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Camouflage in a moving predator: testing for background choice in stalking lionfish (*Pterois miles*)

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Predation is pervasive in the natural world, where predators and prey have evolved spectacular mechanisms to avoid detection and recognition. An example is camouflage through background matching, which allows animals to resemble their background. Animals can move strategically towards backgrounds that match their morphology (background choice) to enhance camouflage. We studied the relevance of background choice in lionfish (*Pterois miles*), conspicuous stalking predators that could take advantage of background matching by resembling corals and other invertebrates in their surroundings. We offered different background combinations to hunting lionfish and we found that they indeed account for their background while hunting, although the response did not support the hypothesis that the preference is determined by background matching. Lionfish deviated towards a rocky background, which closely resembled the substrate where lionfish were caught (rocky reefs in the Mediterranean Sea). We suggest that lionfish showed a preference for a rocky background because in the Mediterranean they live on rocky reefs. While we cannot rule out that background matching played a role in background choice, we suggest that remaining close to a rocky reef while hunting offers lionfish the

best combination of easy access to hiding spots and high availability of prey.

1. Introduction

Predation is ubiquitous, as virtually every animal is either predator or prey at some moment of their life cycle. Therefore, predation has a major role in shaping animal evolution as well as ecosystems [1–7]. A predator–prey interaction can only take place after a predator detects and recognizes a prey, and both parties should benefit greatly from avoiding detection and recognition [8,9]. For a predator, being inconspicuous can delay or reduce reactions in targeted prey, increasing their success. For a prey, being inconspicuous can decrease their chances of being caught or being targeted in the first instance [10]. While empirical evidence shows that if prey are camouflaged, predators take longer to find them and are less likely to attack them [11,12], evidence showing that inconspicuousness enhances the success of predators is scarce [10,13,14]. Predators and prey can detect each other using any combination of their senses and which senses are more prominent depends heavily on the environment and ecological context [15–17]. Underwater, chemical and visual cues are the most studied in predator–prey interactions, either alone or in combination [15,17–20]. Chemical cues can be used by animals for detection from long distances and tend to be prominent in environments where light is scarce or turbidity is high. Conversely, in the (short) ranges of distances and time relevant for predator–prey interactions, visual cues tend to be more important in clear water [19,21]. Contrary to chemical cues, the sight of an animal makes it possible for prey to assess its size and properties more easily than would be possible through chemical cues [15].

Crypsis refers to any mechanism used by living organisms to interfere with detection and recognition. Owing to the importance of visual cues in predator–prey interactions, both predators and prey have evolved a spectacular suite of mechanisms to be visually cryptic. Prey that hide to avoid predator attacks [22] or have a partly transparent body [23,24] are examples of crypsis through interference with visual detection. Camouflage refers to the morphological adaptations that decrease the chance of animals to be detected or recognized [8,25–27]. In camouflage through background matching, animals resemble the background on which they live. Because the visual appearance of many animals is typically inflexible, background matching is often facilitated by background choice; animals choose their background strategically and prefer surroundings that they can match [9]. A common assumption is that background matching can be easily impaired by movement [28], unless animals move to match moving backgrounds or have colour patterns that evolved specifically to conceal motion signals [29,30]. However, many predators move while hunting. Whether this implies that they cannot camouflage through background matching remains enigmatic as studies on camouflage in predators are scarce [10,13,14].

