



Foraging and mating opportunities influence refuge use in the fiddler crab, *Uca mjoebergi*

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Although many animals use refuges to avoid predators, it is often costly to do so. The longer an individual remains in a refuge, the less time it has available for other essential activities, such as foraging and mate searching. Animals should therefore optimize the time spent in a refuge after an attack by adopting a flexible approach to predator avoidance. I examined refuge use in the fiddler crab, *Uca mjoebergi*, under variable foraging and mating contexts on a mudflat in Australia. There were no sex or size differences in refuge use, suggesting that there are no morphological or gender biases in predation risk. Risk-taking behaviour in *U. mjoebergi* was, however, highly flexible and appeared to be strongly dependent on the trade-off between the costs and benefits of hiding. Refuge use varied between optimal foraging and reproductive periods of a semilunar cycle. Loss of foraging time influenced risk-taking behaviour in both males and females since both were quicker to re-emerge when food levels were high. During the reproductive period, crabs took longer to re-emerge because of few foraging opportunities, as well as few mating opportunities since receptive females were rare. However, when mating opportunities for males were experimentally increased by introducing a tethered female, actively courting males engaged in highly risky behaviour and re-emerged after a few seconds, with some males abandoning refuge use completely. Refuge use in *U. mjoebergi* is therefore highly flexible, with the decision to re-emerge influenced by fitness benefits.

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Predator avoidance often conflicts with behaviours such as foraging (Cooper & Pérez-Mellado 2004), fighting (Brick 1998), courtship (Candolin 1997) and mate searching (Brown & Shine 2004). Optimal escape theory predicts that trade-offs between the costs and benefits of predator avoidance will affect the risks an individual is willing to take before fleeing from a predator (Ydenberg & Dill 1986). There is strong empirical evidence that predator avoidance strategies vary as a consequence of these trade-offs (reviewed in Lima & Dill 1990; Lima 1998). Similarly, morphological variation, such as sex and body size, often results in individual differences in predator avoidance strategies (e.g. Shine et al. 2000). Although optimal escape theory has been tested extensively on reptiles, data on other species remain limited

(Cooper 2003). Furthermore, few empirical studies have considered the factors influencing when an animal should re-emerge from a refuge after a predator attack (Martín & López 1999; Jennions et al. 2003; Martín et al. 2005).

Antipredator vigilance often decreases foraging time (Cowlshaw et al. 2004). Similarly, taking refuge from a predator may curtail the time available for other essential activities. Loss of foraging time is often considered one of the main costs of refuge use since little or no foraging occurs in a refuge (Lima & Dill 1990; Martín et al. 2003a). Lost mating opportunities can also be a major cost of refuge use (Martín et al. 2003b), especially when mating opportunities are limited (Hazlett & Rittschof 2000). To reduce these potential costs, individuals should optimize the time spent in a refuge. Individuals may, for example, spend less time in a refuge if there are increased benefits outside (Martín et al. 2003b). The decision to re-emerge should therefore depend on the trade-offs between the costs and benefits of refuge use (Martín & López 1999;

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Cooper & Pérez-Mellado 2004). Animals may therefore minimize the costs incurred from refuge use during essential behaviours by adopting a flexible approach to predators (Martín et al. 2003b). Barnacles, for example, adjust their re-emergence times according to how long they spent feeding before an attack, coming out later if they

predator attack. The tethered female was released immediately after the trial ended. For each plot I used a new tethered female and this was repeated for 15 plots. I measured re-emergence times of noncourting males for 15 plots where no receptive female was present and counted the males that remained on the surface during an attack. No plot or individual was measured twice.

Statistical Analysis

For analysis I used linear mixed models with parameters fitted by using restricted maximum likelihood. The significance of terms was tested with marginal F tests (Pinheiro & Bates 2000, page 90). Time was log transformed to approximate normality and plot identity was set as a random factor. To compare the magnitude of the response between experiments, I calculated the effect size, r , for each trial (Zar 1999, page 386). I then tested for a significant difference in correlation coefficients between tests. Since carapace width and major claw length were highly correlated (Pearson correlation: $r_{299}^2 = 0.85$, $P < 0.001$), all analyses were done using carapace width as a measure of body size. Significance was accepted at $\alpha < 0.05$. All analyses were conducted with the statistical program SPSS 11.5 (SPSS Inc., Chicago, IL, U.S.A.). Data are presented as mean \pm SD.

