Experimental evidence for a seasonal shift in the strength of a female mating preference

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The costs and benefits of mate choice can vary both spatially and temporally. Phenotypic plasticity in mate choice, which could be due to changes in choice criteria (e.g., acceptance thresholds) or shifts in underlying mating preferences (i.e., relative values assigned to different males), can therefore increase reproductive success. We examined shifts in female mating preference for male claw size between 2 seasons (winter and summer) in the fiddler crab *Uca mjoebergi*. We used custom-built robotic crabs in 2-stimulus mate choice experiments conducted in the field. Females showed a consistent preference for larger claw size, but this was significantly weaker during winter. This seasonal difference was observed for 2 successive years. We propose that the change in female preference for claw size is due to a seasonal difference in the value of a larger burrow, which strongly influences burrow temperature. Burrow temperature largely determines larval development rate and larvae release in fiddler crabs is constrained to a narrow time window where survival is optimal. Females appear to alter their preference for burrow width, which is signaled by claw size, between winter and summer, potentially allowing them to optimize developmental time of larvae and/or to reduce mate search costs. *Key words:* female choice, fiddler crabs, mating preference, phenotypic plasticity, sexual selection, *Uca mjoebergi*. [*Behav Ecol* 21:311–316 (2010)]

Variation in female mating preferences at both the individual and the population level will influence the rate and direction of male sexual ornament evolution through sexual selection (Widemo and Sæther 1999). One source of variation is that the costs and benefits of expressing mating preferences can vary both spatially and temporally (Jennions and Petrie 1997). If female mating preferences are fixed, suboptimal mate choice decisions can therefore occur under some conditions (Qvarnström 2001). Consequently, there should be selection for females to facultatively adjust how they choose a mate.

Phenotypic plasticity in mating preferences and/or mate choice criteria will increase female fitness if the costs of plasticity are less than the increase in mean reproductive success that can be gained by shifting away from a fixed preference (Jennions and Petrie 1997). For example, in the collared flycatcher *Ficedula albicollis*, mate choice trials show that a female mating preference for forehead patch size (a trait also sexually selected through its effects on male–male competition) varies seasonally (Qvarnström et al. 2000). Females only prefer males with larger patches toward the end of the breeding season. The level of parental care largely determines breeding success, and males with larger patches modify their behavior late in the breeding season to allocate more resources toward parental care. In contrast, early in the season, males with larger patches allocate more resources toward premating activities, such as seeking out extrapair copulations (Qvarnström 1999). Females that mate with males with large patches late in the season therefore have increased reproductive success due to greater male parental care (Qvarnström et al. 2000). This is 1 of a very limited number of field-based studies that supports the notion that mating preferences are not static traits and

that, furthermore, this behavioral plasticity is adaptive (Reaney and Backwell 2007a; Chaine and Lyon, 2008).

It is worth noting that most studies investigating plasticity in mate choice show variation in choosiness (e.g., a change in the average phenotype of males that mate due to shifts in mating thresholds), rather than directly testing for a change in mating preferences (i.e., which males and females prefer when they are offered a simultaneous choice of mates so that mate sampling costs do not influence choice decisions; e.g., Lynch et al. 2005; Borg et al. 2006). Studies that directly examine shifts in mating preferences tend to be laboratory based, which makes it difficult to determine whether experimentally induced changes in mate choice are adaptive in the field (e.g., Pfennig 2007; Heubel and Schlupp 2008).

Temporal constraints in marine species

In many intertidal species, the tidal cycle determines the optimal time for mating and larval release. Reproductive success is strongly related to both these activities as there is only a small window of opportunity for them to occur (Morgan and Christy 1995). In most intertidal species, reproduction is timed to ensure successful dispersal of larvae that are at the appropriate developmental stage (Christy 1978). Many of these species release larvae on nocturnal maximum-amplitude high tides, when larvae are least likely to be seen by predators and most likely to be transported away from coastal areas into the open sea (Morgan and Christy 1995).

