



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.

Hood Addition Experiment

Following the procedures described above, adjacent burrows of two courting males that did not build hoods ($N = 25$ pairs) were chosen, the movements of the males were recorded for 3 min and then an artificial hood of average dimensions (see Christy et al., 2002) was added to one male's burrow, selected at random. The males were allowed an additional 3 min after emergence to view the added hood and resume courtship before their movements were again recorded for 3 min. For the reasons given above, a sham hood addition was not applied to the male that did not receive a hood.

Video Analysis

The video recordings were played back with the recording camera and viewed on a 15 inch studio monitor in the laboratory. We noted the handedness of each crab and whether it was located to the right or to the left of the female, determined by a line from the female to the midpoint of the line between the males' burrows. Courting males typically keep their large claw and lateral axis directed towards the females they court. Right-handed males may be better able to maintain this orientation if the female is to their left and their burrow is to the right of the female, and vice versa for left-handed males. We therefore divided the males into those courting from burrows on the same or on the opposite side of the female with respect to their handedness. A plastic ruler held against the monitor's screen was used to measure to the nearest 0.5 mm the size of the scale bar allowing us to estimate actual dimensions from the video recording. Crab carapace width and the maximum distance the crabs moved away from their burrows were measured. We also measured the angle between the transverse body axis of each crab and the direction of the crab's burrow three times when the deviation appeared to be the largest. This was done by extending the transverse axis of the crab with a ruler placed on the screen and measuring with a protractor the angle between the extension and a line directly from the centre of the crab to his burrow. We made this measurement only when the male was more than 8 cm from his burrow because at closer distances males can see and orient visually to their burrows (Ribeiro et al., 2006). We used the maximum value of the three measurements for the maximum deviation between the crab's transverse body axis and the home bearing. Finally, we measured the deviation of the male's transverse axis and the home bearing when the crab was furthest from his burrow. Deviations in either direction relative to the home bearing of 0 degrees were converted to a single direction that ranged from 0 to +90 degrees.

Statistical Analysis

We used the Wilcoxon signed-rank test to compare for each experimental pair of males the carapace widths of the males and the maximum distances that the crabs moved from their burrows. We used the Moore's paired test to compare the maximum deviations of the males' transverse body axes from the home bearings and the deviations when males were the furthest away from their burrows. To determine whether the direction of the female relative to the handedness of the male affected the distances the males went from their burrows and deviations of their transverse axes from the bearing to their burrows, we used the Mann–Whitney U test and the Mardia–Watson–Wheeler test, respectively. Oriana version 4.02 (Kovach Computing Services, Anglesey, U.K., www.kovcomp.co.uk/oriana/) was used for circular statistics and STATVIEW version 5.0 (SAS Institute Inc., Cary, NC, U.S.A.) was used for other statistics. Data are presented as mean \pm SD.

Ethical Note

We used each female crab as a decoy to attract courting males for up to three pairs of males and for a total elapsed time of typically <30 min. The tether was removed and the female was released after the last experiment. Females ran from us and sheltered in a nearby burrow when released and showed no apparent negative effects of having been tethered. After we captured and measured the males they too were released immediately in the field back into the local population.

RESULTS

Movements of Males With and Without a Hood

There was no significant difference in carapace size between males that did and did not build hoods (Wilcoxon signed-rank test: $Z = -0.747$, $N = 35$, $P = 0.455$; males with hoods: 12.1 ± 1.6 mm; males without hoods: 12.2 ± 1.6 mm). The maximum distances that the two classes of males moved from their burrows did not differ significantly (Wilcoxon signed-rank test: $Z = -1.556$, $N = 35$, $P = 0.120$; males with hoods: 185 ± 100 mm; males without hoods: 158 ± 79 mm). The direction of the female relative to the handedness of the male did not significantly affect either the maximum distances the males moved from their burrows (Mann–Whitney U test: $U = 475$, $N_1 = 25$, $N_2 = 45$, $Z = -1.066$, $P = 0.286$) or the maximum deviation of the males' transverse body axes from the bearing to their burrows (Mardia–Watson–Wheeler test: $W = 2.713$, $N_1 = 24$, $N_2 = 40$, $P = 0.258$). We therefore did not make these comparisons for the experiments in which we removed or added hoods.

