The strength of a female mate preference increases with predation risk

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When females search for mates and their perceived risk of predation increases, they less often express preferences for males that use conspicuous courtship signals, relaxing sexual selection on production of these signals. Here, we report an apparent exception to this general pattern. Courting male fiddler crabs *Uca beebei* sometimes build pillars of mud at the openings to their burrows in which crabs mate. Females visit several males before they choose a mate by staying and breeding in their burrows, and they preferentially visit males with pillars. Previous studies suggested that this preference is based on a visual orientation behaviour that may reduce females' risk of predation while searching for a mate. We tested this idea by determining whether the female preference for males with pillars increases with perceived predation risk. We attracted avian predators to where crabs were courting and measured the rates that sexually receptive females visited courting males with and without mud pillars. Under elevated risk, females continued to search for mates and they showed a stronger relative preference for males with pillars. Thus, when predation risk is high, females may continue to express preferences that are under natural selection because they help females avoid predation, strengthening sexual selection for use of the preferred signal.

Keywords: female preference; predation risk; sexual selection; sensory trap; fiddler crab

1. INTRODUCTION

Many animals change their courtship behaviour as their risk of predation increases (Magnhagen 1991; Jennions & Petrie 1997). Courtship signals evolve under sexual selection to be conspicuous to the opposite sex but they also often are conspicuous to predators (Wagner & Basolo 2007). Hence, animals may stop courting (Ryan *et al.* 1982), court less (Jones *et al.* 2002) or use less conspicuous signals (Endler 1995) as their predation risk increases. An increase in predation risk also typically constrains mate choice (Jennions & Petrie 1997; but see Bro-Jøgensen 2002). Under high risk, females may reduce their exposure to predators by searching less extensively for a mate (Hedrick & Dill 1993), by failing to express a preference for males that use conspicuous signals (Johnson & Basolo 2003), or by switching to a safer mode of mating (Koga *et al.* 1998). In general, an increase in predation risk results in a decrease in the strength of sexual selection by female preferences for conspicuous male signals and the use of those signals by males (Pomiankowski 1987; Forsgren 1992; Godin & Briggs 1996).

However, it has been suggested (Christy 1995; Dawkins & Guilford 1996) that some female preferences may reduce predation risk (or other costs) to females as they search for mates. Such preferences and sexual selection on the preferred male signals should increase in strength with increasing risk. Here, we test this idea by manipulating perceived predation risk and measuring the strength of a preference for a conspicuous signal used by male fiddler crabs. Previous studies of the courtship behaviour of fiddler crabs (summarized by Christy 2007) strongly suggested that the preference may reduce females' predation risk.

Courting males of 18 species of fiddler crab (genus *Uca*, approx. 100 species, Rosenberg 2001), sometimes build structures from the sediment at the entrances of their burrows to which they attract females for mating and in which females breed (Christy 2007). Females of three species have been shown to prefer to visit males with structures (*Uca beebei*, Christy 1988*b*; Christy *et al.* 2003; *Uca terpsichores*, Christy *et al.* 2002; *Uca lactea*, Kim 2006). A series of field experiments tested the attractiveness of male-built structures and natural objects of similar size (shells, stones, rocks and wood) to receptive and non-receptive females of species that do and do not build structures. Structure attractiveness was measured during courtship, during simulated attack by a predator, and when females spontaneously oriented to structures but predators were absent. These studies (Christy 2007) lead to the hypothesis that fiddler crab courtship structures are attractive because they elicit 'landmark orientation' (Herrnkind 1983), the tendency of crabs that do not have access to burrows to move to nearby objects whether or not a predator is nearby.

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We recently tested this hypothesis by manipulating the predation risk perceived by mate searching female *U. terpsichores* and measuring the frequency per courtship that they approached males with and without sand hoods at their burrow entrances. As predicted by the hypothesis, the attractiveness of males with hoods, but not those without hoods, increased significantly with perceived predation risk (Kim *et al.* 2007). However, we did not establish a link between this measure of preference and male-mating rates. Hence, we could not conclude that sexual selection for structure building may increase with risk. Here, we use a different measure of female preference for structure-building males of the Neotropical fiddler crab *U. beebei*. The measure we chose has been shown to be directly proportional to male-mating rates providing a good, albeit indirect, measure of sexual selection for use of courtship structures.

