by the packages `rnaturalearth` and `rnaturalearth-data` (South 2017).

Results

We received a total of 105 survey responses overall and, after accounting for multiple responses from the same dive shop ($n=4$) and those that did not fulfil the criteria for inclusion ($n=2$), a total of 99 participant responses (each pertaining to a unique dive shop) were suitable for subsequent analysis (18% response rate). From the responses, 88% of participants went diving more than once a week, with the remainder diving more than once a month; our survey therefore targeted regular scuba divers in the region. Overall, 90% of participants observed trumpetfish either "often" or "nearly always" on their dives, and these observations were distributed across the Caribbean (Fig. 1a, b(i)). In contrast, only 24% of participants observed shadowing behaviour either "often" or "always" on their dives (Fig. 1, b(ii), c). Overall, we found the frequency at which participants frequently observed shadowing behaviour was spatially aggregated within the Caribbean, with significant clustering identified up to distances of ~120 km ($p_d=0.004$; Fig. 1d); participants that were within 120 km of one another reported shadowing frequencies that were more similar than would be expected by chance. Observations of infrequently observed shadowing behaviour did not significantly differ from random ($p_d=0.600$; Fig. 1e).

We found a significant effect of habitat upon the shadowing likelihood score (CLMM: $X^2=27.49$, $df=5$, $p<0.001$), with participants more likely to observe trumpetfish shadowing rather than being alone in only one habitat type, namely patchy hard coral/reef flats (Fig. 2a). There was a significant overall effect of host fish (CLMM: $X^2=130.15$, $df=9$, $p<0.001$) upon the frequency of observing trumpetfish shadowing. Pairwise analyses revealed that trumpetfish, tangs, and parrotfish were most often observed to be shadowed (Fig. 2b).

Discussion

Using a targeted citizen science approach, we found that while the frequency of participants observing trumpetfish was high throughout the Caribbean Sea, the frequency of observing trumpetfish shadowing behaviour was geographically clustered within certain areas. Overall, we identify significant spatial aggregation of shadowing behaviour for observations within 120 km of each other, which may infer that the frequency of shadowing behaviour differs in the