RESULTS

There was no significant difference in re-emergence times between males and females ($F_{1,341} = 1.31$, $P = 0.505$; Fig. 1). Females took an average of 48.4 ± 33.8 s ($N = 46$) to

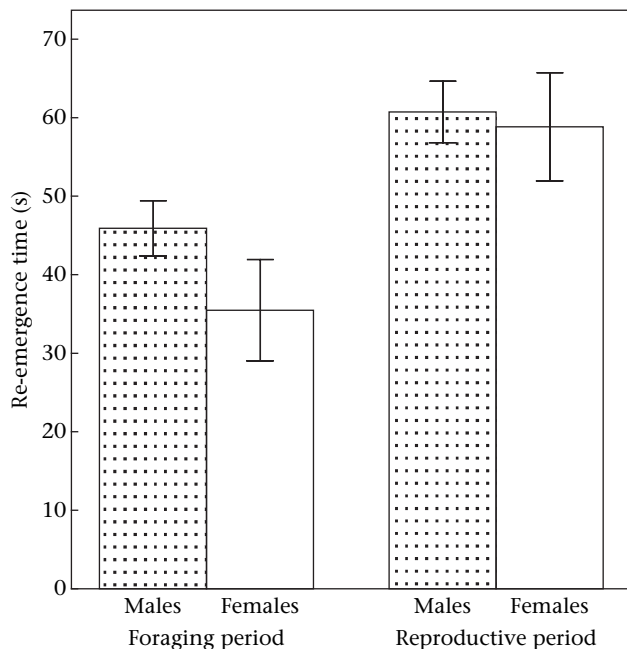


Figure 1. Re-emergence times ($\bar{X} \pm 1$ SE) of males and females during foraging and reproductive periods of a semilunar cycle after a simulated predator attack.

re-emerge after an attack and males took 56.0 ± 47.2 s ($N = 303$). Re-emergence data from males and females were therefore combined. Body size had no effect on re-emergence time during peak foraging ($F_{1,95} = 1.33$, $N = 134$, $P = 0.162$) or reproductive periods ($F_{1,31} = 1.238$, $N = 38$, $P = 0.428$).

Re-emergence times varied significantly between foraging and reproductive periods ($F_{1,52} = 9.01$, $P = 0.004$; Fig. 1). Individuals that were foraging spent an average of 46.1 ± 41.7 s ($N = 168$) in a refuge. During mating periods, when food levels were substantially lower, average re-emergence time increased to 63.2 ± 47.7 s ($N = 181$). Although individuals in feeding plots ($N = 43$) had slightly lower average re-emergence times than those in control plots ($N = 43$), food additions had no significant effect on re-emergence times during the reproductive period ($F_{1,19} = 0.266$, $P = 0.612$; Fig. 2).

When presented with a receptive female, males spent significantly less time in a refuge ($F_{1,29} = 171.22$, $P < 0.001$; Fig. 3), re-emerging 12.7 ± 8.6 s ($N = 56$) after an attack compared to 117.5 ± 85.7 s ($N = 79$) when males were not presented with a female. The percentage of individuals remaining on the surface also increased significantly when a female was present, with 12% of males choosing not to enter their burrows during an attack compared to zero when there was no receptive female ($\chi_1^2 = 12.77$, $P < 0.001$). Furthermore, there was a significant difference between the effect sizes for the comparison of foraging and reproductive periods and those for the comparison of actively courting males and noncourting males ($Z = 9.61$, $N_1 = 58$, $N_2 = 30$, $P = 0.001$). The re-emergence times of actively courting males were therefore significantly shorter than the time individuals spent in a refuge during foraging periods.

