



A mechanism for visual orientation may facilitate courtship in a fiddler crab



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Some social signals are sexually selected both by female mating preferences and by male–male competition for mates. Studies of the behavioural mechanisms that mediate responses to these signals provide insight into how sexual selection operates. Courting male fiddler crabs, *Uca terpsichores*, sometimes build large sand structures called hoods at the openings to their burrows. Hoods attract females to males' burrows for mating because they elicit landmark orientation, a behaviour that is selected by predation. Males also orient visually to their own hoods when errors are introduced experimentally into their nonvisual mechanism for path integration. These errors occur naturally when males move far from their burrows to court females or fight neighbours. Here we explored whether courting males also use hoods as visual beacons to the location of their burrow. Crabs that rely on path integration to orient to their burrow keep their lateral axis closely aligned with the bearing home. We therefore measured and compared the distances males moved from their burrows and the maximum deviations between males' body axes and home bearings for males that did and did not build hoods, males that had their hood removed and males that had a hood added to their burrow. Males with hoods did not range further from their burrows than those without hoods, but they exhibited greater maximum deviations between their body axes and the bearings to their burrows. Hoods may facilitate courtship by allowing males to move more freely than when they rely on nonvisual path integration alone.

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Some male sexual traits are selected both by female preferences and by male–male competition for mates or fertilizations (51 cases compiled and reviewed by [Hunt, Breuker, Sadowski, & Moore, 2009](#)). Examples include the expanded terminal foreleg segment (pala) of a water boatman, *Sigara falleni* ([Candolin, 2004](#)), the yellow throat patch of the rock sparrow, *Petronia petronia* ([Griggio, Serra, Licheri, Monti, & Pilastro, 2007](#)) and the single, greatly enlarged claw of male fiddler crabs (genus *Uca*; [Dennenmoser & Christy, 2013](#)). Studies that measure both modes of selection on such dual-function traits can show whether they favour the same or different features of the traits ([Hunt et al., 2009](#)). However, detailed studies of the behavioural mechanisms that govern preferences and the effects of traits on male–male competition are

required to understand why sexual selection operates as it does (e.g. [Dennenmoser & Christy, 2013](#)).

We showed previously that predation selects for a mechanism for visual orientation in fiddler crabs that females use to choose mates (summarized in [Christy, 2007](#)) and that males use to maintain ownership of their burrow ([Ribeiro, Christy, Rissanen, & Kim, 2006](#)). Here we investigated whether this mechanism also allows courting males to move more freely, perhaps increasing their signalling performance.

Males of some species of fiddler crabs (genus *Uca*), which are well known for having one greatly enlarged claw that they wave as a threat and to attract females for mating, sometimes build courtship structures at their burrows using sand or mud ([Christy, Backwell, Goshima, & Kreuter, 2002](#); [Kim, Christy, & Choe, 2004](#)). The size and shape of these structures ([Crane, 1975](#)), how, when and how often they are built (compare dome building by *Uca pugilator*: [Christy, 1982](#); and hood building by *Uca terpsichores*: [Christy, Backwell, & Goshima, 2001](#)) and their functions as sexual

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signals and in male–male competition vary considerably (e.g. hoods of *U. terpsichores*: Christy et al., 2001, 2002; Zucker, 1981; pillars of *Uca beebei*: Christy, 1988a,b; semidomes of *Uca lactea*: Kim et al., 2004; Yamaguchi, Henmi, & Tabata, 2005; Zhu, Kim, & Choe, 2012). Courtship structures and their functions have been more thoroughly studied in *U. terpsichores* than in any other species in the genus.

A courting male *U. terpsichores* will build a sand hood at the entrance to his burrow on 1 or 2 days during each semilunar mating period; males are synchronized in this behaviour producing marked cycles of hood building that are coincident with cycles of female sexual receptivity and mate choice (Christy, Backwell, & Schober, 2003; Zucker, 1974). Males that build hoods blanch to bright white, feed little, stay on the surface for most of the low tide period and court females vigorously (Christy et al., 2002). Field experiments demonstrated that hoods attract females to males' burrows for mating and that landmark orientation (visual orientation to objects on the surface of the sand; Herrnkind, 1968), a behaviour selected by predation, is the basis of this female preference (Christy, 2007; Kim, Christy, & Choe, 2007).

