



Polyandry occurs because females initially trade sex for protection

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In many species, females mate with multiple males, suggesting that polyandry confers fitness-enhancing benefits. The benefits of polyandry are usually attributed to either the cumulative acquisition of direct material benefits from consecutive mates or genetic benefits resulting from access to greater sperm diversity that facilitates cryptic female choice and sperm competition or simply elevates genetic diversity among offspring. With the notable exception of studies in birds that contrast within-pair and extrapair copulations, the alternative explanation that females receive different benefits from different types of mates is rarely explored. In the fiddler crab *Uca mjoebergi*, females mate multiply using two distinct mating tactics: surface and burrow mating. We found that females gained a different benefit from each type of mating. Females that initially mated on the mudflat surface secured the help of their mate in burrow defence. Male neighbours were significantly more likely to help after mating. In contrast, a female's final mating allowed her to choose the mate that would sire most of her offspring and gain access to a burrow that she then used for breeding. Together, these benefits provide a strong incentive for females to mate multiply.

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Multiple mating (polyandry) by females occurs in most animal taxa (Jennions & Petrie 2000) despite female reproduction rarely being constrained by access to males (Trivers 1972). Polyandry could be directly selected for if it increases a female's lifetime fecundity. This can occur when mating increases female access to material resources necessary for breeding (Gray 1997a; Fedorka & Mousseau 2002) or allows them to replenish depleted sperm supplies (Diaz et al. 2010). It has also been suggested that a female can receive protection from her most recent mate against harassment by other males ('convenience polyandry'; Lovell-Mansbridge & Birkhead 1998; Cordero 1999).

A more controversial claim is that polyandry is under indirect selection because polyandrous females produce offspring with above average net fitness so that they have more grandchildren (i.e. genetic benefits; Simmons 2001; Kokko et al. 2006; Slatyer et al. 2012). In principle, this could even compensate for a slight decline in offspring production (i.e. the effect of polyandry on offspring fitness differs for sons and daughters; Head et al. 2005). Genetic benefits require that females either choose a higher-quality male when they mate a second time or that post-copulatory mechanisms exist that bias paternity towards males that sire fitter offspring (Jennions & Petrie 2000; Pryke et al. 2010; Slatyer et al. 2012).

It is, of course, possible that polyandry confers several benefits, either simultaneously (Fedorka & Mousseau 2002) or sequentially because different mates provide different benefits (Friedl & Klump 2005; Rubenstein 2007). Few studies, however, have explicitly examined the latter aspect of polyandry (but see Fedorka & Mousseau 2002; Friedl & Klump 2005; Fisher et al. 2006; Rubenstein 2007; Townsend et al. 2010). This is despite the large volume of literature on polyandry in socially monogamous birds, where the different contexts of within- and extrapair copulations (EPCs) are grounds to suspect that females might receive diverse benefits from mating. In general, it is simply assumed for most passerine birds that a female's social mate provides direct benefits (e.g. parental care and a breeding territory), and that EPCs are then driven by genetic benefits, even though the evidence for elevated performance of extrapair offspring is weak (Schmoll 2011). In other taxa, especially invertebrates, even fewer studies have tested whether females mate with different males for qualitatively different types of benefits.

In many fiddler crabs, including our study species *Uca mjoebergi*, females will often mate with two or more males in a single reproductive cycle, with 55% of clutches fertilized by two or more males (L.T. Reaney & P.R.Y. Backwell, unpublished data). Females are able to store sperm for long periods (Yamaguchi 1998a), which could theoretically account for multiple paternity clutches (i.e. use of sperm acquired in an earlier reproductive cycle). However, females also utilize two distinct mating tactics in each reproductive cycle. Initial surface matings usually (70% of cases; R.A. Slatyer, unpublished data) involve neighbouring territory holders. There is

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no apparent courtship, and both crabs return to their own burrows after mating (Yamaguchi 1998b; Milner et al. 2010a). Surface mating occurs throughout the semilunar cycle, but is most common earlier in the cycle (around spring tides). Later, during the peak breeding period each semilunar cycle (around neap tides), females vacate their burrow and actively sample courting males (Reaney & Backwell 2007). Males wave their single enlarged major claw and mate-sampling females favour males with larger claws and a faster wave rate (Reaney 2009). Once a female chooses a male, they mate underground in his burrow and remain there until the female fertilizes and releases her eggs (Backwell & Passmore 1996). The female does not emerge to feed during this time and burrow-mating females do not mate again in the same breeding cycle since they are guarded by their mate until they oviposit (Backwell & Passmore 1996). Larval release is carefully timed to coincide with a nocturnal spring tide, which is thought to maximize larval survival (Morgan & Christy 1995; DeRivera 2005). There is often very strong last-male sperm precedence (L.T. Reaney & P.R.Y. Backwell, unpublished data). This begs the question: why do females initially mate on the surface?