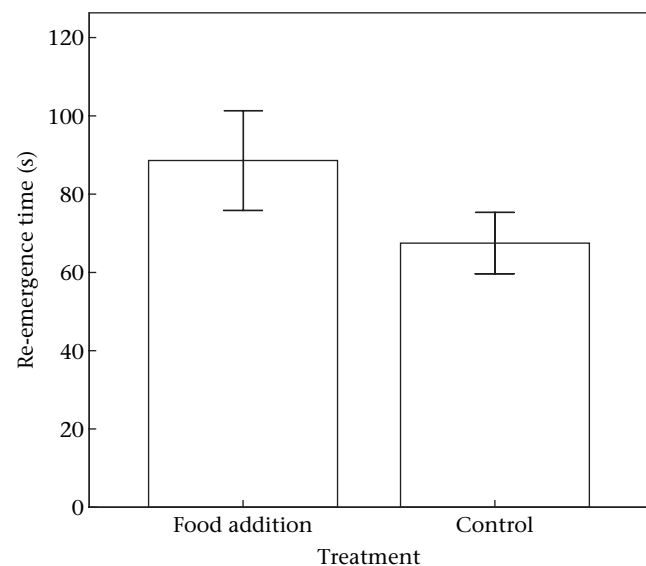


Figure 2. Re-emergence times ($\bar{X} \pm 1$ SE) for food addition and control plots for both males and females after a simulated predator attack. Re-emergences times were measured during the reproductive period of a semilunar cycle.

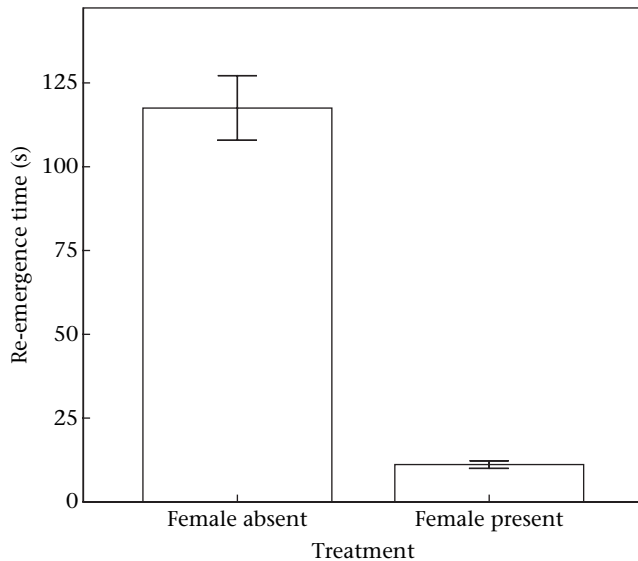


Figure 3. Re-emergence times ($\bar{X} \pm 1 \text{ SE}$) of courting males in the absence and presence of a tethered female after a simulated predator attack. Re-emergences times were measured during the reproductive period of a semilunar cycle.

DISCUSSION

Refuge use in *U. mjoebergi* was not related to either body size or sex. This is surprising since variation in body size and sexual dimorphism between the sexes often results in differences in predation risk, and consequently in predator avoidance strategies (e.g. Shine et al. 2000; Jennions et al. 2003; Roth & Johnson 2004). A fiddler crab male's major claw comprises more than 30–40% of body mass and is often brightly coloured, as in *U. mjoebergi* (Crane 1975). An increase in conspicuousness from the large body and claw size will presumably increase predation risk for fiddler crabs. Indeed, male-biased predation has been reported in some species (e.g. *U. beebei*, Koga et al. 2001). Biased predation risk may in turn result in differential refuge use since more vulnerable individuals may be more reluctant to re-emerge after an attack. This was demonstrated in *U. lactea perplexa*, where males spent more time in a refuge than females did and larger individuals of both sexes took longer to re-emerge (Jennions et al. 2003). In *U. mjoebergi*, however, males and females of all sizes spent similar times in a refuge after an attack. This suggests that increased conspicuousness may not translate directly into increased predation risk in this species and that other factors influence refuge use in males and females. The defensive ability of a male's major claw and increased handling time may, for example, lower the predation risk for conspicuous males (Bildstein et al. 1989; Jordão & Oliveira 2001). The lack of size or sex differences in risk-taking behaviour after an attack may therefore be a result of negligible differences in the relative predation risk between males and females in this population.