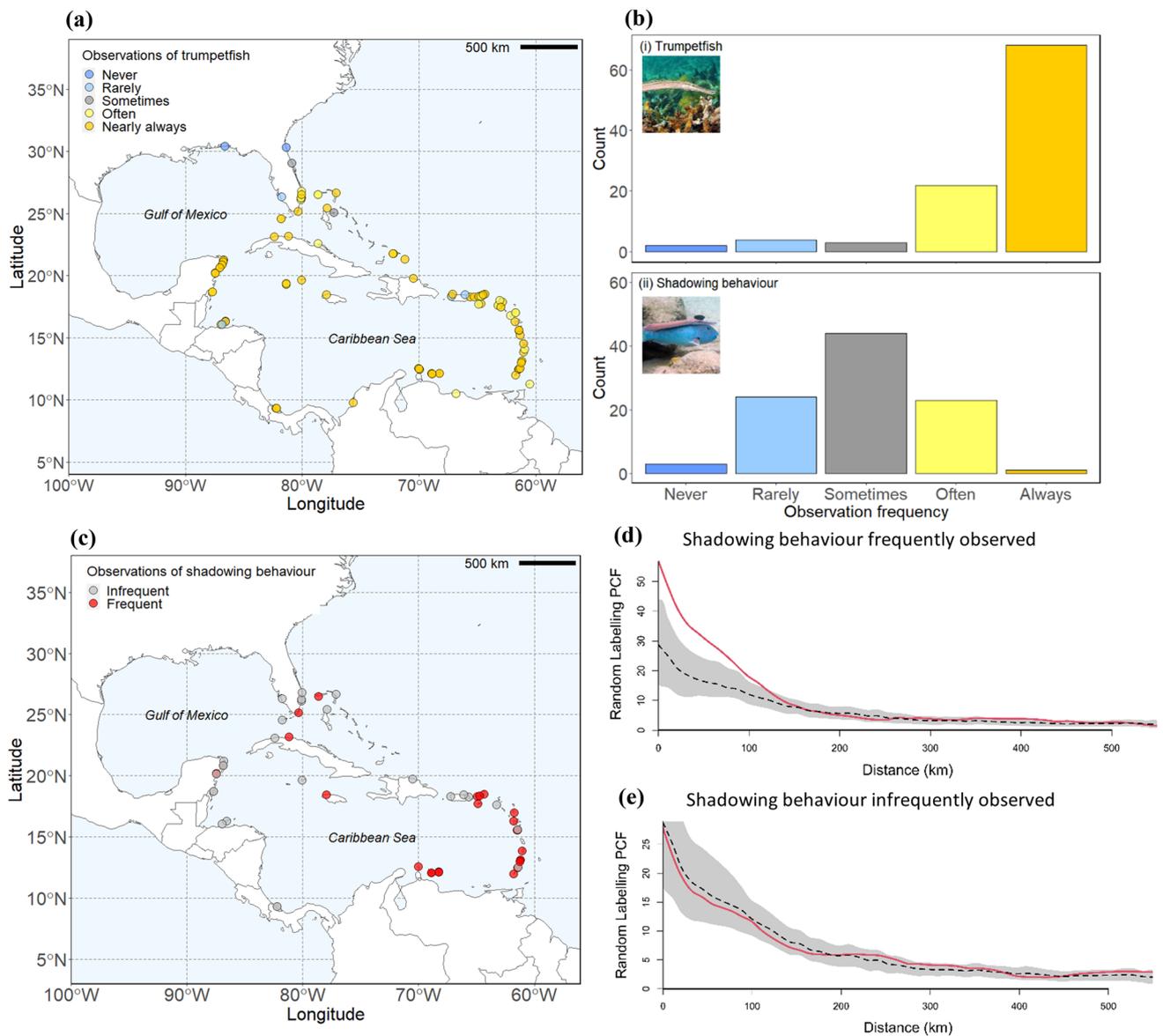


Fig. 1 **a** The distribution and the frequency of observations of trumpetfish by participating dive shops. **b** The number of dives within which participants observed (i) trumpetfish and (ii) trumpetfish shadowing behaviour. **c** The distribution of participants that observed shadowing behaviour, when converting shadowing frequency to a binary response (0=“never” and “rarely”, 1=“often” and “always”). **d** The PCFs of the shadowing behaviour and **e** non-shadowing behav-

our showing observed data (red line) and dive shop distribution (black dashed line). The light grey area represents the dive shop distribution simulation envelope generated from 999 Monte Carlo simulations. There is no significant deviation from the random distribution for non-shadowing behaviour, but shadowing behaviour demonstrates significant aggregation under ~ 120 km

Caribbean between regions of large islands and between small island chains, given that 97% of the islands in the Caribbean Sea are smaller than 100 km². Indeed, our study consolidates the locations in which shadowing behaviour has been previously documented, with high incidences of shadowing behaviour observed around Bonaire (Aronson 1983; Baehr 2007; Auster 2008), including Aruba and Curaçao, and the islands that comprise St Vincent and the

Grenadines (Kaufman 1976). We also identify areas in the British Virgin Islands and the United States Virgin Islands where shadowing is often observed.

While our survey is unable to identify the drivers of this variation in shadowing behaviour, it does identify several ecological correlates that could be responsible for variation in trumpetfish hunting behaviour between different locations. Habitat type appears to influence where shadowing

