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Interspecific attractiveness of structures built by courting male fiddler crabs: experimental evidence of a sensory trap

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Abstract Male fiddler crabs *Uca musica* sometimes build sand hoods and male *Uca beebei* sometimes build mud pillars next to their burrows to which they attract females for mating. Mate-searching females preferentially approach these structures and subsequently mate with structure builders. Here we show that the preference for structures is not species-specific and argue that it may not have evolved for mate choice. When not near burrows, many species of fiddler crabs approach and temporarily hide near objects, suggesting that hoods and pillars may attract females because they elicit this general predator-avoidance behavior. To test this sensory trap hypothesis we individually released female *U. musica*, *U. beebei* and *Uca stenodactylus*, a non-builder, in the center of a circular array of empty burrows to which we added hoods and pillars and then moved a model predator toward the females. All species ran to structures to escape the predator and the two builders preferred hoods. Next, we put hood replicas on male *U. beebei* burrows and pillar replicas on male *U. musica* burrows. When courted, females of both species preferentially approached hoods as they did when chased with a predator. However, males of both species with hoods did not have higher mating rates than males with pillars perhaps because hoods block more of a male's visual field so he

sees and courts fewer females. Sexual selection may often favor male signals that attract females because they facilitate general orientation or navigation mechanisms that reduce predation risk in many contexts, including during mate search.

Keywords Landmark orientation · Mate search risk · Predator avoidance · Sensory trap · *Uca*

Introduction

Processes that occur as a consequence of a female's choice of mates are widely thought to govern the evolution of female preferences based on male traits (Andersson 1994; Espmark et al. 2000). For example, the direct benefits and indicator models propose that variation in female reproductive success or offspring fitness selects for preferences for males with traits that are positively correlated with their material or genetic contributions to their mates or young (Møller 1994; Jennions and Petrie 2000; Møller and Jennions 2001). In Fisher's run-away model (Fisher 1930) preferences evolve because non-random mating establishes genetic correlations between the preference and the preferred trait (e.g., Lande 1981). If processes that are contingent on mating govern preference evolution, then preferences and traits will co-evolve and females should prefer the courtship signals of males of their own species.

A growing number of studies indicate that processes that are independent of mating also affect preference evolution (Kirkpatrick 1987; Ryan 1990, 1998; Basolo 1990; Endler 1992; Christy 1995). Several models, all related to the sensory drive model of communication (Endler 1992; Endler and Basolo 1998), feature female preferences that evolve before preferred traits arise in males. Variation in female fitness as a consequence of mate choice cannot explain the evolution of such preference. Some of these models, for example pre-existing biases (Basolo 1990) and sensory exploitation (Ryan 1990), do not specify what causes preferences to evolve

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either before or after they mediate mate choice (Basolo and Endler 1995; Christy and Backwell 1995). Others models do, and among those, the sensory trap model (West-Eberhard 1984; Christy 1995) is perhaps most explicit. It proposes that female preferences evolve because they are selected for at least one function other than mate choice. For example, females may recognize food by certain stimuli to which they respond with approach. This naturally selected stimulus-response relationship should bias sexual selection in favor of courting males that use signals that are sufficiently similar to food stimuli that females orient to and approach the signaling male (e.g., Proctor 1991; Clark and Uetz 1992; Fleishman 1992; Rodd et al. 2002). Thus, the sensory trap mechanism depends on a model-mimic relationship between some other stimuli and a male trait or signal (Wickler 1965; Christy 1995). A sensory trap hypothesis can be tested with two complimentary experiments that test for mimicry (Christy 1995): (1) the male signal, the alleged mimic, is presented to females in the context thought to select for the response, and (2) the stimuli that elicit the response in that context, the alleged model(s), are presented to females during courtship. If females make the same response to the signal and other stimuli in their usual and transposed contexts, then this would support a mimetic relationship between them and the sensory trap hypothesis.

