

Original Article

Strategic male courtship effort varies in concert with adaptive shifts in female mating preferences

Andrew T. Kahn, Tegan Dolstra, Michael D. Jennions, and Patricia R.Y. Backwell

Division of Evolution, Ecology and Genetics, Research School of Biology, Australian National University, Building 44, Daley Road, Canberra, ACT 0200, Australia

Very few studies have presented compelling evidence for adaptive shifts in female mating preferences. Additionally, there is almost no data on how males adjust courtship effort when female mating preferences change predictably. How should males respond? Should a currently more attractive male increase his courtship effort because he has, for now, a better chance of reproducing? Or should he maintain/lower his courtship effort and conserve energy because he already has an edge on the competition? We experimentally measured female mating preferences and male courtship effort (i.e., male mating preferences) in the fiddler crab *Uca mjoebergi*. Using robotic males, we documented a consistent shift in female preferences for male claw size across each of 6 biweekly mating periods: females tested at the beginning of a mating period preferred large males, whereas those tested at the end preferred small males. This is one of the fastest-known temporal changes in the mean mating preference of a population and supports our prediction of an adaptive response due to time constraints on larval development. Males adjusted their courtship effort across the mating period in concert with the observed daily shift in the mean female mating preference. Interestingly, changes in courtship effort depended on male size. We interpret this shift as males increasing their courtship effort to take advantage of their current attractiveness to females. To our knowledge, this is the first study of the interactions between shifts in female and male mating preferences.

Key words: behavioral plasticity, fiddler crab, mate choice, sexual selection, *Uca*. [*Behav Ecol*]

INTRODUCTION

Female mating preferences and the effort females put into expressing these preferences (choosiness) determine patterns of female mate choice (Jennions and Petrie 1997). Many population studies have reported temporal or geographical variation in female mate choice (e.g., Endler and Houde 1995; Lynch et al. 2005). It is, however, difficult to know whether this variation is adaptive, as the net gains from mating nonrandomly are often poorly understood. This is especially true for indirect genetic benefits (Schmoll 2011; Slatyer et al. 2012). Several studies have made the case that variation in female choice could arise as an adaptive phenotypic response to low mate availability, which favors a greater female mating propensity (e.g., Karlsson et al. 2010) or weaker directional mating preferences (e.g., Fowler-Finn and Rodriguez 2012a, 2012b) to ensure mating occurs in a timely fashion. Similarly, females might be less discriminate in situations where the costs of choosiness are higher (e.g., Borg et al. 2006); indeed, there is evidence from many taxa

that females in poor body condition pay greater costs of choosiness and consequently tend to be less choosy (Cotton et al. 2006).

Temporal variation in female preferences for specific male traits has been reported in numerous species (e.g., Lehtonen et al. 2010). Only a few studies have, however, provided evidence for adaptive shifts in mating preferences based on putative changes in the benefits associated with mating with specific males (Qvarnström et al. 2000; Pfennig 2007; Chaîne and Lyon 2008; Milner et al. 2010). To do so requires both direct measures of mating preferences (i.e., direct experimental mate choice tests rather than simply documenting patterns of mating) and a plausible link between male phenotype and fitness benefits for females. Shifts in female mate preferences are evolutionarily significant because they can dramatically alter the direction and strength of sexual selection on males. Indeed, such shifts could partly explain the maintenance of genetic variation in preferred male traits (i.e., the lek paradox; Kirkpatrick and Ryan 1991) in cases where net sexual selection on these traits is reduced. The potential for the evolution of adaptive shifts in mating preferences exists if the costs and benefits of mating nonrandomly vary predictably over time (Widemo and Sæther 1999). Temporal, population-wide shifts in mating preferences could occur via 2 alternative mechanisms: 1) individual plasticity

Address correspondence to A.T. Kahn. E-mail: andrew.kahn@anu.edu.au.
Received 29 November 2012; revised 13 February 2013; accepted 14 February 2013.

of mating preferences across time or 2) variation in fixed individual preferences, with correlation between preference and timing of mating (Jennions and Petric 1997).

It is well known that the mating preferences of females and males can interact (i.e., mutual mate choice: e.g., Myhre et al. 2012; South et al. 2012). But if female mating preferences shift across time, this raises an obvious, but rarely addressed, question: how does this affect male mate preferences? Male mate preferences have been widely documented (reviews: Bonduriansky 2001; Edward and Chapman 2011) and are predicted to occur when the time to recover after mating is such that a male cannot mate with every female he encounters (Kokko and Monaghan 2001; Wedell et al. 2002). Active rejection of potential mates by males is, however, rare (e.g., Schwagmeyer and Parker 1990). It is more common for male preferences to be expressed as changes in courtship effort (e.g., Svensson et al. 2010; Jordan and Brooks 2012) or investment in ejaculate (e.g., Pizzari et al. 2003; Kelly and Jennions 2011). For male preferences to evolve, there must be variation among females in the reproductive benefits they offer, otherwise there is no benefit to delaying mating. This is likely to occur in taxa where body size and fecundity are positively correlated, which is especially common in species with indeterminate growth (e.g., fish: Wong and Jennions 2003; Lehtonen et al. 2011; crustaceans: Reading and Backwell 2007; Wada et al. 2011). As with females, selection might therefore also favor adaptive shifts in male mate preferences that depend on the availability of, or variability among, potential mates (Heubel and Schlupp 2008).

