ORIGINAL PAPER

Temporal constraints and female preference for burrow width in the fiddler crab, *Uca mjoebergi*

Leeann T. Reaney · Patricia R. Y. Backwell

Abstract We studied sampling behaviour and mate choice in the fiddler crab *Uca mjoebergi*. Once a female selects a mate, she copulates in his burrow and remains there until releasing her aquatic larvae. *U. mjoebergi* occurs in habitats that are inundated only by the highest amplitude spring tides. Females can only release their larvae during these tides, and release before or after will result in complete failure of reproductive effort. Matings occur over a 5-day period near the end of neap tides. Our results suggest that within the mating period, females adjust their larval developmental rates by selecting specific burrows in which to incubate their clutches. We found that at the start of the mating period, females chose larger males as mates. Since male size was positively correlated to burrow width, females were selecting wide burrows and effectively incubating at lower temperatures. This would slow down the developmental rates of larvae. In contrast, females that mated late in the mating period selectively chose small males. By incubating in narrower, warmer burrows, these females may increase the developmental rates of larvae. We propose that females are selecting burrows to influence incubation rate and ensure timely release of their larvae. Female *U. mjoebergi* appear to adjust their preference for the direct benefits of mate choice to increase their reproductive success.

Communicated by C. St. Mary

L. T. Reaney (✉) · P. R. Y. Backwell
School of Botany and Zoology,
The Australian National University,
Canberra, ACT 0200, Australia
e-mail: leeann.reaney@anu.edu.au

Introduction

Mate choice is not always a simple process of acceptance or rejection. Rather, choosy individuals must sample one or more prospective partners and acquire information before selecting a mate (Wittenberger 1983; Jennions and Petrie 1997). Sampling can be costly in terms of time, energy and predation risk (Milinski and Bakker 1992; Gibson and Langen 1996). Furthermore, the timing of fertilisation or egg deposition is often limited by physiological or ecological constraints (Morgan and Christy 1995). These costs and constraints can cause females to adjust their mate choice decisions (Watson et al. 1998; Luttbeg et al. 2001; Lynch et al. 2005).

Flexibility in mate choice decisions may be essential to ensure reproductive success under un-favourable conditions. In guppies, for example, females reduced their preference for brightly coloured males when the perceived predation risk was increased (Godin and Briggs 1996; Gong and Gibson 1996). In species where mate choice is based on both male phenotypic traits and resource quality, females will presumably give priority to direct benefits when sampling costs are high because of their immediate effects (Møller and Jennions 2001). In the common goby, females generally prefer males that already have eggs in their nest. Females avoided these males, however, when oxygen levels were low because they would be unlikely to successfully care for a second clutch (Reynolds and Jones 1999). Individuals are expected to select traits that will increase offspring fitness whilst minimising the costs associated with mate searching and assessment (Gibson and Langen 1996; Jennions and Petrie 1997).

Reproduction in many inter-tidal marine species is reliant on the tidal cycle to ensure successful dispersal of gametes and hatching of larvae (Christy 1978; Morgan and

Christy 1995). Female reproductive success is therefore strongly correlated with the timing of mating, and this is often restricted to small windows of optimal mating periods (Morgan and Christy 1995). Temporal constraints play an important role in fiddler crab mating behaviour (Backwell and Passmore 1996). The safest time for larval release occurs during the largest-amplitude nocturnal high/spring tides (Morgan and Christy 1997; Christy 2003). Consequently, fiddler crabs have developed highly synchronised reproductive activities. Matings occur at discrete times within each semi-lunar tidal cycle to ensure there is sufficient time for oviposition and incubation (Christy 1978). A female mating outside the optimal mating period runs the risk of releasing during an un-favourable tide, which may result in a decrease in offspring survivorship (Morgan and Christy 1995). Although females may gain from spending more time searching and assessing potential mates, when time is limited, they often have to adjust their mate choice criteria to ensure a successful mating (Backwell and Passmore 1996).