Milner et al. (2010a) recently showed that males protect female neighbours against territorial intrusions by foreign males in another fiddler crab, *U. annulipes*. They suggested that this is a form of male mate guarding to retain a female neighbour as a future mate, but did not present evidence that directly linked male protection to surface mating. Here we investigated whether a male provides protection when he mates with a neighbouring female on the surface. We also investigated whether surface mating (1) provides genetic benefits arising from pre- or postcopulatory mate choice or (2) guarantees a sperm supply, allowing females to be more selective in their subsequent choice of mates (Kokko & Mappes 2005).

METHODS

Our study was conducted on mudflats in Darwin, Australia in September–December 2009.

Is There a Direct Benefit to Surface Mating?

To test whether surface-mated males protect females against intruding males, we experimentally created novel male–female neighbours. To do this, we translocated a burrow-owning female from elsewhere on the mudflat into a plastic enclosure placed 8 cm from a resident male's burrow. The enclosure contained an artificial burrow. We allowed the female to acclimatize for 6 min and then removed the enclosure. We then observed the pair for 3 min. In 10 of 34 cases the pair mated. For all 34 pairs we then simulated an intrusion into the female's territory. We captured a male ('intruder') from elsewhere on the mudflat, glued (with superglue) a 3 cm cotton thread to his carapace, tied it to a nail, and embedded the nail into the sediment 5 cm from the female's burrow, on the opposite side to the focal male neighbour. The intruder male (carapace width, CW = 9.9 ± 0.7 mm, $N = 34$) was always smaller than the male neighbour (10.6 ± 0.8 mm), increasing the likelihood of a male neighbour providing a protective response (Backwell & Jennions 2004; Detto et al. 2010). Protection was scored if the focal male made contact with the intruder male within 5 min of emerging from his burrow. We compared how often, and how soon, a male neighbour helped the female to defend her territory when the pair had ($N = 10$) or had not ($N = 24$) surface-mated. No intruder was tethered for longer than 10 min. After each trial the tether was cut close to the carapace, taking care not to damage the carapace, and the crab was released onto the mudflat.

Do Females Surface-mate to Guarantee a Sperm Supply?

We documented clutch production of females when their final mating was either a surface or burrow mating. Surface-mating pairs were located on the mudflat and the female captured. We collected burrow-mated females by individually tracking a mate-sampling female through the entire mate-searching process until she chose a mate. After 2 h, to ensure she had mated (Yamaguchi 1998b), we carefully extracted her from the chosen male's burrow. Females were transported individually, in small containers, to the laboratory. Here they were housed individually in 5×5 cm plastic containers containing sea water (changed daily), and a small rock that allowed the crab to sit out of the water. The containers were placed outside, under shade, and covered loosely with a cloth. Females do not feed while incubating eggs in a burrow, so we did not provide additional food. They were held until they released fertilized eggs or 14 days had elapsed ($N = 56$ surface-mated; $N = 14$ burrow-mated). After this period they were returned to the mudflat. No females died in captivity. Given that this method of housing females does not closely match conditions inside a burrow, we expected it to reduce the general likelihood that females would produce a clutch of eggs. Our main interest was therefore in testing for a difference in the proportion of burrow- and surface-mated females that produced a clutch, rather than in the absolute proportion of females of each type that released eggs. Equal likelihood of clutch production by females following both surface mating and burrow mating would provide support for the hypothesis that females mate on the surface to guarantee a sperm supply that can be used if burrow mating is not possible (e.g. because rain prevented diurnal activity and mate sampling).

Are Females Choosy?