Lionfishes of the species *Pterois miles* and *Pterois volitans* (hereafter, lionfish) are stalking predators and constantly move around the prey that they target. While hunting, lionfish slowly hover over the substrate following individual prey with their pectoral fins fully flared. Stalking can continue for several minutes and often ends with a lionfish striking on a prey from a very short distance and swallowing it whole [31]. This stalking strategy of lionfish seems unaffected by geographical range or level of prey naïveté [31–34]. The mechanisms explaining the success of hunting lionfish and how their unique morphology allows them to slowly approach prey without triggering a reaction are poorly understood [34,35]. Lionfish hunt in clear waters, either on coral reefs (Indo-Pacific and Atlantic Ocean) or on rocky reefs (Mediterranean Sea), where prey should be able to detect or recognize them visually. Understanding the stalking hunting strategy of lionfish will contribute to determining what makes them one of the most successful invasive species in the marine realm [34,35]. Although colourful and complex in appearance, lionfish could become cryptic to their prey through strategic background choices [36]. Here, we test the hypothesis that hunting lionfish make background choices that could allow them to camouflage by strategically orientating their body among colourful reef invertebrates. Testing this hypothesis is important to understand the hunting strategy of lionfish and their success as invaders across different habitats. Our experiments contribute to the study of camouflage in a moving predator and the unique hunting strategy and morphology of a highly invasive predator.

2. Material and methods

We conducted our study as two separate experiments, one in October–November 2023 (hereafter, coral-blue experiment) and one in March–April 2024 (hereafter, multiple-backgrounds experiment). The two experiments were done with two different groups of lionfish. Since the experiments were conducted completely independently and with different lionfish, we present the results separately. We used the same experimental apparatus and procedures and treated the animals in the same manner in the two experiments, unless stated otherwise.

2.1. Animals and husbandry

The lionfish *P. miles* and *P. volitans* are native to the coral reefs of the Indo-Pacific Ocean and Red Sea [37]. The two species are virtually indistinguishable in morphology and appearance and became invasive in the western Atlantic Ocean after releases and escapes from aquaria [34,38]. More recently, *P. miles* has also been invading the Mediterranean Sea after introductions from the Red Sea through the Suez Canal [35,39,40]. Invasive lionfish have spread throughout the tropical reefs of the western Atlantic and are now abundant and well established in the rocky reefs of the eastern Mediterranean [34,35]. Lionfish keep expanding their invasive ranges, both in the western Atlantic and in the Mediterranean [35,41].

We caught lionfish (*P. miles*) from the coastal waters of Crete (Greece), where they are well established as an invasive species. We did this using a combination of SCUBA and free diving with two hand nets from a maximum depth of 18 m, without anaesthetizing the fish. This resulted in two lionfish populations with a wide range of sizes (25 lionfish in the coral-blue experiment, from 14 cm to 36 cm in total length, and 25 lionfish in the multiple-backgrounds experiment, from 11 cm to 35 cm in total length). Lionfish were stocked in a rectangular communal tank (2.5 × 1.5 × 1.5 m) at the Hellenic Centre for Marine Research, Gournes, Greece. The tanks had a constant inflow of water (temperature 18–20°C, salinity 35 mg l^{-1}, pH 7.4) provided by a borehole and a constant outflow which maintained the water level constant (1.36 m during stocking). The tanks were located outside, under a natural photoperiod of approximately 12 and 11 hours of daylight at the beginning of the coral-blue and multiple-background experiment, respectively. The photoperiod gradually changed to reach approximately 10 (coral-blue experiment) and 13 (multiple-background experiment) hours of daylight at the end of the experiments owing to seasonality.

At capture, we assigned an identity to each lionfish following an established methodology based on analyses of their unique barred pattern [42]. The lionfish were fed daily with gilt-head seabream (*Sparus aurata*) provided by a local fish hatchery (for coral-blue experiment: mean total length = 5.6 cm, n = 50, s.d. = 0.5 cm and mean total weight = 3.4 g, n = 50, s.d. = 0.6 g; for multiple-backgrounds experiment: mean length = 5.0 cm, n = 20, s.d. = 0.5 cm and mean total weight = 2.0 g, n = 20, s.d. = 0.6 g). Seabream were stocked in a separate cylindrical tank that received water from the same source as the lionfish tank and were fed daily with commercial pellet. The same seabream (hereafter, prey) used for feeding were used as prey during the experiments.