Mating in fiddler crabs occurs at distinct times (usually over a few days) during each semilunar cycle (Christy 1978). Females that mate outside this time risk reduced offspring survivorship by releasing larvae during unfavorable tides if they wait until larvae are at the correct stage of development (Morgan and Christy 1995) or if they release larvae at the optimal time by releasing larvae that are not at the appropriate developmental stage. Although the timing of larval release is largely determined by the time of mating, temperature also influences the rate of larval development (Yamaguchi 2001). Females might therefore be able to speed up or retard larval development

by selecting an incubation environment, that is, respectively, warmer or cooler than average (deRivera 2005).

In the fiddler crab *Uca mjoebergi*, mating and incubation takes place within a male's burrow (Crane 1975). Ambient air temperature and burrow size largely determine incubation temperature (Christy 1987; Yamaguchi 2001). Wider burrows hold a greater volume of air and are likely to allow fresher cooler air to circulate into the burrow and are therefore less affected by high ambient temperatures. In *U. mjoebergi*, for example, with every 1 mm increase in burrow width, there is a 0.27 °C drop in burrow temperature relative to air temperature (Reaney and Backwell 2007a). Burrow width was strongly correlated with claw size, which, in turn, tends to be positively correlated with male attractiveness (Reaney and Backwell 2007a; Reaney 2008). In a correlational study, Reaney and Backwell (2007a) showed that female choice based on claw size appeared to change over a semilunar mating cycle. Females breeding early in the cycle appeared to preferentially mate with large-clawed males who occupy large burrows, whereas toward the end of the cycle, they prefer small-clawed males who occupy small burrows. They argued that females can adjust the rate at which larvae develop to ensure the timing of larval maturation is optimal with regards to larval release during spring tide and that they do this by decreasing their preference for male size/burrow width over the mating cycle (deRivera 2005; Reaney and Backwell 2007a).

Here, we ask whether the phenotypic correlation between male size and attractiveness seen within a cycle is also observed over a larger seasonal time scale. However, we take an experimental approach to test whether any such shift in mate choice is due to changes in mating preferences rather than other factors that might vary seasonally. Like most tropical species of fiddler crabs, reproduction in *U. mjoebergi* occurs year round (Crane 1975), but average air temperature is not constant over the year. We predict that this will affect female mating preferences because larval development time is determined by burrow size/temperature (Yamaguchi 2001; deRivera 2005). Males with large claws have large burrows, which are relatively cooler than small burrows owned by smaller clawed males (Reaney and Backwell 2007a). We therefore predict that for females to release larvae at the optimal time during the summer, when air temperature is highest, they should strongly prefer large-clawed males, whereas during winter, when air temperature is lowest, they will show a weaker preference and might even prefer smaller clawed males. We therefore tested whether female mating preference changes between the 2 seasons.

METHODS

Study species and site

Uca mjoebergi is a small fiddler crab (carapace width up to 20 mm) that inhabits intertidal mudflats in northern Australia. They occur in dense mixed sex colonies, and both sexes defend territories that are centered on a burrow (Reaney and Backwell 2007b). Males have 1 greatly enlarged major claw, which they wave at females during courtship. During the 6-day mating period, receptive females leave their territories and sample a series of courting males before eventually selecting a mate. During this process, a female does 1 of 3 things: approaches a male and his burrow but then bypasses him and continues sampling; approaches a male, enters and inspects his burrow, and then continues sampling; or approaches a male, enters his burrow, and mates with him (Reaney and Backwell 2007a). After copulation and oviposition, the male leaves his burrow, whereas the female remains to incubate the eggs. The female stays in the burrow until she

is ready to release larvae at the next high-amplitude spring tide.

