Attractiveness of sand hoods built by courting male fiddler crabs, *Uca musica*: test of a sensory trap hypothesis

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Courting male fiddler crabs, *Uca musica,* sometimes build sand hoods at the entrances of their burrows to which they attract females for mating. On average, females visit 17 males in as many minutes before they choose a mate, and they preferentially visit males with hoods. When moving between burrows, fiddler crabs of both sexes sometimes approach and temporarily hide against objects on the surface. Hence, mate-searching females may approach hoods because they resemble (mimic) other objects that crabs approach to reduce their predation risk. We conducted two experiments to test this sensory trap hypothesis. First, we determined whether sexually receptive and nonreceptive female *U. musica* and nonreceptive female *U. stenodactylus*, a species that does not build structures, spontaneously approach hoods (replicas), stones, pieces of wood and shells. As predicted by the sensory trap hypothesis, both species, irrespective of sexual receptivity, approached these objects and neither preferred hoods. Second, to determine whether female *U. musica* show a preference for hoods when they search for a mate, we recorded the frequency with which females approached males with natural hoods, hood replicas, wood, stones and shells. Again as expected, females approached males with these different structures at the same rates. We conclude that hoods are effective mimics of objects that females approach for safety whether they are searching for a mate or not. Males benefit by using this sensory trap because hoods make them more attractive, and receptive females may benefit when they approach hoods because they reduce their mate-search risk.

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Research on sexual selection has expanded rapidly to include studies of the causes of female preference evolution as well as the effects of preferences on the evolution of male traits. Most direct benefits, and all indicator ('good genes') and Fisherian models propose that processes that are contingent on mating produce variation in female or offspring fitness and thereby cause the evolution of female preferences (Andersson 1994; Møller & Jennions 2001). These models show how preferences function as adaptations for mate choice. They are consistent with what might be called the 'existential adaptationist' view that any trait with current utility for a particular function is an adaptation for that function (Reeve & Sherman 1993). These models do not consider how preferences arise or how different origins may affect preference evolution.

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In contrast, the pre-existing biases, sensory exploitation and sensory trap models of sexual selection (Endler & Basolo 1998), each of which can be included in the sensory drive model of communication (Endler 1992), explicitly recognize the importance of history (Williams 1992) in preference evolution. Taking the 'historical adaptationist' view, they propose that preferences are based on features of female sensory, neural and motor systems that evolve before the preferred male traits. These pre-existing female characteristics bias the direction of sexual selection; they favour male traits that are most stimulatory to existing sensory systems or that are most likely to elicit existing responses that improve male mating success. In these models, preferences arise independently of preferred traits, not as adaptations for mate choice. However, neither the pre-existing biases (Basolo 1990) nor the sensory exploitation (Ryan 1990) model specifies the causes of preference evolution. Preferences in these models can arise in many ways, including as nonfunctional by-products of how sensory systems develop. As in other models of preference evolution, once preferences mediate mate choice, they may evolve under direct or indirect selection as new adaptations for mate

choice. In contrast, the closely related sensory trap model (West-Eberhard 1984; Christy 1995) proposes that female responses that mediate mate choice arise and currently are maintained by selection for at least one function other than mate choice. Mate choice is a consequence of a sensory trap response, but the response is not an adaptation for mate choice. For example, females may be attracted by the appearance of food or young and this will bias sexual selection in favour of males with traits that look like food (Rodd et al. 2002) or young (Stålhandske 2002). Thus, the sensory trap mechanism depends on a model–mimic relationship between some other stimuli and a male trait or signal.

At least five lines of study can provide evidence of a sensory trap (Christy 1995). Most convincing perhaps are transposition experiments that test the proposed model–mimic relationship between some other stimuli and a male trait. The basic experimental design includes two reciprocal transpositions: (1) the male trait is presented to females in the context in which females respond to the model stimuli and (2) the model stimuli are presented to females during courtship. The sensory trap hypothesis is supported if females make the same response to the contextually transposed male trait and other stimuli. Here we report the results of transposition experiments in which we tested a sensory trap hypothesis for the function of sand hoods built by courting male fiddler crabs, *U. musica* (Ocypodidae). Males build these structures at the openings of their burrows to which they attract females, who move on the surface between males' burrows, for mating.