2. MATERIAL AND METHODS

This study was done during November and December 2005 on the west bank of the Pacific entrance to the Panama Canal approximately 1 km north of the Bridge of the Americas. *U. beebei* lives in mixed-sex aggregations at an average density of approximately 50 adults m^{-2} (Koga *et al.* 2001) on intertidal mud flats throughout the area. Great-tailed grackles, *Quiscalus mexicanus*, are common predators of *U. beebei* at the study site (Koga *et al.* 1998, 2001).

Like most fiddler crabs, *U. beebei* has a semilunar reproductive cycle with mating occurring over an 8 to 9-day period centred on a 2 to 3-day 'peak' (Morgan & Christy 1995). Each day during this activity cycle numbers from a few up to approximately 80 per cent of courting males build mud pillars at the entrances to their burrows to which they attract females for mating using claw waving and other signals (figure 1, Christy 1987, 1988*a*,*b*). Non-breeding females occupy burrows alone. During low tide they emerge to feed on the surface and they typically range no more than a few centimetres from their burrows to which they return frequently. When females become sexually receptive they may mate and breed in two different ways. Some stay at their burrows, mate on the surface with neighbouring or transient males and then oviposit and incubate their clutch underground in their own burrows. Others leave their burrow and go to the burrow of a male where they mate underground and stay for approximately two weeks while their eggs develop (Christy 1987). We studied mate preferences only of sexually receptive females who left their burrows and searched for mates. Mate searching receptive females can be distinguished from non-receptive females who also sometime leave their burrows and look for new ones, because receptive females seldom receive threats from males and they do not attempt to dig new burrows or obtain them from other crabs through aggression (Christy 1988*b*). Receptive females sequentially approach and stop at the burrows of several males (they 'visit' these males) before they choose one by staying in his burrow whereupon the male plugs the burrow sealing himself and the female below. This ends mate searching for that female. We measured preference as the frequency with which males with and without pillars were visited by sexually receptive females. When a male is visited by a female, she may or may not enter the male's burrow. We observed crabs from a distance through binoculars and it was not always possible to discern whether the female entered the male's burrow. We therefore

Figure 1. Male *Uca beebei* with a mud pillar at his burrow.

recorded as a visit all cases in which a female stopped at a male's burrow regardless of whether she entered it. Previous studies strongly suggest that visitation rates as we recorded them in this study give reliable estimates of mating rates of males with and without pillars. deRivera *et al.* (2003) found that the number of female *U. beebei* seen visiting males was significantly positively correlated with the number of matings in male burrows under both high- and low predation risk. J. H. Christy & U. Schober (1989, 1993, unpublished data) did a detailed video tape study of the mate searching behaviour of 27 sexually receptive females. Tapes were made of all courtship interactions (1030) of these females until they stayed with males in their burrows to mate. Visits were scored using the same criteria we used in the present study; the female stops at a male's burrow and may or may not enter. There was no significant difference in the mating rates of males with and without pillars, which were visited by females (males with pillars: 10 matings from 79 visits, 12.66%; males without pillars: 17 matings from 153 visits, 11.11%; *G*-test of independence, William's correction; $G_{\mathrm{W}} = 0.1173, p > 0.50$). Finally, Christy (1988*b*) showed that under natural levels of risk, females more often visit males with pillars but the presence of a pillar does not affect whether females that enter males' burrows stay and mate. Other, as yet unidentified cues affect mating decisions after females reach males' burrows (Christy & Schober 1994). Together, these studies strongly suggest that the mating rates of males with and without pillars may be directly proportional to the rates with which they are visited by mate-searching females. If perceived predation risk affects female visitation rates to males with and without pillars, it should also affect the mating rates of these males and sexual selection for pillar building.