Here, we investigate the interaction between adaptive shifts in female and male mate preferences. This is an area that has received little empirical attention. Studies of mutual mate choice are not uncommon (e.g., Pryke and Griffith 2007; Hancox et al. 2012), but they usually assume that individuals of each sex have fixed mating preferences. Species where female mating preferences shift in response to external factors allow us to ask a simple, testable question: if female mate preferences for specific male traits change, how does this affect the optimal male courtship effort strategy? One possibility is that a male who is currently more attractive should increase his courtship effort because he has a relatively better chance of reproducing at that time. Alternatively, a male might leverage his increased attractiveness to reduce his mating costs by lowering his courtship effort without any net decline in his likelihood of mating. To our knowledge, theoreticians have not yet addressed which factors determine the optimal patterns of male courtship effort when female preferences vary predictably over time (e.g., over a breeding season).

Here we take advantage of the breeding biology of the fiddler crab *Uca mjoebergi* (Ocypodidae) to provide some empirical answers to the above-mentioned question. Male fiddler crabs attract potential mates by waving their oversized claw. Female *U. mjoebergi* prefer males with a higher wave rate (Reaney 2009) and generally prefer larger males (Milner et al. 2010). A male pays a significant cost to mate because he relinquishes his burrow to a female and must then fight other males to attain a new burrow (Crane 1975). Consequently, males appear to make prudent courtship decisions by waving more intensely toward larger, more fecund females (Reading and Backwell 2007). We conducted simple experiments to test whether

1) there is a consistent, adaptive shift in female mating preferences for male claw size across each breeding period as predicted by constraints on the timing of mating and larval development (see Materials and Methods), and

2) male preferences—manifested as courtship effort (wave rate)—vary across the breeding period in concert with a concomitant shift in female preferences for claw size. If so, is the observed change in courtship such that males increase or decrease their courtship effort when they are most attractive to females?

MATERIALS AND METHODS

The study system

We studied a population of *U. mjoebergi* at East Point Reserve, Darwin, Australia (12.41°N, 130.83°E). *U. mjoebergi* is a small crab (<20-mm carapace width), which occurs in dense, mixed-sex populations on the intertidal mudflats of northwestern Australia. Each crab owns and defends a burrow and a small area of the surrounding mudflat. In the mating period, receptive females leave their burrows and sequentially sample the burrows of several courting males before choosing a mate. Copulation and oviposition occur in the male's burrow, after which he leaves and the female stays to incubate the eggs (Crane 1975).

In fiddler crabs, the optimal timing of mating and larval release is codetermined by the tidal cycle. Larval release is synchronized to occur with nocturnal maximum amplitude high tides, presumably to promote transport of larvae out to sea (Christy 1978; Morgan and Christy 1995). Mating must, therefore, occur during a restricted period within each tidal cycle to ensure that larvae develop before being released; if mating and fertilization occur outside this window, then larvae that develop at the average speed will be at an inappropriate stage of development at the optimal release time.

Our study site is approximately 6 m above sea level, so is only inundated during spring tides (Figure 1). Mating occurs over 5–7 days during neap tides, when the mudflat stays uncovered. Females then release their larvae on the nocturnal maximum amplitude high tide of the second following tidal cycle (Figure 1; unpublished data). This creates variation in incubation duration: females mating at the start and end of the mating period must incubate for 24 and 18 days respectively. Assuming that females have a developmental “target” that their larvae should reach before being released, females mating later in the mating period need their larvae to develop faster than those mating earlier. Females might, however, be able to accelerate or retard

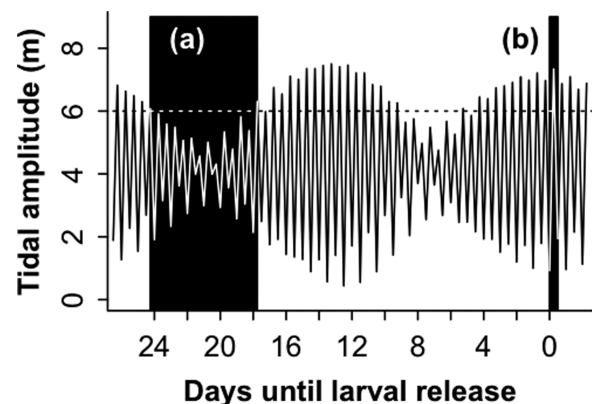


Figure 1

The reproductive cycle of *Uca mjoebergi* with respect to semilunar tidal cycles. The mating period (a) occurs during neap tides when the mudflat remains uncovered (the dashed line is the height above sea level of the study site). Females that mate during that period release their larvae 18–24 days later at a nocturnal tidal maxima (b).

larval development by adjusting the incubation temperature (deRivera 2005), as this is positively correlated with larval development rate (Yamaguchi 2001).

In *U. mjoebergi*, incubation depends on both ambient air temperature and burrow diameter. Wider burrows are cooler than narrower burrows (Reaney and Backwell 2007). We, therefore, predicted a shift across the mating period from females preferring to incubate in wider burrows to narrower burrows. This shift should be manifested as a change in mating preference based on male size (as represented by male claw length) as mating and incubation occur within the male's burrow (Crane 1975) and male size and burrow width are highly correlated (Milner et al. 2010). This prediction is partly supported by an earlier observational study showing that females mated with larger males earlier in the mating period (Reaney and Backwell 2007). In addition, Milner et al. (2010) demonstrated a stronger female preference for large males, thereby favoring a cooler burrow, in summer, when ambient temperatures are higher. It remains to be shown, however, that there is a population-level shift in female mating preferences over a single mating period.