Mate choice in fiddler crabs is often based on the sequential assessment of male phenotypic traits and burrow quality (Backwell and Passmore 1996; deRivera 2005). Male courtship rate is an important indicator of male mating success in *Uca annulipes*, where females preferentially sample males with a faster wave rate than their close neighbours (Backwell et al. 1999). Females often choose mates according to size, selecting males that closely match their body size (e.g. Goshima et al. 1996; deRivera 2005). However, burrow quality is considered the most important determinant of female reproductive success in many fiddler crab species (Christy 1983). If the burrow collapses whilst the female is incubating, she could lose her entire reproductive investment. In *U. pugilator*, females prefer stable burrows that are less likely to collapse during oviposition and incubation (Christy 1983). Burrow quality may also determine incubation rate since air temperature inside a burrow may vary with burrow size (Christy 1987; deRivera 2005).

We studied a population of *U. mjoebergi* to determine if females are flexible in their mate choice decisions for both male and burrow properties when optimal larval release time is highly restricted. *U. mjoebergi* experience extremely high temporal constraints because they occur in the high inter-tidal zone and are inundated infrequently by the tide. This greatly restricts the amount of time available for larval release. Females mating at sub-optimal times are almost certain to experience a failed mating since tidal cover will be absent once their larvae have fully developed. Female *U. mjoebergi*, therefore, have a very limited time available to find a mate and still allow sufficient time for subsequent larval development and successful release. Under such extreme temporal constraints, we predict that females should adjust their preference of both male phenotypic traits and resource quality over the mating period to ensure successful larval incubation within the time available.

Materials and methods

Study species and area

U. mjoebergi is a small fiddler crab that lives in large mixed-sex colonies at high densities on inter-tidal mudflats. As in most fiddler crab species, both sexes are highly territorial, and males aggressively defend burrows (Jennions and Backwell 1996, personal observations). During the mating period, receptive females leave their burrows and sample a number of males before selecting a mate. Courting males wave their enlarged claw to attract sampling females to their burrows. A female can do one of three things whilst sampling for a mate: (1) She can approach a male and his burrow and then bypass him to continuing sampling through the population; (2) approach a male and enter his burrow for a few seconds before continuing to sample; or (3) approach a male, enter his burrow and remain there to mate with him. Once a female has selected a male, the latter seals both of them in the burrow and copulation takes place underground. After oviposition, the male leaves the burrow whilst the female remains until she releases her larvae.

We studied a population of *U. mjoebergi* at East Point Reserve in Darwin, Australia from October 2004 to January 2005. The study population covers an area of approximately 50×200 m. It occurs in the highest inter-tidal zone and is therefore inundated only by the highest diurnal and nocturnal spring tides. As a consequence, the site is inundated for approximately five consecutive days during each 14-day semi-lunar cycle, after which it remains uncovered by high tides for up to 10 days. Females therefore have only 4 or 5 days in which to release their aquatic larvae. To determine population size distribution, we set up 0.5×0.5 m plots ($n=17$) randomly throughout the study site. All individuals in the plots were caught and measured for carapace width and major claw length (males only), as well as nearest neighbouring burrow distance (cm).

Following sampling females

We followed actively sampling females over seven semi-lunar tidal cycles. To follow females without disturbing them, we remained approximately 1.5 m from the female and dropped a numbered bead through a long pipe to mark the location of each visited male. We distinguished between an approach to a male and an approach that was followed by a burrow entry by dropping a second coloured bead at
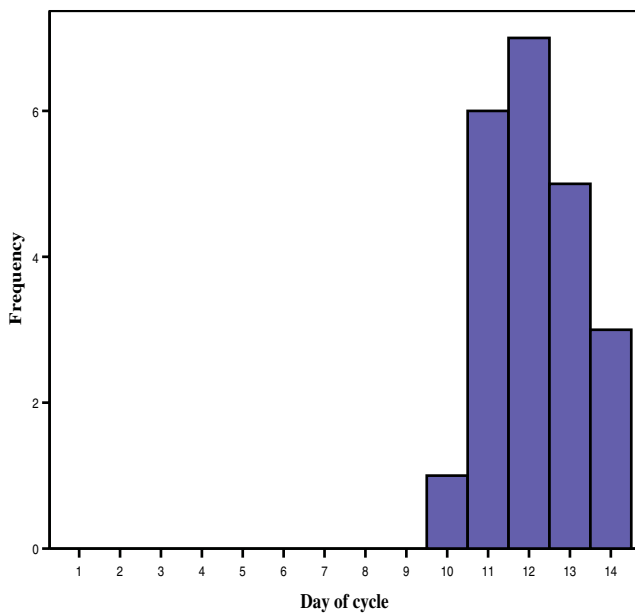
Fig. 1 Frequency of mating over a semi-lunar tidal cycle in *U. mjoebergi*. Matings were documented over seven tidal cycles and occurred over a 5-day period. The highest amplitude spring tides occur on days 1 and 14

