



# No preference for exaggerated courtship signals in a sensory trap

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Courting male fiddler crabs, *Uca terpsichores*, construct unusually large sand hoods at the entrances to their burrows to which they attract females for mating. Females sequentially visit several courting males before they stay with one and mate in his burrow, and they preferentially approach burrows with hoods. While moving between burrows, crabs are at risk of predation by birds and they sometimes run to objects that provide temporary cover. Thus, the female preference for burrows with hoods may help females to avoid predators. Could selection for predator avoidance produce a directional preference for especially large hoods? To examine this possibility, we made multiple replicas of two kinds of hood models with exaggerated dimensions (super models and wall models) and a single model with average dimensions (average models). Super models were four standard deviations taller and two standard deviations wider than average-size natural hoods. Wall models were of average height but near the maximum width of natural hoods; when males 'overbuild', they construct wall-like hoods. We replaced males' hoods with these models and measured their effects on male attractiveness. Males with exaggerated models neither encountered nor attracted more females than did males with average models or natural hoods. Females did not show a directional preference for larger hoods. The attractiveness of hoods may plateau with increasing size because discrimination between average and larger hoods may result in fatal hesitation, preventing the evolution of a directional preference for an exaggerated form of this courtship signal. Males build hoods from pure sand, so males may build unusually large hoods because they are more durable, not because they are better signals.

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Darwin (1871) observed that many male sexual signals and behavioural displays are so exaggerated that they must reduce survival and cannot therefore be favoured by natural selection. Nevertheless, he argued, they may still be beneficial if females have an aesthetic sense that leads them to prefer to mate with males who use the brightest, loudest, most vigorous and otherwise extreme signals and displays. It is now clear that aesthetic sensibilities, as determined by properties of female sensory response systems, do often affect mate choice (Bradbury & Vehrencamp 1998; Endler & Basolo 1998; Ryan 1998; Basolo 2000), and most studies of directional preferences support Darwin's prediction; when females show a bias they prefer courtship signals of greater quantity as measured along nearly every stimulus dimension (Ryan & Keddy-Hector 1992). Females may even harbour unexpressed preferences for supernormal signals (Tinbergen

1951), those with stimulus values that exceed the upper limits of current signal variation (e.g. Andersson 1982). In general, directional, open-ended biases in female mate preferences are thought to govern the evolution of ever more exaggerated male courtship signals until they are checked by natural (mortality) selection (Andersson 1994).

Courting males of at least 18 species of the approximately 100 species of fiddler crabs (genus *Uca*; Rosenberg 2001) build structures of mud or sand at the entrances to their burrows (17 structure-building species are listed in Christy (1988a) and Christy et al. (2001), to which we add *Uca uruguayensis*; P. Ribeiro, personal communication). Males of structure-building species use claw waving and other visual and acoustic (seismic) displays to attract females into their burrows for mating. In most species, males attract females either by approaching them to within a few centimetres and leading them with claw waving and other displays back to their burrows, or by staying close to their burrows and directing vigorous waving to females from a distance. Receptive females visit a dozen or more males in quick succession before they choose one and stay in his burrow (deRivera & Vehrencamp 2001).

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Male courtship structures might attract females at any of three sequential steps leading to mating: (1) from a distance, affecting the rate that males encounter and court females, (2) from nearby, affecting the rate that females approach the males that court them, (3) at the burrow, affecting the rate that females stay and mate with the males they visit. Studies of the functions of the mud pillars built by male *Uca beebei* (Christy 1988a, b) and the sand hoods built by male *Uca terpsichores* (previously *U. musica*) have shown that these structures attract females only at the second step, after a male has directed claw waving to a female. To confirm that females visually orient to structures as they approach courting males, we removed males' hoods and replaced them with hood models positioned a few centimetres to the side of the burrow openings. About 40% of the time, females moved to the hood models, not to the courting males, especially when males did not closely approach and lead the females to their burrows. We also showed that females preferentially moved to hoods over unadorned burrows when they ran from a simulated predator (Christy et al. 2003a) and that hoods effectively mimic pieces of wood, stones and shells to which females run for cover (Christy et al. 2003b). Finally, females were just as attracted to courting males with these natural objects at their burrows as they were to males with hoods (Christy et al. 2003b). We concluded that hoods elicit landmark orientation (Herrnkind 1983; Langdon & Herrnkind 1985) and co-opt for mate choice a behaviour that is selected by predation. Hoods can be said to catch females in a 'sensory trap' (West-Eberhard 1984; Christy 1995) because they elicit a response that mediates mate choice but is selected for another function, predator escape. Females who are caught in this 'trap' may benefit directly; by preferentially moving to hoods, they may move relatively quickly and without error from one male's burrow to the next and thereby minimize their exposure to predators while they are between burrows and without a safe refuge.