The maximum deviation of the male's transverse body axis from the bearing to his burrow was significantly greater for males that built hoods than for those that did not build hoods ($29.4 \pm 8.9^\circ$ versus $23.2 \pm 11.4^\circ$; Moore's paired test: $R = 1.204$, $N = 29$, $P < 0.025$; Fig. 1). When males were furthest from their burrows, males with hoods exhibited greater deviations from the bearing home than males without hoods ($21.1 \pm 10.9^\circ$ versus $15.5 \pm 9.8^\circ$; Moore's paired test: $R = 1.176$, $N = 29$, $P < 0.025$).

Effects of Hood Removal

Before we removed the hood from one male's burrow, there was no significant difference between the two males in the maximum distance that they moved from their burrows (131 ± 70 mm versus 139 ± 59 ; Wilcoxon signed-rank test: $Z = 0.714$, $N = 29$, $P = 0.476$) and the maximum deviation of their transverse body axis from the bearing to the burrow ($25.4 \pm 10.0^\circ$ versus $22.8 \pm 8.0^\circ$; Moore's paired test: $R = 0.6$, $N = 22$, $P > 0.1$; Fig. 2a, b). After we removed one male's hood in each pair, the males that kept their hoods moved significantly further from their burrows than males that had their hoods removed (155 ± 62 mm versus 128 ± 55 mm; Wilcoxon signed-rank test: $Z = -2.162$, $N = 29$, $P = 0.03$) and they exhibited significantly greater maximum deviations of their transverse body axes from the bearing to their burrows ($26.4 \pm 8.0^\circ$) than males that had their hoods removed ($19.4 \pm 5.0^\circ$; Moore's paired test: $R = 1.686$, $N = 22$, $P < 0.001$; Fig. 2c, d). The maximum deviations of the males that had their hoods removed was significantly less than the maximum deviations of the same males before we removed their hoods (Moore's paired test: $R = 1.054$, $N = 22$, $P < 0.05$). The deviation of body axis at the maximum distance that males moved from their burrows was significantly greater for males that kept their hoods than for males whose hoods were removed ($18.3 \pm 6.2^\circ$ versus $12.5 \pm 7.2^\circ$; Moore's paired test: $R = 1.272$, $N = 20$, $P < 0.01$).

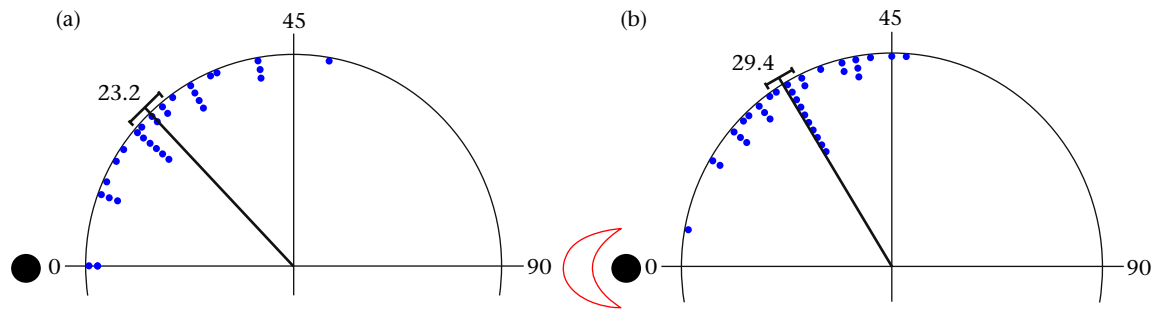


Figure 1. Maximum deviations of the longitudinal body axis of courting male *U. terpsichores* that (a) did not and (b) did build a hood; deviations measured relative to the direction of the males' burrows at 0°. Thick black radii with terminal bars show the mean and the confidence intervals (99%) of the body axis deviations. The location of the burrow is shown by the filled black circle; the presence of a hood is shown by the moon-like shape.

