Current Biology
Magazine

CellPress

Correspondence

Predatory trumpetfish conceal themselves from their prey by swimming alongside other fish

Samuel R. Matchette[1,*],
Christian Drerup[1],
Isla Keesje Davison[2],
Stephen D. Simpson[2],
Andrew N. Radford[2],
and James E. Herbert-Read[1,3]

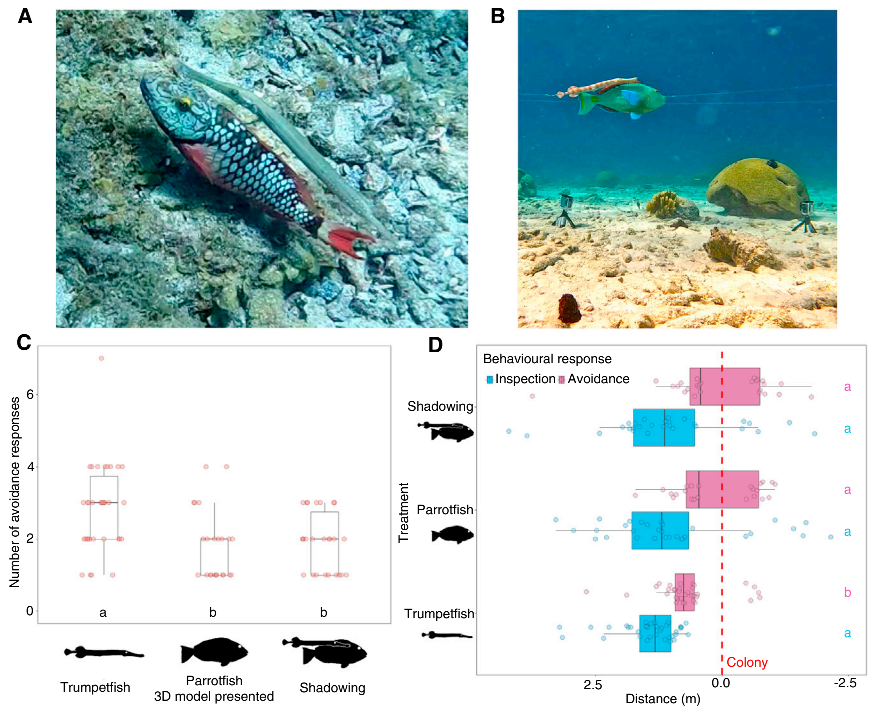

Figure 1. Trumpetfish exhibiting ‘shadowing’ behaviour and the primary measures of damselfish behaviour.
(A) A trumpetfish (top) shadowing a parrotfish (below). (B) A screenshot from an experimental trial: the shadowing trumpetfish treatment (a 3D model of a trumpetfish attached to the side of a 3D model of a parrotfish) is reeled past a colony of bicolour damselfish. (C) The number of avoidance responses exhibited by damselfish in a given trial (n = 36) when presented with each model treatment. Letter labels below the boxes denote the pairwise comparisons between treatments, whereby treatments with the same letter do not statistically differ. (D) The distance from the colony to the model (in metres) when the *first* inspection (blue) and avoidance (pink) responses were exhibited. The dashed red line represents the location of the colony relative to responses: positive distances denote responses that occur *before* the model has reached the colony whereas negative distances denote responses that occur *after* a model has passed by. As seen in panel C, letter labels on the right-hand-side in panel D denote the pairwise comparisons between treatments for their observed inspection (blue letters) and avoidance (pink letters) distances. The box plots in panels C and D show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range. The hollow circles represent the raw data points.

Many animals use camouflage to avoid detection by others, yet even the most inconspicuous objects become detectable against the background when moving[1,2]. One way to reduce detection while moving would be to ‘hide’ behind the movements of objects or other animals[3]. Here, we demonstrate experimentally that a common marine predator, the trumpetfish (*Aulostomus maculatus*), can conceal its approach from its prey by performing a behaviour known as ‘shadowing’ — swimming closely next to another, larger and non-predatory fish[3–5]. Our findings reveal how predators can actively use another animal as a form of concealment to reduce detection by prey.