Optimal foraging and reproductive activities are temporally separated in *U. mjoebergi*. Refuge use during these two periods varied considerably. Both males and females

re-emerged faster after a simulated predator attack during peak foraging times of a semilunar cycle, when food levels were at their highest. When food levels decreased naturally because of the absence of tidal cover, individuals spent longer in a refuge after an attack. The cost of staying in a refuge often varies with food availability and many animals take more risks when food levels are high. For example, the tubeworm, *Serpula vermicularis*, alters its re-emergence time with fluctuating food levels, coming out earlier after an attack when food levels were increased (Dill & Fraser 1997). In the Iberian rock lizard, *Lacerta monticola*, re-emergence time decreased when a lizard had detected food before a predation threat (Martín et al. 2003a). Similarly, *U. mjoebergi* re-emerged sooner from a refuge when food was abundant and foraging was optimal. The natural fluctuation in food availability experienced by *U. mjoebergi* therefore results in variable refuge use during a semilunar cycle. Food additions, however, had no noticeable effect on re-emergence times when food levels were naturally low. This may be because the surface sediment was too dry for efficient foraging during neap tides. Fiddler crabs feed by filtering organic matter out of the surface sediment and this is likely to be easier over spring tides, when the surface remains moist for most of the day (Reinsel & Rittschof 1995). Since tidal cover was absent, food treatments during the reproductive period may have had a weak effect on the benefits of quick re-emergence after a predator attack.

The increase in re-emergence time during the reproductive period of a semilunar cycle is interesting since animals are often less responsive to predators during reproductive seasons (Brown & Shine 2004). In the Iberian rock lizard, for example, males are quicker to re-emerge from a refuge during than after the mating season (Martín et al. 2003b). *Uca mjoebergi*, however, spent more time in a refuge during reproductive periods. Since the OSR is extremely male biased, the probability of encountering a receptive female is likely to be low. Together with a decrease in food levels, few mating opportunities during this period therefore appear to decrease the benefits of quick re-emergence. Predator avoidance, therefore, appears to be the main priority for *U. mjoebergi* when there are few foraging and mating opportunities.

However, when the probability of gaining a mating was high, males were willing to engage in highly risky behaviour. Males presented with a tethered female re-emerged considerably sooner after an attack than males not presented with a female. Furthermore, some males abandoned refuge use entirely, remaining on the surface during the simulated predator attack. When there is a trade-off between mating opportunity and predator avoidance, the degree of risk taking is predicted to increase when the probability of future mating opportunities is low (Clark 1994). A missed mating opportunity is exceedingly costly to males because the OSR is highly skewed towards males. Effect size analysis also revealed that males were less responsive to predators when they risked losing a mating than when they were actively foraging. Lost mating opportunities while in a refuge therefore appear to increase the degree of risk taking substantially in male *U. mjoebergi*.

If this increase in risk-taking behaviour was a result of the perceived predation risk outside the refuge being reduced by the presence of the female, one would expect all individuals to respond similarly. However, only males that were actively courting the female failed to retreat into their burrows or re-emerged quickly, whereas females and males that had not detected her presence always took refuge and stayed in their burrows for considerably longer. Furthermore, during trials when a wandering (burrowless) male within the plot remained on the surface during an attack, his presence did not appear to increase the re-emergence times of individuals in the vicinity (personal observation). Increased mating opportunity is therefore the probable cause of males engaging in highly risky behaviour after a potential predation attack. Other factors are also likely to influence refuge use in *U. mjoebergi* since re-emergence times varied between trials during the reproductive period. This is likely to reflect seasonal variation in refuge use since the study was conducted over several months. Further investigation on this aspect of refuge use is therefore needed.

In sum, refuge use in *U. mjoebergi* is costly in terms of both lost foraging time and missed mating opportunities. When faced with a choice between two mutually incompatible behaviours, an individual is expected to make a decision based on the fitness consequences of each behaviour. When the benefits of one behaviour far outweigh those of the other, individuals may completely abandon the less beneficial behaviour (Morell 2004). *Uca mjoebergi* engaged in risky behaviour when there were increased fitness benefits outside a refuge. When individuals were actively foraging and males were courting a receptive female, the benefits outside a refuge far outweighed those of avoiding another predation attack. By adopting a flexible approach to refuge use when the costs and benefits of refuge use vary, individuals optimize the time they spend hiding from a predator. *Uca mjoebergi* therefore appear to make trade-offs between the costs and benefits of refuge use to increase naturally and sexually selected fitness benefits.

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