

Sexual selection for structure building by courting male fiddler crabs: an experimental study of behavioral mechanisms

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Males of the fiddler crab *Uca musica* sometimes build sand hoods at the entrances of their burrows, to which they attract females for mating with claw waving and other displays. Females significantly more often approached males with hoods than males without hoods, but once at a burrow, they were just as likely to stay and mate whether the male had a hood or not. To determine how hoods affect male attractiveness, we conducted experiments that controlled for other differences in courtship behavior between builders and nonbuilders; we removed hood builders' hoods and we added hood models to nonbuilders' burrows. We then measured the attractiveness of hood builders and nonbuilders with and without hoods. Neither manipulation measurably affected male courtship behavior. The presence of a hood did not increase male–female encounter rates, suggesting that hoods do not attract distant females into a male's courtship range. However, once a male courted a female, she was significantly more likely to approach if he had a real or model hood. We obtained direct evidence that females orient to hoods by replacing them with hood models positioned about 3 cm away from the openings to males' burrows. Females approached the models, not the courting males, about 27% of the time. We conclude that hood building is sexually selected because courted females differentially approach hoods, not because hoods attract distant females and not because females prefer to mate with hood builders. *Key words*: behavioral mechanisms, bowers, courtship, female preferences, fiddler crabs, male-built ornaments, sexual selection, *Uca musica*. [*Behav Ecol* 13:366–374 (2002)]

Sexual selection by female responses to male courtship signals and displays has been implicated in the evolution of diverse male characters that mediate sexual communication at all scales (Andersson, 1994; Darwin, 1871). Experimental studies in which male traits are manipulated are perhaps most convincing (Wilkinson et al., 1987) because they can provide direct evidence that a trait is sexually selected by a female response to its presence, form, or degree of development.

Courting male *Uca musica* build sand hoods at the entrances of their burrows, to which they attract females for mating (Zucker, 1974, 1981). In addition to *U. musica*, males of 16 of the nearly 100 species in the genus (Rosenberg, 2000) build mud or sand hoods, pillars, semi-domes, lips, or rims at their burrows (14 species listed in Christy [1988a] plus *U. perplexa* [Christy, unpublished data], *U. crenulata* [deRivera CE, personal communication], and *U. annulipes* [Backwell, unpublished data]). Like the bowerbirds' bowers (Gilliard, 1969), the display courts of some other birds (Andersson, 1991), and the sand structures built by some cichlid fish (McKaye et al., 1990) and other ocypodid crabs (Jones, 1972; Linsenmair, 1967), fiddler crab structures are "external ornaments" (Andersson, 1991), constructions that exist physically apart from their builders. Unlike male-built nests, hoods are not used during breeding, and they have no utility to either sex beyond their possible role in courtship. The objective of this study was

to determine experimentally how hood building by males of the fiddler crab *U. musica* might be sexually selected by a differential female response to hoods.

Reproductive behavior of *Uca musica*

Uca musica (about 1 cm adult carapace width) lives in mixed-sex colonies on intertidal sand flats and bars in estuaries and bays in the tropical Eastern Pacific, where it breeds year-round (Crane, 1975). Except when mating, crabs occupy burrows alone. Crabs are inactive at night and for 2–3 consecutive days of each biweekly tidal amplitude cycle when low tides occur near dusk and dawn. Consequently, hood building, courtship, and mating follow a biweekly cycle (Zucker, 1976, 1978). Males court from and defend burrows in the middle to upper intertidal zones (Zucker, 1984). Those that court vigorously build hoods and usually blanch to cream or brilliant white, except for bluish wash on the outer lower surface of their single large cheliped. All males probably are hood builders, but they do not blanch and build hoods every day (Christy et al., 2001).

To choose mates, females leave their burrows and move through the area with males who court them with lateral-circular claw waving. Waving males either stay close (typically ≤ 15 cm) to their burrows and move but a few steps back to them when females approach, or they range up to about 1 m from their burrows, approach females closely (≤ 5 cm), switch to rapid vertical waving, and lead them back to their burrows. Females sequentially stop at several males' burrows before they stay in one (Zucker, 1984), and they rarely return to a male after visiting another. Mate choice is indicated when a female stays in a male's burrow and he plugs the entrance and upper shaft with sand. The pair copulates in the burrow, and about 2 days later ($n = 43$) the female produces a clutch of eggs, which she carries attached to her abdominal append-

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Received 12 October 2000; revised 25 June 2001; accepted 31 July 2001.

ages. The male then digs an emergence shaft and leaves the female to incubate in the burrow.

