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Predators hide against similarly coloured species to camouflage on the move

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Many predators aim to approach prey without being detected or identified. Ambush predators often achieve this through camouflage, such as background matching. This strategy is thought to be ineffective for actively moving predators, as motion typically breaks camouflage. However, if animals could select and remain close to similarly coloured moving objects, then camouflage could be achieved on the move. Using detailed natural observations, we demonstrate that colour polymorphic trumpetfish (*Aulostomus maculatus*) selectively choose to 'shadow'—swim closely alongside—other fishes of similar colour to themselves. Specifically, yellow trumpetfish individuals most frequently shadow yellow Spanish hogfish (*Bodianus rufus*), while blue morph individuals most frequently shadow the blue terminal phase of queen parrotfish (*Scarus vetula*). When we experimentally presented three-dimensional models of these shadowing combinations to bicolour damselfish (*Stegastes partitus*) colonies *in situ*, these prey exhibited reduced anti-predator responses towards trumpetfish that were paired with a similarly coloured species versus trumpetfish that were dissimilar in colour to the fish they were shadowing, particularly for the yellow trumpetfish morph. Selecting a similarly coloured moving object (here a fish) represents a novel form of moving camouflage and illustrates how some predators can use strategic decision-making to improve their hunting success on the move.

1. Introduction

To be successful when hunting, many predators need to reach within striking distance of prey before being detected or identified [1,2]. Ambush predators often achieve this through camouflage, adopting colourations that help them blend in with the background while awaiting the approach of prey [2]. For instance, scorpionfish use crypsis to blend in with coral reefs [3], felids have coat patterns that help them to blend in with the mosaic of shadows in foliage-rich habitats [4] and crocodilians remain undetected in murky waters owing to their colouration [5]. Some crab spiders even select flower heads as ambush sites that match their own colouration when waiting for visiting prey [6]. Camouflage is effective, therefore, for predators that remain stationary against their background. By contrast, colour-matching of the background is believed to be ineffective for predators that move when searching for and pursuing prey. Not only does the background that they are viewed against change as they move, but many animals are also sensitive to motion cues and often detect them through achromatic (luminance-based) mechanisms [7–9]. Taken together, this has led to the long-held paradigm that motion 'breaks' camouflage [10–14]. Indeed, many moving predators do not appear to rely on camouflage to remain concealed during hunts. Instead, some species have evolved high speeds (e.g. peregrine falcon, *Falco peregrinus*; [15]), specialized morphology (e.g. eels; [16]) or group hunting (e.g. wolves, *Canis lupus* [17,18]) to catch prey. Others use colouration strategies not to conceal but to misdirect or mislead their prey, such as through aggressive mimicry or aggressive masquerade (see [2] and [19] for extensive reviews).

Moving predators have, however, evolved behavioural strategies to minimize their likelihood of detection, with a particular emphasis on when and how they move [2,12]. For example, white sharks (*Carcharodon carcharias*) adjust their trajectory when approaching surface prey to match the direction of intense sun glare [20], while some falcons and dragonflies approach their prey using trajectories that make them appear motionless in the prey's visual field [21,22]. Alternatively, some predatory species appear to mask their approach by using the movements of other animals. By performing a behaviour known as 'shadowing'—which involves a predator moving closely alongside another, typically non-predatory animal [23–26]—predators can potentially approach their prey without being detected [27]. Contrary to our standard understanding that moving predators do not adopt colours to match their background, anecdotal reports indicate that shadowing predators may select species that match their own appearance to move alongside [23–26]. By choosing similarly coloured species to shadow, predators may achieve camouflage on the move. However, this potential form of motion camouflage has not been empirically tested.

Trumpetfish (*Aulostomus maculatus*) are common predators on coral reefs across the Caribbean and represent an ideal candidate to investigate whether mobile predators can make behavioural decisions about their colouration to enhance concealment while moving. Trumpetfish prey on a diversity of small fish [28] using several hunting strategies [23,26,29], including shadowing behaviour [24,25,27,30]. Trumpetfish are also polymorphic [31], with individuals being reddish-brown (hereafter, 'brown'), silvery-grey with a blue head (hereafter, 'blue'), or xanthic (hereafter, 'yellow'). Blue and yellow morphs are most often observed shadowing (>75% of our shadowing observations, $n = 91$), so they were the focus of our analysis. Blue and yellow colours, which are common in reef fish [32,33], are also of particular interest because their saliency can vary significantly depending on the background against which they are viewed [34,35], which can include other fish. For example, yellow colours are well-camouflaged when viewed against average reef colours but highly salient when viewed against midwater blues [34–36], which may mean a greater pressure for yellow trumpetfish to shadow similarly coloured species.

Here, we test (i) whether blue and yellow trumpetfish morphs are more likely to shadow species that are similar to their own colouration, and (ii) whether trumpetfish that shadow similarly coloured species are less detectable to their prey than those that shadow differently coloured species. First, we used detailed natural observations to quantify which species the two trumpetfish morphs were shadowing and how this shadowing frequency related to the relative abundance of each species. We predicted that each trumpetfish morph would actively select similarly coloured species to shadow rather than simply shadowing the species that are most available. Second, we ran a field experiment to investigate the detectability of blue and yellow trumpetfish to their prey when shadowing the two species that were shadowed most frequently, the terminal phase queen parrotfish (*Scarus vetula*; hereafter 'parrotfish') and the Spanish hogfish (*Bodianus rufus*; hereafter 'hogfish'), which are also blue and yellow, respectively. We presented to a typical prey species, the bicolour damselfish (*Stegastes partitus*; hereafter, 'damselfish'), 3D-printed models of each trumpetfish morph with either a model of a shadowed species of similar colouration or one with a dissimilar colouration. We predicted that damselfish would be less likely to detect trumpetfish models that were paired with a similarly coloured species than those paired with a dissimilarly coloured species.