Female mating preferences

We performed 3-male, female mate choice experiments using custom-built robotic crabs to test whether female mating preferences for male claw size (a proxy of male body size) and wave rate changed across the mating period. This could be due to either individual plasticity or a change in the mating preferences of females that initiate mate choice later in the mating period. Each robot consisted of a plaster replica of a claw attached to a motorized arm engineered to imitate the waving action of a male *U. mjoebergi* (see past studies: Reaney et al. 2008; Milner et al. 2010). We carried out 2 separate experiments:

- 1) *Claw size treatment*: females chose between a small (14 mm long), medium (18 mm), and large (22 mm) claw, all waving at an intermediate rate (8.4 waves/min).
- 2) *Wave rate treatment*: females chose between 3 identical claws (18 mm) that had either a slow (4.2 waves/min), intermediate (8.4 waves/min), or fast (16.8 waves/min) wave rate.

These claw sizes lie within the natural range, as does the intermediate wave rate. The slower and faster wave rates are half and double the intermediate rate, respectively. This ensured that the robots waved in synchrony, which is important as females prefer males that wave immediately prior to another male (see Reaney et al. 2008). The position (left, middle, or right) of specific robotic units was changed daily. The position of specific claw size/wave rate exemplars was changed after every third trial.

We conducted experiments everyday of the mating period for 6 consecutive mating periods (September–December 2011). Trials were conducted in a raised, mud-covered arena (60 × 60 cm) in the field with the 3 robotic crabs arranged in an arc 5 cm apart. The female release point was 20 cm from the males. We tested mate-searching females that had been recently observed sampling the burrow of a courting male. We detected females by looking for areas of the mudflat where males were waving intensively (rather than by tracking burrowless females). This makes it likely that the test females are an unbiased sample of mate-searching females. Females were then captured and held individually in a plastic cup (5 cm diameter) with a small amount of seawater until tested.

At the start of each trial, a female was placed under a clear plastic container (2.5 cm diameter) in the mate choice arena. After she had observed at least 3 waves by each robotic unit, the container was lifted via a pulley mechanism. We scored a choice if she moved directly

toward, and stopped at, the base of a waving robot. The trial ended when she either 1) made a choice, 2) ran immediately after release, 3) touched the edge of the arena, or 4) did not choose within 3 min. If a female did not choose (i.e., 2, 3, or 4), she was retested a maximum of 3 times before being discarded from the data set and released. Each female was used once for the claw size treatment and once for the wave rate treatment (trials were approximately 1 h apart). After testing, we measured the females' carapace widths (± 0.1 mm) using dial calipers. In total, we recorded $N = 457$ and 455 successful trials for the claw size and wave rate treatments, respectively.

Male courtship effort

To test if male courtship effort depended on female size and/or changed across the mating period, we performed a series of wave rate and startle response trials on each day of the mating period for 5 mating consecutive periods (October–December 2011). All focal males had original claws (males with regenerated claws wave faster; Backwell et al. 2000). Stimulus females were burrow owners collected earlier in the day.

No-choice wave rate trials were conducted at each focal male's burrow (see Hayes et al. 2013). We blocked all the other burrow entrances within 20 cm of the burrow with shells from the mudflat and marked out this area with a 5-cm high mesh barrier. A female was then placed 5 cm from the entrance of the focal male's burrow in a 3-cm diameter clear plastic container. The trial began when the male emerged from his burrow and performed his first wave. We recorded the number of waves the males produced for up to 5 min, or until he had not waved for 60 s, in which case the duration from first to last wave was noted. A wave was only counted if the male was facing the female.

Immediately following the wave rate trial, we tested the male's willingness to reemerge from his burrow after being startled by the observer standing up abruptly. Because males had reliable information that a mate-searching female was present, this emergence time reflects a trade-off between the benefits of mating and the risk of predation (Hugie 2003; Jennions et al. 2003). We, therefore, consider the delay until emergence as an additional measure of a male's courtship effort. We recorded how long it took for any part of the male to reappear at the burrow entrance. If the male did not enter his burrow on being startled, a time to reemerge of 0 s was recorded. Finally, the male was caught and his claw length and carapace width, as well as that of the female, were measured with dial calipers (± 0.1 mm). Wave rates and startle responses were recorded for $N = 232$ males.

Statistical analyses

Female mating preferences

To test whether the size (carapace width) of mate-searching females changed over the mating period, we ran a simple linear regression. To test for overall differences in the number of females preferring each type of male (across all mating periods), we performed Pearson's chi-square tests. We tested for shifts in female preferences by producing cumulative link mixed models (ordinal regression: Agresti 2010; Christensen 2011), and testing the effect of individual variables using log-likelihood ratio tests. Ordinal female mate choice was used as the response variable; that is, small, medium, or large for claw size preferences and slow, intermediate, or fast for wave rate preferences. The fixed explanatory variables included in these models were day in the mating period, season of mating period, and their interaction; and female carapace width. Season of mating period was treated as a fixed continuous effect (i.e., 1 for late September, 2 for first period in October, 3 for second period in

October, etc.) rather than a random effect. This is because previous work suggests that female choice varies seasonally (i.e., a potential season-by-day interaction; Milner et al. 2010), and the mating periods we studied were progressively closer to the “wet” season (which starts in late December). The position and identity of the preferred robotic crab unit were included in these models as random effects to account for potential biases, although neither were ever significant predictors of female choice (log-likelihood tests, all $P > 0.56$). All explanatory variables were centered and standardized (mean = 0, standard deviation [SD] = 1) to improve reliability and interpretation of the model (Schielzeth 2010). To further investigate the effect of day of mating period on female preferences for male claw size, separate mixed effect logistic regressions were run for each of the 3 tested claw sizes. Day of mating period and season were treated as fixed explanatory variables and the random variables were as described previously. The relative importance of predictor variables was assessed using Wald’s tests.