METHODS

The Hypothesis and Its Test

During biweekly reproductive periods year-round, 20–60% of courting male fiddler crabs *U. musica* build hoods (Christy et al. 2001). In a previous study we removed hoods from builders' burrows, added hoods (replicas) to nonbuilders' burrows and observed the effects of these manipulations on male courtship and mating success. Hoods increased male attractiveness. As females moved away from one male's burrow to the next, they preferentially approached courting males with hoods, demonstrating experimentally that females visually orient to and approach hoods (Christy et al. 2002). However, hoods did not attract females from a distance and thus did not increase male–female encounter rates, nor did they affect females' mating decisions after they reached males' burrows. Hoods may attract females at relatively close range as they move between males' burrows, because these structures elicit landmark orientation, the general tendency for crabs that are moving on the surface away from the safety of a burrow to approach vertical objects that provide temporary cover and reduce predation risk (Herrnkind 1983; Langdon & Herrnkind 1985; Christy 1988, 1995; Christy & Salmon 1991). In support of this hypothesis, we found that female *U. musica* and *U. stenodactylus*, a species that does not build structures, preferentially approached empty burrows with hoods when we chased them with a model of an avian predator (Christy et al. 2003).

For the present study, we conducted two reciprocal transposition experiments. Our hypothesis proposes that crabs orient to and approach objects, not to escape an attacking predator, although they may use it in this context as well, but more generally to reduce their predation risk whenever they move between burrows, including during mate-search. We therefore compared the spontaneous approach frequencies by female *U. musica* and *U. stenodactylus* to hood replicas and to natural objects that are common on the surface where these crabs live. We released the females on the surface, but did not give them a burrow and did not chase them with a model predator. To avoid the possible confounding effects of the attractiveness of burrow openings, we did not make artificial burrows next to the test objects. We predicted that there would be no differences between the two species in the attractiveness of hoods and these other natural objects. For the second transposition experiment, we replaced males' hoods with hood replicas and natural objects and measured their attractiveness to female *U. musica*. If hoods and these natural objects are equally attractive to mate-searching females, this would support a model–mimic relationship between them and the sensory trap hypothesis.

Study Site

We conducted this study on intertidal sand bars on the west bank of the Pacific entrance of the Panama Canal, about 1 km upstream of the Bridge of the Americas. We tested crabs for spontaneous approach to objects in a circular arena that we made anew daily on the crest of a sand bar at the extreme upper limit of the local distribution of *U. musica*. Crabs in the arena saw test objects against a relatively distant (>200 m) and bright horizon. In the second experiments, we placed objects on males' burrows wherever they occurred. Mate-searching females saw them against a more varied, often closer and darker horizon.

Test Objects

We tested female approach to sand-coated cement replicas of an average-sized hood (see Christy et al. 2001) and to stones, and pieces of shell and decayed wood that we collected from around *U. musica* burrows. These objects are abundant and typically about the same size as hoods. The frontal surface area of the hood replicas was 5.1 cm^2 and the areas of the other objects ranged from about 4 to 6 cm^2. All objects were weathered and eroded. The hood replicas and stones appeared medium to dark brown or grey, the wood pieces were charcoal black and the shells typically were chalk white with patches of light brown or grey. We glued (silicone sealant) U-shaped wire 'legs' on the backs of the objects that we put on males' burrows to help hold them in place.

Spontaneous Approach to Objects

Each day, we lightly scribed in the sand a circle with a 30-cm radius and we marked 16 evenly spaced points on its circumference. We placed, in a randomized sequence, a hood replica, a stone, a shell and a piece of wood on the four points in each 90° sector. For each test, we changed and randomized the sequence of the objects in each sector. The objects occupied 28% of the circumference of the circle, leaving 72% open space. A thin plastic disk, about 8 cm in diameter and covered with sand, was placed in the centre of the arena to prevent crabs from burrowing. We removed the few resident crabs within a 2-m radius of the arena and filled their burrows. We periodically moistened the surface of the arena by spraying it lightly with sea water.

We dug female *U. musica* and *U. stenodactylus* from their burrows, released them individually in the centre of the arena and recorded whether they moved to an object, showing landmark orientation, or out of the arena, showing lack of landmark orientation or orientation to open space. These burrow-resident females had not been mate searching when we caught them and they probably were not sexually receptive. We also captured and tested female *U. musica* that we saw move away from their burrows and visit one or more courting males. These females probably were sexually receptive (Christy et al. 2002). We held the females in covered plastic containers with a small amount of sea water for up to about 30 min before testing them. Immediately after testing, we returned each female to the adjacent natural population. After placing a female in the centre of the arena, the observer stepped back about 3 m and sat low and motionless until the female approached an object or moved out of the arena. This person changed sitting positions by 90° for each test. We conducted the experiments on 12 clear days beginning about 1 h before low tide and ending about 4 h later. We used *G* tests of goodness-of-fit to determine whether females preferentially approached objects over open space and if they had a preference for some objects over others. We compared the approach frequencies between species and classes of females with Fisher's exact test or *G* tests of independence.