In this study we used transposition experiments of the first kind and other manipulations to test the sensory trap hypothesis that the structures that courting males of some species of fiddler crabs build at the entrances to their burrows attract females because they elicit landmark orientation, a behavior that is selected by predation and may reduce female mate search risk (Herrnkind 1972, 1983). Males and females of many species of fiddler crabs approach objects to avoid predation (Crane 1975; Christy 1995). We therefore predicted that the female preference for male-built structures would not be species specific. We tested this by measuring the attractiveness of con- and heterospecific structures, alone and together, both in the context of simulated predation and during courtship. These experiments extend our previous work on this problem (Christy 1988b, 1995; Christy et al. 2002b) to include study of the relationship between the interspecific attractiveness of structures in both the model and the mimic contexts. Our results provide new evidence that natural selection for a behavior that reduces predation risk and is used by many species of fiddler crabs has led to sexual selection for structure building.

Fiddler crab courtship: the role of landmark orientation in mate choice

Females of many species of fiddler crabs, especially in the diverse American clade (Strumbauer et al. 1996; Rosenberg 2001), search for mates by moving sequentially between the burrows of a few to dozens of courting males (Christy 1983, 1987; Backwell and Passmore

1996; deRivera and Vehrencamp 2001; Christy et al. 2002a). When fiddler crabs move more than about 10 cm from a burrow they have entered, they use a non-visual mechanism, possibly based on a memory of recent leg movements, to determine the direct route back to the burrow and safety (Zeil 1998; Cannicci et al. 1999; Zeil and Layne 2002). For each move between males' burrows, mate-sampling females must abandon their non-visual reference to the burrow they have left and go on to the next. If a predator should approach at this moment, the female must quickly find a new burrow or a temporary hiding place. This brief, high-risk situation occurs whenever a crab, male or female, adult or juvenile, moves between burrows. It may be the most common context in which predation selects for landmark orientation, visually guided and rapid approach to objects such as shells, stones, pieces of wood, and parts of plants against which crabs take cover when they are unable to locate burrows (Herrnkind 1972, 1983; Langdon and Herrnkind 1985; Christy et al. 2002b).

Landmark orientation may play an important role in mate choice in structure-building fiddler crabs. Courting males of 17 (Christy et al. 2002a) of the approximately 100 species of fiddler crabs (Rosenberg 2001) build structures at the entrances to their burrows. Sexual selection by female choice for structure building has been described for *Uca beebei*, which builds tall narrow mud pillars (Crane 1975; Christy 1987, 1988a, b) and for *Uca musica*, which builds equally tall but much broader sand hoods (Zucker 1974, 1981; Crane 1975; Christy et al. 2001, 2002a). In addition to building structures, males use claw waving and other displays to attract females to their burrows. Sexually receptive females of both species sequentially visit several males (typically >10) before they choose one by staying in his burrow where the pair then mates (Christy 1987; Christy et al. 2002a). Female *U. beebei* also mate on the surface with neighboring burrow-resident or wandering males and then breed in their own burrows (Christy 1987). In both species, mobile unreceptive females also stop at courting males' burrows even though they eventually occupy burrows alone. Both receptive and unreceptive females preferentially approach structure-builders (Christy 1988b; Christy et al. 2002a), who, on a given day, typically number less than half of the actively courting males (Christy 1988b; Christy et al. 2001).

Using experiments that controlled for differences in color and behavior between hood-builders and non-builders, we showed that the presence of a hood on the burrow of a male *U. musica* increases his attractiveness and we confirmed that females visually orient to and approach hoods as well as courting males (Christy et al. 2002a). However, after a female reaches a burrow, the presence of a hood or, for *U. beebei*, the presence of a pillar, does not affect whether she will stay and mate (Christy 1988b; Christy et al. 2002a); structures attract females but do not subsequently affect female mating decisions. These observations suggest that females approach pillars and hoods because they are salient visual

cues for landmark orientation, a behavior that may reduce a female's risk of predation, particularly from birds such as juvenile and female great-tailed grackles (*Quiscalus mexicanus*), the most common predators of fiddler crabs at our study sites (Koga et al. 1998, 2001; deRivera et al. 2002).