Effects of hoods on courtship

Hoods might increase male courtship success by increasing the rate (frequency) that (1) males encounter and court females, (2) courted females approach males and their burrows, and (3) females mate with the males they approach (Andersson [1989, 1991] and Borgia [1995] discuss the sequential effects of avian display ornaments). Hoods may increase encounter rates in two ways. Fiddler crabs see two-dimensional objects on the surface poorly, and they do not use vision to locate their burrows entrances if they are more than a few centimeters away (Zeil, 1998; Zeil and Layne, 2002). In contrast, they see vertical objects such as hoods, which are as tall as or taller than their eyestalks, exceptionally well (Land and Layne, 1995; Zeil and Al-Mutairi, 1996). With a hood marking his burrow, a male may safely range farther from it and increase the rate at which he intercepts females. Hoods also should be conspicuous to distant females (Figure 1b). As they move between males' burrows, females may preferentially orient to hoods. This response also would increase the rate that hood builders encounter and court females. Similarly, once a male has directed claw waving to a female, she may be more likely to approach if his burrow is marked with a hood (Christy, 1988b; Crane, 1975; von Hagen, 1968). Finally, hoods may signal either male or burrow quality (Backwell and Passmore, 1996; Backwell et al., 1995; Christy, 1983, 1987) and increase the probability that a female will mate with a male once she reaches his burrow. Thus, hood builders may have higher mating rates because they are more likely to encounter and court females, to attract the females they court, and to mate with the females that they attract.

METHODS

We conducted this study in February–April, September, and November 1995, March–May 1998, and January–June 1999. We observed crabs at various locations on shifting sand bars and flats on the west bank of the Pacific entrance to the Panama Canal about 1 km upstream of the Bridge of the Americas. Data for experimental contrasts were taken at the same locations on the same days.

Male courtship success

Male mating rate (frequency) should be the product of the three rates discussed above. We measured the rate that courted females approached males, step 2, and the rate that females mated with the males they approached, step 3. However, we could not reliably determine when a male missed a courtship opportunity so we could not accurately measure male success at step 1. We therefore took an indirect approach and measured the rate that females visited males with and without hoods. Visitation rates are the product of encounter (step 1) and approach (step 2) rates. We used independent measurements of approach rates to determine whether hoods affected encounter rates.

Hood removal and addition experiments

We did two kinds of experiments to control for the possible effects of behavioral differences between hood builders and nonbuilders on male courtship success. We removed the hoods of hood builders, and we added hood models to the burrows of nonbuilders and compared the courtship success of these males to that of hood builders with their hoods pre-

sent and nonbuilders without hoods. A convenient feature of male behavior facilitated the removal experiments. Beginning about 1 h after low tide, when many females are searching for mates, hood builders rarely rebuild their hoods if they are damaged. We therefore created hoodless hood builders by removing their hoods at 1–1.5 h after low tide. For the hood addition experiments, we made replicas of a hood from a latex mold of a real hood. The hood we replicated was nearly symmetrical, and its height (23 mm) and width (33 mm) were within 1 mm of the average hood ($n = 100$). We glued sand from the study area on the replicas so that they looked to us like real hoods (Figure 1c). We observed crab courtship behavior and measured male success under eight experimental and natural conditions. For clarity, we describe the methods, analysis, and results for each separately below.

RESULTS

Attractiveness and mating rates

To determine if hood builders more often attract mates than do nonbuilders, we recorded the responses of individual females to courting males. We watched both receptive and unreceptive females. Receptive females stayed in males' burrows, which the males then plugged. We assume that these pairs mated. Unreceptive females occupied empty burrows or ones from which they displaced the residents. Some of these unreceptive females may have been searching for mates but did not find them. We recorded when we first and last saw each female, whether she approached or passed each male who courted her, whether each male had a hood, and whether she stayed in the male's burrow. From 2 to 46 males courted each female. Using a two-way ANOVA for paired comparisons (Sokal and Rohlf, 1995), we asked whether individual females differentially approached hood builders compared to nonbuilders and whether there was significant variation among females. We considered only females who were courted by at least five males of each class. The response variables were the arcsines of the square roots of the proportions of approaches by each female to builders and nonbuilders. We also asked whether hood builders were differentially attractive to females generally, as expected if there is sexual selection for hood building. Individual females contributed several observations to the total, but only one per courtship and male, so we treated each response as a statistically independent observation (see also Andersson, 1989). We used G tests of independence (with William's correction; Sokal and Rohlf, 1995) to determine whether hood builders were more attractive per courtship (step 2), whether they were equally attractive to receptive and unreceptive females, and whether, after being attracted to a burrow, receptive females preferred to mate with builders (step 3).

We watched 28 receptive females for 17.4 ± 17.95 min (mean \pm SD; range: 2–70 min) until they chose mates and we recorded their responses to 17.5 ± 13.67 males (2–46). We watched 34 unreceptive females for 17.3 ± 12.89 min (2–44 min), and we recorded their responses to 8.9 ± 8.71 males (1–41), about half the mean number that courted receptive females in the same average time. Because we started watching females after they began searching, these values underestimate the true means.

