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Starfish Capture Crabs by Standing on Tiptoe without Apparent Attractive Signaling

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Abstract

Predator–prey interactions are strongly influenced by the relative mobility of the two parties, as mobility determines the strategies available to predators. Predators that are slower than their prey often rely on alternative strategies, such as mimicking non-threatening objects or actively attracting prey. The blue bat star *Patiria pectinifera* uses a distinctive "standing-on-tiptoe" posture to capture the crab *Gaetice depressus*, a species that moves faster than the starfish. To investigate whether *P. pectinifera* uses signals that attract crabs, we observed crab behavior toward starfish exhibiting the tiptoe posture with their behavior toward a slowly elevated stone tile. If starfish use signals, crabs are expected to enter beneath starfish more frequently than beneath a stone tile. Unfortunately, although there are several differences in the experimental conditions between the two treatments, in stone-tile trials, 10 of 25 crabs (40%) entered the space beneath the tile, whereas in starfish trials, 10 of 30 crabs (33%) entered the space beneath the starfish. These results imply that starfish in the tiptoe posture might not lure crabs by using attractive signals. In this context, the tiptoe posture of *P. pectinifera* might represent a form of aggressive masquerade primarily operating in a predatory context.

Key words : Camouflage, Foraging tactics, Predator-prey interaction, Sea star

The relative mobility of predators and their prey strongly influences the strategies predators employ to capture prey (Scharf et al., 2006 ; Moore and Biewener, 2015 ; Smith and Ruxton, 2020). Faster predators may rely on direct pursuit, whereas slower predators must adopt alternative tactics—morphological, chemical, or behavioral—to compensate for reduced mobility. For example, the leaf fish *Monocirrhus polyacanthus* mimics a drifting leaf to ambush prey (Catarino and Zuanon, 2010). Anglerfishes attract prey using lures resembling small fishes (Pietsch and Grobecker, 1978).

We previously observed that the starfish *Patiria pectinifera* captured the shore crab *Gaetice depressus*, despite moving much more slowly (Gushiken and Wada, 2024). During these interactions, the starfish displayed a distinctive "standing-on-tiptoe" posture, elevating its central disk on the extended tips of its arms after contact with the crab (see Results). Crabs that moved beneath the disk were captured. Why crabs enter this vulnerable position is unclear ; they may misidentify the posturing starfish as a non-threatening object (e.g., crevice), or the starfish may emit signals that attract crabs (e.g., food-like chemical cues or tube-foot movements). Here, we tested these two hypotheses by observing crab responses to *P. pectinifera* in the tiptoe posture and their responses to a slowly elevated stone tile. If starfish use signals, crabs are expected to enter beneath starfish more frequently than beneath a stone tile.

To test crab responses to starfish, we collected 47 individuals of *P. pectinifera* (arm length 54.3 ± 4.0 mm [mean ± SD]) and 235 individuals of *Gaetice depressus* (carapace width 11.9 ± 1.7 mm) from May to July 2023 from a rocky shore at Kattoshi, Hakodate Bay, Japan (41°44′N, 140°36′E). The study site consists of a mosaic of gravelly areas, exposed bedrock, and boulder fields. In particular, the boulder fields contain interstitial spaces of various sizes formed by stones, which serve as refuges for the crab *G. depressus*. *The crabs* are frequently found in gravelly and bedrock areas, and the starfish are also most commonly observed in these habitats. Thus, the habitats of the two species overlap extensively, and individuals of both species are observed in close proximity in the field.

Starfish were housed individually in aquaria (L 310 × W 155 × H 225 mm ; glass walls with white plastic bottoms) filled with seawater collected from the study site and held unfed for three days. Crabs were maintained communally in a separate aquarium under the same conditions (15°C, continuous LED illumination). For starfish trials, five crabs were introduced in an aquarium containing a starfish, and behavior was recorded from above for 99 h using a 1-s interval time-

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lapse video (GZ-R480, JVC) (n = 47 replicates). We recorded (1) whether the starfish initiated tiptoe posture in contact with a crab, (2) duration of the posture, (3) whether the crab entered beneath the disk, and (4) whether prey capture occurred. Maximum movement speeds for the two species in 310-mm aquarium sections were estimated from a random subset of videos (4 of 47 videos per species).

To test crab responses to an inanimate object, we used a square stone tile (L 95 × W 95 × H 9 mm) that could be lifted at one end by pulling an attached thread (Fig. S1). Twenty-five crabs (carapace width 13.1 ± 1.6 mm) were tested individually in July 2025 in aquaria (L 207 × W 139 × H 93 mm ; blue plastic walls and bottoms) filled with seawater collected from the study site. After a 2 min acclimation period, the tile was slowly raised over 10 s once a crab had remained in contact with it for 5 s. We recorded whether the crab entered the space beneath the tile within 10 min.