Approach to Objects During Courtship

Beginning at about 30 min before low tide, we replaced the hoods on males' burrows with hood replicas, shells, stones and pieces of wood. We left the natural hood on every fifth burrow. This created an approximately even spatial arrangement of males with five kinds of objects at their burrow entrance. From six to 25 sets of objects were set out each day, depending on the local abundance of hoods. Nevertheless, males with natural hoods always were more abundant in the observation area than were males with any one kind of artificial object. Beginning at the time of low tide, we recorded whether individual mate-searching females passed or approached the males who courted them. After we had recorded the responses

of a female to about four males ($\bar{X} \pm \text{SD} = 3.7 \pm 2.14$), we watched a new and different female. Over 11 days we recorded 422 responses from 114 females. We treated each response, including those from the same female, as an independent observation, because each courtship was a unique male–female combination. We used *G* tests with William's correction to determine whether the relative frequencies with which females approached courting males depended on the kinds of objects on their burrows. In a previous study (Christy et al. 2002), we observed individual *U. musica* females respond to at least five males with hoods and five males without hoods. This allowed us to use a two-way analysis of variance (ANOVA) to analyse the relative attractiveness of the two male classes, while keeping the responses of individual females separate. Females approached courting males with hoods more often than they did those without hoods, and we found no significant variation between females. Furthermore, our conclusions about relative male attractiveness remained unchanged when we used a *G* test to analyse the responses from all females (Christy et al. 2002). Thus, we feel confident in the conclusions we have drawn from pooling several observations from each female in the present study and using *G* tests of independence to detect preferences for some objects over others. Statistical power analysis follows Cohen (1988).

RESULTS

Spontaneous Approach to Objects

Females of both species and reproductive condition approached objects on the circumference of the arena significantly more often than they moved between these objects and towards empty space outside the arena (Table 1). *Uca musica* females showed a significantly stronger approach response to objects than did *U. stenodactylus* females (Fisher's exact test: $N=338$, $P<0.001$). The reproductive condition of *U. musica* females did not affect the frequency with which they approached objects compared to empty space (Fisher's exact test: $N=184$, $P=0.65$, power to detect a medium effect=1).

The four equally available kinds of objects were not equally attractive to all females (Table 2). However, there were no differences in the rates that female *U. musica* and *U. stenodactylus* approached the four kinds of objects (Table 2). This was true when the responses of (nonreceptive) *U. stenodactlyus* were compared with those of nonreceptive *U. musica* ($G_3=3.46$, $P=0.327$, power to detect a medium effect=0.807), or both nonreceptive and receptive *U. musica* combined ($G_3=0.17$, $P=0.983$, power to detect a medium effect=0.934). Receptive and nonreceptive *U. musica* females differed significantly in their frequency of approach to the four kinds of objects ($G_3=10.77$, $P=0.013$; Table 2). Nonreceptive females primarily approached hood replicas and receptive females most often approached wood. Shells were the least attractive objects to all females.

Table 1. Spontaneous approach by female fiddler crabs towards objects (hoods, wood, stones, shells) on the circumference of the test arena versus their movement between these objects towards empty space outside the arena

Species, reproductive status	Out of the arena	Towards an object	Total	% Towards an object	G
U. musica, nonreceptive	38	62	100	62	49.75
U. musica, receptive	29	55	84	65	50.51
U. stenodactylus, nonreceptive	93	61	154	40	9.58

Females were released individually in a 60-cm-diameter circular arena with 16 objects evenly spaced on its circumference. The G statistics are for goodness-of-fit tests of the null hypothesis that females would approach objects or move between objects and towards empty space in proportion to the relative amount of the circumference occupied by objects (28%) and by open space (72%). All P values were <0.05.

Table 2. Spontaneous approach by female fiddler crabs to four kinds of objects

Species, reproductive status	Hood	Wood	Stone	Shell	Total	G
U. musica, nonreceptive	29	22	7	4	62	29.38
	47%	35%	11%	6%		
U. musica, receptive	12	23	17	4	55	14.53
	22%	42%	31%	7%		
U. stenodactylus, nonreceptive	20	22	13	5	61	14.25
	33%	36%	21%	8%		

Females were released individually in a 60-cm-diameter circular arena with 16 objects, four of each kind, evenly spaced in randomized sequence on its circumference. The G statistics are goodness-of-fit tests of equal approach frequencies to the four kinds of objects. All P values were <0.05.

Table 3. Approach frequencies by mate-searching female U. musica (N=114) to courting males at burrows with natural hoods, hood replicas, pieces of wood, stones and shells

Object on male's burrow	Pass	Approach	Total	% Approach
Natural hood	58	101	159	64%
Hood replica	24	37	61	61%
Wood	27	38	65	59%
Stone	32	45	77	58%
Shell	24	36	60	60%
Total	165	257	422	61%

G test of independence between approach frequency and object type: $G_4=0.83$, $P=0.934$, power to detect a medium effect=1.