To test whether mating is nonrandom with respect to male size and claw type (original or regenerated; Lailvaux et al. 2009), we demarcated 15 randomly placed 25×25 cm plots on the mudflat and caught all males within each plot to obtain a population sample ($N = 63$ males). We then compared the CW and claw type to that of surface-mated and burrow-mated males ($N = 127, 17$, respectively). These two measures were chosen because (1) male size is known to influence female choice in *U. mjobergi* and (2) claw type affects fighting ability (Reaney et al. 2008; Reaney 2009; Milner et al. 2010b). We supplemented data on claw type by including data from 34 burrow-mated males from our earlier study (Reaney et al. 2008). We expected to see evidence for selectivity in the choice of males for both surface and burrow matings if females mate multiply for some form of genetic benefit. Alternatively, if selective mate choice only occurs when burrow mating, this would be consistent with surface mating providing a different type of benefit that is unrelated to male size or claw type.

Summary statistics are presented as mean \pm SD, except where otherwise stated. We set $\alpha = 0.05$ (two-tailed).

RESULTS

Is There a Direct Benefit to Surface Mating?

Males that surface-mated with a female were significantly more likely to protect her against an intruder than those that did not (10/10 versus 14/24; Fisher's exact test: $P = 0.017$). Furthermore, males that surface-mated responded significantly more quickly to the presence of an experimental intruder (37.2 ± 16.5 s versus 172.0 ± 24.0 s; Mantel–Cox test: $\chi^2_1 = 19.101$, $P < 0.001$).

Do Females Surface-mate to Guarantee a Sperm Supply?

Clutches were produced significantly more often after burrow than surface mating (1/56 versus 6/14; Fisher's exact test: $P < 0.001$). Surface mating was therefore far less likely to lead to sperm use, even though all females were monitored for sufficient time to ensure that they should have released eggs (i.e. to coincide with the nocturnal spring tide).

Are Females Choosy?

Surface-mated males, burrow-mated males and the random sample of males in the population differed significantly in size ($F_{2, 53.4} = 8.52$, $P = 0.001$; CW of population: 10.3 ± 1.6 mm, $N = 63$; surface-mated: 10.5 ± 1.3 mm, $N = 127$; burrow-mated: 11.4 ± 0.8 mm, $N = 17$). Burrow-mated males were significantly larger than both the population sample (least significant difference pairwise test: $P = 0.001$) and surface-mated males ($P = 0.004$). In contrast, surface-mated males did not differ in size from the population average ($P = 0.517$).

In the population sample, 86% (51/59) of males had an original major claw. Similarly, 84% (94/112) of surface-mated males still had their original claw. In contrast, all of the burrow-mated males had their original claw (51/51). Burrow-mated males more often had an original claw than males in the general population (Fisher's exact test: $P = 0.007$) or than surface-mated males ($P = 0.003$). The proportion of surface-mated males with an original claw did not differ from that in the general population ($P = 0.823$).

DISCUSSION

The available evidence suggests that female *U. mjobergi* are often polyandrous because they initially surface-mate with a neighbour and later leave their own burrow to burrow-mate and oviposit elsewhere. This scenario implies that polyandry occurs because females accrue distinct benefits in each mating context. Another possibility is that polyandry provides genetic benefits because it generates the potential for sperm competition and/or cryptic female choice.

Large *U. mjobergi* males help smaller male neighbours repel intruders (Backwell & Jennions 2004). These territorial 'coalitions' allow the protecting male to avoid costly territorial interactions with a new male resident (Getty 1987; Detto et al. 2010). Recent studies of the related *U. annulipes* show that males will also protect neighbouring females (Detto et al. 2010; Milner et al. 2010a). Milner et al. (2010a) hypothesized that protection is a form of precopulatory mate guarding because retaining a female neighbour increases the likelihood of gaining future surface matings. In the current study we found an increase in the speed and likelihood of protection of females after surface mating in *U. mjobergi*, suggesting that this male behaviour could have the additional, nonmutually exclusive function of acting as a form of postcopulatory mate guarding (i.e. to decrease the likelihood that the already mated female is evicted and then surface-mates again with another male when she locates a new burrow). This type of guarding behaviour is common in species with last-male sperm precedence as it ensures a higher share of paternity (Diesel 1991; Alcock 1994). Male protection appears to be an important mechanism allowing competitively inferior females, which lack a major claw, to defend their burrow against intruding males until they are ready to leave their burrow for burrow mating (Backwell & Jennions 2004; Milner et al. 2010a). To the best of our knowledge, this is the first experimental evidence for any species that females obtain greater protection as a direct benefit of mating with a male, where protection helps females defend their own resource (i.e. their

territory) rather than simply deters direct male sexual harassment (i.e. a form of 'convenience polyandry'; see Cordero 1999).