In starfish trials, we recorded 59 tiptoe postures from 47 starfish. Of these, 30 were initiated during direct contact with a crab, and 29 occurred without contact. Thus, direct contact was not required to elicit the posture. The mean posture duration was 44.4 ± 57.9 min (n = 59). The mean time until capture was 15.4 ± 13.8 min (n = 11) from elevating its central disk. Crabs entered the space beneath the starfish in 14 of the 30 contact-initiated postures (Fig. 1), compared with only 1 of the 29 postures initiated without contact. Of the 11 successful captures, 10 followed contact-initiated postures. Starfish movement was far slower than that of crabs (1.44 ± 0.23 mm/s vs. 34.38 ± 2.08 mm/s, n = 4 for each species), confirming that crabs would likely outrun pursuing *P. pectinifera*.

In stone-tile trials, 10 of 25 crabs (40%) entered the space beneath the tile. By contrast, in starfish trials, among tiptoe postures that were initiated while the starfish were in contact with crabs, 10 of 30 crabs (33%) entered the space beneath the starfish within 10 min, regardless of whether they were eventually captured (Fig. 1). However, the possibility that differences in the number of crabs per trial and the color of the experimental aquaria influenced the results cannot be excluded. We nonetheless consider it unlikely that these factors substantially affected crab responses once the contacted object was lifted. Because the experimental conditions were not identical between the two trial types, no statistical comparisons were performed ; nevertheless, the proportions of crabs entering the space were similar between the two trial types.

Our results provide no evidence that the tiptoe posture of *P. pectinifera* functions as an attractive signal for crabs. Grace (1974) suggested that the space between starfish and the substrate could act as a trap for small animals seeking a crevice. *Gaetice depressus* has also been reported to use the space between stones and the substrate as a refuge (Sakamoto et al., 2006). *Gaetice depressus* may therefore respond to *P. pectinifera* exhibiting a tiptoe posture in a manner similar to its response to a stone tile, which is analogous to a natural crevice.

Camouflage, broadly defined as traits that prevent detection or recognition, encompasses crypsis, mimicry, and masquerade (Skelhorn et al., 2010 ; Skelhorn, 2018 ; Smith and Ruxton, 2020). Crypsis reduces the likelihood of detection, mimicry involves resemblance to another organism, and masquerade entails resemblance to an inedible object. Because these traits may provide benefits for both predatory and defensive contexts, no species is known to exhibit masquerade

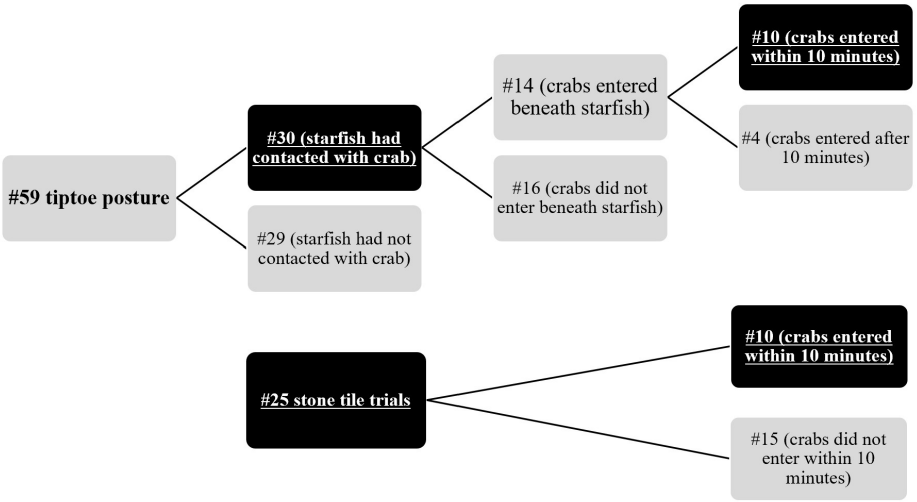

Fig. 1. Across starfish trials, standing on tiptoe behavior was observed 59 times. Of these, 30 events were initiated while the starfish was in contact with a crab. In 14 of 30 events, the crab entered beneath the starfish, and in 10 of 14 events, this occurred within 10 minutes of initiation. Thus, in 10 of the 30 contact-initiated tiptoe events, crabs entered beneath the starfish within 10 min. By contrast, in the stone-tile trials, 10 of 25 crabs entered beneath the stone tile within 10 minutes.

exclusively for predatory benefit (Smith and Ruxton, 2020). The starfish *Solaster dawsoni* is a known predator of *P. pectinifera* ; however, *P. pectinifera* can sense bioactive substances released by *S. dawsoni* and has not been reported to exhibit tiptoe behavior in response to this predator (Ukai et al., 2002), suggesting that this posture is unlikely to function as a defensive trait. Instead, our findings seem to support the hypothesis that the tiptoe posture functions as a form of aggressive masquerade, representing a rare example of masquerade operating in a predatory context. Further investigation into how crabs perceive and recognize the starfish will be essential for clarifying the mechanisms underlying this interaction.

Supplemental information

The online version of this article contains supplemental information :

Supplementary Fig. 1. Experimental setup showing a plastic aquarium (length 207 mm × width 139 mm × height 93 mm) containing a square stone tile (95 mm on each side) placed on the bottom. The tile could be tilted to create a space between the substrate and the tile by pulling a thread wrapped around the tile.

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