Under certain circumstances, males also visually orient to their own hoods to find their burrows. Fiddler crabs regularly range up to 30 cm from their burrow to feed or court yet they cannot see the opening to their burrow when they are more than a few body lengths (5–10 cm, depending on crab eye height) away (Zeil & Layne, 2002). They therefore use a nonvisual mechanism based on path integration to home directly to their burrow (Cannicci, Fratini, & Vannini, 1999; Layne, Barnes, & Duncan, 2003a, 2003b; Zeil, 1998). The operation of this mechanism is revealed by the close alignment of the transverse axis of the crab with the true bearing to its burrow (Layne et al., 2003b; Zeil, 1998). In an experiment to determine whether females orient visually to hoods (Christy et al., 2002), males' natural hoods were removed and replaced with hood mimics positioned 3 cm to one side of the entrances to males' burrows. In 94 cases males ranged far from their burrows and courted distant females, movements likely to introduce errors in path integration. In eight (8.5%) of these 94 courtships the males returned, not to their burrows, but to the displaced hoods. Use by males of hoods to orient visually to their burrows when errors are introduced into their mechanism for path integration was subsequently confirmed experimentally (Ribeiro et al., 2006). In addition, males without hoods that range far from their burrows to court or to fight neighbours are sometimes unable to relocate their burrows, leaving them to wander and fight resident males for a new burrow (Christy, 2007). Landmark orientation by males to their own hoods improves their ability to retain their burrows and attract mates. Hoods also allow males to find their burrows more quickly (Ribeiro et al., 2006) which presumably reduces their risk of predation. Thus, hood building is sexually selected by both a female preference and male–male competition because hoods elicit landmark orientation in both sexes, reducing their risk of predation during courtship (Kim et al., 2007) and improving male resource-holding ability (Ribeiro et al., 2006).

Hoods may affect male behaviour in another way favoured by sexual selection. Kim, Kim, and Choe (2010) found that, like male *U. terpsichores*, male *U. lactea* orient visually to their courtship structures, which, in this species, are relatively low and massive semidomes. In addition, males with semidomes moved greater distances from their burrows to court females and moved more freely, as shown by greater maximum deviations between their transverse body axis and the bearing to their burrows, than males that had built semidomes but had them removed experimentally. Here we explored whether male *U. terpsichores* also move further from their burrows and move more freely when they have a hood

on their burrow. We extended the approach taken by Kim et al. (2010) to include comparisons between males that did and did not build hoods and males that did not build hoods but had them added to their burrows. This allowed us to determine whether use by a male of a hood as a beacon is contingent on the male having built a hood.

METHODS

Study Site and Species

The study was conducted on the sand beach at Punta Culebra located about 0.5 km south of Naos Island, on the east side of the Pacific entrance to the Panama Canal, Republic of Panama (8° 54'N, 79° 31'W) from 15 October to 25 November 2005. Tides at this site are semidiurnal and range in amplitude from about 2 to 6 m. *Uca terpsichores* lives in the upper intertidal zone along about 40% of this beach (about 10 × 60 m). After tides recede, crabs of both sexes emerge from their burrows and are active on the surface for about 7–8 h each day when the habitat is exposed by the diurnal low tide.

Movements of Males With and Without a Hood

About 1 h after low tide, when males finished building their hoods and were courting vigorously, adjacent burrows of a courting male with a hood and a courting male without a hood ($N = 35$ pairs) were marked. These males seldom interacted aggressively with each other and never with other males, all of which had burrows at least 30 cm away from the pair. A reproductively active female, one that was seen responding to courting males by approaching and moving between their burrows, was caught and tethered with light string to a thin wooden stake. The stake was inserted into the sand in the centre of a computer compact disk laid flat on the surface and covered with a thin layer of sand. The disk was positioned 40 cm from each of the two males forming the apex of a regular isosceles triangle. The female could move at most 5 cm from the stake and the disk prevented her from burrowing. The focal males approached and directed lateral claw waving towards the tethered female. A camcorder mounted on a tripod was positioned with the lens directed down 50 cm above and centred between the two males' burrows. A plastic scale 15 cm long was placed on the ground between the two burrow openings and was recorded for 5 s. The scale was removed and the video recording continued for 5 min. During recording, the observer moved at least 5 m from the crabs and did not move. The focal males typically returned to the surface and began courting the tethered female within a minute after the observer moved away.

Hood Removal Experiment

One hour after low tide, when males will not rebuild their hoods if they are removed (Christy et al., 2002), two adjacent burrows of actively courting males with hoods were marked ($N = 29$ pairs). A female and camera were arranged as described above. The males were recorded for 3 min after which the hood of one male, chosen at random, was removed and the crabs were recorded for another 3 min. We used a 3 min recording period because the previous study, using a 5 min period, indicated that differences between treatments were apparent within 3 min. We did not do a sham hood removal for the male that kept his hood. Both males escaped into their burrows when we removed the hood of one male and both returned to the surface at about the same time. Hence, hood removal had no apparent effect on the readiness of the male to resume activity on the surface.

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