Hoods are, relative to male size, the largest structures built by courting male fiddler crabs (Crane 1975; Christy et al. 2001). Here we report the results of field experiments to determine whether female *U. terpsichores* prefer hoods that are as large as or larger (supernormal) than the largest hoods. Our objective was to discover whether a directional bias in the preference might have contributed to the exaggeration of this signal and whether this bias is open-ended.

## METHODS

### Study Site

We conducted this study on intertidal sand beaches, bars and flats on the west bank of the Pacific entrance to the Panama Canal between the Bridge of the Americas and Rodman Naval Station, about 1 km north. *Uca terpsichores* lives in mixed-sex colonies with one crab per burrow, except for mating pairs. Although the sexes are spatially intermixed, usually only vigorously courting males occupy burrows at the drier upper limit of the distribution.

## Models

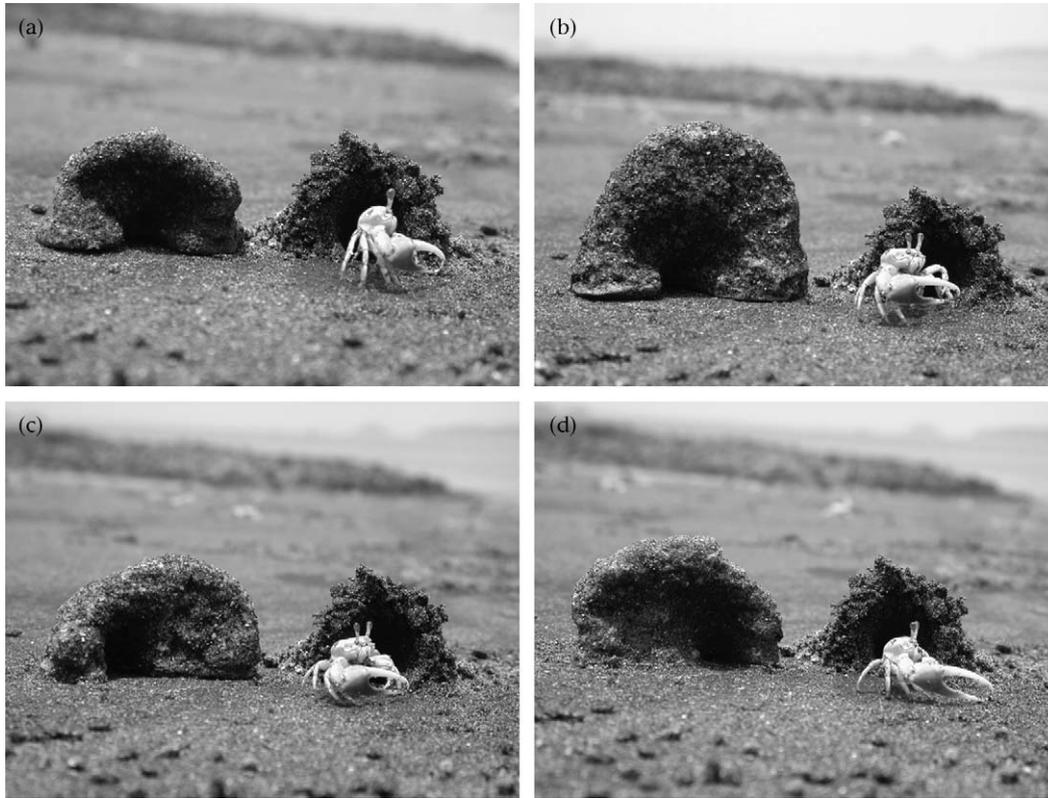
We tested the attractiveness of two kinds of hood models (super models and wall models) whose dimensions were exaggerated relative to those of the average hood (Fig. 1). On average ( $\bar{X} \pm \text{SD}$ ,  $N = 100$ ; Christy et al. 2001), hoods in the study area were  $23.3 \pm 3.17$  mm high,  $33.3 \pm 5.35$  mm wide at their base, and wider ( $0.57 \pm 0.061$  of total width) on the side opposite the male's large claw (Fig. 2a, b). Supernormal models, 'super models', exaggerated hood height and overall size; they were 35.5 mm high, about four standard deviations higher than average, taller than any natural hood that we measured, and 45 mm wide, about two standard deviations wider than average (Figs 1b, 2a). Super models were nearly symmetrical, with 0.54 of their width on the wider side (Fig. 2b). Wall models also were 45 mm wide but only 22.8 mm high, just less than average (Figs 1c, d, 2a), and they were very asymmetrical (0.69; Fig. 2b). We extended the walls of the wall models to the left or right. In the experiments described below, we matched the typical asymmetry between males and their hoods by giving 'left-handed' models to right-handed males and vice versa. Hood models were based on a single concrete cast of a real hood of average dimensions that we built up with modelling clay. We made latex moulds of the exaggerated models and cast numerous replicas in grey concrete, to which we glued sand from *U. terpsichores* habitat so that they appeared realistic to us. We also used replicas of the average-sized hood (Figs 1a, 2a, b) as controls for possible model effects, although no model effects have been found previously (Christy et al. 2002).