2. Methods

(a) Observations of shadowing behaviour

We collated observations of shadowing behaviour from three sources: those (i) filmed during the collection of individual trumpetfish behavioural data (i.e. focal follows), (ii) filmed during the collection of trumpetfish abundance data (i.e. transects), and (iii) opportunistically filmed in the period immediately before or after experimental data collection. Focal follows ($n = 54$, 18 for each trumpetfish morph) comprised a SCUBA-diving researcher an individual trumpetfish for 10 min while positioned 2–3 m behind and above the animal, and were conducted between April and May 2022. Transects ($n = 185$) comprised a researcher swimming parallel with the reef drop for 15 min (translating to approx. 200 m of reef) approx. 5 m above the reef floor, and were conducted from April to December 2022, March to May 2023 and April to May 2024. Opportunistic observations ($n = 37$) were collected from March to May 2022 and from April to May 2024. For observations during focal follows and transects, filming was completed using two GoPro cameras (Hero 10; 3840 × 2160 px, 30 fps, linear angle) fixed to a stereo camera rig, whereas only a single GoPro (with identical settings) was used for opportunistic encounters. All observations were collected across 12 reef sites around the Caribbean island of Curaçao (see electronic supplementary material, table S1).

For all filmed observations of blue and yellow trumpetfish morphs, we noted the colour morph of the trumpetfish and the shadowed species, as well as the date and dive location. Although trumpetfish can be observed swimming amongst shoals of fish (e.g. blue tangs, *Acanthurus coeruleus* [24]), we limited our observations of shadowing behaviour to those involving an interaction with a single other fish. For individuals that exhibited shadowing on more than one occasion during a focal follow ($n = 2$), only the species that they shadowed first was recorded. From all relevant shadowing observations, and for each of the two trumpetfish colour morphs, we calculated the proportion that pertained to each species recorded.

(b) Abundance of shadowed species

To quantify the likely abundance of all fish species that we knew were shadowed, we examined a long-term monitoring dataset of fish assemblages on the reefs surrounding Curaçao (for the first iteration, see [37]). The latest iteration (2023) followed an identical methodology to the work outlined in Sandin *et al.* [37]: multiple line transects were conducted throughout October 2023 across 129 reef sites along the Southwest coastline of Curaçao. These transects comprised a SCUBA swimming researcher moving parallel with the reef drop for 30 m at the reef floor, recording the number of each species encountered within 2 m of their swimming path, as well as estimating the size of each individual (to the nearest 5 cm). From this dataset, we isolated the transects that corresponded to the 12 reef sites where our shadowing observations were collected. A total of five transects were completed at each of these 12 sites. From these transects, we totalled the observations of all species that had previously been identified as having been shadowed by a yellow and/or blue trumpetfish morph. Observations were made at the species level and therefore did not account for the distinction of reproductive phase in the parrotfish species; adults of these fish are sequential hermaphrodites and exist in one of two visually distinct phases (initial and terminal). Instead, we used the estimated total body length to assign a phase to each parrotfish observed, with size correlating with the age of transition between phases [38]. To ensure our size thresholds were conservative, we assumed an individual was in the initial phase if it was below 30 cm total length for *Scarus vetula* or *Sparisoma viride*, and below 20 cm total length for *Scarus iseri* and *Sparisoma rubripinne* [38].

(c) Active species selection

We then compared the relative proportion of shadowing events observed for a given species with the relative availability of that species. If, for example, trumpetfish shadow species in accordance with their relative abundance (i.e. the most abundant species are shadowed most and *vice versa*), then the relative difference between shadowing frequency and availability for each species should be negligible. Alternatively, if the frequency with which trumpetfish shadow a given species significantly differs from the availability, then we can infer that trumpetfish are actively selecting—or avoiding—a given species for shadowing. The majority of our shadowing observations related to two species, the terminal phase queen parrotfish (*S. vetula*) and the Spanish hogfish (*B. rufus*), and these possess colourations that are very similar to each of the trumpetfish morphs studied (i.e., blue and yellow, respectively; figure 1). We therefore deemed it most likely that species selection by shadowing trumpetfish was determined by a colour similarity between the two fish, and our behavioural experiment focused on these two species as a result.

(d) Behavioural experiment

(i) Three-dimensional model generation

We generated 3D models of three species of fish: the trumpetfish (blue and yellow morphs) and the two shadowed species, the hogfish (yellow) and the parrotfish (blue) (figure 1). As with Matchette *et al.* [27], we used a digital model of the trumpetfish previously procured from TurboSquid (product ID: 1251130; TurboSquid, New Orleans, LA, USA) to create 3D model trumpetfish. We procured two additional digital models as the basis of the 3D model hogfish (product ID: 1144115) and parrotfish (product ID: 1098903). All models were manipulated in Blender (Blender v.3.1.2, Amsterdam, The Netherlands; www.blender.org/), FreeCAD (FreeCAD v.0.19; www.freecad.org/) and PrusaSlicer (v.2.3.3; Prusa Research, Prague, Czech Republic; www.prusaslicer.net/) to facilitate model joining and printing, the latter completed using an Original Prusa i3 MK3S$^+$ (Prusa Research, Prague, Czech Republic) with clear 1.75 mm PETG filament (TecBears, Kwun Tong, Hong Kong). The final 3D models had total lengths that fell within the natural size range for each species [29,39]: the trumpetfish measured 55.5 cm (although wild individuals can be up to approx. 90 cm), the hogfish model measured 55.6 cm (wild individuals up to approx. 60 cm) and the parrotfish model measured 58.8 cm (wild individuals between approx. 30 and 60 cm; [38]). In total, we printed three 3D models for each trumpetfish morph and the hogfish and two for the parrotfish.