We found no evidence that females mate on the surface for genetic benefits, because surface mating was random with respect to male size and claw type, and males provide no information about their courtship abilities (i.e. no waving displays) prior to surface mating. In short, surface matings are with neighbours that are a random sample of the male population. Additionally, females collected after surface mating rarely (<2%) produced a clutch of fertilized eggs. Given that female fiddler crabs can store fertile sperm for at least 10 months (Yamaguchi 1998a), this suggests that ensuring an adequate sperm supply to breed in the current reproductive cycle is an unlikely explanation for surface mating. So why do females that can readily surface-mate then also go on to burrow-mate, which is the main cause of polyandry?

Burrow mating implies that females either prefer to use the sperm of burrow-mated males to fertilize their eggs (for genetic benefits) and/or that they gain additional direct benefits by burrow mating. Current evidence for genetic benefits of polyandry is equivocal (Schmoll 2011; Slatyer et al. 2012), but females might elevate offspring fitness by burrow mating with higher-quality males that gain the bulk of paternity because of strong last-male sperm precedence. Consistent with this claim, females preferentially burrow-mated with males that were larger than the population average, but whether male size is correlated with offspring fitness is unknown.

No males with a regenerated claw obtained a burrow mating. This result is unrelated to burrow-mated males being larger, as the likelihood of possessing an original claw decreases with body size (i.e. age, as fiddler crabs have indeterminate growth; Reaney et al. 2008). Maintaining an original claw seems unlikely to be related to genetic quality. In many species, however, the quality of male-held resources (e.g. a nest or territory) is a key criterion for female mate choice and is positively correlated with male weaponry (Emlen 2008; Kelly 2008). In fiddler crabs, original-clawed males are better competitors than either females or males with regenerated claws. Original-clawed males might therefore possess higher-quality burrows (Reaney et al. 2008; Lailvaux et al. 2009). In other fiddler crabs, females choose mates based on burrow features that optimize larval development rate and timing of release, thus improving larval survival (Backwell & Passmore 1996; DeRivera 2005). It is therefore plausible that burrow mating provides a direct benefit because it enables females to obtain a burrow well suited to breeding. This hypothesis warrants testing by making a direct comparison of the burrow characteristics of a female's original burrow and those of the male with which she burrow-mates, as well as a comparison between the burrows of males with original and regenerated claws.

The question 'Why do females that surface-mate go on to burrow-mate?' can also be rephrased to ask: 'Why do females not simply burrow-mate straight away?' The most likely answer is that this is costly. After a female has burrow-mated the male guards her and she remains underground where she is unable to feed. Females that remain in their own burrows until shortly before the optimal time for oviposition (i.e. during the neap tide period) therefore have more time to forage. The 'price' they appear willing to pay is to surface-mate with a neighbour to gain greater protection while they continue to feed.

When females gain qualitatively different benefits from different males, polyandry can be considered to arise as a by-product of selection acting separately in each context. Only a handful of studies have explicitly demonstrated that polyandry is beneficial because it provides different benefits in different mating contexts. In birds, a few studies have shown that EPCs provide a nutritional reward (Tryjanowski & Hromada 2005), access to additional territorial

space (Gray 1997b), more nest materials (Hunter & Davis 1998) or extra helpers at the nest (Rubenstein 2007; Townsend et al. 2010). Many more studies have tested for potential genetic benefits of EPCs, which would explain polyandry via a 'different benefits' model if females 'trade up' from a social mate (who provides direct benefits) to an extrapair mate (which will sire fitter offspring), but the evidence from these studies is unclear (reviewed in Schmoll 2011). In many studies of invertebrates, successive matings appear to provide the same type of benefit that accumulates with each successive mating (Gwynne 2008; e.g. nutrients are transferred at each mating), but further studies are required to assess the generality of a multibenefit model of polyandry when females mate with successive males under different conditions.

In summary, polyandry in *U. mjoebergi* appears to occur because surface and burrow mating confer different types of benefits. We suggest that polyandry is primarily a by-product of selection favouring both types of benefits rather than being directly selected for as is the case when, say, greater offspring genetic diversity is beneficial (Mattila & Seeley 2007).

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