There are few mechanisms by which organisms can minimise the salience of their movement[1,2]. Some animals move in a way that mimics the motion of nearby objects such as vegetation (for example, swaying behaviour), whereas others use illusory body patterns to reduce their likelihood of capture[1,2]. An alternative approach to conceal movement, which has received little attention, is for animals to maximise their visual occlusion by ‘hiding’ behind other moving objects[3]. Whereas a fully occluded animal remains largely undetectable, partially occluded animals may also benefit from this form of concealment by being less recognisable. In habitats where there are opportunities for animals to use other moving animals to hide behind, this could help conceal their movement from onlookers. In principle, this strategy is not limited to prey hiding from predators but could also benefit predators that aim to stealthily approach their prey.

On coral reefs, several predatory species of fish exhibit a behaviour referred to as ‘shadowing’[6], also termed ‘riding’[3] or ‘aligning’[5], whereby an individual swims very closely alongside a larger heterospecific. Unlike nuclear hunting events, where groups of predators follow one another for increased access to prey[6], shadowing behaviour often involves a predator swimming alongside a non-predatory species[7]. The most documented example of shadowing behaviour is by the trumpetfish, a common piscivore found across Caribbean coral reefs that often follows herbivores such as parrotfish[3–5] (Figure 1A and Video S1). Shadowing behaviour has been suggested to enable a trumpetfish to remain concealed alongside the other animal as it approaches its prey[3,5,6,8], thus reducing its potential striking distance, but this proposed function has never been tested.

To test experimentally if shadowing behaviour allows trumpetfish to approach their prey more closely without being detected, we generated multiple 3D models of trumpetfish and a frequently shadowed species, the stoplight parrotfish (*Sparisoma viride*; Figure S1A), that were presented *in situ* to a common trumpetfish prey species, bicolour damselfish (*Stegastes partitus*). These damselfish form highly localised colonies within structures on the reef substrate and exhibit characteristic anti-predatory responses[6]. Thirty-six colonies (mean ± SD number of fish per colony = 9 ± 6) were used across three locations (12 colonies per location) in Curaçao, Netherland Antilles; colonies at each location were at least 15 m apart. Each colony received three treatments in a randomised block design: a trumpetfish (non-shadowing), a parrotfish (non-predatory) and a combination of the two (a trumpetfish attached to the side of a parrotfish, i.e., shadowing) (see Supplemental information). 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 in the process, which was positioned halfway between the two (Figure 1B and Figure S1B). Using videos and a stereocamera setup, we quantified common antipredator responses of the damselfish to these passing models.

Overall, damselfish behavioural responses towards a shadowing trumpetfish more closely resembled those towards a non-predatory parrotfish than those towards a non-shadowing trumpetfish. Specifically, shadowing trumpetfish were inspected for a shorter duration (t.ratio = 10.44, df = 58.4, $p < 0.001$; Figure S1C), inspected by a smaller proportion of each colony (t.ratio = 11.69, df = 82, $p < 0.001$; Figure S1D), and induced fewer avoidance responses (t.ratio = 3.91, df = 55, $p < 0.001$; Figure 1C) compared to the non-shadowing trumpetfish; there were no significant differences in responses compared to the parrotfish treatment (Data S1A). In addition, although the distance at which the first inspection event was observed did not differ significantly between treatments (LMM: LRT = 4.53, df = 2, $p = 0.104$; Figure 1D), treatment did have an effect on the distance at which the first avoidance response was observed (LRT = 9.20, df = 2, $p = 0.010$; Figure 1D); damselfish showed avoidance behaviour to the shadowing trumpetfish when it was closer to the colony compared to the non-shadowing trumpetfish (t.ratio = 2.45, df = 56.5, $p = 0.045$; Data S1A).