We applied a morph- or species-specific texture to all four model types. For the two trumpetfish morph models, the process used was identical to that in Matchette *et al.* [36]. In short, we extracted colours from standardized photographs of two fresh trumpetfish cadavers (one yellow morph and one blue morph) and used these as the palette to create a fish texture manually. While some colours may change following death, we were limited to using photographs of cadavers owing to the unavailability of standardized photographs of live trumpetfish *in situ*, but we ensured that photographs were taken as soon as possible following death (within 30 minutes). We then converted each fish texture to a foldable ‘skin’ using the software Pepakura Designer (Tamasoft, Tokyo, Japan; www.pepakura.tamasoft.co.jp/pepakura_designer/), printed it out onto waterproof paper (ToughPrint) and wrapped it around the corresponding physical model. To ensure that, when printed, the colours matched the originally extracted colours, we transformed both colour sets into anemonefish colour space (*Amphiprion akindynos*, an Indo-Pacific member of the Pomacentridae family and our closest available proxy for the bicolour damselfish) and compared the difference between the two. If the difference generated a just noticeable difference (JND) [40–42] that was greater than 1, we adjusted the original RGB values (i.e. increased or decreased them) and the process was repeated. Photograph transformation and subsequent colour analysis were completed using open-source MATLAB code from the *TrumpetfishColour* repository [43]. We used the same process for the hogfish and parrotfish models, with the only difference being that we sourced the original colours from online photographs of each species *in situ* (hogfish: Florent’s Guide To The Tropical Reefs

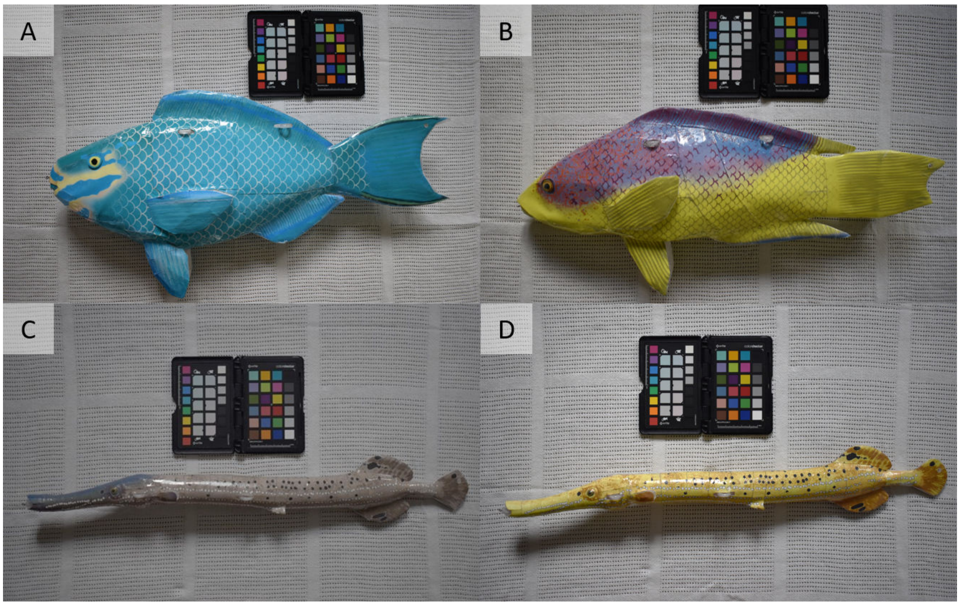

Figure 1. Photographs of the models used in the experiment, which included two fish species that are commonly shadowed: *Scarus vetula* (A) and *Bodianus rufus* (B), and the blue (C) and yellow (D) colour morphs of the trumpetfish, *Aulostomus maculatus*. When presenting a shadowing interaction, the trumpetfish model was attached to the other species using bespoke in-built hoops.

https://reefguide.org/pixhtml/spanishhogfish10.html; parrotfish: Florent's Guide To The Florida, Bahamas and Caribbean Reefs https://reefguide.org/carib/pixhtml/queenparrot11.html).

While the use of online photographs is not optimal, we did not have access to any fresh cadavers at the time of the study, and there are no standardized open-access photographs of these species nor spectrophotometry data for their external colouration. However, to assess the general suitability of using colours of fish from online photographs, we compared the colours extracted from the trumpetfish cadaver photographs with colours extracted from a set of online trumpetfish photographs ($n = 10$ for each morph). To match the already-transformed cadaver photographs, we first transformed the online photographs, sourced from https://openverse.org/, into anemonefish colour space [43]. We then randomly extracted 100 pixels from each photograph and compared the chromatic contrasts between the cadaver photographs and each online photograph using the JND metric [40]; the larger the JND, the greater the dissimilarity between the two pixels. For this, the blue trumpetfish morph was subdivided into two body regions, which were analysed separately: the head, which is primarily blue, and the body, which is silvery grey. The colouration of the yellow trumpetfish morph is uniform across both regions. Overall, across the three regions, 85% of colour comparisons generated a JND that fell below 2 (electronic supplementary material, figure S1), implying that colour differences are unlikely to be perceptible to the viewer [40]. We therefore predict that, by using online photographs to colour the shadowed species, any error in perceived colour should be minimal.