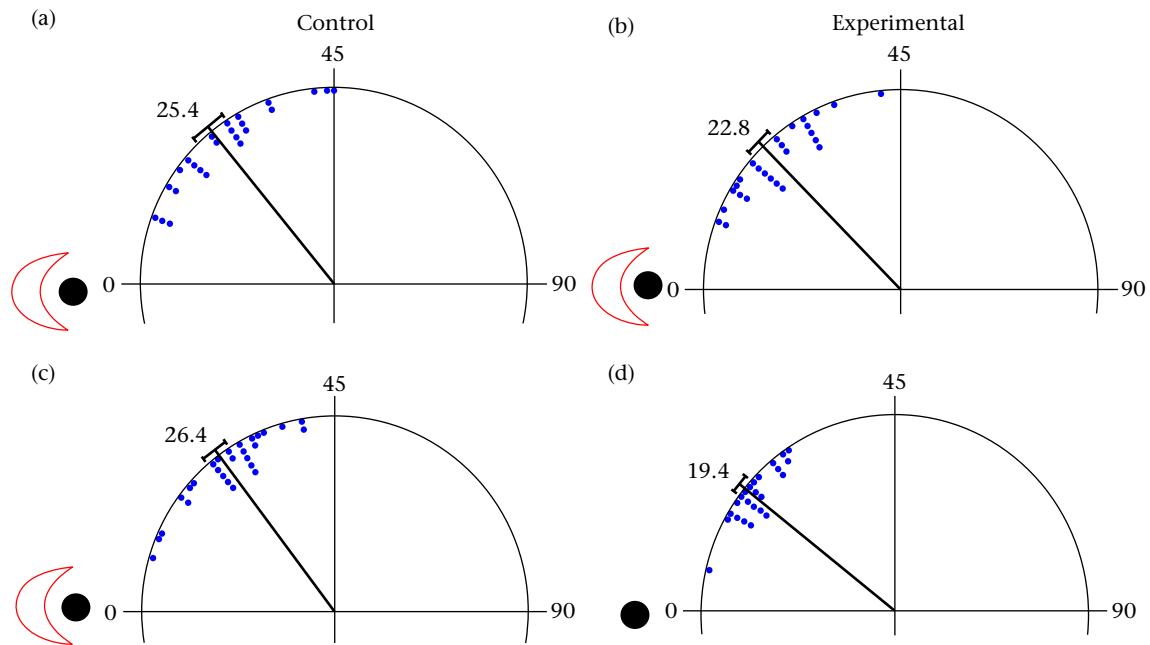


Figure 2. Maximum deviations of the longitudinal body axis of courting *U. terpsichores* that built hoods (a, b) before and (c, d) after we removed the hoods from half the males' burrows; deviations measured relative to the direction of the males' burrows at 0°. (a, c) Control males that kept their hoods; (b, d) experimental males whose hoods were removed. Symbols as in Fig. 1.

Effects of Hood Addition

Before we added a hood to one male's burrow, neither the maximum distances the two males without hoods moved from their burrows (118 ± 75 mm versus 115 ± 82 mm; Wilcoxon signed-rank test: $Z = -0.129$, $N = 25$, $P = 0.897$) nor the maximum deviation of their transverse body axes from the bearings to the males' burrows ($19.5 \pm 10.5^\circ$ versus $19.7 \pm 9.8^\circ$; Moore's paired test: $R = 0.766$, $N = 18$, $P > 0.1$; Fig. 3a, b) differed significantly. After we added a hood to one male's burrow, the maximum distances the males moved away from their burrows did not differ significantly (hood added: 141 ± 46 mm; no hood: 147 ± 87 mm; $Z = -0.578$, $N = 25$, $P = 0.563$). The deviations of the transverse body axes of the males from the bearing to their burrows at the maximum distance they moved from their burrows also did not differ significantly (hood added: $16.3 \pm 7.8^\circ$; no hood: $13.1 \pm 10.5^\circ$; Moore's paired test: $R = 0.567$, $N = 21$, $P > 0.1$). However, the maximum deviations of the transverse body axes of the males with hoods from the bearings to their burrows were significantly greater

than those of the males with added hoods: $23.5 \pm 6.9^\circ$; no hood: $18.0 \pm 8.7^\circ$; Moore's paired test: $R = 1.439$, $N = 23$, $P < 0.005$; Fig. 3c, d) and also greater than that of the identical male before adding hoods (Moore's paired test, $R = 1.317$, $N = 24$, $P < 0.01$).