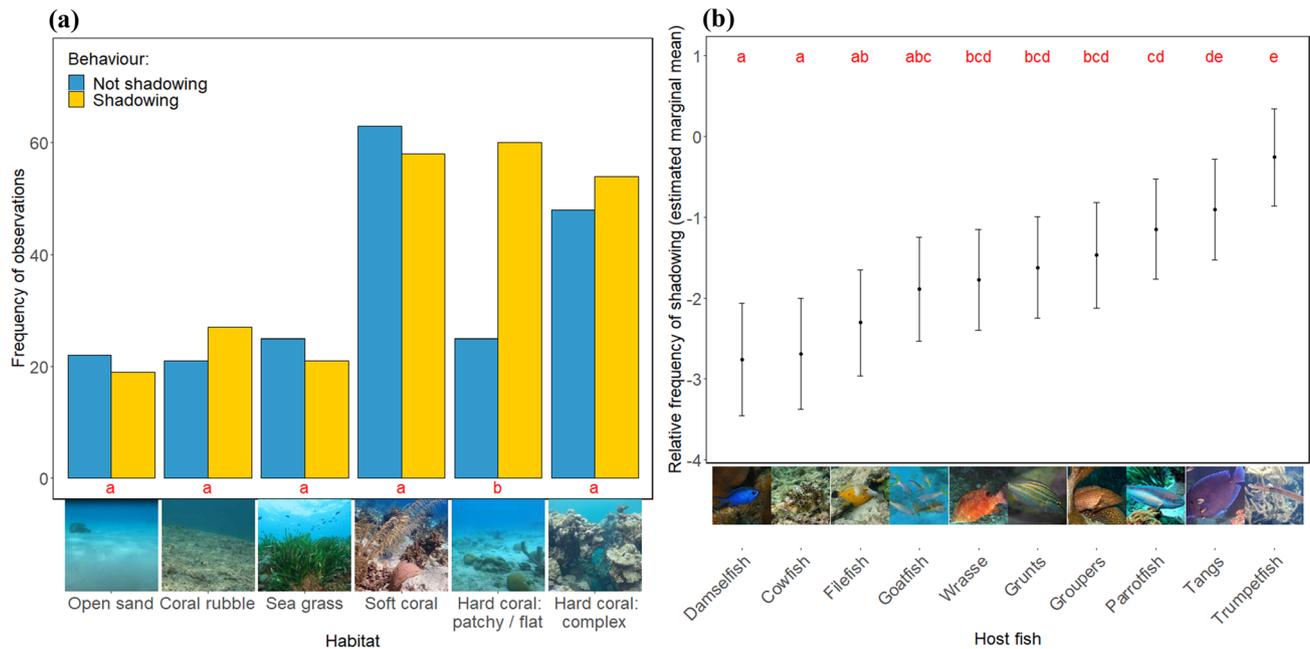


Fig. 2 **a** The frequency that participants most often observed trumpetfish not exhibiting shadowing behaviour (blue bars) or trumpetfish exhibiting shadowing behaviour (yellow bars) in different habitat types. Letter labels (red) below the bars denote the pairwise similarity between habitat types based on their shadowing likelihood scores. The similarity between groups is computed using the emmeans and cld functions from the emmeans package (Lenth et al. 2020). **b** The

comparison of estimated marginal means (emmeans) for shadowed hosts, also computed using the emmeans package (Lenth et al. 2020). Higher emmeans indicate shadowing behaviour was more often observed with this host. As with the habitat type comparison, letter labels (red) denote the similarity between hosts for observations of trumpetfish shadowing. Error bars denote 95% confidence intervals

behaviour is more or less likely to occur, with trumpetfish more likely to be observed shadowing than swimming alone in patchy hard coral/reef flat habitats. In these patch reef flat areas, trumpetfish may be using shadowing behaviour to reduce the saliency of their approach (relative to lone trumpetfish), given that these habitats typically host an abundance of potential prey (unlike open sand or coral rubble areas), but offer less visual cover than other habitats such as complex hard or soft coral. Indeed, this finding corroborates prior research that found the occurrence of mixed-species foraging associations to be more frequent within habitats with less visual cover (Auster and Lindholm 2008). Our analyses deliberately only compared the observation frequency of shadowing versus non-shadowing within each habitat, because differences in the availability of habitats between different dive shops would not make it possible to compare whether shadowing or non-shadowing behaviour was more common between different habitat types. Indeed, the relative availability of each habitat type is likely to differ between dive shop locations, and therefore the tendency for trumpetfish to shadow may also be governed the availability of different habitat types. Mapping the availability of each habitat type for all locations and assessing the distribution of trumpetfish and their hunting behaviour between these sites would therefore be worthwhile.