We then compared the appearance of each trumpetfish morph relative to each shadowed species. We photographed one model of each morph or species alongside a colour standard (ColorChecker Passport Photo 2) from above at approximately 0.5 m, against a white fabric background and under diffuse sunlight. Each image was transformed to anemonefish colour space using the same methods described above. After the background was removed in each image, we compared the pairs of images in three ways. First, we compared the overall colour difference using the *getColorDistanceMatrix* pipeline (with the 'earth mover's distance' method) in the *colordistance* package [44] (electronic supplementary material, figure S2A). Through the *getHistList* function, this pipeline bins the colours present in each image ($n = 27$ bins, across three colour channels), reducing and normalizing the amount of colour data present. In doing so, we could directly compare both the identity of the colours present (that best represent each image) and their relative proportions, the latter being a significant component of each model's overall saliency. From each image comparison, a single 'colour distance' score was generated; the larger the colour distance, the greater the dissimilarity between the two images. To complement this approach, and to assess the difference between colours using a real-world metric, we randomly extracted 500 pixels from each image and calculated the JND in chromatic contrast between each pixel pair (electronic supplementary material, figure S2B) using the same open-source code outlined above [43]. Finally, because trumpetfish may also select hosts based on their achromatic contrast (rather than on their chromatic contrast), we used the same approach to calculate the achromatic contrast between pixel pairs (electronic supplementary material, figure S3). In each case, the larger the JND, the greater the dissimilarity between the two colours. We used independent linear models (function *lmer* in the *lme4* package [45]) to assess the chromatic contrast and achromatic contrast (both square root transformed) between models in each combination (nominal; see electronic supplementary material, f). When model combination was significant, we computed pairwise comparisons using the *emmeans* and *cld* functions from the emmeans package [46]. While the achromatic contrast between model combinations did not differ significantly (LM: LRT = 3.85, d.f. = 3, $p = 0.278$; electronic supplementary material, table S2; electronic supplementary material, figure S3), the chromatic contrast did (LRT = 282.14, d.f. = 3, $p < 0.001$; electronic supplementary material, table S2; electronic supplementary material, figure S2B).

(ii) Experimental set-up and procedure

We presented each damselfish colony with six treatments: two non-shadowing treatments ((i) blue trumpetfish model alone and (ii) yellow trumpetfish model alone) and four shadowing treatments, the latter involving the attachment of a trumpetfish model to one of the shadowed species models using translucent 3 mm cable ties. Of the four shadowing treatments, two treatments involved a combination between a trumpetfish and a shadowed species that was similar in their colouration: (iii) yellow trumpetfish shadowing the yellow hogfish and (iv) blue trumpetfish shadowing the blue parrotfish. The other two shadowing treatments involved a combination between a trumpetfish and a shadowed species that were dissimilar in their colouration: (v) yellow trumpetfish shadowing the blue parrotfish and (vi) blue trumpetfish shadowing the yellow hogfish.

We presented each treatment *in situ* to 40 colonies of bicolour damselfish, which live in groups among semi-isolated structures on the reef floor [47]. The colonies were located on four reef sites around Curaçao (n = 10 colonies per site; see electronic supplementary material, table S1). All species and colour morphs have been observed across all four reef sites, as well as all four shadowing combinations (SRM, personal observation, 2022). Trials were conducted between 9:00 and 11:00 by the same two researchers on SCUBA, in an identical manner to those in Matchette *et al.* [27]. Specifically, each trial consisted of the relevant model(s) being hand-reeled along a clear nylon line from one tripod to another, passing over the colony, which was positioned halfway between the two (approx. 6 m from each tripod; electronic supplementary material, figure S4). For the two non-shadowing treatments, trumpetfish were presented horizontally, in a manner previously described as their 'search' position [47,48]. For all shadowing treatments, the trumpetfish was attached to the shadowed species on the side nearest the colony, such that the trumpetfish was always visible to the colony during its approach and departure (i.e. not occluded by the shadowed species). We counterbalanced treatment order and the model ID (1–3 for yellow trumpetfish, blue trumpetfish and hogfish; 1–2 for parrotfish) in a random-block design for each site.

We positioned two cameras ('Focal'; GoPro Hero 10; 3840 × 2160 px, 30 fps, linear angle)—one on either side of the colony—to capture the damselfish behaviour; one captured the approach of the model and one captured its departure. We fixed two further cameras ('Stereo'; GoPro Hero 10; 3840 × 2160 px, 30 fps, linear angle) to a stereo camera rig (left and right) and positioned it approx. 3 m away, perpendicular to the reeling direction, to capture the full journey of the model(s) from tripod to tripod. All cameras were synchronized using a burst of clear 'tank bangs': an elasticated ball that 'dings' against the SCUBA air tank. We gave each colony 5 min to acclimate before the start of each trial.

(iii) Video processing

For each trial, we synchronized videos from both the focal and stereo cameras (using the tank bangs) and trimmed them down to four short clips per trial. The subsequent focal and stereo clips were used to quantify different aspects of the experiment.

First, we used the stereo camera clips to assess whether each 3D model was reeled past a given colony at a similar speed. To do this, we extracted the position of the model from the stereo camera clips in six regularly spaced frames, spanning the journey of the model towards and beyond the colony. With this, we calculated the mean speed of each model as it moved between these frames and, using a linear mixed model (function *lmer* in the *lme4* package [45]), we compared the reeling speeds between each treatment (nominal fixed effect) across all trials. Colony ID was provided as a random effect. We found that the reeling speeds of each model treatment did not significantly differ (non-shadowing blue trumpetfish: 0.36 m s^{-1} ± 0.14; non-shadowing yellow trumpetfish: 0.36 m s^{-1} ± 0.15; blue trumpetfish shadowing hogfish: 0.37 m s^{-1} ± 0.15; blue trumpetfish shadowing parrotfish: 0.37 m s^{-1} ± 0.16; yellow trumpetfish shadowing hogfish: 0.38 m s^{-1} ± 0.17; yellow trumpetfish shadowing parrotfish: 0.38 m s^{-1} ± 0.14; mean ± 1 s.d.; χ^2: = 3.78, d.f. = 5, p = 0.582; electronic supplementary material, figure S5).

Both the focal and stereo camera clips were used to analyse the behavioural responses exhibited by each damselfish colony. We initially scored the behavioural responses in the focal camera clips using the event-logging software, BORIS [49]. Specifically, we organized the subsequent damselfish responses into two behavioural clusters: responses relating to inspection behaviour and responses relating to avoidance behaviour.