Male courtship effort

Male carapace width and claw length were highly correlated (Pearson’s product–moment correlation: $r = 0.948$, $t_{230} = 45.044$, $P < 0.001$). Given this tight correlation, we used male carapace width as our proxy for male size in all further analyses and relative claw length (the standardized residuals from a simple linear regression of claw length as predicted by carapace width) as a measure of male investment into a sexual trait (which is likely to be correlated with his condition, sensu Rowe and Houle 1996). Multiple linear regression was used to assess whether male wave rate varied with male size, relative claw length, female size, day of mating period, and season. The following 2-level interactions were included: male-by-female size (to test for assortative mating preferences) and male size-by-day in mating period (to test if the relationship between male courtship effort and day of mating period varied with male size). Each data point was weighted by the duration of waving. The significance of predictor variables and interactions was assessed using Wald’s tests. We also tested the effect of the predictor variables (and interactions) on the time males took to reemerge ($\log[x + 1]$ transformed to reduce heteroscedasticity and improve normality of residuals) using the same approach.

Summary statistics are given as mean \pm SD. All statistical analyses were performed using R version 2.12.2.

RESULTS

Female mating preferences

The mate-searching females used in mate choice trials had, on average, a carapace width of 8.4 ± 1.1 mm. There was a weak trend for the average size of females to decrease across each mating period (Wald’s test: $\beta = -0.048$, $\zeta = -1.783$, $P = 0.075$).

Claw size treatment

We found clear evidence for a within-mating period shift in female preferences for male claw size. Across all mating periods, females significantly preferred the large claw (number of females preferring small: 145; medium: 136; large: 176; $\chi^2_2 = 8.672$, $P = 0.013$). However, there was also a significant effect of day of mating period on the preferred claw size (log-likelihood ratio test: $\chi^2_2 = 55.475$, $P < 0.001$; Figure 2). The within-mating period pattern did not differ seasonally (season \times day interaction: $\chi^2_1 = 1.284$, $P = 0.257$) nor did the overall level of preference for claw size (season: $\chi^2_2 = 1.284$, $P = 0.526$). Female carapace width had no effect on preference ($\chi^2_1 = 0.534$, $P = 0.465$), so

the slight daily decline in the size of mate-searching females (i.e., those tested) across each mating period cannot readily explain the observed change in claw size preferences.

When analyzed individually the proportion of females that preferred the large claw declined significantly across the mating period (Wald’s test: $\beta = -0.593$, $\zeta = -5.581$, $P < 0.001$; Figure 2a); conversely, the preference for the small claw increased significantly across the mating period ($\beta = 0.803$, $\zeta = 6.933$, $P < 0.001$; Figure 2c). The proportion of females preferring the medium claw did not vary significantly across the mating period ($\beta = -0.135$, $\zeta = -1.291$, $P = 0.197$; Figure 2b). Taken together, these data suggest that female preferences are for larger males at the start of the mating period and shift toward preferring smaller males later on.

Wave rate treatment

Females displayed a strong preference for the fastest wave rate (number of females preferring slow: 49; intermediate: 139; fast: 274; $\chi^2_2 = 30.070$, $P < 0.001$). This preference appeared to be relatively fixed; there was no significant effect of female carapace width (log-likelihood ratio test: $\chi^2_1 = 0.969$, $P = 0.325$), season ($\chi^2_2 = 1.663$, $P = 0.435$), day in the mating period ($\chi^2_2 = 0.740$, $P = 0.691$), or their interaction ($\chi^2_1 = 0.056$, $P = 0.813$).

Male courtship effort

The size range of females used to elicit male courtship signalling (mean carapace width 8.6 ± 1.2 mm) was very similar to that of naturally mate-searching females. The carapace width of the tested males was, on average, 11.0 ± 1.3 mm, with a mean claw length of 17.6 ± 3.5 mm. Males waved at a mean rate of 13.5 ± 4.6 waves/min. Most males continued waving for the entire 5-min sampling period (198/232). The rest were spread relatively evenly across a range of 24–275 s.

We found evidence for strategic courtship effort by males. Wave rate varied significantly with male and female size (carapace widths), as well as across the mating period (Table 1a and Figure 3). In particular, there were positive effects of both female size and day of the mating period on male wave rate. Male size itself was not significant, but we found a significant positive interaction between male and female size and a significant negative interaction between male size and day of mating period. Neither relative claw length nor season had a significant effect on wave rate (Table 1a). The net result of these effects can be summarized as follows: large males do not noticeably vary their courtship effort (i.e., wave rate) across the mating period, but they wave significantly more when courting a larger female; small males, on the other hand, show a clear increase in courtship effort across the mating period, but do not noticeably wave more at larger females (Figure 3).

There were strong effects of male and female size on the time males took to reemerge after being startled (Table 1b). Males reemerged significantly sooner when presented with larger females, and larger males tended to take longer to reemerge. There was also weak, but significant, effects of day in the mating period and season, with males tending to reemerge faster later in each mating period and sooner toward the end of the breeding season (Table 1b). There was no significant effect of relative claw length on time to reemerge. Unlike male wave rate, there were no significant interactions between male and female size or between male size and day of the mating period (Table 1b).