2.2. Experimental apparatus

After two weeks of acclimation, we placed an experimental apparatus in one of the corners of the tank (figure 1a). The apparatus (figure 1b) consisted of two panels (70 × 50 cm) that allowed us to present combinations of different background combinations to hunting lionfish. We used three patterns on the panels: blue, coral and rock (figure 1c). The patterns were two-dimensional, printed representations of corals and rocks in natural size. A frame of PVC pipes at the bottom of the tank ensured that the panels were held at the same distance and angle throughout the study. During trials, a prey was presented at the end of the apparatus inside a clear jar 8 cm in diameter. The jar was added to or removed from the tank through ropes that could be handled from the side of the tank. We used white pebbles at the bottom of the jar to ensure that it sank and remained stable during a trial. The distance between the entrance of the apparatus and the centre of the prey jar was 80 cm. We placed a white bar at the bottom of the tank to connect the centre of the entrance with the closest part of the prey jar. This white bar marked the closest approach trajectory to the prey jar and had marks every 20 cm to facilitate measurements and calibrations during video analysis.

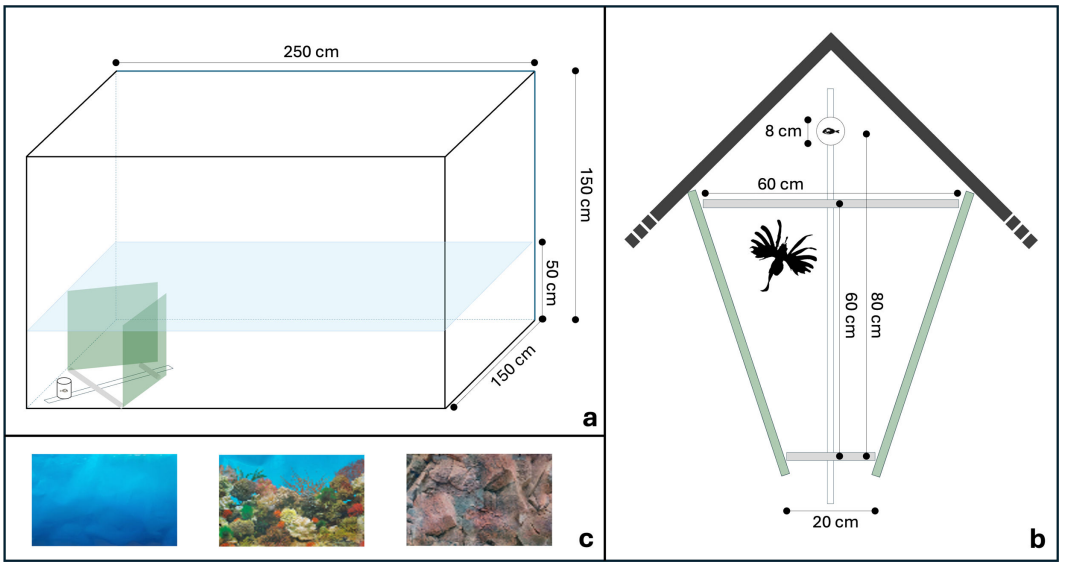

Figure 1. Overview of the tank during the experiments (a), measurements and position of the experimental apparatus (b), and patterns used as backgrounds (c).

The patterns were presented in three background combinations: coral-blue, rock-blue and coral-rock. In the coral-blue experiment, we only tested the combination coral-blue, while in the multiple-backgrounds experiment, we tested all three combinations. Each combination was presented over the course of multiple days, using the same image in each treatment. Within each combination, we randomized the side on which each pattern was presented across days. This was done to correct for any laterality in our fish or potential other unknown environmental features that may have affected the lionfish trajectory in the apparatus.