Inspection behaviour by a colony was defined as at least one individual facing and swimming towards the model [27]. For this behavioural cluster, using a Python script from Dunkley *et al.* [50] and a bespoke MATLAB script, we first extracted from the stereo camera clips the position of each 3D model relative to the nearest edge of the colony at the time of each behavioural response. With this, we could quantify (a) the distance that each 3D model was from the colony when the first inspection behaviour was exhibited. In addition, we also quantified (b) the duration of time that a colony spends inspecting each 3D model.

Avoidance responses involved at least one individual moving rapidly towards the colony shelter. For this behavioural cluster, we quantified (a) the distance between each model and the colony when the first avoidance response was exhibited and (b) the number of avoidance responses exhibited by a colony. If multiple individuals exhibited avoidance responses (i.e. if an individual sequentially responds to another conspecific's avoidance), we defined independent avoidance responses as those occurring more than half a second (15 video frames) from another (as in Matchette *et al.* [27]).

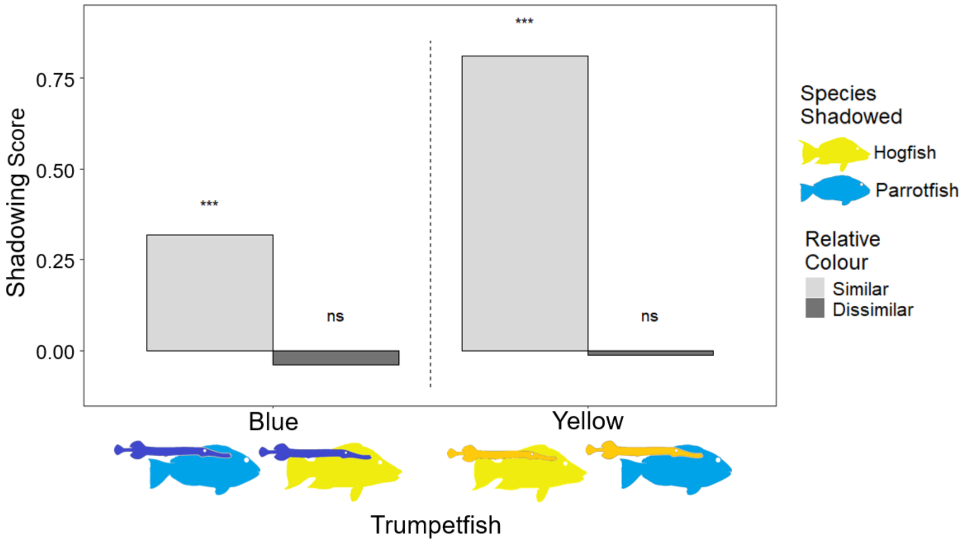

Figure 2. The shadowing score for each fish species shadowed (hogfish or parrotfish) by blue and yellow trumpetfish morphs. Shadowing scores were calculated by subtracting the availability of a given species (i.e. the proportion of the total number of all observed shadowed species) from the shadowing observation frequency for that species (i.e. the proportion of all shadowing events involving this species). For each shadowed species, one trumpetfish morph was similar in colouration, while one was dissimilar. Shadowing scores that do not significantly differ from zero ('ns' $p > 0.05$) indicate a shadowing frequency that reflects the relative availability of that species, whereas shadowing scores greater than zero indicate a shadowing frequency that is greater than that expected by abundance alone (***$p < 0.001$). For raw counts of each shadowing combination, see electronic supplementary material, figure S6.

(e) Statistical analysis

(i) Active species selection

We performed all statistical analyses in R v. 3.3.2 (R Foundation for Statistical Computing, https://www.r-project.org/). To quantify species selection, it was important to use a quantitative measure that accounted for both the relative frequency of shadowing as well as the relative abundance. We therefore used a proportion *z*-test to compare the relative abundance of the hogfish and the parrotfish (i.e. the proportion of each from all fish observations) and the frequency with which they are shadowed by each morph (i.e. proportion of all shadowing observations that involved these species).

(ii) Behavioural experiment

We used mixed models to analyse the damselfish responses to control for repeated testing of the same colonies. Initially, we assessed how the behavioural state of the trumpetfish model (i.e. shadowing or non-shadowing, irrespective of colour) influenced each response variable (electronic supplementary material, table S3). We then focused on the shadowing treatments by analysing the interaction between the colour of the trumpetfish (nominal) and the colour of the shadowed species (nominal), testing the significance of the interaction for each response variable by comparing models with and without the term using the *anova* function (electronic supplementary material, table S4). For the behavioural cluster relating to inspection responses by damselfish, we used independent linear mixed models (LMMs) to assess how the interaction of colours influenced the distance from the colony when the latter first inspected the model and the total time that a colony spent inspecting (square-root transformation). Likewise, we used LMMs to assess how the interaction of colours influenced the responses relating to avoidance behaviour, namely the distance at which the colony first initiated an avoidance response and the number of avoidance responses (square root transformation). For all models, colony ID was included as a nested random effect within reef site, denoted in lme4 syntax as (1|site/colony ID). To check the assumptions of each model, we used the *DHARMa* package [51] to interpret the dispersion and distribution of the residuals.

(f) Ethics

All procedures were approved by the University of Cambridge Animal Welfare and Ethical Review Body (OS2024/01).