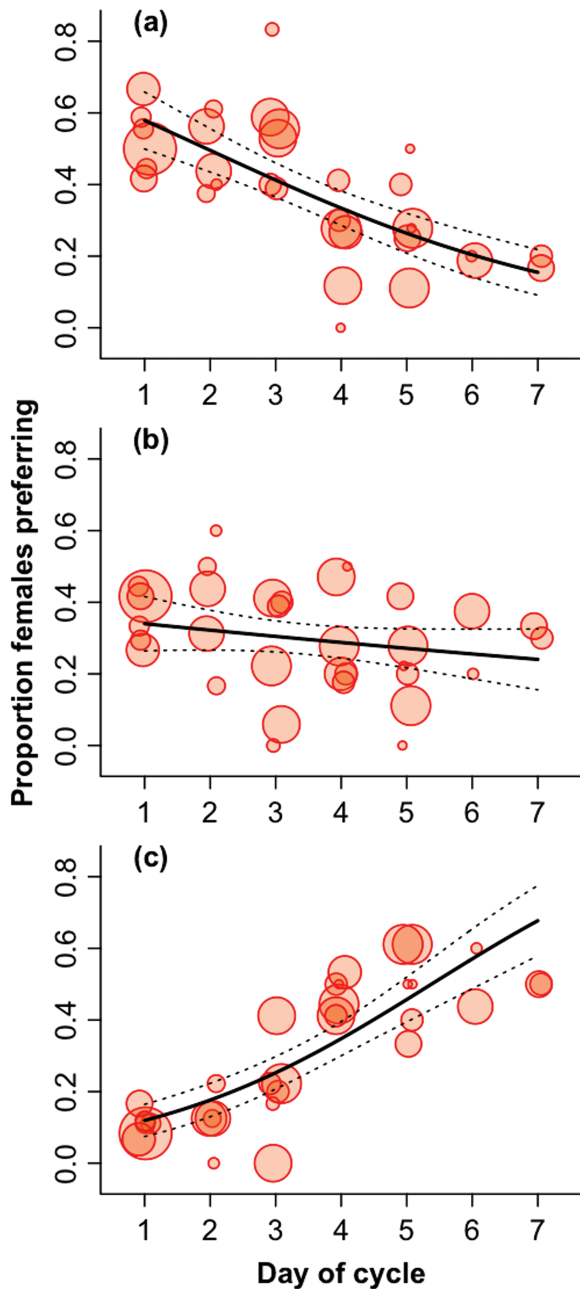


Figure 2

Female preferences for robotic male crabs based on claw size: (a) large claw (22 mm), (b) medium claw (18 mm), and (c) small claw (14 mm). Each data point represents the proportion of females preferring that male per day for a single mating period ($n = 6$ periods). The area of each dot represents the number of females sampled that day (range: 4–27). The solid lines are the fitted logistic regression models, and the dotted lines are 95% confidence intervals for these models. Points are jittered slightly to aid distinction.

DISCUSSION

Female mating preferences

Many field studies report changes in female mate choice over a breeding season. This cannot be solely attributed to changes in female mating preferences, however, because many factors affect which female mates with which male (e.g., female–female competition, male mate choice). It is, therefore, necessary to conduct

controlled choice experiments repeatedly across a breeding season to quantify mating preferences. Although a few studies have done so and temporal changes in female preferences have been observed in some species, it is often unclear how, or even whether, this variation is adaptive. Consequently, very few studies have convincingly shown that female mating preferences shift across a breeding season and also provided a plausible explanation as to why this variation might have evolved (e.g., [Qvarnström et al. 2000](#)). Here, we used an experimental test to document a clear shift in the preference of female *U. mjoebergi* for larger-clawed males across each biweekly mating period ([Figure 2](#)). The observed shift in female mating preferences is in the direction predicted due to putative changes in the direct benefits of female choice. Specifically, we suggest that temporal constraints affect the optimal rate of temperature-dependent larval development, thereby leading to female choice of males whose burrows are of the appropriate temperature for a given time of mating ([Reaney and Backwell 2007](#); [Milner et al. 2010](#)).

We interpret these results as being the outcome of individual females having phenotypically plastic mating preferences that change over the mating period. We did not incontrovertibly demonstrate this, however, as we did not repeatedly test the same female across the mating period. Unfortunately, this is a logistic impossibility because females have to be tested on the day on which they decide to initiate mate searching. The population-level shift in preferences we observed could also arise if there are among-female differences in preferences for male size and females adjust the time at which they mate accordingly. We suggest, however, that this is unlikely. Females need to accrue energetic resources before they can reproduce (because they spend many days incubating without feeding). Given the patchy nature of food resources, it seems unlikely that females could consistently ensure they have adequate stores available to make it sensible to breed at a predetermined time. Individual female plasticity in the timing of breeding, therefore, seems more probable. Regardless of the interpretation, however, we have demonstrated that *U. mjoebergi* exhibits one of the fastest-known shifts in predicted sexual selection on males due to changes in population-level female mating preferences: the mean female preference for male size reversed within a 7-day period.

Our data corroborate previous work that shows that female *U. mjoebergi* prefer faster-waving males ([Reaney 2009](#)). Perhaps unsurprisingly, female preferences for wave rate did not vary across the mating period; wave rate is an unreliable cue of male size so it is not correlated with burrow temperature. In general, most species have strong and consistent female preferences for higher male sexual display rates ([Ryan and Keddy-Hector 1992](#)). This could be due to a sensory bias, or because wave rate is a good predictor of male condition, which is correlated with benefits that do not vary reliably over time (e.g., genetic benefits or a lower likelihood of the male being diseased). It is also unclear how much variation in wave rate actually occurs in the field among the relevant set of males. Males tend to wave in synchrony when a female approaches ([Reaney et al. 2008](#)). This is why we isolated males during our courting effort trials. Our measure of male wave rate is best viewed as a male's willingness to mate (hereafter “courtship effort”); but this measure might not work in all fiddler crab species: see [Hayes et al. 2013](#)). This is not necessarily the wave rate produced when competing with rivals.