the burrows that were entered. A mating was confirmed when the female remained in the burrow, and the male either displayed mate guarding behaviour at the burrow entrance or sealed the entrance with a sand plug. This behaviour indicates a successful mating because females that were removed from a burrow once the male left always produced a clutch of eggs (unpublished data). Sampling time was recorded from when the female was first detected to when she entered the mated males' burrow. The distance between each successively sampled burrow was then measured to determine the total distance travelled by the female. Since it was not always possible to detect a female the moment she began sampling, the measures we obtained are under-estimates of female sampling behaviour. Whilst the female was being followed, a second person filmed the visited males as they courted the female using a Sony DCR-TRV16E digital video camera. Wave rate of sampled males was determined using the event recording programme Jwatcher ©. To confirm that our tracking and marking methods did not disturb the sampling process, we observed ten sampling females from a stationary position ±3 m away and compared the number of visits made to the number recorded whilst tracking females.

Once a mating was confirmed, the mated pair and all visited males were caught and measured for carapace width and major claw length (mm). Since it was impossible to make accurate casts of burrows in the type of substrate that covered the study site, burrow width and length were measured as potential indicators of burrow quality. Burrow width (mm) was measured as the distance between the sides

at the widest part of the burrow aperture using callipers. Burrow length (mm) was measured by pushing a flexible tube down the burrow and measuring the inserted length with a ruler.

Measuring burrow temperature

Burrow temperature from a subset of burrows that were randomly selected within the population were measured for internal temperature. We used a Physitemp temperature recorder (model BAT-12) consisting of an insulated cord connected to a digital reading metre by a terminal microphone plug that measured temperature to the nearest 0.1°C. Surface air temperature was taken immediately before each burrow was measured for internal temperature and burrow width. Temperature readings were taken at the entrance of each burrow and 5 cm down the length of the burrow shaft. A third temperature reading was taken if the probe could be inserted further than 5 cm into the burrow without obstruction. This measurement was used to calculate the rate of temperature decrease inside the burrow.

Statistical analysis

All data were tested for normality or transformed to approximate normality before using parametric tests. Sampling data were analysed using linear mixed models using REML to estimate parameters, with female identity as a random factor to control for multiple data points from the same female. Female carapace width was set as a covariate to control for female size. In the case of pair-wise comparisons, alpha levels were adjusted using sequential Bonferroni procedure. Burrow temperature data were analysed using general linear models with surface air temperature set as a covariate, thereby controlling for daily variation in outside temperature. All analyses were conducted using SPSS 13.

Results

General sampling description

Unlike most fiddler crab species, peak sampling time for *U. mjoebergi* occurred near the end of neap tides (first/last quarter moon) rather than over spring tides. Matings occurred over five successive days within a semi-lunar cycle (Fig. 1). Females sampled an average of 2.2±1.6 SD males (range: 1–6; $n=22$ females) and never visited the same male twice. Sampling females that were observed from a stationary position sampled 2.0±1.1 SD males. The marking method is therefore unlikely to have affected the sampling process since there was no difference in the

Table 1 Spearman's correlations and two-tailed probability values

	Day of mating period	Female carapace width	Total distance travelled	Number of males sampled
Total sampling time	0.328	−0.045	0.847	0.847
	(22)	(22)	(21)	(21)
	0.136	0.841	<0.001*	<0.001*
Number of males sampled	0.349	−0.079	0.983	
	(22)	(22)	(21)	
	0.111	0.726	<0.001*	
Total distance travelled	0.369	−0.051		
	(21)	(21)		
	0.100	0.828		
Female carapace width	0.062			
	(22)			
	0.785			

Sample sizes are indicated in parentheses. Alpha levels are adjusted with sequential Bonferroni procedure
*Significant P values

number of males sampled when burrows were marked or un-marked.