We manipulated perceived predation risk using established methods (Koga *et al.* 1998; deRivera *et al.* 2003). We selected a small area (48 m^2) that was bounded naturally by unsuitable habitat and that had a high density of *U. beebei*. We bisected the area by erecting a straight, 0.5 m high brown fabric fence across the middle. The fence prevented crabs on each side from seeing crabs and predators on the surface on the opposite side. Using stakes and string we delimited five 2×2.4 m permanent rectangular plots on each side. We performed the experiments daily during 17 days spanning most of two semilunar reproductive periods. On the first day of each period, we observed crabs on both sides of the area to determine whether there was a difference in activity.

Table 1. Summary statistics (means ±s.d.) for the two sides of the observation area ($n = 17$ days).

variable	predation risk		statistic	p-value
	high (food added)	low (no food)		
no. of predator visits/day	26.41 (±17.68)	3.53 (±3.97)	$Z = -3.516$	<0.0001
no. of courting males/day	318.71 (±59.24)	330.65 (±58.83)	$Z = -1.231$	0.218
no. of pillar builders/day	150.12 (±38.37)	168.59 (±55.62)	$Z = -0.757$	0.449
no. of non-builders/day	160.41(±30.57)	170.24 (±58.33)	$Z = -0.260$	0.795
percent pillar builders/day	47.5% (±10.5%)	49.3% (±9.7%)	$Z = -1.254$	0.209
no. of mate searching females/day	15.88 (±6.50)	15.70 (±7.10)	$Z = -0.259$	0.796
percent visits to pillar builders/day	78.3% (±11.5%)	57.3% (±12.0%)	$Z = -3.621$	0.0003
total visits to pillar builders	316	244	$G_1 = 33.33$	<0.0001
total visits to non-builders	84	160		

From the second day onward, just before the time of low tide, we scattered one handful of dry dog food on one side of the area, alternating sides daily. The dog food attracted great-tailed grackles which also fed occasionally on the crabs. We waited until low tide to attract grackles because more than 50 per cent of pillar-building males usually have built their pillars by this time and females are just beginning to search for mates (Christy 1988*a*,*b*). Hence, the experiment was designed to allow us to measure the effect of perceived predation risk on the rates that males with and without pillars were visited by sexually receptive females but not on the rate males built pillars on a given day (see Koga *et al.* 1998 and deRivera *et al.* 2003 for the effects of perceived predation risk on pillar building).

Two persons, one on each side of the area, observed the crabs through binoculars from at least 2 m away, far enough so that the crabs and grackles behaved normally. Beginning at low tide and continuing for 2.5 hours, each observer recorded the following data for each of the five plots per side in each 30 min interval: during the first 10 min, the maximum number of courting (claw waving) males with and without pillars, during the next 20 min, the number of times receptive females visited males with and without pillars (each of the five plots were observed for 4 min in randomized sequence), and the number of times grackles caused crabs to hide in their burrows (recorded as 'predator visit' to the plot). Receptive females that have begun to move away from males' burrows respond to the immediate threat from a predator by moving quickly back to the burrows they are leaving. We did not include these 'return visits' in our count of visits to males. All visits we counted were made when predators were temporally absent from the vicinity, males had resumed courtship on the surface and females moved to courting males they had not previously visited. These 'forward visits' constitute female mate searching behaviour; they are not made in direct response to the threat of a particular predator. We recorded one to five visits from each female, then located another female and recorded her responses to courting males. Females typically move several metres while searching for a mate and they seldom loop back and pass a second time through a given area. Hence, they very rarely visit a given male a second time once they have left his burrow and visited another male. We therefore assume that each of the visits we counted came from a unique courtship interaction between a given male and female. After 30 min, the observers changed sides so that individual observational or recording biases were distributed equally between the two sides each day.

Since the side of the flat that received food changed daily, possible side effects were balanced between the treatments, and possible sequential effects unrelated to the treatments were balanced between the sides. For each day, we summed the values of the variables across the five plots in each half of the area and used these sums as the values of the variables for that day and side. Hence, there was a single value of each variable for each side and day. Summary statistics are means±s.d. We recorded 804 female visits to males; high-risk side: 278 females averaging 1.48±0.90 visits per female; low-risk side: 275 females averaging 1.51±0.88 visits per female. We based our analysis on the total number of visits to the two classes of males per side per day. We calculated the relative visitation rates to males with pillars for each day and side as visits to males with pillars/total visits to males with and without pillars for that day. We used the Wilcoxon signed-rank test to compare the means of the dependent variables between the food added (high risk) and food not added (low risk) treatments.