Methods

Study site

Our primary study sites were sand and mud flats on the west bank of the Pacific entrance to the Panama Canal about 1 km north of the Bridge of the Americas. We studied landmark orientation by *U. musica* in the context of simulated predation on a sand beach on the western shore of Culebra Island, which is located about 5 km southeast of the bridge along the approach channel to the Panama Canal. We did the transposition experiments in 1992–1993 and the rest of the study from November 1998 to April 1999.

Attractiveness of hoods and pillars in the context of predation

We recorded the responses of female *U. beebei*, *U. musica* and *Uca stenodactylus* to the approach of a model of a great-tailed grackle. Courting male *U. stenodactylus* do not build structures nor do they typically lead females to their burrows with claw waving as do the structure-building species. Instead *U. stenodactylus* males make rapid radial movements, typically with their large claw held high, in all directions away from and back to their burrow entrances. These movements sometimes appear to startle nearby females and reveal their locations to the displaying males. Males attempt to intercept these females and herd, or capture and carry them to their burrow (Crane 1975; Christy and Salmon 1991). Like *U. beebei*, male *U. stenodactylus* also approach neighboring females, often without waving or other obvious display, and mate with them on the surface near the females' burrows.

We individually released females of the three species in a slight depression in the center of a circle, 40 cm in diameter, which we scribed on the sand. Sixteen equally spaced artificial burrows, 1.5 cm in diameter, were made around the circumference of the circular arena. In one set of experiments we added model hoods to every other burrow. In another set we alternately added model hoods and pillars to the burrows. Models faced the center of the arena. A second circle with a 10 cm radius was very lightly scribed concentric to the larger circle. After being released, females usually groomed themselves and then moved slowly away from the center of the circle. When a female crossed the inner circle, we moved a model of a grackle, which was suspended by a wire from a long thin pole, directly and quickly toward the female. The starting position of the model was about 3 m from the female. This simulated a running approach, a common hunting mode of grackles (Koga et al. 2001). To reduce that chance that movements of nearby resident crabs affected the behavior of our test subjects, we removed all crabs and filled all burrows within a 2-m radius of the center of the arena. In response to the approaching model, a few females "froze" (pressed their sternum to the sand and did not run), but most ran out of the circle or to a burrow with or without a structure. When females ran to structures or unadorned burrows they typically followed a curved or angular path away from the predator and approached an object directly only when they were close to it. This suggests that they visually oriented to burrows and structures as they were running from the predator, not before. We omitted the few "freeze responses" from the data, as we were interested in the orientation responses of females that run from predators.

We obtained females by digging them from their burrows and we used each only once, typically within 30 min of capture. Be-

fore capture, these females were burrow residents that were feeding, not searching for mates. Such females typically have small poorly developed ovaries and are not ready to mate (J.H. Christy and T. Koga, unpublished). If the sensory trap hypothesis is wrong, and females approach structures because this response is selected for mate choice, these females would be less likely to approach structures compared to females who were searching for mates before capture. Thus, by using females who were not mate-searching we have conducted a conservative test of the sensory trap hypothesis. We did two goodness-of-fit *G*-tests (William's correction has been applied to all *G*-tests; Sokal and Rohlf 1995). First, we tested whether crabs ran to burrows more often than expected by chance as determined by the relative proportions of the circumference of the arena that were occupied by empty space or burrows and structures. Second, we asked whether the crabs that ran to burrows preferentially approached burrows with hoods over unadorned burrows or, if both burrows had structures, whether they preferred hoods or pillars.