Our study was undertaken at East Point Reserve, Darwin, Australia. The site lies in the highest section of the intertidal zone and is only inundated by the highest amplitude spring tides (Reaney and Backwell 2007a). Females therefore have about a 4-day period in which it is possible to release larvae. We only ran mate choice trials over the first 3 days of the 6-day mating period during neap tide. This was done to control for an already documented weaker female preference for larger clawed males later in the mating period (Reaney and Backwell 2007a).

Average monthly temperature

Half-hourly temperature readings for Darwin Airport from July 2007 to December 2008 were obtained from the Australian Bureau of Meteorology. The average monthly temperatures for July through December were then calculated.

Burrow diameter measurements

To establish whether crab size and burrow size are correlated, we used dial calipers to measure carapace size, major claw size, and burrow diameter to the nearest 0.1 mm for 55 randomly selected males.

Size preference experiments

A series of 2-choice experiments were performed using a custom-built robotic crab system. In brief, each robotic crab produces a claw movement engineered to resemble closely that of a courting male *U. mjoebergi*. The system used consisted of a control box and 2 identical crab units. Each crab unit had a motor housed in a plastic container that controlled the movement of a rigid metal arm. Wave rate was set at 8.4 waves/min (close to the population average), and both claws waved in synchrony to avoid a leadership effect (Reaney et al. 2008). Replica claws were temporarily attached to the robotic crab arm. Three experiments were performed using 3 different claw combination pairs: (1) 14.6 versus 19 mm, (2) 14.6 versus 21.2 mm, and (3) 19 versus 23 mm. Female choice for each combination of claw sizes was tested 4 times across 2 years (September 2007, November/December 2007, July 2008, and December 2008; for *N* see Table 1). From here on, July and September will be referred to as "winter" and November and December as "summer."

Mate choice experiments were performed in a cleared area of mudflat in situ that contained the 2 robotic crabs placed 5 cm apart and 20 cm from the female release point. All conspecific and heterospecific crabs within 2 m of the choice arena were removed and released elsewhere on the mudflat. Naturally occurring mate searching females, identified when they were observed sampling the burrow of a courting male, were captured on the mudflat and placed in a container with water to prevent dehydration. A female was then placed under a clear plastic container at the release site. The robotic crabs were activated and the female left under the container for at least 3 wave cycles. The container was then lifted using a remotely triggered lever. We scored a positive choice if a female moved in a direct line and stopped at the base of a waving robotic unit (for video footage see Reaney et al. 2008). A trial was discarded if the female ran immediately after being released or did not make a choice within 3 min. Each female was used in 1 trial per experiment. Female size in winter and summer 2007 did not significantly differ (9.60 ± 0.74 mm vs. 9.42 ± 0.92 mm, $t_{88} = 0.985$, $P = 0.327$). However, pooled across all experiments, tested females were smaller in winter than summer

Table 1

Mean ± standard deviation temperature and female size per claw combination per season and binomial test results for size preference experiments and the effect size *r*

Season	Year	Claw combinations (mm)	Average temperature (°C)	Female size (mm)	N	P	r
Winter	2007	14.6 versus 19.0	27.02 ± 3.34	9.60 ± 0.74	40	0.636	0.075
		14.6 versus 21.2	27.02 ± 3.34	9.61 ± 0.89	40	0.081	0.319
		19.0 versus 23.0	27.02 ± 3.34	9.29 ± 0.86	40	0.430	0.125
	2008	14.6 versus 19.0	23.87 ± 4.30	8.35 ± 1.05	35	0.175	0.229
		14.6 versus 21.2	23.87 ± 4.30	8.35 ± 1.05	35	0.175	0.229
		19.0 versus 23.0	23.87 ± 4.30	8.35 ± 1.05	35	0.736	0.057
Summer	2007	14.6 versus 19.0	28.74 ± 2.67	9.42 ± 0.92	50	0.001	0.465
		14.6 versus 21.2	28.74 ± 2.67	9.38 ± 0.81	50	0.000	0.792
		19.0 versus 23.0	28.74 ± 2.67	9.38 ± 0.82	50	0.015	0.344
	2008	14.6 versus 19.0	29.01 ± 2.53	9.79 ± 0.77	40	0.000	0.763
		14.6 versus 21.2	29.01 ± 2.53	9.79 ± 0.77	40	0.000	0.647
		19.0 versus 23.0	29.01 ± 2.53	9.79 ± 0.77	40	0.000	0.592