### Tests of Attractiveness: Super Models

The fiddler crab eye has an equatorial zone of acute vertical resolution that the crab keeps aligned with the horizon (Zeil et al. 1986; Zeil & Al-Mutairi 1996). Fiddler crabs are best able to detect objects that are tall enough to be imaged in their acute zone. This may explain, in part, why they preferentially orient to tall vertical objects (Langdon & Herrnkind 1985) and it may put a premium on the height of the structures that males build to attract females. Compared to no hood at all, hoods of average height are not more likely to attract females from a distance or to increase male-female encounter rates (Christy et al. 2002). However, the attractiveness of unusually tall hoods was not tested. In this study, we determined whether super models increase male-female encounter rates, the first step leading to mating, and whether super models are subsequently more attractive to females as they approach the males that court them. This second step is when males with hoods are demonstrably more attractive than are males without hoods.

### Encounter frequencies

Although we can recognize when an encounter occurs by observing that a male directs courtship to a female, we cannot determine when an encounter could have



**Figure 1.** Model hoods used to test the effects of hood dimensions on male attractiveness. Models were made of concrete and were coated with sand. Models are on the left and a natural hood and the male fiddler crab, *Uca terpsichores*, that built it are on the right of each frame. (a) Average model; (b) super model; (c) 'left-handed' wall model (asymmetrical to the right when viewed from the front), as might be built by this right-handed male; (d) 'right-handed' wall model.