3. Results

(a) Trumpetfish select similarly coloured species to shadow

A total of 70 shadowing events were recorded for blue and yellow trumpetfish morphs. Of these, 32% were of trumpetfish shadowing the blue terminal phase queen parrotfish (*Scarus vetula*; hereafter 'parrotfish') and 21% were of trumpetfish shadowing the primarily yellow Spanish hogfish (*Bodianus rufus*; hereafter 'hogfish'), with the remaining 47% of observations

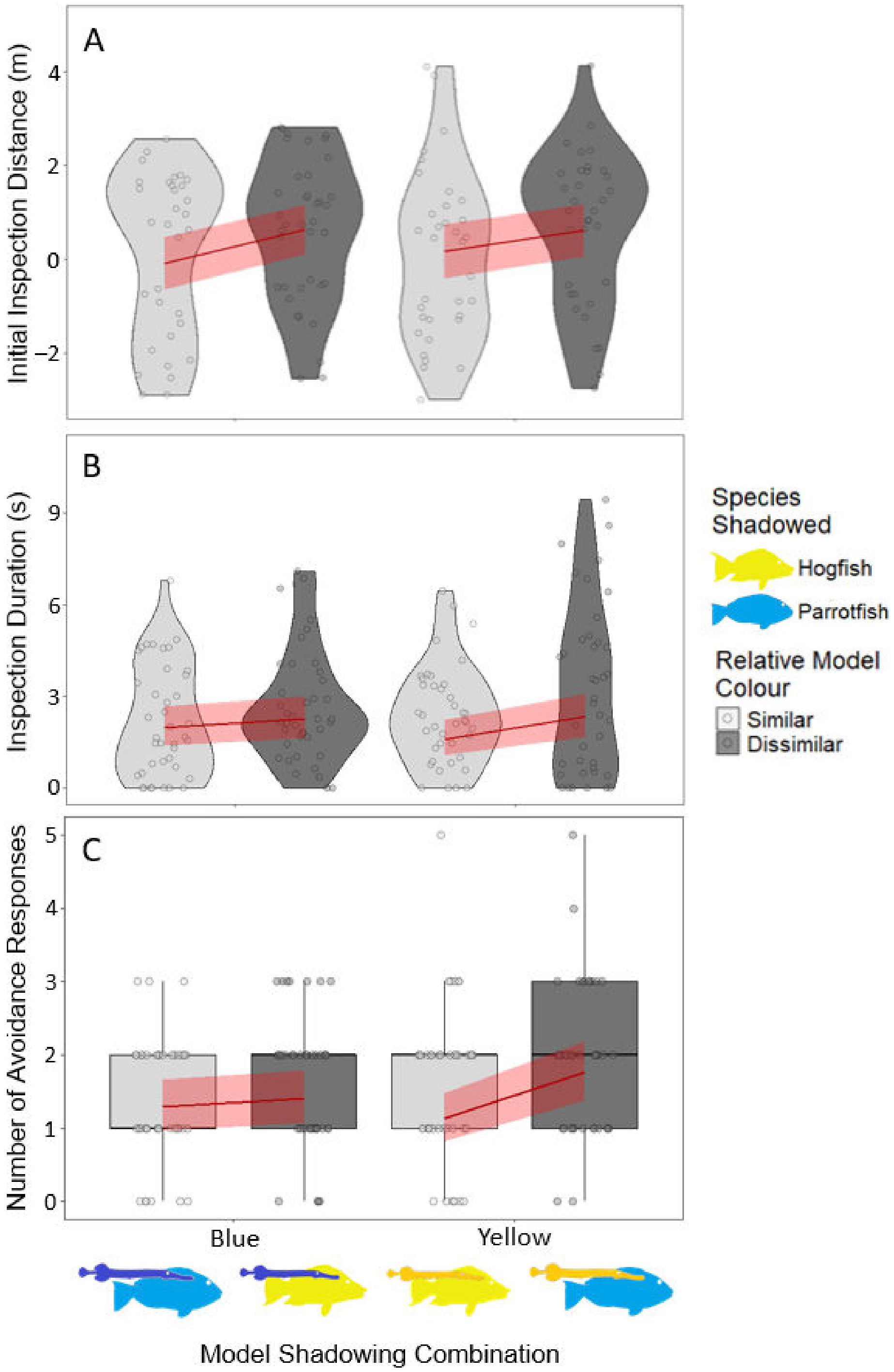

Figure 3. The distance between each shadowing trumpetfish model and the damselfish colony at the time of first inspection (A), the time spent inspecting each shadowing trumpetfish model (B) and the number of avoidance responses exhibited (C). There were four shadowing model combinations: a blue trumpetfish shadowing either a yellow hogfish or a blue parrotfish, and a yellow trumpetfish shadowing either a yellow hogfish or a blue parrotfish. For each shadowed species, one trumpetfish morph was generally similar in colour, while one was generally dissimilar. In (A), positive values indicate inspection prior to the model passing the colony, while negative values indicate inspections that occurred after the model had passed the colony. In (A) and (B), violin plot curves indicate the density of data points; the hollow circles represent the raw data points. In (C), box plots show the median and 25th and 75th percentiles, with the whiskers indicating values within 1.5 times the interquartile range and hollow circles representing the raw data points. In all cases, data points are jittered for ease of viewing. Red lines denote model-based estimates for the interaction between shadowed species and trumpetfish morph, while pink ribbons denote the 95% confidence intervals; both metrics were generated using the *ggpredict* function from the *ggeffects* package [52].

divided amongst six other species (electronic supplementary material, figure S6). Given that the parrotfish and hogfish possess similar colourations to the blue and yellow trumpetfish morphs, respectively, we asked if these morphs were selected to shadow each species more than expected given their relative abundance. Observations of yellow trumpetfish shadowing the yellow hogfish were more numerous than expected (proportion z-test: $\chi^2 = 165.59$, d.f. = 1, $p < 0.001$; figure 2), as were observations of blue trumpetfish shadowing the blue parrotfish ($\chi^2 = 69.98$, d.f. = 1, $p < 0.001$; figure 2). By contrast, the frequency of yellow trumpetfish shadowing the blue parrotfish ($\chi^2 = 0.29$, d.f. = 1, $p = 0.593$) and of blue trumpetfish shadowing the yellow hogfish ($\chi^2 = 0.85$, d.f. = 1, $p = 0.357$) did not differ significantly from expected given the relative abundance of each species (figure 2).