DISCUSSION

We showed previously that hood building by courting male *U. terpsichores* (Christy et al., 2001) is sexually selected by a female preference (Christy et al., 2002) and probably by indirect male–male competition for maintaining ownership of a burrow (Ribeiro et al., 2006). Hood building may also be naturally selected by predation because males with hoods find their burrows more quickly and from a greater distance. Here we showed that courting male *U. terpsichores* with a hood, either one they built or one we added to their burrow, exhibited greater deviations between their transverse body axes and the bearings to their burrows including, for males with natural hoods, at the moment they were furthest from their burrows. Males that did not build a hood but had one

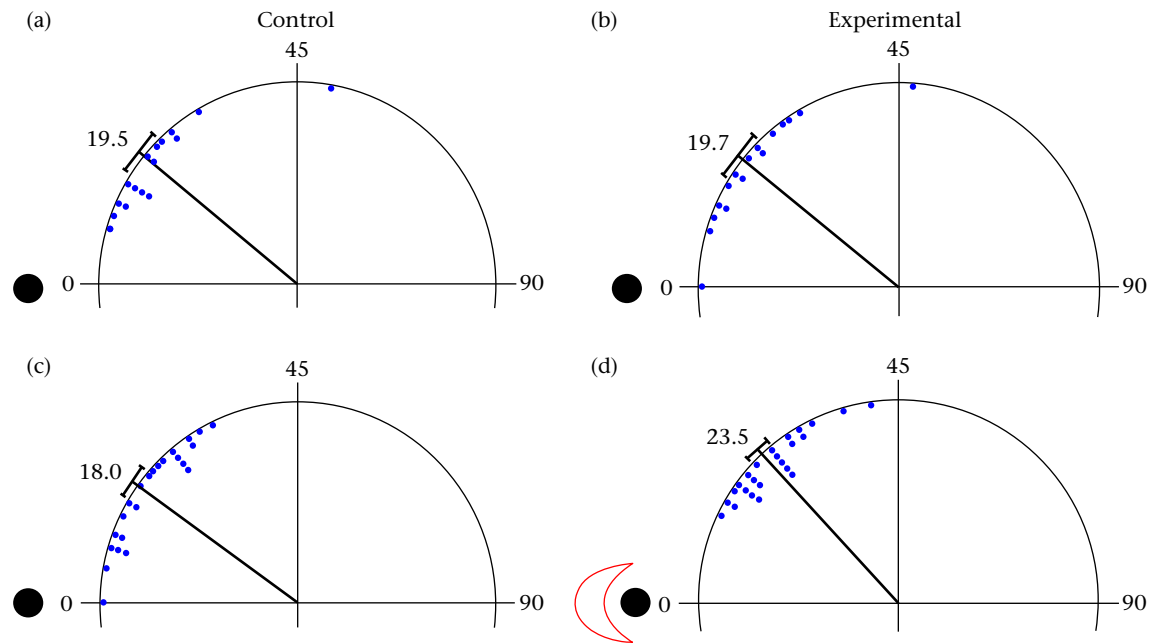


Figure 3. Maximum deviations of the longitudinal body axis of courting male *U. terpsichores* that did not build hoods (a, b) before and (c, d) after we added hoods to burrows; deviations measured relative to the direction of the males' burrows at 0°. (a, c) Control males without hoods; (b, d) experimental males with added hoods. Symbols as in Fig. 1.

added to their burrow also moved more freely after the addition, indicating that use of the hood as a beacon is not contingent upon having built the structure. However, we did not detect an effect of the presence of the artificial hood on male body orientation when the male was at the maximum distance from his burrow. In all three experiments, males with hoods did not move further from their burrows than males without hoods. This could be an effect of the rather short periods of observation during which the males directed courtship to the same equidistant female. The effect of the presence of a hood was most evident across all three experiments in the freedom with which males moved when they courted the distant female. We suggest that this effect may improve male performance in courtship and hence generate yet another mode of sexual selection favouring hood building.

