

Risk-taking behavior predicts aggression and mating success in a fiddler crab

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Evidence is growing that an individual's propensity to take risks in the presence of a predator is correlated to behaviors that can affect individual fitness. We examined whether risk-taking behavior predicts aggression, surface activity levels, and mating success in male fiddler crabs, *Uca mjoebergi*. Risk-taking behavior was highly consistent among individuals, remained stable over time, and was unrelated to male size. We found that males that took greater risks in the presence of a potential predator also behaved more aggressively when searching for a new territory. In addition, bold males exhibited higher surface activity levels and spent more time courting females compared with their shy counterparts. Although risk-taking behavior was independent of other sexually selected traits, it accurately predicted male mating success in *U. mjoebergi*. We suggest nonsexually selected traits, such as risk taking, may represent important behavioral predictors of success in other species. *Key words*: aggression, correlated behavior, fiddler crab, mating success, risk-taking behavior. [*Behav Ecol* 18:521–525 (2007)]

Sexually selected traits, such as size, song, and coloration, have proved to be accurate predictors of male fighting and mating success in many taxa (Andersson 1994). Little attention, however, has been paid to the potential role of nonsexual behavioral traits in predicting individual success. However, there is an increasing number of studies showing behavioral variation is often repeatable among individuals and correlated to behaviors that can affect fitness (Dall et al. 2004; Dingemanse et al. 2004; Sih, Bell, and Johnson 2004). For example, exploratory behavior in the great tit (*Parus major*) is correlated to both adult survival and reproductive success (Dingemanse et al. 2004; Both et al. 2005), and male three-spined sticklebacks (*Gasterosteus aculeatus*) that are quick to resume foraging after a predator attack are also more competitive foragers (Ward et al. 2004).

An individual's propensity to take risks in the presence of a predator has been shown to correlate to seemingly unrelated behaviors in a growing number of species, including spiders (Riechert and Hedrick 1993), fish (Ward et al. 2004), lizards (Stapley and Keogh 2004), birds (Westerberg et al. 2004), and domestic dogs (Svartberg 2002). Such correlations may be the result of a suite of behaviors evolving together rather than as independent traits (Sih, Bell, Johnson, and Ziemba 2004). Over an individual's lifetime, this limited plasticity may explain why individuals exhibit maladaptive behaviors in some situations. For example, in the cannibalistic fishing spider (*Dolomedes triton*), females that respond boldly toward predators are also more likely to kill and cannibalize courting males before mating has begun (Johnson and Sih 2005). Conversely, there is also support that individual variation in risk-taking behavior can be adaptive in other contexts. For example, male guppies (*Poecilia reticulata*) that actively inspect predators experience lower predation risks (Godin and Davis 1995) and are preferred by females, irrespective of their coloration (Godin and Dugatkin 1996). Behavioral variation in predator avoidance often occurs among morphologically similar individuals (e.g., Coleman and Wilson 1998; Brodie and Russell 1999),

suggesting that if risk-taking behavior is correlated to other behaviors and independent of sexually selected traits, it may represent an important behavioral predictor of success in many species.

Here we test if risk-taking behavior in the presence of a predator is an accurate behavioral predictor of male success in 3 unrelated contexts in the fiddler crab, *Uca mjoebergi*. When confronted by predators, fiddler crabs rapidly retreat into their burrows. The time spent underground is costly in terms of missed foraging, courting, and mating opportunities (Backwell et al. 1998; Jennions et al. 2003; Reaney forthcoming), but rapid reemergence is risky because the threat may not have passed. Individuals must therefore play a "waiting game" with the predator, deciding how long to delay reemergence and potentially expose themselves to another attack (Hugie 2003).

We classified males according to their risk-taking response when approached by a potential aerial predator. Bold males were classified as those willing to take greater risks and reemerge soon after a predation attack, whereas shy males remained in the safety of their burrows for longer. Individuals that take risks in threatening situations are expected to behave riskily in other situations, such as in explorative, aggressive, and courtship contexts (Coleman and Wilson 1998). We therefore determined whether individual variation in risk-taking behavior in *U. mjoebergi* was consistent among individuals and correlated to aggressiveness, activity levels, and mating success, with the a priori prediction that bold males will exhibit riskier behavior in all contexts. Specifically, we predicted that bold males will take greater risks and 1) behave more aggressively when searching for a new burrow, 2) have higher levels of surface activity, and 3) increase investment in conspicuous courtship displays and therefore be more successful at attracting females compared with shy males.

MATERIALS AND METHODS

Study species

Uca mjoebergi is a small fiddler crab that inhabits the northern coastlines of Australia. Whereas females have 2 small feeding claws, male *U. mjoebergi* have one enlarged, yellow major claw, which they use for both male–male competition and attracting females. They occur in dense mixed-sex aggregations, and both sexes aggressively defend their burrows. Burrows

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are essential for protection from desiccation and tides, and individuals will readily retreat into them when confronted by a potential predator (Reaney forthcoming). In the study area, *U. mjoebergi* are frequently preyed upon by a number of avian predators, including bee eaters (*Merops ornatus*), common sandpipers (*Actitis hypoleucos*), and mangrove kingfishers (*Todiramphus chloris*) (Reaney LT, personal observation). Burrow properties, such as stability and size, are also important determinants of female mate choice (Backwell and Passmore 1996). Receptive females leave their burrows to sample several males before choosing a mate, while males vigorously wave their enlarged claw to attract females to their burrow. Once a female has chosen a mate, the male seals the burrow, where they both remain until she has extruded her eggs. The male then leaves the burrow, whereas the female remains for the duration of her incubation period. Reproduction is concentrated over 7–9 days around neap tides each semilunar tidal cycle.