Receptive females ($n = 12$) who were courted by at least five builders and five nonbuilders were significantly ($F_{1,11} = 14.404$, $p < .005$) more attracted to builders (mean approach rate: to builders = 0.823; to nonbuilders = 0.642). There was no significant variation among receptive females ($F_{1,11} = 1.646$, $p > .10$) in approach rates, but the power of this test to detect even a medium effect was low at 21% (Buchner et



Figure 1

Male *Uca musica* with natural or model hoods. (a) A blanched male at the entrance of his burrow. (b) Males and hoods viewed from approximately the elevation of crabs' eyes showing the sharp contrast between these dark structures and the bright sky. The three spheres just below the horizon are balls of sediment made by *Uca stenodactylus*, a larger species. (c) A hood model added to the burrow of a nonbuilder. (d) A hood model positioned about 3 cm away from the entrance of a builders' burrow.

Table 1
Female responses to courting hood-building and nonbuilding males

Female	Female response			Totals	%
	Male	Pass	Approach		
Receptive	Hood builder	27	142	169	84.0 ^a
	Nonbuilder	111	212	323	65.6 ^b
	Totals	138	354	492	
Unreceptive	Hood builder	11	74	85	87.1 ^c
	Nonbuilder	94	129	223	57.9 ^d
	Totals	105	203	308	

Frequencies are the responses of 28 receptive and 34 unreceptive females to courtship from 492 and 308 males, respectively. *G* tests of independence: ^{a,b} $G_W = 19.697$, $p < .001$; ^{c,d} $G_W = 23.095$, $p < .001$; ^{a,c} $G_W = 0.411$, $p > .50$; ^{b,d} $G_W = 3.389$, $p > .05$.

al., 1997; Faul and Erdfelder, 1992). Unreceptive females received too few courtships for this analysis.

Hood builders were more attractive than were nonbuilders and equally so to receptive and unreceptive females. Nonbuilders also attracted both classes of females at the same frequency (Tables 1 and 2). The presence of a hood did not significantly affect the frequency that females stayed at males' burrows to mate (Table 2). Sample sizes for these tests were sufficient (≥ 254) to give a power of $> 99\%$ to detect a small effect (Cohen, 1988). Hence, builders were differentially attractive, but we found no evidence that females subsequently preferred to mate with them. Multiplying these rates gives 0.07 matings/courtship for hood builders, about 40% greater than the nonbuilder rate of 0.05 matings/courtship.

The result that hoods do not affect mating decisions after females approach males' burrows appears to be robust. During a hood addition experiment (described below), we recorded a median rate of 0.4286 visits/h to builders with natural hoods ($n = 36$). In another study (Christy et al., 2001), hood-builder mating rates averaged 0.09 matings/day ($n = 27$ days, > 150 males/day) and varied little with hood abundance. We estimate that these males received 1.072 visits/day (0.4286 visits/h \times 2.5 h courting/day), giving 0.084 matings/visit (0.09 matings/day \div 1.072 visits/day), closely comparable to the estimate of 0.085 matings/visit we obtained from following individual females (Table 2).

Behavior of hood builders and nonbuilders

Behavioral differences other than hood building between builders and nonbuilders may contribute to differences in their attractiveness. On 3 days we used scan sampling at 5-min intervals to record male behavior with respect to seven activities: feed, wave-feed (waving while feeding), wave, threaten (includes threaten-feed, a rare activity), fight, in burrow, and other (includes self-maintenance). We observed males for 3 h from 1 h before to 2 h after low tide. At low tide we noted whether each built a hood and his degree of lightening (dark, medium, white). We expected (Christy, 1988b) that hood builders would court more and feed less than nonbuilders. We used one-tailed Mann-Whitney *U* tests (Sokal and Rohlf, 1995) to compare the courtship frequencies (wave + wave-feed) of the two classes of males, with each male contributing a single frequency value. We compared the frequency of aggression (threat + threaten-feed + fight) between builders and nonbuilders with a two-tailed test because we could not predict the direction of the difference. We used a *G* test to determine if hood building and body brightness are associated, and we examined the value of Somer's *d*, which measures the

Table 2
Responses of receptive females to courting hood-building and nonbuilding males

Female	Male	Female response		Totals	% Mate
		Leave	Mate		
Receptive	Hood builder	130	12	142	8.5 ^a
	Nonbuilder	196	16	212	7.6 ^b
	Totals	326	28	354	

Frequencies are the responses of 28 receptive females who stopped at the burrows of 142 hood building and 212 nonbuilding males. *G* test of independence: ^{a,b} $G_W = 0.093$, $p > .50$.

strength and direction of association between ordinal variables in rectangular tables (+1 to -1; Wilkinson et al., 1996).