The number of sampled males was positively correlated with both distance travelled (50.2 ± 73.4 cm) and total time spent sampling (330.6 ± 413.2 s), and none of the three measures declined as the cycle progressed (Table 1). Females did not simply move between adjacent burrows as the distance between successively sampled burrows was significantly larger than the distance between nearest neighbour burrows (Mann–Whitney U test, $Z=7.15$, $P<0.001$; sampled burrows: 40.6 ± 23.1 cm, $n=26$; nearest neighbouring burrows: 12.6 ± 5.3 cm, $n=95$).

Female choice for male size

The two measures of male body size, carapace width and major claw length, were highly correlated (Pearson correlation: $r=0.91$, $P<0.001$, $n=49$). All statistical analyses for male size were therefore done using major claw length only. Females sampled males that were significantly larger than those in the general population ($t_{1,104}=2.35$, $P=0.02$; sampled males: 15.7 ± 2.6 mm, $n=49$; males from population: 13.9 ± 4.6 mm, $n=57$). Furthermore, the sampling pattern of individual females was related to their size, with larger females sampling bigger males (Pearson correlation:

$r=0.385$, $P=0.006$; all sampled males: $n=49$). Male wave rate showed no relationship with male size (Pearson correlation: $r=0.005$, $P=0.98$, $n=19$). There was insufficient data to determine if the wave rate of sampled and mated males varied through the mating period, but our limited data gave no indication of this.

There was significant temporal variation in the size of the males that females selected as mates. When female size was controlled for, the size of the mated male significantly decreased as the mating period progressed (Table 2). The drop in mated male size was not caused by temporal variation in female size since the size of sampling females did not change over the mating period (Table 1). The decline was also not a result of larger males being absent later in the mating period as the size of surface active males did not vary (Darby DA and Backwell PRY unpublished data). In fact, the size of rejected males remained consistent throughout the mating period (Table 2). There was a significant negative relationship between day of mating period and the size difference between the mated male and the average size of the previously sampled males (Table 2), with 83% of females mating early in the cycle (first 3 days) choosing a male larger than the average size of males sampled compared to only 50% of females during the last 2 days). Furthermore, the size of males selected as mates

Table 2 Partial correlations controlling for female size

	Burrow width of mated male	Burrow length of mated male	Mean size of rejected males	Size difference between mated and rejected males	Mated male size
Day of mating period	−0.555	0.205	0.187	−0.757	−0.634
	(22)	(22)	(12)	(12)	(22)
	0.009*	0.347	0.186	0.007*	0.002*

Sample sizes are indicated with parenthesis. Alpha levels are adjusted with sequential Bonferroni procedure
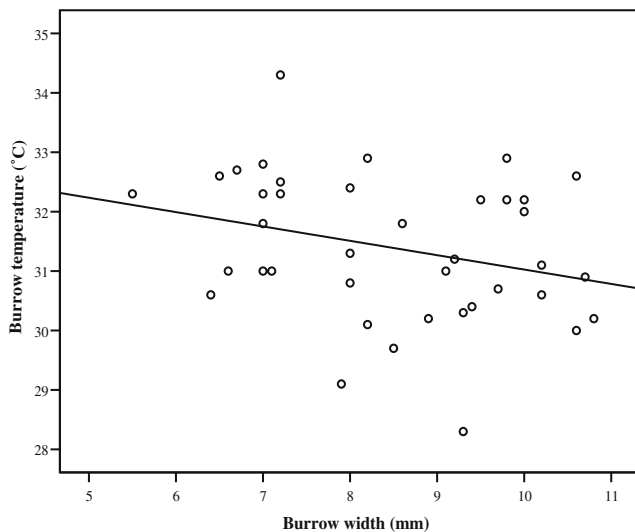*Significant P values

Fig. 2 Relationship between burrow width and internal burrow temperature (5 mm down the burrow shaft)

early and late in the cycle differed; during the first 2 days of the mating period, females selected significantly larger males as mates compared to those females that mated during the last 2 days ($F_{1,13}$=11.18, P=0.006; early: 17.9± 3.0 mm, n=7 late: 15.3±1.6 mm, n=8).