3. RESULTS
Great-tailed grackles significantly more often visited the side of the mud flat to which food was added (table 1). Owing to the small size of the area ($24\ m^2$ on each side), each time a bird visited, nearly all crabs on that side retreated into burrows, where they hid until the predator left. There was no significant difference in the number of courting males, the number of males with pillars or the proportion of males with pillars between the treatments. There also was no significant difference in the number of mate-searching females between the two treatments. Courtship activity (maximum number of courting males) did not decrease with an increase in perceived predation risk (the number of times crabs entered their burrows in response to grackles, table 1). However, predation risk had a marked effect on the rate males with pillars were visited by receptive females. The relative visitation rate to males with pillars was significantly greater on the side with greater perceived risk (78% versus 57%, table 1) and this difference was seen on all 17 days of the experiment (figure 2).

4. DISCUSSION
The results of our study provide a clear exception to the general pattern that females reduce mate searching and are less likely to express preferences under elevated predation risk. Sexually receptive female *U. beebei*,
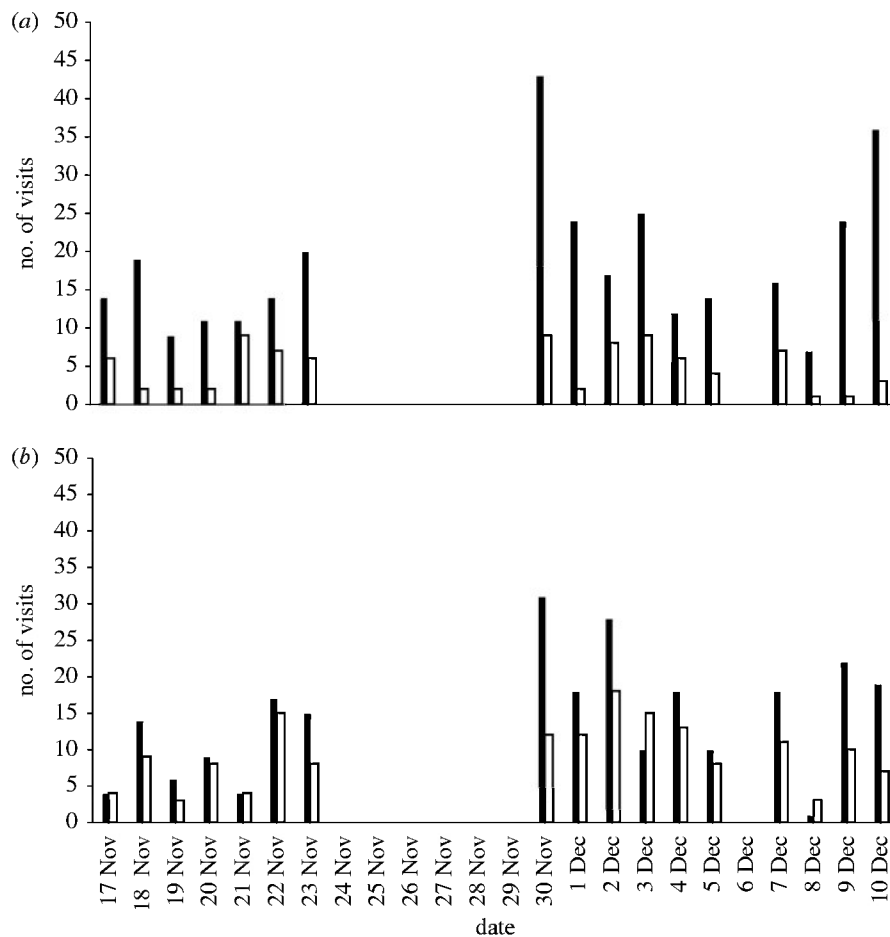
Figure 2. Distribution of the number of females visiting males with pillars (black bar) and without pillars (white bar) in the environment with (*a*) high predation risk and (*b*) low predation risk.