Approach to Objects During Courtship

There was no significant difference in the attractiveness of males with natural hoods, hood replicas, pieces of wood, stones, or shells to mate-searching female U. musica (Table 3). Females approached males with these structures about 60% of the time, a frequency comparable to the 63% spontaneous approach rate to objects by female U. musica when not mate searching. Approach rates to males without natural hoods or hood replicas typically are about 20% less than to males with these structures (Christy et al. 2002).

DISCUSSION

The results from both transposition experiments support the hypothesis that female U. musica approach hoods because they are suitable objects for landmark orientation, a behaviour selected by predation, and not for mate choice. When released into an arena without burrows or males, females of both species and reproductive condition approached objects on the circumference of the arena significantly more often than they moved between these objects and towards empty space outside the arena. This confirms that both species approach objects when they cannot enter a burrow for cover

(Christy 1995; Christy et al. 2003), even when they are not chased by a predator. Because *U. stenodactylus* do not build structures, but show the behaviour, selection for approaching objects during mate-search is not necessary for the maintenance of this behaviour. However, the response was much stronger in *U. musica*, perhaps because hoods are both abundant and reliable indicators of safe places (males' burrows) in this species' habitat. In earlier experiments (Christy 1995), female *U. panamensis* approached the mud pillars built by male *U. beebei* more often than did female *U. beebei*, *U. musica* and *U. stenodactylus*. Like *U. stenodactylus*, *U. panamensis* does not build structures. However, it lives on cobble beaches in burrows under stones. Hence, its habitat abounds with objects to which crabs can orient and find cover, perhaps explaining why this species shows the highest object approach frequency of any species tested to date. The response threshold, but not the presence of approach mediated by landmark orientation, may vary with the utility of this risk-reducing behaviour, which in turn may depend on the abundance of objects to which crabs can orient for safety. Selection for efficient predator avoidance may produce positive frequency-dependent sexual selection for structure building; the more males build structures, the more useful they become for reducing predation risk, the lower the female threshold for approaching structures and the greater their attractiveness, thus strengthening selection for structure building.

Females of both species more often spontaneously approached wood and hoods, the darker objects, and least often approached the chalk-white shells in the arenas. The arenas were on the top of a sand ridge so that the crabs viewed the objects against the bright sky or reflective sea surface. Perhaps the poor contrast of the white shells and the better contrast of the darker objects against the generally bright background affected their attractiveness. Mate-searching *U. musica* spontaneously approached wood more often that hoods, but nonreceptive females preferred hoods. If background contrast explains differences in attractiveness between these objects, then both species should have preferred charcoal black wood. Nevertheless, these results do not support the claim that females are selected to approach hoods for mate choice. If this were true, then hoods should have been most attractive to mate-searching females rather than to nonreceptive females.

The second transposition experiments showed that mate-searching female *U. musica* were just as attracted to males with wood, stones and shells at their burrows as they were to males with hoods and hood replicas. Although hood building may lower the threshold for approaching objects, females apparently do not distinguish between hoods and other objects, even when approaching courting males and their burrows. This strongly supports the proposed mimic–model relationship between hoods and other objects that is the basis of the sensory trap hypothesis. It implies that the tendency for crabs to approach hoods and other objects is a single response, not two context-dependent responses that are superficially similar, one that has been selected for reducing predation risk (approach objects other than

hoods) and the other for mate choice (approach hoods). We suggest that a context-dependent switch between two such responses has not evolved because the response has the same risk-reducing function whenever crabs move on the surface between burrows, including during mate-search. If females enjoy the same direct benefit whether responding to a model or a mimic, there would be no selection for discriminating between them. This is not to say that females are unable to distinguish hoods from other objects, only that they do not show differential responses to them. Precise resemblance between model and mimic is unnecessary when receivers benefit from responding to both.

Reduction in mate search costs may be a common benefit of sensory trap preferences (Christy 1995; Dawkins & Guilford 1996). When females benefit from responding to sensory trap signals, selection for females to discriminate between mimic and model should be weak. Indeed, the attractive properties of mimetic male traits that elicit these and other kinds of beneficial responses may be quite abstract as long as they reliably elicit a female response that increases male reproductive success. A hint of colour, a subtle touch, or the suggestion of a shape may be sufficient. Given our human sensory and cognitive biases, it will be difficult for us to recognize such mimics and their models. Abstract and, to us, often cryptic resemblances may explain at least some of the great diversity of the seemingly bizarre and arbitrary male courtship signals. Fortunately, whether they do or not, can be determined empirically. As illustrated by this study, transposition experiments can be used to test the model–mimic relationship upon which all sensory traps rely.

Acknowledgments

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