(b) Shadowing a similarly coloured fish improves trumpetfish concealment

Overall, irrespective of colour, shadowing trumpetfish provoked less acute anti-predator responses from the damselfish than treatments with non-shadowing trumpetfish, as demonstrated by Matchette *et al.* [27]. Specifically, shadowing trumpetfish were first inspected at a closer distance (LMM: likelihood ratio test (LRT) = 35.40, d.f. = 1, $p < 0.001$; electronic supplementary material, figure S7A) and for less time (LRT = 116.39, d.f. = 1, $p < 0.001$; electronic supplementary material, figure S7B) than non-shadowing trumpetfish. By contrast, the distance at which the first avoidance response was exhibited by damselfish did not differ significantly between shadowing and non-shadowing trumpetfish (LRT = 1.12, d.f. = 1, $p = 0.289$), although fewer avoidance responses were exhibited towards shadowing trumpetfish than non-shadowing trumpetfish (LRT = 9.56, d.f. = 1, $p = 0.002$; electronic supplementary material, figure S7C).

For shadowing treatments, the colour of the trumpetfish relative to the shadowed species influenced the magnitude and timing of damselfish responses. Specifically, there was a significant interaction between the shadowed species' colour and the trumpetfish's colour for the distance at which the colony first inspected the model (LMM: $\chi^2 = 5.83$, d.f. = 7, $p = 0.016$), the duration of time that colonies spent inspecting the 3D models ($\chi^2 = 4.16$, d.f. = 7, $p = 0.041$) and the number of avoidance responses exhibited ($\chi^2 = 5.87$, d.f. = 7, $p = 0.015$). When compared with treatments where models were dissimilar in colour, the colour-similar treatments were first inspected closer to the colony (figure 3A), inspected for less time (figure 3B) and provoked fewer avoidance responses (figure 3C). However, the distance at which the damselfish first exhibited an avoidance response did not differ between colour treatments ($\chi^2 = 0.60$, d.f. = 7, $p = 0.439$).

4. Discussion

Trumpetfish actively selected species to shadow that more closely resembled their own colouration and, when recreated with 3D models, prey responded to these combinations later and less strongly than trumpetfish combined with dissimilar models, particularly for the yellow trumpetfish morph. By enhancing their concealment, shadowing a similarly coloured species is therefore likely to improve the hunting success of mobile predators.

There are two mechanisms that may underlie the benefit of colour shadowing to trumpetfish: either the damselfish are unable to detect the trumpetfish or are unable to identify it. If misdetection acts, colour-matched shadowing may represent a novel form of motion camouflage, replicating the effect of background matching but on the move. By positioning themselves against a moving background that better matches their appearance, trumpetfish may conceal their approach while moving. Alternatively, colour-matched shadowing may alter the ability of damselfish to identify the trumpetfish, instead misclassifying it as a part of the shadowed species. This mechanism has previously been proposed for the shadowing behaviour exhibited by the soapfish, *Diploprion drachi* [25]. This would represent an unusual form of aggressive mimicry, whereby a part of an animal is mimicked rather than the whole organism [2]. Further investigation is required to tease these two mechanisms apart. In each case, to remain camouflaged, the trumpetfish needs to minimize its apparent motion relative to its background [10–14], which here is the moving shadowed species. In this way, we predict that trumpetfish may also be exhibiting some degree of motion mimicry, whereby they are controlling their speed to match that of the shadowed species so that they remain positioned next to them. Additional experiments are needed to address this and could use pneumatic or electromagnetic devices to alter the relative speeds or movement of the two species as they approach the prey. Crucially, owing to our placement of the trumpetfish on the near side of the damselfish colony, our experimental results cannot be explained by occlusion; this was previously assumed to be the mechanism by which shadowing provided an advantage [27] but, until now, had not been explicitly tested. However, occlusion may still play a significant role, especially in cases where there is a substantial colour dissimilarity between the two species, such that the relative position of the trumpetfish as it approaches (i.e. occluded or not) becomes much more important. Indeed, Matchette *et al.* [27] also demonstrated that shadowing was generally more beneficial than not shadowing, even for a brown trumpetfish shadowing a bluish parrotfish.

In our experiment, the colour shadowing effects were generally more pronounced for shadowing combinations with the yellow trumpetfish model than with the blue trumpetfish model. Yellow colours may generally be more salient to damselfish than blues, which is reflected by an increased responsiveness by the damselfish when viewing the yellow trumpetfish against the blue parrotfish. By contrast to the uniformly blue parrotfish, the yellow hogfish is not entirely yellow, with individuals possessing a purplish saddle on their dorsal side (see figure 1B), which can be variable in its shape, size and shade ([39] and SRM, personal observation, 2024). Therefore, the relative saliency of the blue trumpetfish, if viewed against this region, may be less than when viewed against the yellow parts of the hogfish, resulting in lower overall damselfish responsiveness. Similarly, the colour of the blue trumpetfish is also not uniform; the blue colouration is limited to the head and snout, while their body is typically silvery grey. This colouration may therefore lead to the blue trumpetfish being generally less conspicuous when viewed against a greater range of backgrounds, reflected in our observations of blue trumpetfish shadowing a greater number of species than yellow trumpetfish (electronic supplementary material, figure S6).