Builders ($n = 37$) and nonbuilders ($n = 75$) spent about the same relative amount of time feeding and courting (Figure 2), but they distributed their time differently between these activities. Hood builders fed significantly less ($U = 2130.5$, $p < .001$; one-tailed), and they courted significantly more ($U = 1086.5$, $p < .031$; one-tailed), spending nearly half (47.4%) their time waving without feeding. Both classes of males spent little time on aggression (4.7%). Male brightness and hood building were significantly positively associated ($G_W = 6.476$, $p < .05$; Somer's $d = 0.245 \pm 0.097$, $p < .01$); 62% (23/37) of hood builders but only 43% (33/77) of nonbuilders blanched to white at low tide. These behavioral and color differences could contribute to the greater attractiveness of hood builders.

Effects of hood removal on hood builder behavior

The effects of hoods on attractiveness can be inferred directly from the hood removal experiments only if this manipulation does not affect attractiveness by changing male courtship behavior. On 5 days we marked the burrows of 18–36 hood builders. Beginning at low tide, we used scan sampling to record their behavior with respect to the activities listed previously. At 1.5 h after low tide we removed the hoods from every other burrow and resumed observing for another 1.5 h. We used a one-tailed Mann-Whitney *U* test to determine whether males, half of whom had their hoods removed, courted less after the manipulation.

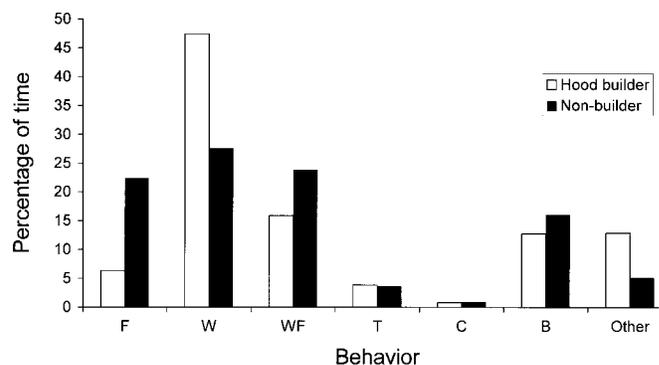


Figure 2
Behavioral correlates of hood building. The time budgets of hood building ($n = 37$) and nonbuilding ($n = 75$) males were calculated from the mean relative frequencies with which males were observed in seven activities: F, feeding; W, waving; WF, wave-feed; T, threat; C, combat; B, in burrow; other, all other activities, including self-maintenance and burrow maintenance.

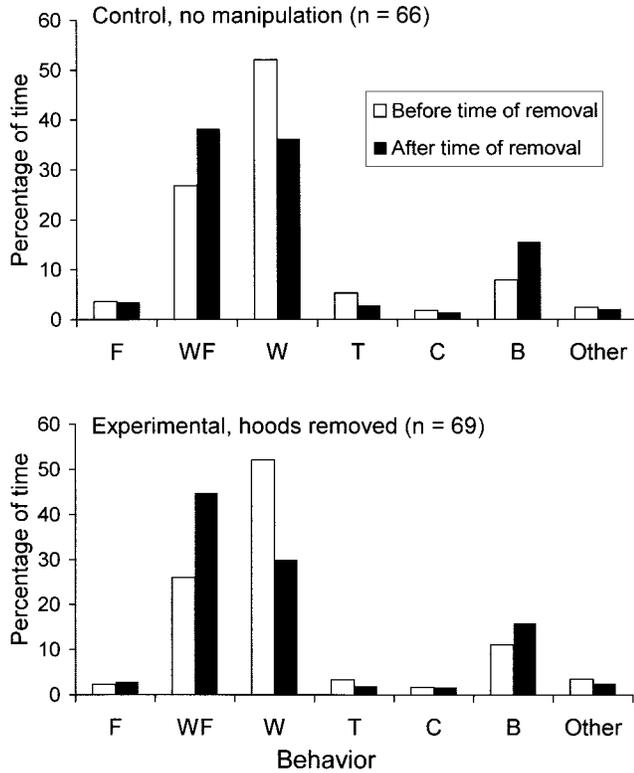


Figure 3
Effects of hood removal on male behavior. The time budgets of hood-building males are shown for 1.5-h periods before and after we removed hoods from approximately half of the males. Percentages of time are calculated from the mean relative frequencies with which we saw males in each of seven activities: F, feeding; W, waving; WF, wave-feed; T, threat; C, combat; B, in burrow; other, all other activities, including self-maintenance and burrow maintenance.