Fiddler crabs that are moving on the surface away from their burrows usually keep their transverse body axis closely aligned with the bearing to their burrow (Zeil, 1998). However, in some species, actively courting males may make complex and rapid rotational movements (e.g. the 'circus display' of *Uca stenodactylus*, Christy & Salmon, 1991; *Uca perplexa*, How, Hemmi, Zeil, & Peters, 2008; *Uca elegans*, How & Hemmi, 2008) that result in males breaking this alignment and abandoning use of path integration to find their burrow. *Uca terpsichores* males will approach and follow passing females and direct claw waving to them by keeping the side of their body with the large claw oriented towards the female. This can result in rotation of the male's body, a movement that can introduce errors in path integration causing a male to fail to find his burrow if he does not have a hood (Ribeiro et al., 2006). Our results suggest that the presence of a hood allows males to shift between using path integration and visual orientation to find home and that this change permits males to move more freely when courting. The female in these experiments was tethered and could move little. Even so, males with hoods moved more freely when they courted the female. More typically, males detect, approach and court females that are moving at a distance between the burrows of other males. The closer the courting male comes to the female the greater will be

the deviation of his transverse axis from home as he keeps lateral claw waving directed towards the moving female. In this context, signal competition among males to attract the female should most favour use of hoods as 'back-up' visual beacons to the location of the male's burrow.

Structure building has been shown to be condition dependent in several species (Backwell, Jennions, Christy, & Schober, 1995; Kim & Choe, 2003; Kim, Sakamoto, Henmi, & Choe, 2008) but it seems unlikely that the ability of a male to rotate his body axis during courtship would itself depend on his condition. Males with hoods are more attractive to females and females orient visually to hoods (Christy et al., 2002). Differences between males with and without hoods in their movements during courtship may, however, also contribute to the measured difference in attractiveness.

Our understanding of how selection affects hood building by *U. terpsichores* is based on our studies of the behavioural mechanisms that govern both female and male responses to hoods. Attention to mechanism is integral to studies of how sensory drive (Endler, 1990), sensory bias (Basolo, 1990), sensory exploitation (Ryan, 1990), sensory traps (Christy, 1995) and, more generally, cognitive biases (Ryan & Cummings, 2013) govern signal evolution. The most general result is that sexual selection for hood building is a consequence of the operation of mechanisms that crabs use for visual orientation and that these mechanisms are strongly selected by predation (Christy, 2007; Kim et al., 2007). Females differentially approach and visit males with hoods (the preference) and males orient visually to hoods to find their burrows when path integration fails (increasing performance in indirect male–male competition to maintain burrow residency) because these responses in both sexes reduce predation risk. Thus, natural selection is responsible for the mechanism by which sexual selection on hood building operates.

Our understanding of the linkage between natural and sexual selection for hood building provides insight into sexual selection for semidome building by *U. lactea*, a species that is seldom prey of shorebirds. Approximately 90% of courting males of this species build semidomes (Kim et al., 2004) which, like hoods, are attractive to females (Zhu et al., 2012). Unlike female *U. terpsichores* (Christy

et al., 2003), however, unless female *U. lactea* are exposed to a mock predator, they are attracted to semidomes only during the reproductive period when females are seeking mates. Like male *U. terpsichores*, male *U. lactea* use semidomes as beacons to the location of their burrow but they move much more freely with maximum deviations between their transverse axis and the home bearing up to 43°. Structure building in this species may be favoured primarily by the beneficial effect of structure on the ability of males to court freely yet relocate their burrows and by the response of females to structures when they are seeking mates. However, because avian predation is so rare, that response may seldom benefit females directly by keeping them safe during mate search (as for female *U. terpsichores*; Kim et al., 2007). Other, perhaps indirect, benefits may favour the preference when predation risk is low (Zhu et al., 2012).

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