Male courtship effort

We found evidence for variation in courtship effort by male *U. mjoebergi*. Larger males greatly increased their wave rate when

Table 1
Summary of multiple linear regression models of (a) strategic male courtship and (b) transformed ($\log[x + 1]$) male reemergence time, with Wald's tests

Response	Predictor	β	z	P
(a) Male wave rate	Intercept	13.645	47.318	<0.001
	Male carapace width (M)	-0.391	-1.351	0.178
	Female carapace width (F)	0.915	3.145	0.002
	Relative claw size	-0.314	-1.060	0.290
	Day of mating period (D)	0.816	2.822	0.005
	Season	0.091	0.314	0.754
	M × F interaction	0.600	2.053	0.041
	M × D interaction	-0.556	-2.030	0.044
(b) Transformed time to reemerge	Intercept	2.877	42.440	<0.001
	Male carapace width (M)	0.262	3.860	<0.001
	Female carapace width (F)	-0.181	-2.627	0.009
	Relative claw size	0.033	0.479	0.632
	Day of mating period (D)	-0.143	-2.087	0.038
	Season	-0.156	-2.286	0.023
	M × F interaction	-0.018	-0.263	0.793
	M × D interaction	0.097	1.497	0.136

Highlighted rows are significant predictor variables; light gray: positive effect; dark gray: negative effect. The coefficients (β s) presented here are for centered and scaled variables.

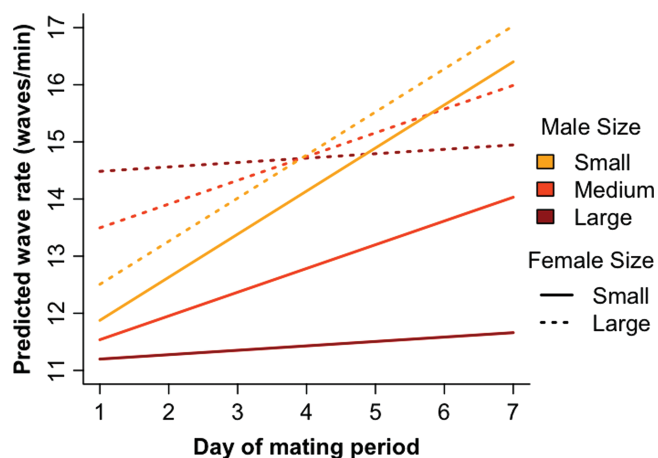


Figure 3

Predicted male courtship effort (waves per minute) from our multiple linear regression in relation to day of the mating period, male size, and female size. Male and female size (carapace width) were included in the model as continuous variables but are categorized here for illustrative purposes. Male size categories are for carapace widths equivalent to claw lengths of 14, 18, and 22 mm (i.e., the same categories as used in the female preference trials; Figure 2). Female size categories are 1 SD below and above the mean carapace width (7.4 and 9.8 mm).

presented with larger females. This appears to be adaptive, as males pay a high cost of mating (burrow loss) and larger females are far more fecund: there is an estimated 9-fold difference in fecundity between the largest and smallest females that we used in our male courting effort trials (see equation in Reading and Backwell 2007). This makes it somewhat surprising that small males did not also

dramatically increase their waving toward larger females. A partial explanation is that some females are physically too large to be accommodated in a small male's burrow. Thus, small males that invest in courting large females are wasting their energy. This is only a partial explanation, however, because it only applies to a subset of the male–female pairings we tested. Possible evidence for this explanation comes from the observed trend that smaller mate-searching females were collected later in the cycle. If large females cannot mate with the smallest males, they should avoid mating late in the cycle, when narrow burrows are desirable. All these arguments are, however, verbal, and formal theoretical models are needed to test their validity and internal consistency.

We tested whether courtship effort varied across the mating period based on the assumption (confirmed by the shift in female mating preferences) that male “physical attractiveness” changed. Males with a given level of attractiveness due to their physical appearance might be able to elevate their net attractiveness by increasing their courting efforts (Kokko 1997). Available theoretical models do not, however, predict how males should respond to population shifts in female mating preferences. We found that male courtship effort (and hence male mate preferences) changed across the mating period in concert with the shift in female preferences, albeit in a male size-specific manner. In particular, we found that small males significantly increased their courtship effort across the mating period, consistent with an increase in the attractiveness of smaller clawed males. In contrast, large males showed neither a decline nor an increase in courtship effort across the mating period. A similar pattern has been found in the closely related *Uca annulipes* (Jennions and Backwell 1998), suggesting that similar shifts in mating preferences might exist in this species.

One explanation for size-dependent changes in male courting effort over the mating period stems from our finding that medium-sized males increased their courtship effort. This is not a statistical

artifact; when we consider only males with 16- to 20-mm long claws (~35% of males sampled), there was a significant positive effect of day of mating period on courting effort (same approach as in Table 1; $\beta = 0.976$, $\zeta = 2.207$, $P = 0.027$). This is intriguing as we found no evidence that the proportion of females preferring medium males (18 mm claw) varied across the mating period (Figure 2b). We suggest that, on average, male courtship effort increases because the future reproductive costs of mating might decline over the mating period (i.e., mating at the end is advantageous because the time spent establishing a new burrow occurs outside the mating period). Large males might actually decrease their courtship effort as their attractiveness to females decreases, but this is masked by a general increase in courting effort for all males across the mating period. To test this explanation will require future studies of the relative costs of mating at different times for *U. mjoebergi*.

Given that female mating preferences appear to shift across the mating period due to extrinsic constraints on larval development, it is likely that females adjust their behavior according to environmental cues of the relative time during the mating period. One potential cue for females is the level of water in their burrows, which will be greatly influenced by tidal cycles. From our correlational results between female and male mate preferences, it is, however, unclear whether males are responding to these same cues or instead to the behavior of females (i.e., a direct cue of the males' attractiveness). One could attempt to disentangle these alternatives by investigating the mating behavior and preferences of captive fiddler crabs in a controlled environment and their interactions with individuals collected from the field.