Hood removal had no significant effect on male courtship or aggressive behavior. Before we removed hoods, males in both groups spent about the same amount of time courting (78.9%, hoods later removed; 78.1%, hoods left on). After we removed hoods, males in both groups waved less and wave-fed more (Figure 3), giving an overall slight decline in courtship (74.7%, hoods removed; 74.5%, hoods left on). There was no significant difference between the two groups in the reduction in percentage of time waving ($U = 2459.5$, $p = .422$) or in the increase in percentage of time wave-feeding ($U = 2675.5$, $p = .079$), with a power of 82% for each test to detect a medium effect (Buchner et al., 1997; Faul and Erdfelder, 1992). Rates of aggression were low, and they decreased slightly for both groups after we removed hoods (Figure 3).

Effects of hood removal on attractiveness

On 7 days, we marked 80–200 hooded burrows by placing a small stick about 15 cm from each one. At 1 h after low tide we removed the hoods from every second burrow, creating an approximately even spatial distribution of builders with and without hoods. Nonbuilders also were present throughout. We watched individual females for several courtships but usually not until they chose mates. We recorded whether the female passed or approached each male who courted her and the status of the male. We used G tests of independence to determine if approach frequencies depended on male status.

Builders with their hoods were significantly more attractive

Table 3
Female responses to courting hood-building males, with and without their hoods, and to nonbuilding males

Male	Female response		Totals	% Approach
	Pass	Approach		
Hood builder				
Hood present	80	223	303	73.6 ^a
Hood removed	104	121	225	53.8 ^b
Nonbuilder				
No hood	756	412	1168	35.3 ^c
Totals	940	756	1686	

Frequencies are the responses of 146 females to courtship from approximately 1254 males. (We do not know the exact number of males because we did not count the nonbuilders that we saw court females each day.) G tests of independence: ^{a,b} $G_W = 22.204$, $p < .001$; ^{b,c} $G_W = 26.570$, $p < .001$.

than were builders without their hoods, who in turn were significantly more attractive than nonbuilders (Table 3). The first difference indicates that hoods directly affect attractiveness. The second difference suggests that frequent waving and a light color also contribute to male attractiveness.

Effects of hood removal on visitation and encounter rates

On 9 days we marked 50–120 burrows with hoods. At about 1 h after low tide we removed every second hood, creating an approximately even spatial distribution of builders with and without hoods. For the next 1.5–2 h we recorded each time we saw a female visit a male at a marked burrow and whether he had a hood. We watched a given female for only a few visits, and then shifted our attention to another. We tallied visits at 10-min intervals and noted when any male mated, left, or was ousted from his burrow or disappeared.

The distributions of visitation rates (visits/h) to both groups of males were bimodal, as many males were never visited. We used a G test of independence to determine whether visit frequencies of 0 or ≥ 1 depended on male status. The distributions of visitation frequencies ≥ 1 were strongly skewed to the right. We therefore compared the median (rather than the mean) visitation rates between the two groups of males (Fisher's Exact test; Sokal and Rohlf, 1995).

We saw 807 visits to 460 builders with and 378 builders without hoods. Eliminating 45 males that we saw for less than 30 min, builders with hoods were significantly ($G_W = 12.481$, $p < .001$) more likely to be visited at least once (56.8%, 252/444) than were builders without hoods (44.1%, 154/349). Considering males who received ≥ 1 visit, the median rates were 0.923 visits/h to males with hoods and 0.754 visits/h, to males without hoods, a nonsignificant difference (Fisher's Exact test, $p = .457$, tails; $n = 377$, power $> 99\%$ to detect a small effect).

Shifting the analysis from individual visitation rates to the sample of visits, we used G tests of goodness-of-fit (Sokal and Rohlf, 1995) to test two hypotheses. First, we asked whether the relative proportions of visits to builders with and without hoods differed from those expected based on the relative amount of time males in the two groups courted weighted by the relative proportions of visits when they courted. For each group we calculated the sum, across males, of the number of minutes each was active during each 10-min observation period. We then multiplied these sums by the proportions of the 807 visits that we observed during each of the periods and summed these values across periods. These group sums, each divided by the grand sum for the two groups, gave the ex-

Table 4
Female responses to courting hood-building and nonbuilding males, with and without model hoods

Male	Female response		Totals	% Approach
	Pass	Approach		
Hood builder + natural hood	127	229	356	64.3 ^a
Hood builder + model hood	52	160	212	75.5 ^b
Nonbuilder + model hood	84	134	218	61.5 ^c
Nonbuilder, no structure	563	363	926	39.2 ^d
Totals	826	886	1712	

Frequencies are the responses of 185 females to courtship from about 948 males (see footnotes of Table 2). G tests of independence: ^{a,b,c,d} $G_W = 140.037$, $p < .001$; nonsignificant subsets with $\alpha = 0.05$; ^{a,b} $G_W = 7.811$; ^{a,c} $G_W = 0.474$.

pected proportions of visits to each group under the null hypothesis of equal visitation rates. The observed frequencies of visits to the two groups did not fit the expected frequencies ($G_W = 13.432$, $p < .001$). Hood builders with hoods were visited more often (observed – expected: 518–467 = 51), and those without hoods were visited less often (289–340 = –51) than expected.