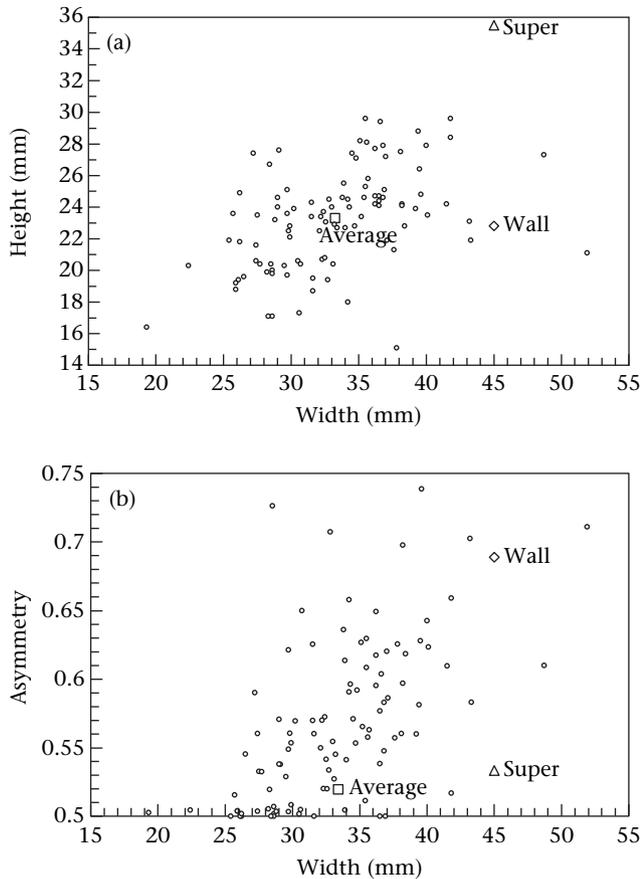
occurred but did not. For direct measures of the effect of courtship structures on male–female encounter frequencies, one needs to establish an objective criterion for when an encounter could take place and then record the number of times that the male and female do and do not encounter each other. We have not been able to do this. Therefore, we measured the effects of courtship structures on male–female encounter frequencies indirectly by measuring the frequencies that females stopped at burrows with different structures (visit frequency) and the frequency that females moved to the males from each structure category that courted them (approach frequency). Visit frequencies are the product of encounter frequencies and approach frequencies. Hence, we measured two of these frequencies and solved for the unknown third. We determined whether the different male and hood model combinations affected encounter frequencies by comparing (*G* test of goodness-of-fit with William's correction Sokal & Rohlf 1995) the relative visit frequencies to each male and structure combination with the relative frequencies that are expected based only on the approach frequencies to the same combinations (see also Christy et al. 2002). This tests the null model of no effect of structure type on encounter frequencies.

We found previously (Christy et al. 2002) that removing hoods does not affect male courtship and that females visually orient to hoods as well as to the courting male. Here

we assume that models of different size do not affect male behaviour differently and that differences in the responses of females to male–model combinations are determined by differences in their responses to the structures.

#### Visit frequencies

On each of 4 days, about 30 min before low tide, we marked 120 hooded burrows with small sticks placed about 15 cm from each burrow. For every three adjacent males, we left the natural hood on the first burrow and replaced the hoods on the second and third with average and super models, respectively. Thus, 40 males of each male–model combination were approximately evenly distributed across the observation area. We changed the location of our observations daily to minimize the chance of observing the same males on subsequent days. Beginning at low tide and continuing until about 30 min before the rising tide covered the area, we tallied the number of times females visited males with the different hoods. We continuously scanned the area to record the responses of as many mate-searching females as possible. We did not identify individual females, so our tally probably included several visits by each female. We noted the time when males lost their burrows, mated or ceased active courtship for other reasons or had a badly damaged hood (if a natural one), and we subsequently excluded them from the pool



**Figure 2.** Dimensions of natural hoods ( $\circ$ ), average model hoods ( $\square$ ), wall model hoods ( $\diamond$ ) and super model hoods ( $\triangle$ ) used to test the effects of hood dimensions on male attractiveness. (a) Hood height in relation to width. (b) Hood asymmetry in relation to width. Asymmetry is the larger proportion of the total width of a hood on either side of the burrow opening.

of males who could receive visits. We used a  $G$  test of goodness-of-fit to determine whether the males with different structures received the relative number of visits expected based on the relative amount of time that they were available for visits.

#### Approach frequencies

We recorded the frequency that females approached courting males without hoods and courting males with natural hoods, average models and super models. On each of 9 days, about the time of low tide, we replaced natural hoods of 15–30 males with models of each kind. We watched individual mate-searching females for several courtship interactions and recorded whether they passed or approached each male. Each courtship was a unique male–female pair, and we treated each as a statistically independent observation. Use of more than one observation per female does not bias conclusions about mate preferences in this species (Christy et al. 2002). We used  $G$  tests of independence to determine whether the frequencies with which females approached males depended on the kind of structure they had.