(9.01 ± 1.09 mm vs. 9.58 ± 0.87 mm, $t_{141} = -3.653$, $P < 0.001$). There was, however, no effect of female size on their claw size preference (see Results). To test this, we conducted *t*-tests comparing the size of females that chose the larger versus the smaller claw in each of the 12 experiments. We then converted all 12 experimental outcomes to the effect size *r*, using the formula $r = Z/n^{1/2}$ (where *Z* was obtained from the *P* value for the experiment and *n* is the sample size; Rosenberg et al. 2000). We then calculated the mean effect size in a random effect meta-analysis for the Fisher-transformed *r* values to test whether it differed from 0 (Rosenberg et al. 2000).

The lack of a within-season female size effect suggests that the seasonal difference in female size is unlikely to explain any seasonal difference in female choice.

Furthermore, due to the presence of a major claw in males, large female are easily able to fit down the burrows of relatively small males (e.g., a female with a carapace width of 11.5 mm can easily fit down the burrow of a male with a carapace width of 10 mm and major claw length of 14.6 mm). Therefore, any observed seasonal change in preference cannot be explained by a seasonal change in the range of males that females are able to mate with due to burrow width constraints.

For all 2-choice experiments, any potential side bias was eliminated by alternating the presentation of test stimuli between sides across trials. There was no detectable side bias (left vs. right: 248:247; $N = 495$, binomial test, $P > 0.999$).

Female preferences were first tested with binomial tests (2-tailed) with $\alpha = 0.05$. To compare the strength of the female preference for claw size between the 2 seasons, we converted all

experimental outcomes to the effect size *r*. We then calculated the mean effect size in each season and tested for a significant difference in Fisher-transformed *r* between the 2 seasons by running a random effects model with season as a grouping factor in Metawin 2.0 and testing whether Q_b was significantly larger than expected (Rosenberg et al. 2000).

RESULTS

The monthly air temperature in summer (November to December) was 1.72 (2007; $t_{2372} = 17.14$, $P < 0.001$) to 5.14 °C (2008; $t_{2026} = 42.65$, $P < 0.001$) hotter than in winter (July to September; Figure 1).

Both claw length and carapace width were strongly correlated with burrow diameter ($r = 0.92$ and 0.90, $n = 55$).

For each individual experiment, during winter, females showed no significant preference for claw size ($P = 0.081$–0.736), whereas during summer, females showed a significant preference for larger claws in all experiments (all $P < 0.015$; Table 1).

When pooling data across all 12 experiments, females showed a significant preference for claw size as the mean effect was significantly greater than 0. The strength of the effect of claw size on female mating preference was significantly greater in summer than in winter (meta-analysis: $Q_b = 17.76$, degrees of freedom = 1, $P = 0.003$, $r_{winter} = 0.176$, $r_{summer} = 0.728$). In both seasons, however, the mean effect was significantly greater than 0 (Figure 2).

There was no significant difference in the size of females choosing the larger over the smaller claw in any of the 12
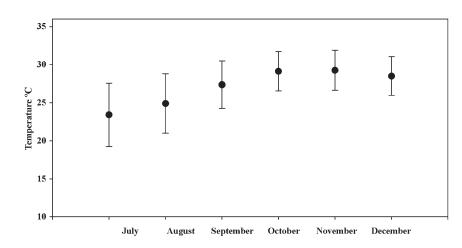

Figure 1
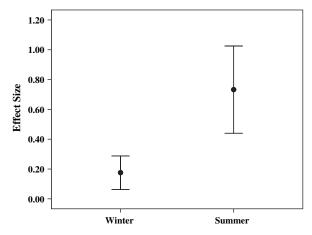Average monthly air temperature for Darwin Airport (2007–2008). Mean ± standard deviation.