We predicted that hunting lionfish adjust their approach trajectory to present themselves against backgrounds that match their morphology and coloration. Specifically, we expected lionfish to deviate consistently towards coral backgrounds, regardless of the alternative. In choosing our backgrounds, we did not account for the visual system of prey owing to the large variety of prey that lionfish feed on [31,43]. We could therefore not measure quantitatively which backgrounds could be best for lionfish to camouflage. Rather, we chose the patterns because they represent realistic backgrounds that lionfish can have while hunting in nature: coral reefs in their native range and the invaded western Atlantic, rocky reefs in the invaded Mediterranean and open water present in any range. We also tested for any effect that might be simply owing to colour preference by analysing two additional colour combinations: blue-black and coral-black (see the electronic supplementary material).

2.3. Experimental procedures

At the start of an experimental day, we lowered the water level to 50 cm in preparation for the experiments. Preliminary observations ensured that changes in water level did not affect the behaviour of the animals. In this way, lionfish could only enter the apparatus through the entrance. We then lowered the prey jar into the apparatus and waited for a lionfish to enter. A trial started the moment a lionfish (focal lionfish) entered the apparatus. In the cases when another lionfish approached the apparatus while the focal lionfish was approaching a prey, we placed a metal net (gate) at the entrance to prevent the second lionfish from entering and interfering with the trial. Lionfish are typically not impacted by manipulations in their surroundings. However, to exclude any interference with the swimming trajectory, the gate was only lowered after the focal lionfish reached the middle length of the apparatus (i.e. approx. 40 cm). In pilot trials, we found that this operation did not interfere with the behaviour of focal lionfish and prey. A trial ended when the focal lionfish struck on the plastic jar, when it lost interest in the prey, or after 5 min from the start of the trial. We defined loss of interest based on the position and orientation of the pectoral fins of the focal lionfish, flared and perpendicular to the body of the fish when hunting and parallel to its body when not hunting. At the end of a trial, we removed the prey jar from the apparatus and filmed the focal lionfish on either side with a camera on a PVC handle for individual identification. After filming, we gently guided the lionfish outside of

the apparatus. Before any subsequent trial, we replaced the prey in the jar with a new individual that had never been involved in the experiments. Every trial was filmed by a camera (GoPro Hero 7 Black) held on top of the apparatus by a PVC frame. The same camera model was used for the videos for individual identification at the end of a trial.

2.4. Video analyses

We analysed a total of 273 trials (80 in the coral-blue experiment and 193 in the multiple-backgrounds experiment). This was after filtering the videos and discarding trials that were unsuitable to analyse (46 in the coral-blue experiment and 18 in the multiple-backgrounds experiment). We decided to discard a video whenever it was impossible to identify the focal lionfish or whenever there was some accidental misalignment or malfunction in some of the elements of the apparatus. The videos were analysed with the free, open-source software Tracker (v. 6.1.5), and the identification of our individuals was done visually from the individual identification videos [42]. For every trial, we determined the position of the lionfish in the apparatus in an X–Y coordinate system: X represents the position of the lionfish along the reference bar and Y represents the orthogonal distance of the lionfish from the bar. We determined the lionfish X and Y coordinates every 1 s of video (measurement points), starting from the moment a lionfish entered the apparatus. These measurements were taken based on the midpoint of a line connecting the lionfish eyes. The Y position was then standardized by interpolation at the following X coordinates: 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 55, 60, 65, 70 and 75 cm. This was done to ensure that we had Y measurements that were equidistant along the X-axis (one every 5 cm) and that every trial had the same maximum number of data points (i.e. 15 X coordinates and corresponding Y coordinates). We also measured the body orientation of the lionfish, defined as the angle between the main axis of the lionfish body and the reference bar. Data on the lionfish's body orientation were collected and interpolated in the same manner as Y coordinates. For each measurement point of lionfish position, we also scored Y coordinate of the prey inside the jar.