Attractiveness of hoods and pillars during courtship

The sensory trap hypothesis predicts that the relative attractiveness of hoods and pillars to female *U. musica* and *U. beebei* during courtship should be the same as their relative attractiveness in the context of predation. This prediction follows from our assumption that hoods and pillars elicit the same predator avoidance response from females of both species in both contexts. To test this, beginning about 1 h after low tide, when males no longer build or repair their structures (Christy et al. 2002a), we removed the pillars from every other *U. beebei* burrow in an area with abundant pillars and added hood models to these burrows. We put out about 25 hood models on each of 10 days during the 4–5 day period in the middle of each biweekly cycle that most mating occurs. On 11 different days, also during periods of intense courtship and mating, we removed about 25 hoods from every other *U. musica* burrow and replaced them with pillar models. These manipulations created each day a spatial array of alternating burrows with natural male-built structures and with model structures of the other species. However, males with natural hoods or pillars always were more abundant in the observation areas. For approximately the next 2 h each day we recorded whether courted females approached or passed males with their own or the other species' (model) structure. We did not include controls for the manipulations (e.g., hoods replaced with hood models) because previously we found no difference between the attractiveness of real and model structures (Christy et al. 2002a). We observed the responses of 159 female *U. beebei* to (mean \pm standard error) 6.5 ± 0.48 courtships per female and the responses of 127 female *U. musica* to 5.2 ± 0.41 courtships per female. Females did not revisit males so each courtship was a unique male-female interaction. We treated each of the several observations of courtship from each female as an independent observation (sample sizes for the *G*-tests are the number of courtships, not females). We are confident that this procedure has not biased our conclusions. In a previous study in which we used the same basic procedures to measure the relative attractiveness of male *U. musica* with and without hoods (Christy et al. 2002a), we found that relative approach frequencies were statistically the same whether based on a single measure for each female or multiple observations per female. In addition, there was no significant variation among females in the relative frequencies that they approached males with and without hoods. We used *G*-tests of independence to determine whether the frequency with which females approached the males who courted them depended on the presence, absence or kind of structure on the males' burrows.

Mating frequencies

We did an experiment to determine if differences in the frequencies that females approach courting males with their own and the

Table 1 Responses of female fiddler crabs in a circular test arena to the approach of a model of a grackle. Females could either run out of the arena or approach empty burrows with or without hoods

Species	Out of arena		To a burrow		G^a	No hood		Hood		%	G^b
	Obs.	Exp.	Obs.	Exp.		Obs.	Exp.	Obs.	Exp.		
<i>U. musica</i>	28	139	138	27	363.8*	22	69	116	69	84	69.9*
<i>U. beebei</i>	19	132	138	25	395.3*	18	69	120	69	87	84.1*
<i>U. stenodactylus</i>	21	127	130	24	360.8*	39	65	91	65	70	21.3*

* $P < 0.001$

^a G -test of the hypothesis that females did not preferentially approach burrows. The expected frequencies were calculated from the proportions of the circumference of the circular arena that were occupied by burrows, with and without hoods (0.16) and by empty space (0.84)

^b G -test of the hypothesis that females who ran to burrows approached burrows with and without hoods in proportion to their equal relative abundance (0.50)

other species' structure affect male mating frequencies. The results would indicate whether sexual selection might favor a heterospecific structure. At about 1 h past low tide we placed small plastic chips near approximately 100 burrows of *U. musica* with hoods or of *U. beebei* with pillars. Moving sequentially from burrow to burrow, we replaced every second hood with a pillar model, or every second pillar with a hood model. For the reasons given previously, controls were unnecessary. At 30–45 min before the tide covered the burrows, we counted the number of males in plugged and open burrows indicating, respectively, that they had and had not attracted mates (Christy et al. 2001). We used Fisher's exact tests to compare mating frequencies between males with their own or with the other species' structure.

When statistical tests of hypotheses gave non-significant differences, we did power analyses following the procedures either in Cohen (1988) or in the on-line manual (Buchner et al. 1997) for the computer shareware program G*Power (Faul and Erdfelder 1992). We used Cohen's (1988) conventions for small (0.10), medium (0.30), and large (0.50) effect sizes and his effect size index w for contingency tables (p 221).