continued to search for mates and these females significantly more often visited males with pillars when their perceived predation risk was relatively high. If, as we have argued, visitation rates are correlated with male mating rates, then sexual selection for pillar building may increase with predation risk. Whether it does or not may relate importantly to the timing of the increase in predation risk in the daily activity cycle. In previous studies (Koga *et al.* 1998; deRivera *et al.* 2003), grackles were attracted before and during the daily pillar-building period, which suppressed pillar building, while we attracted birds only after pillars were built. Hence, when perceived risk was high, females in these previous studies could not safely search for mates by orienting to pillars because relatively few males built them. This may explain why fewer females in these studies left their burrows to search for mates under elevated predation risk.

Courtship structures of fiddler crabs can be regarded as sensory traps because they elicit a female response that increases the male's chance of mating but has a function other than mate choice (West-Eberhard 1984; Christy 1995). It is often assumed that female responses to sensory trap courtship signals are costly and that these costs produce selection for females to escape the trap (e.g. Stuart-Fox 2005). To the contrary, the results of this study and previous studies of the basis of the response in landmark orientation strongly suggest that the response is beneficial because it helps females reduce their risk of predation as they search for mates. Females that are searching for new burrows but not

mates also preferentially approach courting males with structures (*U. beebei*: Christy 1988*a*,*b*, unpublished data 1985–1989, 1993; *U. terpsichores*: Christy *et al.* 2002) as expected if the response has a function other than mate choice. Thus, landmark orientation may reduce predation risk whether or not it also mediates a mate preference (Christy 1995; Dawkins & Guilford 1996).

Preferential orientation by female fiddler crabs to males who have structures by their burrows may produce a mating bias for those males. Thus, in addition to natural selection for predator avoidance, the response may also be exposed to both direct and indirect sexual selection (*sensu* Fuller *et al.* 2005; Kokko *et al.* 2006) as a consequence of reproduction between females with the preference and males with the trait. For example, structure builders may provide better burrows for breeding (though this does not appear to be true for *U. beebei*; Christy & Schober 1994), creating direct sexual selection on the preference. In addition, structure building may be correlated with heritable male traits that increase the fitness of the attracted female or her offspring, creating indirect sexual selection on the preference. For example, pillar building by male *U. beebei* appears to depend on male condition (Backwell *et al.* 1995). Provided that male condition has a heritable genetic basis, females may gain indirect benefits by mating with pillar builders.

If the female response to courtship structures has been affected by direct or indirect sexual selection then one might expect females that have stopped at and entered males' burrows to prefer to stay and mate if they

have structures. Neither *U. beebei* (Christy 1988*a*,*b*; J. H. Christy & U. Schober 1989, 1993, unpublished data) nor *U. terpsichores* (Christy *et al.* 2002) show such a preference. This lack of an effect of structures on mating decisions once a female has reached a male's burrow would be expected if the preference (approach structure) is shaped only by direct selection for predator avoidance. In this case, the fitness benefits of preferentially visiting a male with a structure would end once the female has reached his burrow. Although there are several approaches to test for direct and indirect sexual selection on sensory biases (Christy 1995; Endler & Basolo 1998; Rodríguez & Sneddon 2004) a full accounting of the effects of different modes of selection on mating preferences is extraordinarily difficult and unlikely to be forthcoming (Kokko *et al.* 2003).

Sexually selected signals often reduce the survival of signallers because they are conspicuous and attract predators and parasites (reviewed by Jennions *et al.* 2001; Kotiaho 2001). However, it has recently been shown that the sand hoods built by male *U. terpsichores* (Ribeiro *et al.* 2006) and the semi-domes built by male *U. lactea* (Kim *et al.* submitted) help males locate and return to their burrows quickly and may thereby reduce males' vulnerability to predation. Hence, male-built structures may help both males and females reduce their predation risk during courtship. If so, then both sexual and natural selection may favour pillar building.

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