Figure 2
Strength of mating preference in winter compared with summer. Mean and 95% confidence intervals for effect size *r* (*n* = 6 per season).

experiments (*t*-tests, all *P* > 0.13, *n* = 35–50). The mean effect of female size on choice of the larger claw was not significant, given *r* = 0.043 (95% confidence interval: −0.02 to 0.097). The positive value of *r* indicates that, if anything, larger females more often chose the smaller claw, which makes the seasonal trend highly unlikely to be explained by the seasonal difference in female size.

The strength of the female mating preference for male claw size in *U. mjoebergi* changes between seasons. The female preference for larger clawed males in winter was significantly weaker than that in summer when the mean temperature was 1.7–5.1 °C hotter. Although none of the results for individual experiments undertaken in winter indicated a significant mating preference based on claw size, a meta-analysis showed that the mean effect size for the strength of the female preference for claw size in winter was significantly greater than 0 (r_{winter} = 0.176). This is indicative of a weak size-based preference. To have an 80% likelihood of detecting a significant preference at the 0.05 level in a single experiment would require a sample size of about 250 trials. This is a sample far larger than that seen in most mate choice trials, where median values are probably in the range *n* = 30–50. This highlights the importance of interpreting nonsignificant results with caution (Jennions et al. 2001).

DISCUSSION

Female *U. mjoebergi* show a seasonal change in the strength of a mating preference for male claw size. During hotter months, the strength of female mating preference for larger clawed males was significantly stronger than during cooler months. We propose that the change in female preference for claw size is due to a seasonal difference in the value of a larger burrow, which strongly influences burrow temperature and therefore incubation temperature.

Reaney and Backwell (2007a) showed that strong temporal constraints appear to cause females to modify their preference for burrow width more than a 2-week mating cycle to optimize larval developmental time. They observed a decline in the mean size of mated males over the mating period and attributed this to large males having cool burrows that slow larval development and small males having warm burrows that elevate larval development. We suggest that the same process is occurring seasonally due to a similar change in temperature, albeit over a longer time scale, which selects for a tem-

poral shift in mating preferences. It should be noted, however, that Reaney and Backwell (2007a) only observed the pattern of size-based male mating success and, although unlikely, it is possible that this changed over the mating period even if the female mating preference remained constant (e.g., male–male competition might be stronger earlier in the cycle and favor larger males).

We propose that the seasonal decline in the strength of the female preference for claw size has arisen due to a reduction in the value of a larger burrow. Claw size provides a long-distance signal of burrow size and, by extension, incubation temperature (deRivera 2005). A previous study showed that with every 1 mm increase in burrow width, there was a 0.27 °C drop in burrow temperature (Reaney and Backwell 2007a). Larval development rate in *U. mjoebergi*, like many arthropod species, is largely determined by incubation temperature, and reproductive success in this species is strongly influenced by the timing of larval release (e.g., Wear 1974; Christy 1978; Moriyasu and Lanteigne 1998; Yamaguchi 2001; deRivera 2005). If females are to successfully release larvae on time, they need to adjust their preference for burrow size as ambient temperature changes. In summer, when average air temperature is substantially higher, females should show a greater preference for large males with bigger burrows so as to select an incubation environment that is cool enough to prevent overly rapid development of larvae and a decline in female reproductive success (Christy 1983, Reaney and Backwell 2007a).