We also measured the time it took male *U. mjoebergi* to reemerge after being startled into their burrows. This reflects a trade-off between the risk of predation and the benefits of surface activities such as foraging and mating (Hugie 2003; Jennions et al 2003). In our experimental setup, males had reliable information that a mate-searching female was present. We, therefore, consider re-emergence time as another measure of a male's courtship effort. Males reemerged sooner when presented with larger females, corroborating our findings based on measurement of male wave rate. We also found that, overall, males reemerged more quickly toward the end of the mating period. This finding strengthens our earlier argument that the costs of mating for males decrease over the mating period so that a male's incentive to mate increases. Finally, we found that males tended to reemerge sooner as the season progressed. The reasons for this finding are currently unclear. One prosaic explanation is that it is an artifact of the crabs becoming partly habituated to the presence of researchers over the course of the study. This could be tested for by seeing whether females show a similar change in reemergence times over the season and by collecting data from new sites in each mating period.

CONCLUSIONS

In the past, the focus of studies of adaptive variation in mating preferences has typically been on how females adjust their behavior in response to context-dependent changes in the costs and benefits of mating with different male types. Here we show that not only do female preferences shift following a pattern predicted by the direct benefits of mating with different-sized males, but that males also show a concurrent shift in their preferences expressed as the effort they invest into trying to acquire a mate. Our results suggest that males are either adjusting their courtship effort in direct response to

cues from females or in response to other cues that indirectly indicate the benefits of expending energy to court. The interplay between male and female mate choice is a far more dynamic process than current theory can accommodate. Future research should investigate whether, and to what extent, female mating behavior modulates patterns of male courtship effort in a broader range of taxa.

FUNDING

This research was funded by the Australian Research Council (M.D.J. and P.R.Y.B.) and the Australian National University (A.T.K. and T.D.).

We thank Sophia Callander, Tim Maricic, Isobel Booksmythe, and Hanna Kokko for discussion and assistance, as well as the valuable contribution of Paco Garcia-Gonzalez and 2 anonymous reviewers.

Handling editor: Paco Garcia-Gonzalez

REFERENCES

- Agresti A. 2010. Analysis of ordinal categorical data. 2nd ed. New York: Wiley.
- Backwell PRY, Christy JH, Telford SR, Jennions MD, Passmore NI. 2000. Dishonest signaling in a fiddler crab. *Proc R Soc Lond B*. 267:719–724.
- Bonduriansky R. 2001. The evolution of male mate choice in insects: a synthesis of ideas and evidence. *Biol Rev*. 76:305–339.
- Borg AA, Forsgren E, Amundsen T. 2006. Seasonal change in female choice for male size in the two-spotted goby. *Anim Behav*. 72:763–771.
- Chaine AS, Lyon BE. 2008. Adaptive plasticity in female mate choice dampens sexual selection on male ornaments in the lark bunting. *Science*. 319:459–462.
- Christensen RHB. 2011. Analysis of ordinal data with cumulative link models—estimation with the ordinal package. R-package version 2011.09-13. Available from: <http://cran.r-project.org/web/packages/ordinal>.
- Christy JH. 1978. Adaptive significance of reproductive cycles in the fiddler crab *Uca pugilator*—a hypothesis. *Science*. 199:453–455.
- Cotton S, Small J, Pomiankowski A. 2006. Sexual selection and condition-dependent mate preferences. *Curr Biol*. 16:R755–R765.
- Crane J. 1975. Fiddler crabs of the world Ocypodidae: genus *Uca*. Princeton: Princeton University Press.
- deRivera CE. 2005. Long searches for male-defended breeding burrows allow female fiddler crabs *Uca orenulata* to release larvae on time. *Anim Behav*. 70:289–297.
- Edward DA, Chapman T. 2011. The evolution and significance of male mate choice. *Trends Ecol Evol*. 26:647–654.
- Endler JA, Houde AE. 1995. Geographic variation in female preferences for male traits in *Poecilia reticulata*. *Evolution*. 49:456–468.
- Fowler-Finn KD, Rodriguez RL. 2012a. The evolution of experience-mediated plasticity in mate preferences. *J Evol Biol*. 25:1855–1863.
- Fowler-Finn KD, Rodriguez RL. 2012b. Experience-mediated plasticity in mate preferences: mating assurance in a variable environment. *Evolution*. 66:459–468.
- Hancox D, Hoskin CJ, Wilson RS. 2012. Evening up the score: sexual selection favours both alternatives in the colour-polymorphic ornate rainbowfish. *Anim Behav*. 80:845–851.
- Hayes CL, Booksmythe I, Jennions MD, Backwell PRY. 2013. Does male reproductive effort increase with age? Courtship in fiddler crabs. *Biol Lett*. 9:2012078.
- Heubel KU, Schlupp I. 2008. Seasonal plasticity in male mating preferences in sailfin mollies. *Behav Ecol*. 19:1080–1086.
- Hugie DM. 2003. The waiting game: a “battle of waits” between predator and prey. *Behav Ecol*. 14:807–817.
- Jennions MD, Backwell PRY. 1998. Variation in courtship rate in the fiddler crab *Uca annulipes*: is it related to male attractiveness? *Behav Ecol*. 9:605–611.
- Jennions MD, Backwell PRY, Murai M, Christy JH. 2003. Hiding behaviour in fiddler crabs: how long should prey hide in response to a potential predator? *Anim Behav*. 66:251–257.
- Jennions MD, Petrie M. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biol Rev*. 72:283–327.