Our experimental results indicate that shadowing behaviour likely reduces detection of trumpetfish by their prey, allowing trumpetfish to approach closer to prey before provoking an avoidance response. Although the exact mechanism behind the reduced responses of prey to shadowing trumpetfish remains unknown, we predict that either the partial or total occlusion of the trumpetfish by the shadowed fish reduces the ability of prey to detect the trumpetfish, although other mechanisms including distraction or misclassification may also operate. Given that visual search strategies typically involve the detection of specific animal features (for example, body outline), visual occlusion will have a significant influence on an animal's success when searching for predators or prey. Although the use of physical visual cover (such as rocky outcrops, vegetation) will often be crucial for predators' foraging success[9], the use of other animals may serve as an important alternative concealment strategy when cover is unavailable. Indeed, trumpetfish are more often observed shadowing than hunting alone in less structurally complex habitats[7]. Given the global degradation of coral reefs[10], we may therefore expect an increase in such foraging strategies. Although we provide evidence that shadowing can serve to conceal trumpetfish from their prey, the benefits of this behaviour may be multi-faceted. For example, if the shadowing species is a small mesopredator, then these animals may also profit from being less detectable by their own predators while shadowing[3]. The same mechanism may also be used to reduce detection from aggressive or highly territorial species. Overall, our study demonstrates how animals can use other animals for visual concealment, and further illustrates the diversity of strategies that have evolved in predator–prey arms races.

SUPPLEMENTAL INFORMATION

Supplemental information includes experimental procedures, data availability links, author contributions, one figure, one dataset, and one video and can be found with this article online at https://doi.org/10.1016/j.cub.2023.05.075.

ACKNOWLEDGEMENTS

This project was funded by the Whitten Programme in Tropical and Aquatic Biology, the Fisheries Society of the British Isles (FSBI-RG21-208), and the Association for the Study of Animal Behaviour. S.M. was supported by the Office of Naval Research Global (N62909-21-1-2005). We would like to thank Simon Chen for 3D printing guidance, the Marine Behavioural Ecology Research Group for useful discussion, and four anonymous referees for their helpful comments. We would also like to thank Prof. Mark Vermeij (CARMABI, Curaçao) and the staff at B Diving (Playa Cas Abou, Curaçao) and The Dive Shop (Piscadera Bay, Curaçao) for their on-site support.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

We support inclusive, diverse, and equitable conduct of research.

REFERENCES

1. Stevens, M., and Ruxton, G.D. (2019). The key role of behaviour in animal camouflage. Biol. Rev. *94*, 116–134.
2. Cuthill, I.C., Matchette, S.R., and Scott-Samuel, N.E. (2019). Camouflage in a dynamic world. Curr. Opin. Behav. Sci. *30*, 109–115.
3. Ormond, R.F.G. (1980). Aggressive mimicry and other interspecific feeding associations among Red Sea coral reef predators. J. Zool. *191*, 247–262.
4. Eibi-Eibesfeldt, T. (1955). Über Symbiosen, Parasitismus und andere besondere zwischenartliche Beziehungen tropischer Meeresfische. Z. Tierpsychol. *12*, 203–219.
5. Aronson, R. (1983). Foraging behavior of the west Atlantic trumpetfish, *Aulostomus maculatus*: use of large, herbivorous reef fishes as camouflage. Bull. Mar. Sci. *33*, 166–171.
6. DeLoach, N., and Humann, P. (1999). Reef Fish Behavior: Florida, Caribbean, Bahamas First (Jacksonville, FL: New World Publications).
7. Matchette, S.R., Mitchell, E.G., and Herbert-Read, J.E. (2022). Spatial clustering of trumpetfish shadowing behaviour in the Caribbean Sea revealed by citizen science. Mar. Biol. *169*, 1–9.
8. Lukoschek, V., and McCormick, M.I. (2000). A review of multi-species foraging associations in fishes and their ecological significance. Proc. Ninth Int. Coral Reef Symp. *I*, 467–474.
9. Cresswell, W., Lind, J., and Quinn, J.L. (2010). Predator-hunting success and prey vulnerability: Quantifying the spatial scale over which lethal and non-lethal effects of predation occur. J. Anim. Ecol. *79*, 556–562.
10. Alvarez-Filip, L., Paddack, M.J., Collen, B., Robertson, D.R., and Côté, I.M. (2015). Simplification of Caribbean reef-fish assemblages over decades of coral reef degradation. PLoS One *10*, e0126004.

[1]Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK. [2]School of Biological Sciences, University of Bristol, Bristol BS8 1TQ, UK. [3]Department of Biology, Lund University, Lund 223 62, Sweden.
*E-mail: sammatchette@gmail.com (S.R.M.)