#### Tests of Attractiveness: Wall Models

Wall models were about the same height as natural hoods, so we had no reason to expect, based on our previous research and our understanding of the visual system of fiddler crabs, that they would be more attractive to females from a distance. Hence, we did not measure the possible effect of wall models on visit rates or encounter rates. However, when males make exaggerated courtship structures, they build them wider, like the wall models, not wider and taller, like the super models. If a directional female preference has shaped hood design, then wall models should be more attractive to females than natural hoods once females are courted by males.

We followed the same general, analytical and statistical methods described above to test whether wall models affected the frequency that courting females approached males. When measuring the attractiveness of super models we found, as in previous studies (Christy et al. 2002), that hood builders that had their hoods removed were significantly less attractive to females than were hood builders that had hoods on their burrows. Therefore, we excluded hoodless hood-building males from this experiment, leaving the comparisons between males with natural hoods and those with average, super and wall model hoods.

We define a sexually receptive female as one that chooses a mate during a given activity period and a non-receptive female as one that does not choose a mate. Both receptive and nonreceptive females move on the surface, approach courting males and stop at male burrows. Receptive females move more quickly and directly between males, feed little and seldom investigate empty burrows or attempt to take over burrows from other females. We made most of our observations during peak days of the biweekly courtship cycle and we made every effort to record the responses only of receptive females. Nevertheless we probably watched some nonreceptive females. However, the resulting errors should be small, because receptive and nonreceptive females do not differ in their responses to courting males with hoods or in their responses to courting males without hoods (Christy et al. 2002), suggesting that their responses to hoods of different sizes may be similar as well.

We followed the procedures in Cohen (1988) to conduct power analyses for all nonsignificant statistical tests of hypotheses.

## RESULTS

#### Visits to Super Models

Over the 4 days of this experiment we accumulated 66 411 male-minutes of observation on males with natural hoods (proportion of total = 0.302), average models (0.347) and super models (0.351). We had slightly fewer observation minutes of males with natural hoods because some hoods disintegrated during each observation period but none of the concrete models did. We saw 944 visits. We used these proportions to calculate the expected visit frequencies to males with the different structures under

the null hypothesis that the kind of structure that a male had did not affect the frequency that he was visited. The differences between the observed and expected visit frequencies under the null model were extremely small and nonsignificant ( $G_2 = 0.1276$ ,  $P = 0.938$ ; Table 1). With  $N = 944$ , the power to detect a small effect ( $w = 0.10$ ) was about 80%.

### Approach to Super Models

Over 9 days we observed 1596 interactions between 203 females and hood-building males without hoods, with natural hoods, with average models and with super models. The frequencies with which females approached these males differed significantly ( $G_3 = 128.9505$ ,  $P = 0.000$ ; Table 2); females approached males without hoods less often than males with hoods. There was no significant difference in the approach frequencies of females to males with natural hoods, average models or super models ( $G_2 = 0.9437$ ,  $N = 604$ ,  $P = 0.624$ ; power to detect a small effect approximately 58%).

### Encounter Rates of Males with Super Models

There was no significant difference in female encounter rates of males with natural hoods, average models and super models ( $G_2 = 1.3114$ ,  $N = 944$ ,  $P = 0.519$ ; power to detect a small effect approximately 80%).

### Approach to Wall Models

Over 13 days we observed 485 interactions between 106 females and courting males with natural hoods, average, super and wall model hoods. There was no significant difference between the frequencies that females approached males with these different hoods ( $G_3 = 1.0527$ ,  $P = 0.789$ ; Table 3). Wall models, models of the largest hoods that males build, were not more attractive (power to detect a small effect approximately 36%).

## DISCUSSION

Female preferences for more intense, frequent or otherwise extreme male courtship signals are fundamental for

**Table 1.** Female visit frequencies to courting hood-building male *Uca terpsichores* with natural or model hoods

Type of hood	Observed visits	Expected visits	Observed–expected
Natural hood	280	285	–5
Average model	331	328	+3
Super model	333	331	–3
Total	944		

The expected frequencies were calculated from the proportions of the total observation time (66 411 male-minutes) that males with the different hoods were available for visits; natural hoods: 0.302; average models: 0.347; super models: 0.351.