- Jordan LA, Brooks RC. 2012. Recent social history alters male courtship preferences. *Evolution*. 66:280–287.
- Karlsson K, Eroukmanoff F, Svensson EI. 2010. Phenotypic plasticity in response to the social environment: effects of density and sex ratio on mating behaviour following ecotype divergence. *PLoS ONE*. 9:e12755.
- Kelly CD, Jennions MD. 2011. Sexual selection and sperm quantity: a meta-analysis of strategic ejaculation. *Biol Rev*. 86:863–884.
- Kirkpatrick M, Ryan MJ. 1991. The evolution of mating preferences and the paradox of the lek. *Nature*. 350:33–38.
- Kokko H. 1997. Evolutionarily stable strategies of age-dependent sexual advertisement. *Behav Ecol Sociobiol*. 41:99–107.
- Kokko H, Monaghan P. 2001. Predicting the direction of sexual selection. *Ecol Lett*. 4:159–165.
- Lehtonen TK, Svensson PA, Wong BBM. 2011. Both male and female identity influence variation in male signalling effort. *BMC Evol Biol*. 11:233.
- Lehtonen TK, Wong BBM, Lindstrom K. 2010. Fluctuating mate preferences in a marine fish. *Biol Lett*. 6:21–23.
- Lynch KS, Rand AS, Ryan MJ, Wilczynski W. 2005. Plasticity in female mate choice associated with changing reproductive states. *Anim Behav*. 69:689–699.
- Milner RNC, Detto T, Jennions MD, Backwell PRY. 2010. Experimental evidence for a seasonal shift in the strength of a female mating preference. *Behav Ecol*. 21:311–316.
- Morgan SG, Christy JH. 1995. Adaptive significance of the timing of larval release by crabs. *Am Nat*. 145:457–479.
- Myhre LC, de Jong K, Forsgren E, Amundsen T. 2012. Sex roles and mutual mate choice matter during mate sampling. *Am Nat*. 179:741–755.
- Pfennig KS. 2007. Facultative mate choice drives adaptive hybridization. *Science*. 318:965–967.
- Pizzari T, Cornwallis CK, Løvlie H, Jakobsson S, Birkhead TR. 2003. Sophisticated sperm allocation in male fowl. *Nature*. 426:70–74.
- Pryke SR, Griffith SC. 2007. The relative role of male vs. female mate choice in maintaining assortative pairing among discrete colour morphs. *J Evol Biol*. 20:1512–1521.
- Qvarnström A, Pärt T, Sheldon BC. 2000. Adaptive plasticity in mate preference linked to differences in reproductive effort. *Nature*. 405:344–347.
- Reading K, Backwell PRY. 2007. Can beggars be choosers? Male mate choice in a fiddler crab. *Anim Behav*. 74:867–872.
- Reaney LT. 2009. Female preference for male phenotypic traits in a fiddler crab: do females use absolute or comparative evaluation? *Anim Behav*. 77:139–143.
- Reaney LT, Backwell PRY. 2007. Temporal constraints and female preference for burrow width in the fiddler crab *Uca mjoebergi*. *Behav Ecol Sociobiol*. 61:1515–1521.
- Reaney LT, Sims RA, Sims SWM, Jennions MD, Backwell PRY. 2008. Experiments with robots explain synchronized courtship in fiddler crabs. *Curr Biol*. 18:R62–R63.
- Rowe L, Houle D. 1996. The lek paradox and the capture of genetic variance by condition dependent traits. *Proc R Soc Lond B*. 263:1415–1421.
- Ryan MJ, Keddy-Hector A. 1992. Directional patterns of female mate choice and the role of sensory biases. *Am Nat*. 139:S4–S35.
- Schielzeth H. 2010. Simple means to improve the interpretability of regression coefficients. *Methods Ecol Evol*. 1:103–113.
- Schmoll T. 2011. A review and perspective on context-dependent genetic effects of extra-pair mating in birds. *J Ornithol*. 152:265–277.
- Schwagmeyer PL, Parker GA. 1990. Male mate choice as predicted by sperm competition in thirteen-lined ground squirrels. *Nature*. 348:62–64.
- Slatyer R, Mautz B, Backwell PRY, Jennions MD. 2012. Estimating genetic benefits of polyandry from experimental studies: a meta-analysis. *Biol Rev*. 87:1–33.
- South SH, Arnqvist G, Servedio MR. 2012. Female preference for male courtship effort can drive the evolution of male mate choice. *Evolution*. 66:3722–3735.
- Svensson PA, Lehtonen TK, Wong BBM. 2010. The interval between sexual encounters affects male courtship tactics in a desert-dwelling fish. *Behav Ecol Sociobiol*. 64:1967–1970.
- Wada S, Arashiro Y, Takeshita F, Shibata Y. 2011. Male mate choice in hermit crabs: prudence by inferior males and simple preference by superior males. *Behav Ecol*. 22:114–119.
- Wedell N, Gage MJG, Parker GA. 2002. Sperm competition male prudence and sperm-limited females. *Trends Ecol Evol*. 17:313–320.
- Widemo F, Sæther SA. 1999. Beauty is in the eye of the beholder: causes and consequences of variation in mating preferences. *Trends Ecol Evol*. 14:26–31.
- Wong BBM, Jennions MD. 2003. Costs influence male mate choice in a freshwater fish. *Proc R Soc Lond B*. 12:912–915.
- Yamaguchi T. 2001. Incubation of eggs and embryonic development of the fiddler crab *Uca lactea* (Decapoda Brachyura Ocypodidae). *Crustaceana*. 74:449–458.