Models

For the transposition experiments, we used hood models that we sculpted from clay and pillar models that we carved from cork stoppers. For the experiments on the attractiveness of structures to mate-searching females we needed a large number of durable models so we cast concrete replicas of a real hood (see Fig. 1 in Christy et al. 2002a) and pillar from latex molds of these structures. We colored the models with ink or glued sediment to their surface so that they appeared natural to us. All models were 22 mm high. At their bases, the hood models were 32 mm wide and the pillar models were 19 mm wide. These values are within 1 mm of the average dimensions for hoods ($n=100$; Christy et al. 2001) and near the maximum of those for pillars ($n=95$, J.H. Christy and U. Schober, unpublished). We used relatively large pillars so that the heights of the models, possibly an important stimulus dimension (Zeil et al. 1986; Land and Layne 1995; Zeil and Al-Mutairi 1996), were equal.

Results

Attractiveness of hoods and pillars in the context of predation

Significantly more female *U. musica*, *U. beebei* and *U. stenodactylus* than expected ran from the model predator to burrows than out of the arena, and to burrows

with hoods than to unadorned burrows (Table 1). The three species approached hooded burrows at significantly different frequencies ($G=13.373$, 2 df , $P < 0.005$, $n=406$). Hoods were equally attractive to the two structure builders ($G=0.468$, 1 df , $P=0.494$, $n=276$, power >0.99 to detect a medium effect) and significantly less attractive ($G=12.80$, 1 df , $P < 0.001$, $n=406$) to *U. stenodactylus*, the non-building species.

When given a choice between escaping a predator by running out of the arena or to burrows with hoods or pillars, again significantly more females of all species than expected ran to burrows (Table 2). The two structure builders preferentially approached hoods at very similar frequencies of about 70% ($G=0.164$, 1 df , $P=0.685$, $n=258$, power >0.99 to detect a medium effect). Female *U. stenodactylus*, the non-builder, did not prefer hoods (58%) to pillars (Table 2, power >0.92 to detect a medium effect).

Attractiveness of hoods and pillars during courtship

Female *U. musica* approached courting males with hoods, with pillar models and without structures at significantly different frequencies (Table 3). Males with unadorned burrows were relatively unattractive and males with hoods were significantly more attractive than were males with pillars ($G=4.277$, 1 df , $P=0.039$, $n=391$), but the effect size was small at $w=0.091$.

Similarly, female *U. beebei* approached males with pillars, hoods or without structures at significantly different frequencies (Table 3). They least often approached males without structures. They significantly more often approached males with hoods than they did males with pillars, their own species' structure ($G=8.634$, 1 df , $P=0.003$, $n=333$) and the effect size was larger at $w=0.138$.

Female *U. musica* and *U. beebei* were equally attracted to males with hoods ($G=0.039$, 1 df , $P=0.844$, $n=440$, power >0.99 to detect a medium effect) and just so to males with pillars ($G=3.10$, 1 df , $P=0.078$, $n=513$, power >0.99 to detect a medium effect). The response of female *U. beebei* to courting males of their own species with

Table 2 Responses of female fiddler crabs in a circular test arena to the approach of a model of a grackle. Females could run out of the arena, to burrows with model hoods or to burrows with model pillars

Species	Out of arena		To a burrow		G^a	Pillar		Hood		%	G^b
	Obs.	Exp.	Obs.	Exp.		Obs.	Exp.	Obs.	Exp.		
<i>U. musica</i>	21	123	129	27	328.2*	41	65	88	65	68	17.5*
<i>U. beebei</i>	21	123	129	27	328.2*	38	65	91	65	71	22.3*
<i>U. stenodactylus</i>	27	129	130	28	311.4*	55	65	75	65	58	3.078, n.s.