**Table 2.** Approach frequencies by 203 females to courting hood-building male *Uca terpsichores* without hoods or with natural, average or super model hoods

Type of hood	Pass	Approach	Totals	% Approach
None	584	408	992	41
Natural hood	95	239	334	72
Average model	44	90	134	67
Super model	42	94	136	69

the operation of good genes (indicator) and Fisher's (1958) two-step mechanisms of sexual selection (Andersson 1994; Bradbury & Vehrencamp 1998; Kokko et al. 2003). In contrast, directional preferences are not required for the evolution of signals that elicit responses governed by biases in sensory systems, such as those mediating sensory traps (Christy 1995; Endler & Basolo 1998). Biases exist at all levels in sensory response systems and they can evolve for many reasons (Basolo 2000), not only because individuals benefit from responding to stimuli of greater quantity. Courtship signals that are tuned to these biases will be most effective, whether or not they are exaggerated. However, signal degradation during transmission often may favour signals of greater quantity simply because they are easier to detect. This pertains especially to signals that attract receivers to senders. Thus, sensory response biases may often produce preferences based on perceived signal intensity (Parker 1983) or 'efficacy' alone (Guilford & Dawkins 1991; Johnstone 2000; Ryan & Cummings 2005), leading to signal exaggeration. We therefore expected that female *U. terpsichores* would prefer larger hoods. Our sample sizes were, in general, large enough to detect with reasonable confidence even a small directional preference.

Female *U. terpsichores* did not prefer hoods of a size near the upper extreme of the current distribution of hood sizes (wall models), nor did they prefer hoods that were larger than those males ever make (super models). Compared to natural hoods and average models, super models were not more attractive to females from a distance, nor were super models or wall models more attractive to females as they viewed and interacted with courting males. Comparisons of the time budgets of males with and without structures (Christy 1988b; Christy et al. 2002) and experiments in which males were given supplemental food (Backwell et al. 1995; T. Kim & J. Christy, unpublished

**Table 3.** Approach frequencies by 106 females to courting hood-building male *Uca terpsichores* with natural hoods or average, super or wall model hoods

Type of hood	Pass	Approach	Totals	% Approach
Natural hood	37	72	109	66
Average model	38	66	104	64
Wall model	36	52	88	59
Super model	32	52	84	62

data) indicate that structure building depends on male condition. Indeed, individual males build hoods, court most vigorously and feed relatively little on only 1–2 days during each 8–10-day biweekly reproductive cycle (Christy et al. 2001). The presence of a hood and perhaps its size (although this has not been shown) both may indicate a male's phenotypic condition. Yet females are not more likely to stay and mate with males with hoods after they have reached their burrows and they are not more attracted to males with larger hoods. These results illustrate that one cannot deduce whether or how females may benefit from a mate preference from the observation that production of the preferred signal depends on male condition.

One possible reason why unusually large hoods were not more attractive is that females did not perceive the size difference between average and larger hoods. This seems unlikely. The fiddler crab *U. pugilator* responds to objects as small as 1–1.3° angular size moving at 1°/s at or above their visual horizon (Land & Layne 1995; Layne et al. 1997). As *U. terpsichores* females approach a male's hood, they see the expanding upper edges of the hood above their visual horizon (hoods are taller than crabs' eyes) and we assume that they respond similarly. *Uca terpsichores* density averages about 12 hood-builders/m where we observed them (Christy et al. 2001). Assuming an even distribution of male burrows, the mean distance between nearest neighbours would be about 30 cm (Clark & Evans 1954). Females orient to hoods when they are moving between males' burrows. Assuming females begin orienting to hoods while they are about 20 cm away and that they approach at about 5 cm/s, a moderate walking speed, an average hood will increase in apparent height at about 2.18°/s, and a super hood will loom larger at about 3.34°/s, well within the female's likely perceptual and response thresholds.