We infer that colour-matched shadowing is effective because damselfish are using chromatic rather than achromatic vision to identify shadowing trumpetfish. Differences in the chromatic contrast of trumpetfish and shadowed species aligned with the behavioural responses of the damselfish, whereas the achromatic contrast between models did not differ between shadowing combinations. This is perhaps surprising given that the detection of motion cues tends to be driven by achromatic visual mechanisms [7–9]. However, because shadowing trumpetfish are either perceptually static relative to their background or misclassified as part of the other species, colour-matched shadowing probably represents an object discrimination task, rather than the detection of a moving object. Indeed, across the animal kingdom, chromatic contrast is often more powerful than achromatic contrast for object detection and discrimination (e.g. [53–56]), particularly in environments with variable illumination like shallow marine environments [57–59]. Moreover, the motion of the shadowed species may introduce visual noise for the viewer and reduce the requirement for precise chromatic similarities. Additional resources, such as calibrated *in situ* photographs of live trumpetfish and their shadowed species, are required to complete our understanding of how prey truly perceive trumpetfish and the species that they shadow.

Shadowing behaviour appears to be most prevalent in coral reefs (e.g. [25,60]), which suggests that there are specific conditions that dictate when this strategy is adopted. For example, the predator needs to be mobile, exploring habitats that contain both opportunities to shadow (i.e. high local abundance of organisms) and a high density of different prey species. Second, the intended prey species most probably has a sufficiently good visual system (e.g. colour sensitivity and spatial resolution) that cannot be easily overcome by the predator simply approaching in isolation (i.e. not shadowing) and instead requires a further level of deception. Third, there may be physical limitations for the predator. For instance, shadowing behaviour requires a high degree of locomotive control to remain positioned next to the shadowed species on the move. Other important physical limitations include the size and shape of the predator relative to the shadowed species. While predators that are smaller than the shadowed species would benefit most (with the potential to be fully occluded), predators that have a shape that, in isolation, may be more recognizable or detectable to prey may also significantly benefit from shadowing. For example, some prey species are hypersensitive to the long thin shape of the trumpetfish [36,48], hence the latter may benefit by shadowing species that break up a considerable proportion of their silhouette. Indeed, neither the Spanish hogfish nor the terminal phase queen parrotfish typically exceeds the length of trumpetfish [29], yet shadowing interactions involving these species are very common. There may even be cognitive limitations for the predator; unlike animals that choose between habitats, where decisions are typically infrequent and involve fixed structures (e.g. inhabiting one flower versus another), selecting a species to shadow requires trumpetfish to make dynamic decisions on the move about when and whether to shadow a nearby species. Finally, the relative colouration between species adds a greater weight to these decisions for trumpetfish as they, unlike other shadowing species (e.g. cheek-lined wrasse, *Cheilinus diagrammus* [25]), are unlikely to be able to alter their chromatic appearance before or during an interaction [31] to better match the species they are shadowing (although some degree of intensity-based change is likely; SRM, personal observation, 2023). Understanding the conditions underlying the emergence of these behavioural strategies is particularly pertinent given that coral reefs are also undergoing a great degree of change and thus shadowing decisions by predators may be affected. For example, the opportunity to shadow in some coral reefs may be reduced by the large-scale removal of frequently shadowed species, such as the historic overfishing of parrotfish in the Caribbean Sea [61]. In addition, coral reefs are becoming more degraded and fragmented [62–64] and are therefore offering less physical cover to predators, which may increase the prominence of shadowing behaviour [30].

The observation that blue and yellow trumpetfish actively selected to shadow the hogfish and the parrotfish raises several questions about the mechanisms underlying species selectivity. One possibility is that individuals from each morph learn to shadow species that increase their hunting success, analogous to predators learning the colours and patterns associated with aposematic prey [65]. In this case, we would expect juvenile trumpetfish to display little to no species selectivity and instead develop shadowing preferences with experience. Alternatively, if the colouration of each morph is genetically determined, as suggested [31], then different morphs may also have inherent preferences to shadow particularly coloured species. Trumpetfish may also be selective because they can identify their own colouration and hence seek out similarly coloured species to shadow, much in the same way that some predators and prey choose backgrounds according to their own appearance (e.g. [6,66–68]). Indeed, the eyes of trumpetfish are positioned high on the head and have some degree of rotation, and therefore they may be able to see a large proportion of their snout, a region where an individual's colour is also most pronounced (SRM, personal observation, 2022). Moreover, this species is predicted to be dichromatic like the closely related [69] Indo-Pacific trumpetfish (*Aulostomus chinensis*) [70,71], and therefore their visual assessment of other fish may instead be more sensitive to achromatic differences (i.e. lighter morphs choose species that have high luminance, and *vice versa*). Whether colour shadowing is driven by learning, genetics or self-perception remains to be tested but this represents a crucial question in our understanding of how these predators select other fish to shadow. How a morph selects a species may also influence their broader ecology; if the species that each morph shadows differs in their habitat exploration, then the prey encountered (and targeted) by each morph may also differ.

Overall, our findings illustrate a novel colouration strategy that helps conceal a predator when hunting on the move. Pursuit predators face many decisions when hunting, such as where, when and how to hunt. Here, we demonstrate how the colouration of the predator itself can therefore be a major component of this decision-making process, and the consequences that these decisions may have for their foraging success.

Ethics. All procedures were approved by the University of Cambridge Animal Welfare and Ethical Review Body (OS2024/01).

Data accessibility. Data can be found on the data depository, figshare (https://figshare.com/s/931c31604b137a121afb).

Supplementary material is available online [72].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. S.R.M.: conceptualization, formal analysis, investigation, methodology, project administration, validation, visualization, writing—original draft, writing—review and editing; N.M.H.: investigation, writing—review and editing; J.S.: investigation, writing—review and editing; C.D.: investigation, writing—review and editing; S.W.: formal analysis, validation, writing—review and editing; A.N.R.: conceptualization, formal analysis, methodology, writing—original draft, writing—review and editing; J.H.-R.: conceptualization, formal analysis, methodology, supervision, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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