* $P < 0.001$, n.s. $P > 0.05$

^a G -test of the hypothesis that females did not preferentially approach burrows, with either structure, to avoid the predator. The expected frequencies were calculated from the proportions of the circumference of the circular arena occupied by burrows with pillars or hoods (0.18) and by empty space (0.82)

^b G -test of the hypothesis that females who ran to burrows approached burrows with pillars and burrows with hoods in proportion to their equal relative abundance (0.50)

Table 3 Attractiveness of *U. musica* males courting from burrows without a structure, with hoods, or with pillar models and of *U. beebei* males courting from burrows without a structure, with pillars or with hood models. The G -tests are of the hypothesis that female responses are independent of the presence or type of structure on a male's burrow

Species	Female response				
	Structure	Pass	Approach	% Approach	G
<i>U. musica</i>	Hood	63	263	81	37.8*
	Pillar	53	142	73	
	None	194	305	61	
<i>U. beebei</i>	Hood	23	91	80	38.1*
	Pillar	110	208	65	
	None	101	86	46	

* $P < 0.001$

Table 4 Mating frequencies of hood building *U. musica* males with hoods and with pillar models, and of pillar building *U. beebei* males with pillars and with hood models. G -tests are of the hypothesis that mating frequencies are independent of the type of structure on males' burrows

Species	Outcome				
	Structure	Did not mate	Mated	% Mated	G
<i>U. musica</i>	Hood	312	31	9.0	0.969, ns
	Pillar	319	24	7.0	
<i>U. beebei</i>	Hood	571	15	2.6	0.486, n.s.
	Pillar	567	19	3.2	

n.s. $P > 0.05$

U. musica's hoods, was striking. Moving quickly, females often would pass and then abruptly reverse direction and dash back to a male with a hood. Females seldom respond so dramatically to males with pillars.

Mating frequencies

There were no significant differences in the mating frequencies of males of either species with their own or the

other species' structures (Table 4). The power to detect a significant difference in *U. musica* ($n=686$) given the small expected effect size of 0.091, was moderate at 0.664, while that for *U. beebei* ($n=1,172$) to detect the larger expected effect size of 0.138 was high at 0.997. A previous 2-month study of mating frequencies at >9,500 *U. musica* burrows with natural hoods gave an average of 0.09 matings/burrow/day (Christy et al. 2001), the same value we obtained in this study with a much smaller sample. Although the power of our test of *U. musica* mating rates is only moderate we are confident that the results are accurate; the greater attractiveness of hoods to females of both species was not reflected in higher mating rates of males with hoods.

Discussion

The purpose of this study was to test the hypothesis that female *U. musica* and *U. beebei* approach males with hoods and pillars because these structures elicit landmark orientation, a behavior that is selected by predation and that may reduce female mate search risk. Using transposition experiments, we showed previously that female *U. musica* and *U. beebei* preferred to run to burrows with pillars over unadorned burrows to escape a simulated predator (Christy 1995). In this study we found that both also preferred to run to burrows with hoods (Table 1). Our test subjects were not searching for mates when they were captured and they were unlikely to approach structures for mate choice. The simplest functional interpretation of this behavior is that it reduces a female's predation risk when she is moving between burrows even when she is not looking for a mate. Female *U. stenodactylus*, a species that does not build structures, also ran to pillars and hoods showing that this behavior is maintained in females that could not possibly benefit from using the response during mate search. However, this species approached pillars at a slightly lower frequency (Christy 1995) and hoods at a significantly lower frequency (this study) than did the females of the two structure building species. Hence, the response is present in all three species but is less developed in the one that

does not build structures (for a counter example see Christy 1995).

If female responses to male courtship signals that result in preferences are adaptations for mate choice and co-evolve with preferred male traits, then, allowing for environmental effects, comparisons between species should reveal species-specific correlations between male signals and female responses (Ryan 1994). We found no evidence of such signal-response tuning in our experiments. When chased, female *U. beebei* and *U. musica* both preferentially approached hoods. It could be argued that there is selection for both species to seek refuge by running to the larger structure, either because it provides better cover, or simply because it is more conspicuous; preferences for con-specific signals may be evident only during courtship, when females identify males of their own species and choose among them. However, we found no evidence that females' responses to these two structures depended on context. Females of both species preferentially approached hoods during courtship, just as they did when they ran from the model predator. We suggest that larger (broader) hoods simply are more conspicuous than pillars and that both structures elicit the same risk-reducing response in both species in both contexts.