2.5. Statistical analyses

We analysed whether approaches deviated significantly from the shortest approach trajectory: a lionfish swimming straight towards the prey along the reference line. We tested this on the interpolated Y values and body angles for each X value to test whether they significantly deviated from 0. In the multiple-backgrounds experiment, analyses were done separately for each background combination. Y coordinates were first corrected for the Y coordinate of the prey inside the jar, which was subtracted from the Y value of the lionfish to calculate the lionfish's relative Y coordinate. For each response variable and background combination, we fitted a generalized linear mixed model with X coordinate as a fixed predictor and lionfish identity random predictor. When appropriate, we added an interaction term between the X coordinate and lionfish identity (random slope) and the random effect of trial (nested in lionfish identity) [44]. We used the models to make predictions on our response variables and considered these statistically significant if their 95% confidence interval (CI) did not overlap with 0. We used R 4.4.1 [45] for all statistical analyses and data visualizations.

3. Results

In the coral-blue experiment, we observed 17 lionfish participating in 80 trials. Lionfish only deviated significantly from the shortest trajectory towards the prey jar at the end of their approach (1.06 cm at X = 70, CI: 0.00, 2.13) but changed their body orientation at multiple points in their trajectory (2.03° at X = 40, CI: 0.26, 3.83; −3.03° at X = 65, CI: −4.84, −1.27; −5.30° at X = 70, CI: −7.36, −3.27) (figure 2). In the multiple-backgrounds experiment, we observed 22 lionfish participating in 193 trials. For most background combinations, lionfish did not deviate significantly from the shortest trajectory towards their prey (figure 3). When given the choice between coral and rock, lionfish deviated towards rock (−1.56 cm at X = 5, CI: −2.76, −0.40; −1.78 cm at X = 10, CI: −2.96, −0.62; −2.03 cm at X = 15, CI: −3.18, −0.87; −2.26 cm at X = 20, CI: −3.43, −1.09; −2.30 cm at X = 25, CI: −3.47, −1.14; −2.36 cm at X = 30, CI: −3.53, −1.21; −2.17 cm at X = 35, CI: −3.36, −1.01; −1.99 cm at X = 40, CI: −3.15, −0.83; −1.85 cm at X = 45, CI: −3.05, −0.69; −1.55 cm at X = 50, CI: −2.73, −0.41; −1.34 cm at X = 55, CI: −2.54, −0.16) and changed their body angle towards coral (2.81° at X = 30, CI: 0.23, 5.29; 3.07° at X = 35, CI: 0.46, 5.74; 3.18° at X =

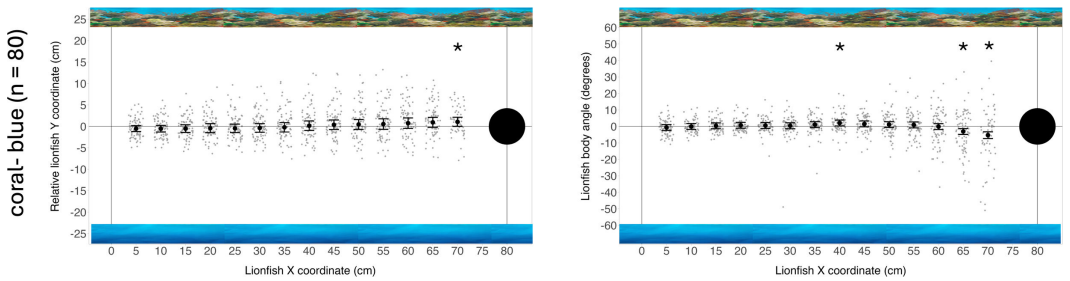

Figure 2. Deviations in relative distance (left) and body angle (right) from closest approach trajectory in lionfish approaching prey in the coral-blue experiment. The black circle at $X = 80$ represents the prey jar, and the grey dots show the (jittered) raw data of the relative Y coordinate and body orientation of lionfish at every X value. The black dots show the model predictions with their 95% CIs, and asterisks highlight confidence intervals that do not overlap with 0.