Consistency of risk-taking behavior

We studied a population of *U. mjoebergi* at East Point Reserve, Darwin (Australia) from October to December 2004 and 2005. We classified males as bold or shy according to their risk-taking response to a potential aerial predator. Males were assessed during the nonmating periods (spring tides) of 8 semilunar cycles. To elicit a predation response, a manual pulley system was constructed that ran an artificial model bird across a 3-m section of mudflat in a downward slope from approximately 100 to 20 cm above the mudflat. The movement of the model caused all individuals in close vicinity to retreat into their burrows. A 35 × 35-cm plot was positioned midway along the pulley system, and burrows within the plot were marked with numbered flags. The model was released over the plot once all males were surface active. Reemergence time for each male was measured from the moment the model was released until the focal male had fully emerged from his burrow. Over 2 tidal cycles, we initially recorded the reemergence time of 211 males to generate a distribution curve. These males were not used in the experiment. Using this distribution, we classified males that were subsequently measured as bold or shy if their reemergence time fell in the first or last third of the distribution, respectively (Figure 1). We were, therefore, examining males that represented more than half of the population. Males that engaged in risky behavior and reemerged soon after the simulated predation attack (≤ 25 s) were classified as bold, whereas those that delayed reemergence (≥ 50 s) were classified as shy. To establish how consistent this anti-predator response was among individuals, the model was flown over each plot twice, with a 5-min time interval between each trial. Only males that remained bold or shy in both trials were caught and measured for carapace width and major claw length (millimeter) and used in further experiments.

Context 1: aggressiveness

We measured aggressiveness of bold and shy males in terms of their ability to obtain a new burrow. This was done over the spring tides of a semilunar cycle. Each male was released into the population by placing him under a lid attached to a pulley system, which allowed the lid to be remotely lifted after a few seconds. This ensured the surrounding crabs had reemerged before the focal male was released, preventing him from going to the nearest undefended burrow. Each male was followed until he had gained a new burrow, noting whether he evicted a territorial male, a female, or took over an empty burrow. We recorded the time taken, distance traveled, and the number of fights each male was involved in until he gained a new burrow.

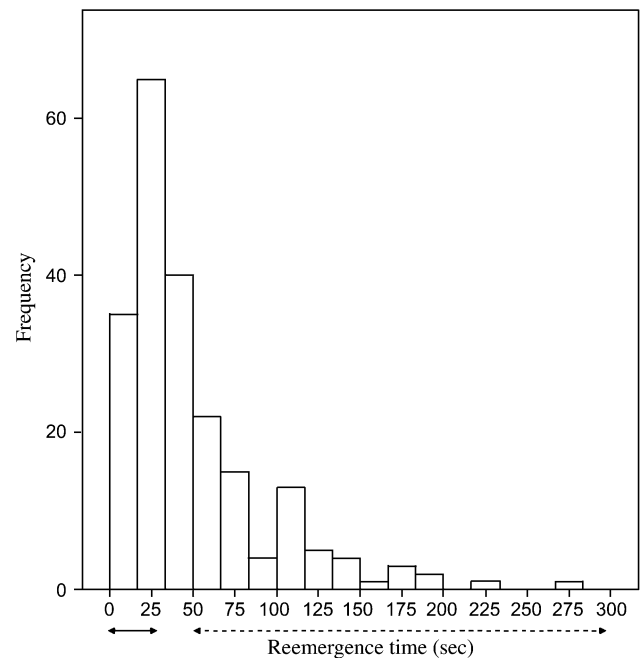


Figure 1

The distribution of reemergence times after a potential predator attack of 211 males used to classify subsequent bold and shy males (49.28 ± 44.23 s). Males that reemerged ≤ 25 s (arrow) were classified as bold, whereas those that reemerged ≥ 50 s (dashed arrow) were classified as shy.

Context 2: daily activity levels

Daily activity levels can vary in 2 ways in *U. mjoebergi*. First, not all males choose to emerge from their burrow each day during low tides (Backwell PRY, unpublished data). Second, when males are surface active, they can spend varying amounts of time outside their burrows on the surface (Reaney LT, personal observation). We therefore determined if there was any variation in daily activity levels in bold and shy males by placing them in 50 × 50 cm diameter enclosures constructed at the study site. Each enclosure was made of plastic mesh and fitted with a strip of plastic rimming along the top edges to prevent males from escaping or entering. Enclosures ($n = 14$) were stocked with equal proportions of bold and shy males (either 2 or 3 of each type) with similar-sized major claws (difference in length: 1.64 ± 0.74 mm; $n = 14$, range: 0.7–3.0 mm; this size difference is negligible as the natural size range in this population can be as large as 18.5 mm). Males were temporarily marked as bold or shy by gluing shaped opaque tags on their dorsal carapace. This allowed quick identification of males during observations and had no adverse affect on their behavior (see Backwell et al. 1995). For 3 successive days during neap tides and at peak daily activity periods, each enclosure was monitored for 1) the number of bold and shy males that were surface active that day (daily presence) and 2) those males that were active, how many times they were present on the surface during 6 instantaneous samples taken at 1-min intervals. Each enclosure was observed from a sufficient distance so as to not disturb the males.