Second, we tested the hypothesis that there was no difference between the relative proportions of visits to the two male groups and those expected based on their relative attractiveness per courtship (step 2). If we fail to reject this hypothesis, then we have no evidence that builders with hoods received disproportionately more visits because they encountered and courted more females (step 1). The expected frequencies for this test were calculated from the products of the expected frequencies in the previous test and the relative frequencies that courted females approached builders with and without hoods (Table 3). Dividing each of these values by their sum gave the expected relative proportions of visits to the two groups. There was no significant difference between the observed and expected frequencies of visits ($G_W = 0.441$, $p > .50$; observed – expected; hood present: 518–527 = –9; hood removed: 289–280 = 9; power > 80 % to detect even a 0.05 difference in relative frequencies relative to the null expectations; Cohen, 1988). Hoods did not enhance male–female encounter rates.

Effects of hood addition on attractiveness

On 9 days we marked the burrows of 20–30 builders and nonbuilders that were approximately evenly distributed across the observation area. Just before low tide, we removed builders' hoods and replaced them with model hoods, and we added models to the burrows of neighboring nonbuilders. This manipulation produced four spatially intermixed groups of males: builders with natural and model hoods and nonbuilders with and without model hoods. We watched individual females for a few courtships and recorded whether they passed or approached each male who courted them and the male's group membership.

There was a significant difference in attractiveness among males in the four groups. Nonbuilders without hoods were relatively unattractive compared to males with hoods, who did not differ greatly in attractiveness (Table 4; power > 99% to detect a small effect in all nonsignificant tests). The presence of a hood increased male attractiveness. Unlike the results of the hood removal experiment, the more frequent waving and the brighter color of builders did not.

Effects of hood addition on visitation and encounter rates

Using hood removal, we found no evidence that hoods increased the rate that males encountered and courted females.

We therefore predicted that the addition of hood models to nonbuilders' burrows also would not increase these rates. On 5 days, beginning at about 30 min before low tide, we marked 60 builders' and nonbuilders' burrows. The manipulation described above was done creating the same four groups of spatially intermixed males. For the next 2–2.5 h, we recorded and tallied at 10 min intervals each time we saw a female visit a male and whether the male had a natural or model hood. We noted any change in male status. The analysis followed the procedures described above, except we used a G test to compare median visitation rates between the four classes of males (Sokal and Rohlf, 1995).

We saw 836 visits to 529 males: 130 nonbuilders, 128 nonbuilders with model hoods, 136 builders with natural hoods, and 135 builders with model hoods. Eliminating four males that we watched for < 30 min, whether a male received at least one visit did not depend on his group membership ($G_W = 4.2448$, $p > .10$, $n = 525$, power > 99% to detect a small effect). For males that received at least one visit, the median rates (visits/h) were 0.429 to nonbuilders without hoods, 0.800 to nonbuilders with model hoods, 0.775 to builders with natural hoods, and 0.857 to builders with model hoods. These medians were not significantly different ($G_W = 2.657$, $p > .10$; $n = 353$, power > 99% to detect a medium effect).

There was a marginally significant difference between the observed and expected frequencies of visits to these four groups of males ($G_W = 7.859$, $p = .049$; observed – expected; nonbuilders: 176–207 = –31; nonbuilders with models: 201–203 = –2; builders with natural hoods: 219–210 = 9; builders with models: 240–216 = 24). Nonbuilders without hood models received substantially fewer visits and builders with models received substantially more visits than expected. However, the observed frequencies of visits to the four groups differed significantly in the direction opposite that expected from their differential attractiveness and their availability for visits. Nonbuilders without hoods received more visits and builders with model hoods fewer visits than expected ($G_W = 15.083$, $p < .01$; observed – expected; nonbuilders: 176–135 = 41; nonbuilders with models: 201–207 = –6; builders with natural hoods: 219–224 = –5; builders with models: 240–270 = –30). Hoods reduced the rates at which males encountered and courted females.