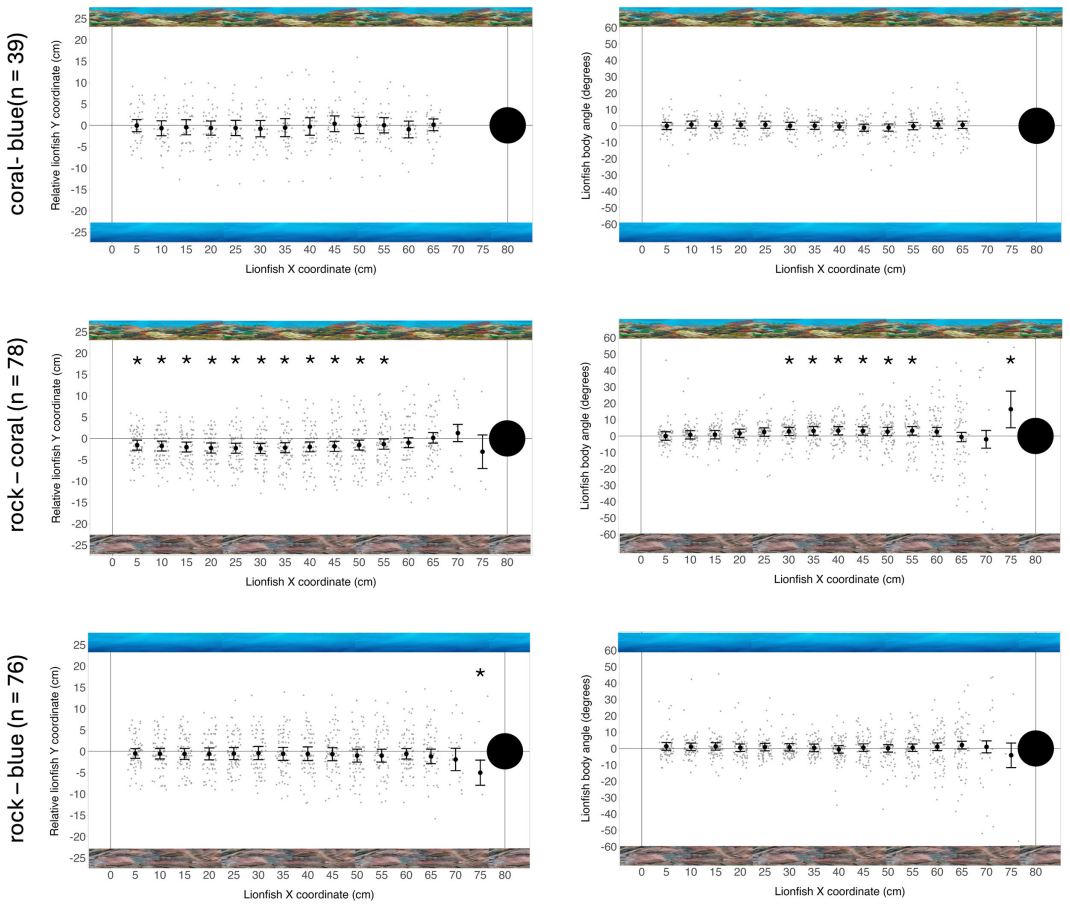

Figure 3. Deviations in relative distance (left) and body angle (right) from closest approach trajectory in lionfish approaching prey with different background combinations in the multiple-backgrounds experiment. The black circle at $X = 80$ represents the prey jar, and the grey dots show the (jittered) raw data of the relative Y coordinate and body orientation of lionfish at every X value. The black dots show the model predictions with their 95% CIs, and asterisks highlight CIs that do not overlap with 0.

40, CI: 0.57, 5.72; 3.06° at $X = 45$, CI: 0.50, 5.62; 2.63° at $X = 50$, CI: 0.10, 5.24; 3.19° at $X = 55$, CI: 0.53, 5.75) (figure 3). Similarly, lionfish deviated towards rock at the end of their approach when given the choice between blue and rock (−5.03 cm, CI: −7.96, −2.07 at $X = 75$; figure 3). Additional comparisons showed no drastic differences in coral-black and blue-black combinations (see the electronic supplementary material).