Female choice for burrows

We found a similar temporal pattern in the width of burrows in which females chose to mate. Burrow width of mated males decreased significantly as the mating period progressed (Table 2). Females mating early in the mating period (first 2 days), mated in burrows that were significantly wider than those females mating late in the cycle (last 2 days; $F_{1,13}$=9.25, P=0.01 early: 9.1±1.2 mm, n=7 late: 7.9±0.6 mm, n=8). Male size was highly correlated with burrow width (Pearson correlation: r=0.696, P<0.001, n=49). Burrow length of mated males, however, did decline over the mating period (Table 2) nor was it correlated with male size (Pearson correlation: r=0.151, P=0.30, n=49).

Burrow temperature

Burrow width significantly influenced the temperature of the burrow shaft, with narrower burrows having higher internal temperature, when controlling for daily variation in air temperature ($F_{1,38}$=5.01, P=0.03, n=39; Fig. 2). For every 1-mm increase in burrow width, there was a corresponding decrease of 0.27°C in burrow temperature. There was no significant difference in the rate of temperature drop inside wide and narrow burrows ($F_{1,21}$=2.52, P=0.13, n=22), suggesting that, with increasing length, internal burrow temperatures will remain higher in narrower burrows.

Discussion

Female *U. mjoebergi* are highly constrained by the amount of time available for successful larval release because they are inundated by only the highest diurnal and nocturnal tides. Although mate searching and courtship occurred over a relatively short period compared to other fiddler crab species (Christy 1983; Backwell and Passmore 1996; deRivera 2005), females still actively discriminated between males. The average distance between successfully sampled burrows exceeded that between neighbouring burrows. This, together with the fact that sampling females behaved in a very distinctive manner, approaching males quickly and deliberately close to his burrow, suggests that females were selectively approaching preferred males and not merely the closest males to her. Females also sampled males that were larger than the average male in the population, suggesting large males have a mating advantage in this population. However, female choice for male size did not remain consistent throughout the mating period. There was a significant decrease in the size of mated males as the tidal cycle progressed. The size of sampling females did not vary as the mating period progressed, nor was there any change in the size of surface active males throughout the semi-lunar cycle. Females therefore had similar-size males available to sample throughout the mating period. Furthermore, although females were mating with different-size males, the size of sampled males did not decrease throughout the mating period. Females mating early in the mating period selected significantly larger males, of those sampled, compared to females that mated late. Female *U. mjoebergi* appear to actively avoid selecting larger males as mates as the mating period progresses.

Temporal constraints have been shown to affect female choosiness for male size in *U. annulipes* (Backwell and Passmore 1996). Although females preferentially selected larger males at the start of the mating period, they dropped their mate choice criteria for male size as sampling time became limited. As a consequence, females became less choosy and mated randomly with respect to male size later in the mating period. Female *U. mjoebergi*, however, do not appear to be less selective for male size as the cycle progresses. There was no temporal variation in the time females spent sampling, the distance travelled or the number of males they sampled. If females were becoming less selective during the mate choice process, they should be more willing to mate with the first male they encounter (Real 1990). For example, in three-spined sticklebacks, females that are forced to hold their eggs are more likely to engage in courtship and enter a males' nest than control females (Luttbeg et al. 2001). However, *U. mjoebergi* females did not mate more readily with smaller males later in the cycle. The drop in mated male size therefore appears to be the result of females actively

selecting different-size males as the mating period progressed. The differences in sampling behaviour between *U. mjoebergi* and *U. annulipes* are intriguing. This population of *U. mjoebergi* is certainly under much higher temporal constraints compared *U. annulipes*, possibly causing the observed difference in sampling behaviour between these closely related species.