Orientation to displaced model hoods

Our hood manipulations may have changed male behavior in some unknown way that affected attractiveness. To obtain direct evidence that courted females approach hoods, we did an experiment in which females could approach either the courting male as he entered his burrow or his hood. On 8 days, beginning at about 1.5 h after low tide, we removed hoods from 54 burrows and replaced them with models, each

Table 5
Female approach frequencies to courting males and their burrows or to model hoods placed 3 cm away from the burrow entrances

Male behavior	Approach direction	Object approached		Totals
		Male and burrow	Model hood	
Courted but did not closely lead the female	Front	18	9	27
	Back	12	15	27
	Burrow side	37	3	39
	Hood side	6	19	25
	Subtotals	73	46	119
Courted and closely led the female	Front	41	2	43
	Back	7	2	9
	Burrow side	34	1	35
	Hood side	1	6	7
	Subtotals	83	11	94
Totals		156	57	213

We placed models next to the burrows of 432 males.

facing in the direction of the hood it replaced. Each model was positioned so its center was about 3 cm to one side of the burrow and its nearest edge was about 0.5 cm away from the opening (Figure 1d). Provided that courting males return to their burrows and not the models, this manipulation would spatially separate orientation cues from the male and hood. We placed models on alternate sides of the burrows on successive days. We watched individual females for one to a few courtships. For each that resulted in an approach, we recorded whether the male came close to the female and then led her to his burrow, whether the female and male ended their approach at the burrow opening or the model hood, and whether the female approached from the 90° sector (estimated by eye) in front, in back, on the side with, or on the side without the model.

Females approached model hoods about 27% of the time (Table 5). Where they stopped depended on the direction from which they approached. Females that approached from the side with the hood usually (25/32, 78%) stopped at the hood, and those that approached from the side with the burrow opening usually (71/75, 95%) stopped at the opening ($G_w = 58.781$, $p < .001$). Because they approached from the side, these females must have seen hoods and males in near alignment. They often stopped at the object they encountered first, making it uncertain to which of the nearly aligned objects they were orienting. Females that approached from the front and back sectors should have seen hoods and males at greater angular separations. Where these females stopped depended on whether males closely led them to their burrows ($G_w = 19.620$, $p < .001$). When not closely led, females often (24/54, 44%) oriented to hoods, whereas closely led females rarely did (4/52, 8%). In two of the latter four cases, and in eight cases total, males also approached the hood models, not their burrow openings. Crabs that stopped at the models often probed the sand where the burrow opening should have been. Both sexes sometimes visually orient to hoods, and they apparently recognize them as cues to the presence and location of burrows.

DISCUSSION

The purpose of this study was to determine whether and how a female response to the sand hoods built by courting male *U. musica* selects for hood building by increasing the mating frequency of hood builders. We recorded the responses of wandering females to courting males, but we do not know if

all females were receptive. This probably has not biased our results because both receptive and unreceptive females differentially approached hood builders at the same relative rates.

Receptive females significantly more often approached courting hood builders than nonbuilders, and builders significantly more often attracted both receptive and nonreceptive females than did nonbuilders. Once attracted to males' burrows, receptive females were equally likely to stay and mate whether the male had a hood or not. Female *U. beebei* who enter males' burrows also show no preference for pillar builders (Christy, 1988b). Hoods and pillars may attract females, but they apparently do not subsequently affect mate choice.

Pillar building by *U. beebei* is a condition-dependent behavior (Backwell et al., 1995) and pillar builders allocate more time, and presumably more energy, to waving at the expense of feeding compared to nonbuilders (Christy, 1988b). We also found this pattern when we compared the behavior of hood-building and nonbuilding *U. musica*. The presence of a hood, a male's bright white body color, his energetic claw waving without feeding, and perhaps other correlated display traits all possibly contribute to his attractiveness.

We did hood removal and addition experiments to control for the possible effects of the behavioral and color differences between builders and nonbuilders on their attractiveness. We first showed that hood removal did not change male courtship behavior, and we assume the same for hood addition. Hood builders without their hoods were significantly less attractive than were builders with their hoods, but they were significantly more attractive than were nonbuilders without hoods. Hence, hoods made males more attractive, but when they were removed, other traits of hood builders contributed to their greater attractiveness. When we added hood models to nonbuilders' burrows, we increased their attractiveness to that of hood builders with natural or model hoods, again showing that hoods make males attractive. However, in this experiment, the differences in behavior and color between builders and nonbuilders, both with hoods, did not measurably affect their attractiveness; the contribution of hoods to attractiveness was paramount. Finally, the displaced hood experiment demonstrated unequivocally that females approach hoods, especially (40% of approaches) when males do not closely lead females to their burrows. These three experiments provide strong evidence that hood builders are preferentially attractive because courted females differentially orient to and approach hoods when they leave a male's burrow and are not

closely led to the next one by another male. Why are hoods attractive in this specific spatial, temporal, and social context?