4. Discussion

We analysed the trajectory of lionfish approaching prey with different background combinations and found that lionfish adjust their trajectory according to their surroundings. Contrary to our predictions, lionfish did not deviate consistently towards a colourful and complex coral background but deviated towards a rocky background when the alternative was a coral background and showed no consistent deviations with other background combinations. Lionfish showed no consistent changes in trajectory when they had a choice between blue and black background or between a coral and a blue or black background, suggesting that colour and pattern complexity by themselves do not explain the deviations observed in our experiments.

We suggest that deviations towards rocky backgrounds are driven by a preference for the substrate that the lionfish in our study were most familiar with. We caught lionfish in the Mediterranean, and our individuals had no experience with corals or similarly colourful structures [46–48]. In the Mediterranean, hunting close to rocks is probably favourable for lionfish as their prey are found on this substrate, which they typically move towards to seek shelter from predators [46,47,49]. In addition, lionfish are almost exclusively found on rocky habitat in the Mediterranean, usually partly hidden in crevices [42]. Remaining close to potential hiding places offered by rocks could be a way for lionfish to protect themselves from potential predators through hiding. There is a paucity of information on what predators lionfish may have, and they are unlikely to be preyed upon as adults [34,35]. This suggests that higher prey availability and proximity to hiding places offered by rocky reefs is probably why lionfish deviated towards rocky backgrounds in our experiments.

We conducted our experiments in the daylight and at 50 cm depth. In the wild, lionfish are crepuscular hunters and often live and hunt at depths deeper than 10 m [31,34,50,51]. In these conditions, light intensity and colours are altered by water selectively filtering out different wavelengths at different depths. In particular, the red component of the light spectrum is almost completely filtered out from depths of 10 m and the characteristic red bars of lionfish tend to acquire a brown or dark grey tone [36,52]. Therefore, in natural circumstances, a rocky reef with swaying algae could offer lionfish more opportunities to camouflage than the blue open sea. In our experiment, it is possible that lionfish showed a preference for the background that would allow them to best camouflage in the wild (i.e. grey rocks, as opposed to colourful corals or blue). This aspect could be tackled in future experiments by analysing the reaction (or lack thereof) of prey when approached by lionfish with backgrounds of the same structural complexity, but different colour compositions reflecting those found at different depths. In future experiments, the choice of backgrounds could account for the visual system of prey and should include more than one pattern per treatment to control for any reaction that predator or prey might show against a specific pattern.

There may be mechanisms other than background matching making lionfish visually cryptic to prey. For instance, rather than specifically matching their background, lionfish could resemble inanimate objects such as algae or coral branches drifting in the current (mimicry). This would allow them to be successful regardless of their background and could explain their success across habitats and ranges [31,50,53]. If lionfish were heavily relying on camouflaging with coral backgrounds, they would not be as successful in the eastern Mediterranean, where structurally complex corals are rare or absent at depths shallower than 30 m [46–48]. In addition, given the preference of lionfish for demersal and benthic prey [31,43,49,54], it is likely that lionfish are seen against the blue background of the open sea by most of their prey in natural situations, and mimicking floating objects can be predicted to be more effective than background matching in this type of scenario as well. It is challenging to test for the relevance of mimicry experimentally, since it is usually impossible to determine whether a prey detected a predator without recognizing it or did not detect it in the first place [55]. This challenge is especially important in a context where prey are naïve to lionfish and are likely to not recognize them as a threat, even when detected [31].