Larger hoods may be more salient visual cues to the locations of males' burrows but they did not elicit a stronger orientation response. It is likely that small hoods that are lower than the female's visual horizon are less conspicuous and do not readily elicit approach, but this remains to be determined. There are significant positive but weak correlations between male body size and hood height ( $R^2 = 0.0585$ ) and width ( $R^2 = 0.0754$ ,  $N = 100$ ; Christy et al. 2001); either small males build relatively large hoods or large males build relatively small ones, or both. This pattern is inconsistent with directional selection for medium- and large-sized males to build as large a hood as possible. One possibility is that hoods are categorical signals of species identity that are constrained to certain distinctive dimensions. Several observations indicate that this is not the case. First, hoods and the pillars of *U. beebei* are not necessary for mate choice. They affect the frequency with which females will approach males but not whether they will stay and mate (Christy 1988b; Christy et al. 2002). Second, structure building is notoriously variable within and between populations (Crane 1975), making structures, at best, unreliable signals of species identity. Third, structure preferences are not species specific (Christy et al. 2003a). Fourth, *U. terpsichores* typically live on pure sand flats

and bars with few or no other fiddler crabs close by. At the lower edge of its distribution, female *U. terpsichores* occasionally encounter courting male *U. stenodactylus* and *U. deichmanni*, neither of which build structures and both of which have highly distinctive claw-waving displays totally unlike that of *U. terpsichores*. *Uca terpsichores* females readily distinguish and reject (with a specific body-bobbing display) courting males of both species on the basis of their behaviour alone (Zucker & Denny 1979). In summary we find no support for the idea that females have a categorical preference for hoods as a species recognition signal.

Unlike biases that are incidental consequences of how sensory systems develop, the responses that produce sensory trap mate preferences have a history of selection for some other function. This should constrain sensory trap signals to conform to the stimuli that elicit the response for the other function (Christy 1995); the response should produce signals that are better mimics of their models. This prediction has been confirmed in studies of (1) the orange colour spots on the tails of male guppies, *Poecilia reticulata*, that mimic fruits from the cabrehash tree, *Sloanea laurifolia* (Rodd et al. 2002), (2) the yellow terminal tail stripe of some males of some species of Goodeinae fish that probably mimic damselfly larvae (Macías-García & Ramirez 2005), and (3) the white silk-wrapped nuptial gifts that male nursery web spiders, *Pisaura mirabilis*, display to females that mimic females' egg sacs (Stålhandske 2002).

However, sensory trap responses may not always produce directional selection for ever-closer conformity of male signals to model stimuli. Females respond to the mimetic signal as they do the model but the stimulus properties of the signal may be relatively free to vary depending on the rules that females use to recognize models. In a previous study we tested the prediction that females should approach hoods as they do other objects that they use for landmark orientation. We found no differences in the rates that mate-searching females approached males with natural hoods or males whose hoods were replaced with average models, stones, shells or pieces of wood (Christy et al. 2003b). Females respond categorically to these objects despite their many physical differences. The present study extends these results by showing that large hood size also does not affect the strength of the female approach response. We suggest a simple functional explanation. When a predator is hunting near a crab that does not have immediate access to a burrow, including a female as she moves between the burrows of potential mates, the crab may do best to run to the nearest object, press its body against it and remain still. This movement, combined with the crab's typically mottled colour pattern, should make it less conspicuous because it will no longer be seen as a distinct object on the surface of the sand or mud flat. It may be vital to make this response quickly. If a crab discriminated between potential objects on the basis of size, colour or texture, and perhaps passed one in favour of another, the delay in its run to cover might well be fatal. Hence, selection to reduce predation risk may result in a general orientation response to nearby objects of some minimum size,

not one based on selective discrimination between potential safe sites. This may explain why the preference that results from co-option of landmark orientation for mate choice is expressed to a relatively broad range of objects and why the mimetic relationship between hoods and other objects need not be exact.

Our results do not explain why male *U. terpsichores* build relatively large courtship structures. One simple possibility is that structures with nearly vertical walls built of fine moist sand become unstable as the sand dries. As we observed, some natural hoods crumbled or blew away as the activity period advanced. Hence, males may build large hoods to make them durable, not because females prefer them.

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