We had expected that the greater attractiveness of hoods to mate-searching females of both species would result in higher mating frequencies of male *U. musica* with natural hoods and male *U. beebei* with model hoods. To the contrary, males of both species with hoods and pillars mated at frequencies that were not statistically different. Mating rates are the product of the rate that males encounter and court females, the rate that females approach the males that court them and the rate they stay and mate with the males they approach (Christy et al. 2002a). From this and previous studies we know that courted females preferentially approach males with hoods and pillars. These observations suggest two possible reasons why males with hoods and pillars had equivalent mating rates. First, after females approached males they may have discriminated against those with the other species' structure. This level of discrimination would be somewhat surprising because previous research showed that even the presence or absence of a hood or a pillar does not affect the likelihood that a female will mate with a male once she visits his burrow. Second, hoods may decrease the rate that males encounter and court females. Indeed, this was the case in one of two previous experiments in which we measured the effects of hoods on encounter rates (Christy et al. 2002a). Hoods may decrease encounter rates because they prevent males from seeing and courting some females that pass behind the hood. This cost of missed courtships might balance the contribution of hoods to attractiveness and result in no net gain in mating frequency. Regardless of the mechanism, there apparently is no benefit for male *U. beebei* to build larger, hood-like pillars. Since structure building is costly (Backwell et al. 1995; Christy et al. 2001) there may be selection for *U. musica* to build narrower, less attractive, but equally effective pillar-like hoods. However,

even broad, robust hoods made of the fine sand where *U. musica* lives often crumble or blow away in the wind. Hence, males probably would not be able to profit if they built less costly but extremely fragile pillar-like hoods.

Studies of Darwin's finches (Podos 2001), sticklebacks (Rundel et al. 2000), African cichlids (Seehausen et al. 1997) and lekking forest birds (Endler and Théry 1996) show how ecological factors can shape patterns of sexual signaling by changing the signaling environment, and by changing selection on the traits with which males signal (Orr and Smith 1998). Clearly, the evolution of courtship signals is affected by processes that operate apart from and in addition to female mate preferences based on those signals. Our study indicates that processes that are unrelated to sexual communication for mate choice also affect preference evolution. Mate searching takes time and energy and often exposes females to an increased risk of predation (Backwell and Passmore 1996; Gibson and Langen 1996; Jennions and Petrie 1997; Koga et al. 1998). These costs will bias sexual selection in favor of signals that elicit orientation, navigation or predator avoidance responses that facilitate safe, efficient searching (Dawkins and Guilford 1996). Thus, mate preferences often may be complex expressions of receivers' sensory-neural-motor systems that perform multiple functions and so are shaped by many processes before and after they play a role in courtship. If preferences typically have multiple utility, then models of preference evolution that invoke singular processes, for example, selection for choice of males that will contribute in a specific way to female or offspring fitness, probably are incomplete.

There is evidence that pillar and hood building are condition-dependent behaviors (Backwell et al. 1995; Christy et al. 2001). Females who are attracted to structure builders may mate high quality males and the consequent fitness benefits may strengthen this preference. But, we would argue and as our study suggests, the evolution of landmark orientation and approach to structures may be governed not by the benefits of mating good-condition males, these may be incidental, but by the benefits of reduced predation risk whenever crabs move between burrows, including during mate search. We emphasize that the sensory trap mechanism of sexual selection, though based on mimicry, a form of deceit, does not predict the evolution of costly preferences (Christy 1995, 1997; Christy et al. 2002b). The effects of sensory trap preferences on female fitness must be assessed across the contexts in which the preferences function, including during mate choice. Studies of sexual communication should be undertaken from a broad perspective with the goal of understanding how diverse processes interact and jointly affect the evolution of male courtship signals and female responses to them.

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