Our study contributes to investigating camouflage in motion: lionfish move as they approach their prey through their stalking strategy [31,50], a different strategy from that of ambush predators such as scorpionfishes found in their same family (Scorpaenidae) [36,56,57]. Theory suggests that movement can easily break camouflage [9] and this could explain why lionfish did not deviate towards the most colourful and complex backgrounds in our experiments; camouflage through background matching is not effective in a fish that, while hunting, moves relatively to its background. There is evidence suggesting that stick insects (*Extatsoma tiaratum*) can enhance their camouflage by moving, since they match the movement pattern of the twigs on which they live [29]. While marine invertebrates do sway

under the action of currents, this is a rhythmic movement that may simply be too different from a lionfish swimming in a trajectory that follows that of their prey. In our experiments, the backgrounds were not moving, but future experiments could investigate the effect of moving corals on the hunting strategy of lionfish. This could be done either by using real or realistic imitations of invertebrates in a context where different currents can be applied or by presenting backgrounds in a virtual reality apparatus where the movement of structures can be manipulated [58].

A mechanism that has been suggested to apply specifically to camouflage in motion is motion dazzle: high-contrast patterns composed of repeated elements such as lines or stripes may help animals camouflage when they are moving [9,59,60]. Clear examples of such patterns in the natural world are lionfish bars and zebra (*Equus zebra*) stripes, which seem to make these animals conspicuous in their environments but could make them more difficult to detect when they are moving. Experiments with humans suggest that the trajectory and speed of moving objects is more difficult to determine compared to that of moving objects with a uniform colour pattern [59,60]. This could make it difficult for prey to determine whether a lionfish is approaching them and at what speed. Motion dazzle could also explain the unusual colour pattern of lionfish, which differs markedly from that of sit-and-wait scorpionfishes known to rely on camouflage [56,57]. Virtual presentations of lionfish with different colour patterns could exploit the lionfish-prey system as a model to investigate this fascinating mechanism from the perspective of a predator [61,62]. Similar to mimicking floating objects, motion dazzle could work regardless of lionfish surroundings.

Finally, our experiments differ from others in that we looked at camouflage as a mechanism that can increase success in predators. Experiments on other animals (including predators) tend to look at camouflage from the perspective of animals trying to evade predation [63–65]. However, theory suggests that predators and prey could both benefit from camouflage [8]. This area of study deserves more experiments and dedicated experimental set-ups, ideally on animals that are both predator and prey, to disentangle the relative importance of camouflage in becoming better at preying as opposed to evading predation [14,66].

In conclusion, lionfish account for their background when hunting and change their approach trajectory towards their prey depending on available backgrounds. The main factor underpinning these changes in trajectory could be a preference in lionfish to hunt close to the substrate that they are most familiar with, which could offer them better foraging opportunities and lower risk of predation. Future experiments should test for alternative mechanisms that prevent detection and recognition in lionfish prey such as mimicking floating objects and motion dazzle. These studies will help elucidate how the unique appearance of lionfish evolved and what makes them so successful at interacting with their prey. Experiments like these are paramount to pinpoint what makes such a great predator and what allows lionfish to be so successful at predation and invasion across contexts. In addition, studying these mechanisms will give insights into the potential benefits of camouflaging as a predator and on camouflage in moving animals, two fields of study that can benefit from more empirical evidence.

Ethics. Capture of live lionfish by SCUBA and free divers was allowed by the local authorities through a sample collection permit (permit number: 6ΡΔΛ4653Π8-Ι9Ρ). Maintenance of wild lionfish in captivity and experiments on their interactions with prey was approved by the ethics committee of the Hellenic Centre for Marine Research (permit number: 121/29.08.2023).

Data accessibility. The data sets and R script can be accessed on Dryad [67].

Supplementary material is available online [68].

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

Authors' contributions. D.B.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, supervision, validation, visualization, writing—original draft, writing—review and editing; C.N.: conceptualization, data curation, formal analysis, methodology, software, writing—review and editing; V.R.: conceptualization, data curation, formal analysis, methodology, software, writing—review and editing; G.S.: project administration, resources, supervision; T.D.: project administration, resources, supervision; M.M.: resources, writing—review and editing; S.C.: resources, writing—review and editing; A.K.: conceptualization, project administration, supervision, validation, 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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