The diversity of shadowed host fish also largely reflects that of prior literature, with some fish groups found to be more frequently shadowed by trumpetfish than others, namely tangs and parrotfish (Kaufman 1976; Aronson 1983; Baehr 2007). There are two primary reasons why some species may be more shadowed than others. First, some aspect of the appearance or ecology of these species may make them more likely to be shadowed. For example, larger fish species or those of a specific colour (Aronson 1983; Lochmann 1989) may provide better visual concealment, whereas non-predatory species may also be favoured as they may be less likely to startle the intended prey. Indeed, both tangs and parrotfish are non-predatory and, in the case of parrotfish, large in size—though tangs form very large tight shoals that are also known to be readily shadowed by trumpetfish (Kaufman 1976). Second, certain species may simply be more numerous across the region of interest, or within a given habitat, making them more likely to be shadowed. In addition, the abundance of potential hosts will also show spatial and temporal variation, which may in turn shape the distribution of shadowing behaviour in this region. For example, spatial changes in parrotfish abundance can be mediated by extensive fishing (Jackson et al. 2014) and legislative protection (Mumby et al. 2006), while the abundance of both parrotfish and surgeonfish undergo seasonal changes

(Kopp et al. 2012). We collected our survey results over a four week period across July and August 2020, however, collecting answers over different times of the year may be able to capture any temporal variation in shadowing behaviour. We were not able to quantify the relative appearance or abundance of host species in the current study, nor were we able to capture further time points; however, we believe that these remain pertinent factors underlying the prevalence of shadowing behaviour and warrant further empirical investigation. Overall, the observations that the prevalence of shadowing behaviour is associated with certain habitat types and host species is an important finding in light of habitat loss and biodiversity. Given the loss of coral reefs due to bleaching and extreme weather events (Hughes et al. 2003, 2017; Pandolfi et al. 2003), and given a reduction in biodiversity of potential host species (Diaz et al. 2019), this could change the occurrence of interspecific behavioural interactions, such as shadowing behaviour.

Citizen science was paramount for the success of this study, especially given the time and finances that would be necessary for other methods of data collection over such a large spatial scale. Indeed, the data we collected, representing close to a hundred independent observations over thousands of square kilometres, would not have been financially or practically feasible over the same timeframe (4 weeks). However, it is also important to consider the limitations of citizen science. For example, the accuracy of a participant's observations will be a function of their experience with both the study organism and the wider ecosystem, and hence there will be variability across participants in their ability to classify a given behaviour and identify the species involved. While we attempted to mitigate this by targeting regular divers and by using a simple scale in the survey, the complex nature of some behavioural interactions, which can be brief, unpredictable, and easily misclassified, may also compound this variability. Indeed, this may be evident from the finding that trumpetfish were most often observed shadowing other trumpetfish, despite this contradicting the proposed function of shadowing behaviour. Instead, this is likely to represent a misclassification of shadowing behaviour with the social interactions of trumpetfish, which are superficially similar (personal observation), or as part of a nuclear hunting event, which may involve multiple trumpetfish (DeLoach and Humann 1999). Moreover, to increase the clarity of the study aims, our survey concerned all occurrences of shadowing behaviour by trumpetfish, whereas shadowing behaviour can involve trumpetfish aligning with an individual host or associating with a shoal of heterospecifics (Kaufman 1976; Aronson 1983). While many treat the two as equivalent strategies, it may be prudent in future to treat these behaviours as independent subgroups given that the relative costs and benefits for the host fish may differ in each instance.

Future standardised empirical and experimental work will be needed to confirm the geographical clustering of trumpetfish's shadowing behaviour in the Caribbean, as well as testing the ecological factors that are proposed as underpinning the purported distributions. Nevertheless, our study represents a major step in mapping the prevalence of this unusual hunting behaviour and identifies ecological correlates that could be responsible for this distribution. In addition, our study highlights how valuable targeted citizen science approaches can be to generate observations and hypotheses in marine systems over large spatial scales and in a cost-effective way.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00227-022-04057-4>.

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Author contributions JH-R conceived the idea for the study; SM collated the participant list and coordinated the delivery of the survey; SM and JH-R designed the survey, conducted statistical analysis, and drafted the manuscript. EGM conducted random labelling analyses. All authors gave final approval for publication.

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Data availability Data can be found on the data depository, Dryad, using the following URL: https://datadryad.org/stash/share/YTd68t_LXwXMGKGLDbPoxE3fqlzxpvn6orKlxykrsk.

Code availability Not applicable.

Declarations

Conflict of interest We declare that there is no conflict of interest.

Ethics approval All procedures were approved by the University of Cambridge Psychology Research Ethics Committee (PRE.2020.080).

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