Reduced direct benefits are 1 potential cause of a weaker preference for claw size during winter. Smaller warmer burrows during winter are probably less important than a larger cooler burrow during summer because it is easier for a female to increase than decrease incubation temperature. This asymmetry occurs because, although incubation generally takes place at the bottom of a burrow, females could move up the burrow toward the entrance to increase the incubation temperature (Christy 2003). In contrast, females are limited in their ability to decrease incubation temperature as the burrows have a finite depth that is restricted by the water table and complex spatial variation in soil structure (Christy 1987). This has been illustrated in *U. mjoebergi*, where burrow depth varies very little between males that differ greatly in size (Reaney and Backwell 2007a) Therefore, during winter, but not summer, females could position themselves precisely in the burrow cavity to accelerate embryo development rates and compensate for a drop in ambient air temperature or any error in the timing of oviposition (Christy 2003). One might then expect small males to dig wider burrows during summer, but there are probably high costs to this due to greater risks of predation or eviction when there is a mismatch between male and burrow size.

One key question is why females show any preference for large-clawed males during winter? Although the direct "thermal" benefit of mating with a large-clawed male is reduced during winter, there are still potential indirect benefits. For example, across the year, large-clawed males still have greater mean mating success than small-clawed males. The population variation in male size is largely a product of variation in male age as growth is indeterminate. This makes it less likely, but not impossible, for a female preference to be partly favored by indirect genetic benefits (i.e., production of more attractive sons) if there is also heritable age-independent variation in claw size (Andersson 1994; Kokko et al. 2006). These benefits might be enough to maintain a weak female mating preference when sampling costs are low (i.e., search time, predation risk, and desiccation risk; Smith and Miller 1973; Backwell and Passmore 1996). This was the case in our experimental study as females were offered a simultaneous choice of males. If, however, we had been observing naturally occurring

sequential mate choice, it is less clear whether we would have detected the same temporal shifts in male size-based mating success due to the higher sampling costs.

Although we have not directly shown that incubation duration changes with burrow size and/or season, the documented effect of temperature on crustacean larval development is strong. At present, we suggest that the best explanation for our results is that female mate choice preferences shift due to changes in temperature. Nevertheless, further data are required to substantiate this argument: Ideally, we need to quantify the relationship between incubation duration and burrow size in winter versus summer. We can also test the prediction that, all else being equal, the decreased benefits of being selective in winter should results in shorter mate searching forays.

In summary, we have shown seasonality in the strength of female mate preference and by extension a reduction in selection on ornament size during part of the year. Only a handful of studies have shown such seasonal switches in mate selection (collared flycatchers: Qvarnström et al. 2000; 2-spotted goby: Borg et al. 2006; field cricket: Velez and Brockmann 2006; sailfin mollies: Heubel and Schlupp 2008). Although this seasonal plasticity indicates there can be high flexibility in mating decisions, the adaptive link between a change in mating preference and the benefits accruing to females from mating with a specific male phenotype often remains uncertain. In *U. mjoebergi*, however, we have identified a change in mating preference that appears to occur at 2 scales (seasonally and within a biweekly tidal cycle) both of which can be accounted for by the same adaptive explanation based on burrow temperature.

Understanding the cause and effect of phenotypic plasticity in mating preferences is of huge importance (Jennions and Petrie 1997). Spatial and temporal variation in mating preferences have numerous implications for the process of sexual selection, evolution of mate choice, and the evolutionary dynamics of preferences and exaggerated traits (Chaine and Lyon 2008). Furthermore, this phenotypic plasticity could provide a mechanism by which multiple male ornaments arise and are maintained and genetic variation for male traits preserved (Ellner 1996). Social and physical environments are rarely stable, and flexibility in mating preferences might allow females to select males that best suit their current needs. Such plasticity is likely to be common. We predict that closer inspection will show that species that live in highly variable environments that change predictably (e.g., those with strong seasonality or strong altitudinal clines) and/or have prolonged mating seasons will display adaptive phenotypic plasticity in mating preferences. This is especially likely when mate choice confers direct benefits. When there are only indirect genetic benefits to mate choice, however, the situation is more complicated because gene–environment interactions make it difficult to use the current phenotype of a male (i.e., his attractiveness) to predict the fitness of offspring who might develop in another environment (Kokko and Heubel 2008).

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