Fiddler crabs use vision to locate their burrow openings only at very close range (Zeil, 1998; Zeil and Layne, 2002). Resident crabs that are feeding away from their burrows (Cannicci et al., 1999; Zeil, 1998) and crabs that are moving between burrows (Zeil and Layne, 2002) use a nonvisual mechanism, probably based on leg odometry (Zeil and Layne, 2002), to integrate their movements away from their burrows so that they can return quickly and directly to them. This mechanism is manifest by the frequent small changes a crab makes in its body orientation that keep its transverse axis nearly aligned with the bearing to its burrow (Zeil, 1998; Zeil and Layne, 2002). Female *U. musica* used this mechanism as they departed from males' burrows. However, as they moved farther away, we often noted that they abruptly changed their body orientation and apparently abandoned their path map to the burrow. This was most obvious when they made clear angular changes from their departing directions and either followed males to their burrows or approached males who waved at them but stayed close to their burrows. This is the precise spatial and temporal context in which hoods attract females, perhaps because they are a conspicuous and reliable visual guidepost to males' burrows. Thus, hoods may elicit landmark orientation, visually mediated differential orientation, vertical objects (Langdon and Herrnkind, 1985). This behavior is expressed soon after crabs settle from the plankton (Herrnkind, 1972), is thought to reduce predation risk (Herrnkind, 1983), and is widespread in the genus (Christy, 1995).

Bird bowers usually are built in dense vegetation where only nearby females can see them (Andersson, 1991; Borgia, 1995). In contrast, crabs and cichlid fishes build their structures in relatively open habitats where distant females may see and be attracted to them, increasing the rate that builders encounter and court females. Thus, crab and fish courtship structures might function like the long-range advertisement calls of many passerines, anurans, and orthopterans. Courting male *U. musica*, and especially *U. beebei* (Christy, 1988b), often occur in high-density patches. Courting males of other fiddler crabs also aggregate, forming groups some have compared to leks (Croll and McClintock, 2000; Greenspan, 1980). *U. beebei* and *U. musica* females may differentially orient to aggregations of courting males (Zucker, 1981; but see Christy, 1988a), but the signals or cues that may attract them are unknown.

We studied the possible mid-range (roughly ≤ 1 m) attractiveness of hoods by asking whether they affect the rate that males, within the high-density areas where we observed them, encounter and court females. Visitation rates to hood builders with their hoods intact and removed fit the rates expected from their differential availability for visits and their differential attractiveness. Hence, distant females probably do not orient to hoods. The hood addition experiments gave an unexpected result. Nonbuilders with models received more visits than did nonbuilders without models. However, when we corrected for differences in the availability of males for visits and in their attractiveness to females per courtship, nonbuilders without model hoods received about 30% more visits than expected. This suggests that there may be a cost to having a hood that sometimes exceeds the benefit due to the attractiveness of this structure. One possibility is that a hood may block a sector of a male's vision (Zucker, 1974), preventing him from seeing and courting females who pass behind his hood. However, we cannot explain why we may have detected this cost in only one series of observations.

We have identified a female response to hoods that establishes a consistent relationship between hood building and male courtship success and thus selects for this behavior. Our

results do not exclude the possibility that hood building is sexually selected by other mechanisms. During the displaced hood experiment, in 8 of 213 courtships, males oriented to the hood models, not to the openings of their burrows. Nearly every day during this study we saw a few bright-white males follow females as they responded to courtship from other males. These rogue males did not have burrows. They courted and threatened the females they followed, and they fought the males at the burrows they visited. We twice saw resident males become rogues. Both were nonbuilders that had followed females to neighbors' burrows and then were unable to relocate their own burrows, despite searching for them in the generally correct area (Zeil, 1998). These observations suggest that a male's path integration mechanism sometimes fails or becomes unreliable. When it does, he may use his hood as a guidepost to relocate his burrow. Thus, hood building may be sexually selected both because females are preferentially attracted to hoods and because hoods increase male resource-holding ability.

The possibility that hoods currently have two sexually selected functions suggests a new avenue for understanding how structure building may have evolved. Initially, structures must have been too small to be conspicuous to relatively distant females, but they may have made burrow openings more visible to males as they searched for them close by. Even now, some species of fiddler crabs make low lips or rims (Christy et al., 2001) that perhaps only help males find their burrows. In some species, directional selection favoring larger structures for males might have made them large enough to elicit landmark orientation from mate-searching females. Thus the function of hoods as a sexual signal that we have demonstrated in this study may have arisen as an incidental effect of the function of proto-hoods for male orientation, with both functions now capitalizing on landmark orientation, a behavior that is selected by predation.

We thank W. Eberhard, M. Jennions, and J. Zeil for their detailed and helpful critical comments on an earlier draft of this paper and the Smithsonian Tropical Research Institute and the Japanese Ministry of Education, Culture, and Science for their generous support.

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