Burrow width was highly correlated with male size. As a result, females selecting smaller males at the end of the mating period were therefore mating in narrower burrows. Burrow width had a significant influence on burrow temperature, with narrower burrows having higher internal temperatures compared to wider burrows. Females mating in wide and narrow burrows therefore experience very different internal temperatures whilst incubating. By altering their preference for burrow width as the cycle progressed, females may be selecting burrows that optimise incubation rate. A sampling *U. mjoebergi* female will often approach a courting male and briefly enter his burrow before continuing to sample other males. Since entries are often too brief to allow the female to fully descend the burrow, females may be assessing the width and perhaps temperature of the burrow entrance, and not depth, when making a mate choice decision.

In many arthropod species, higher incubation temperatures result in shorter development time (e.g. Moriyasu and Lanteigne 1998; Briere et al. 1999). Female *U. mjoebergi* that mate late are choosing burrows with higher internal temperatures. If narrower burrows increase incubation rate, this may allow females to release larvae earlier than if they were in wider, cooler burrows. Since females only have 5 days to release larvae, females mating at the end of the mating period may be at risk of releasing their larvae when they are no longer covered by the nocturnal high tides. Similarly, females mating early in the cycle will lose their entire reproductive investment if they release before there is tidal cover. By incubating in wide burrows at the start of the mating cycle and narrow burrows near the end, females may alter the developmental rate of larvae to ensure that they are ready for release during an optimal tidal cover.

There are other possibilities as to how females ensure they release larvae at the correct time and their apparent reversal of burrow preference. Burrow temperatures may vary naturally through the tidal cycle. However, given the reasonably constant diurnal air temperatures experience at the study site, this is unlikely to have a large effect on female choice. The study population is also situated in an area of hard muddy sediment, which provides very stable burrow structure. The susceptibility of burrows collapsing is unlikely to be a factor affecting female choice for burrows. Another possibility is that the quality of the females change over the mating period, and this may affect developmental time.

Burrow width has, however, been shown to influence incubation rates in another fiddler crab species, *U.*

crenulata (deRivera 2005). Females that were transferred to burrows wider or narrower than the one initially selected released larvae outside the highest-amplitude nocturnal tides. In this species, however, incubation time was negatively correlated with burrow width, but burrow temperature was never directly measured. Certainly, wider burrows should allow cooler, fresher air to circulate and be less affected by high temperatures from the surface substrate as a result of holding a higher volume of air. In accordance with this, we found that wider burrows had lower internal temperatures compared to narrow burrows. Variable temperatures inside the burrows during incubation may explain why developmental rates did not increase in narrow burrows in *U. crenulata*. Daily fluctuations to high temperatures can often inhibit development growth (Hagstrum and Milliken 1991; Georges et al. 2005). Larval release in *U. mjoebergi* is concentrated on the highest nocturnal spring tides, with 60% of females releasing on a single night ($n=31$; unpublished data). This strongly suggests that females can manipulate developmental rate to ensure successful larval release.

The extreme temporal constraints experienced by *U. mjoebergi* appear to cause females to alter their preference for burrow width to optimise developmental time of larvae. In systems where females assess both male phenotype and resource quality, the direct benefits from burrow quality are likely to outweigh the indirect benefits gained by selecting high quality males (Møller and Jennions 2001). When sampling costs are high, females are likely to prioritise traits depending on their relative affects on fitness (Fawcett and Johnstone 2003). Females are expected to maintain high levels of choosiness for direct benefits since their effects are immediate (Halliday 1983; Møller and Jennions 2001). Since burrow quality is such an important determinant of female reproductive success in fiddler crabs, it is not surprising that extreme temporal constraints cause females to adjust their preference for burrow width, and thereby the direct benefits of mate choice, presumably to increase their reproductive success.

References

Backwell PRY, Passmore NI (1996) Time constraints and multiple choice criteria in the sampling behaviour and mate choice of the fiddler crab, *Uca annulipes*. Behav Ecol Sociobiol 38:407–416

Backwell PRY, Jennions MD, Christy JH, Passmore NI (1999) Female choice in the synchronously waving fiddler crab *Uca annulipes*. Ethology 105:415–421

Briere JF, Pracros P, Le Roux AY, Pierre JS (1999) A novel rate model of temperature-dependent development for arthropods. Environ Entomol 28:22–29

Christy JH (1978) Adaptive significance of reproductive cycles in fiddler crab *Uca pugilator*—a hypothesis. Science 199:453–455

Christy JH (1983) Female choice in the resource-defense mating system of the sand fiddler crab, *Uca pugilator*. Behav Ecol Sociobiol 12:169–180

Christy JH (1987) Female choice and the breeding behavior of the fiddler crab *Uca beebei*. J Crustac Biol 7:624–635

Christy JH (2003) Reproductive timing and larval dispersal of intertidal crabs: the predator avoidance hypothesis. Rev Chil Hist Nat 76:177–185

deRivera CE (2005) Long searches for male-defended breeding burrows allow female fiddler crabs, *Uca crenulata*, to release larvae on time. Anim Behav 70:289–297

Fawcett TW, Johnstone RA (2003) Optimal assessment of multiple cues. Proc R Soc Lond B 270:1637–1643

Georges A, Beggs K, Young JE, Doody JS (2005) Modelling development of reptile embryos under fluctuating temperature regimes. Physiol Biochem Zool 78:18–30

Gibson RM, Langen TA (1996) How do animals choose their mates. Trends Ecol Evol 11:468–470

Godin J-GJ, Briggs SE (1996) Female mate choice under predation risk in the guppy. Anim Behav 51:117–130

Gong A, Gibson RM (1996) Reversal of a female preference after visual exposure to a predator in the guppy, *Poecilia reticulata*. Anim Behav 52:1007–1015

Goshima S, Koga T, Murai M (1996) Mate acceptance and guarding by male fiddler crabs *Uca tetragonon* (Herbst). J Exp Mar Biol Ecol 196:131–143

Hagstrum DW, Milliken GA (1991) Modeling differences in insect development times between constant and fluctuating temperatures. Ann Entomol Soc Am 84:369–379

Halliday TR (1983) The study of mating choice. In: Bateman P (ed) Mate choice. Cambridge, Cambridge, pp 3–52

Jennions MD, Backwell PRY (1996) Residency and size affect fight duration and outcome in the fiddler crab *Uca annulipes*. Biol J Linn Soc Lond 57:293–306

Jennions MD, Petrie M (1997) Variation in mate choice and mating preferences: a review of causes and consequences. Biol Rev 72:283–327

Luttbeg B, Towner MC, Wandesforde-Smith A, Mangel M, Foster SA (2001) State-dependent mate-assessment and mate-selection behavior in female threespine sticklebacks (*Gasterosteus aculeatus*, Gasterosteiformes: Gasterosteidae). Ethology 107:545–558

Lynch KS, Rand AS, Ryan MJ, Wilczynski W (2005) Plasticity in female mate choice associated with changing reproductive states. Anim Behav 69:689–699

Milinski M, Bakker TCM (1992) Costs influence sequential mate choice in sticklebacks, *Gasterosteus aculeatus*. Proc R Soc Lond B 250:229–233

Møller AP, Jennions MD (2001) How important are direct fitness benefits of sexual selection. Naturwissenschaften 88:401–415

Morgan SG, Christy JH (1995) Adaptive significance of the timing of larval release by crabs. Am Nat 145:457–479

Morgan SG, Christy JH (1997) Planktivorous fishes as selective agents for reproductive synchrony. J Exp Mar Biol Ecol 209:89–101

Moriyasu M, Lanteigne C (1998) Embryo development and reproductive cycle in the snow crab, *Chionoecetes opilio* (Crustacea: Majidae), in the southern Gulf of St. Lawrence, Canada. Can J Zool 76:2040–2048

Real L (1990) Search theory and mate choice. I. Models of single-sex discrimination. Am Nat 136:376–404

Reynolds JD, Jones JC (1999) Female preference for preferred males is reversed under low oxygen conditions in the common goby (*Pomatoschistus microps*). Behav Ecol 10:149–154

Watson PJ, Arnqvist G, Stallmann RR (1998) Sexual conflict and the energetic costs of mating and mate choice in water striders. Am Nat 151:46–58

Wittenberger JF (1983) Tactics of mate choice. In: Bateman P (ed) Mate choice. Cambridge University Press, Cambridge, pp 435–447