Context 3: courtship effort and mating success

We measured the courtship effort of bold and shy males in each enclosure by determining 1) wave rate and 2) time spent courting. We measured wave rate (waves/second) by filming bold and shy males when they were actively courting a sampling female using a Sony digital video camera. The event

recorder program JWatcher was then used to calculate waves per second. To determine if there was any difference in the time bold and shy males invested in courtship display, we took 6 instantaneous samples of males at 1-min intervals and noted which males were displaying. This was measured for each enclosure over 3 successive days during neap tides of the semi-lunar cycle at peak activity periods.

The mating success of bold and shy males was determined by conducting a female choice experiment. An actively sampling female from the population was caught and released into an enclosure. To minimize any stress from the capture, the female was placed in a small container in the middle of the enclosure that was covered with a piece of light material. This allowed the female to emerge in her own time and encouraged natural sampling behavior. A new female was used for each mating trial, and only those that actively sampled males were recorded. During each mating trial, we recorded the number of bold and shy males that were surface active while the female was sampling and noted which males were sampled and which male was eventually selected as a mate. A mating was confirmed when the male either guarded the entrance to his burrow or sealed the burrow entrance. Under natural conditions, this behavior is a good indicator of a successful mating (Reaney LT, unpublished data).

Persistence

To determine if the bold–shy response to predators remained stable over time, we measured reemergence times of males after a simulated predator attack (as described above) within the enclosures approximately 7 days after they were initially classified. Because reemergence times naturally vary throughout the semilunar tidal cycle (Reaney forthcoming), bold and shy males could not be classified with the time categories previously determined. We therefore recorded the absolute time each male took to reemerge after a potential predation attack.

Statistical analysis

All data were tested for normality before performing parametric analyses. Carapace width and major claw size for bold and shy males were compared using independent *t*-tests assuming unequal variances. Number of fights and distance traveled before gaining a new burrow were log transformed to approximate normality. We performed a general linear model with bold/shy as a fixed factor and major claw size as a covariate to control for the potential effects of male size on the number of fights (major claw size and carapace width are highly correlated; $r_s = 0.865$, $P < 0.001$). Distance traveled or time taken to find a new burrow were not affected by male size and were therefore excluded from the final models. Assumptions of models were verified using residual plots. We used a *G*-test to determine whether there was a difference in the proportion of bold and shy males that fought for a new burrow. Where linear mixed models were applied, restricted maximum likelihood was used to estimate parameters. Enclosure identity was treated as a random factor because multiple data points were collected from the same enclosure. To determine whether bold males spent more time on the surface than shy males, we calculated the proportion of instantaneous samples that each male within an enclosure was active on the surface. These values were averaged across males and days to yield a single value for each enclosure for bold and shy males. This method was repeated for daily presence and time spent courting for bold and shy males. Only 12 enclosures were analyzed for daily presence (some males escaped due to faults in 2 enclosures) and time spent courting (no waving activity during data collection). We then used paired tests

(Wilcoxon signed ranks) to determine whether bold males had higher levels of daily activity and spent more time courting females than shy males. One-tailed probability tests (P_1) were applied where we predicted bold males would engage in riskier behavior than shy males. Data are reported as mean \pm 1 standard deviation (SD), and all statistical analyses were performed using SPSS 14.

RESULTS

Size effects and repeatability of risk taking

There was no significant difference in the size of bold ($n = 44$) and shy ($n = 39$) males in either carapace width ($t_{1,81} = 0.65$, $P = 0.52$; bold males: 10.4 ± 1.2 mm; shy males: 10.2 ± 1.4 mm) or major claw length ($t_{1,81} = 0.37$, $P = 0.71$; bold males: 15.4 ± 3.2 mm; shy males: 15.1 ± 3.3 mm). Most males were consistent in their response to the aerial predator, with 62% (117/190) remaining in the same category in the second trial (binomial test: $P = 0.002$). Of these males, 44 remained bold, 43 shy, and 30 intermediate. We were therefore testing a valid representation of the population and not merely the extremes. Of the males that showed an inconsistent response between the 2 trials, only 12 males (17%) switched between a shy and a bold reaction over the 2 trials. Bold males still reemerged significantly sooner than shy males approximately a week after they had been initially classified ($F_{1,37} = 3.55$, $P_1 = 0.04$; bold males: 104.2 ± 62.0 s, $n = 22$; shy males: 149.2 ± 100.3 s, $n = 17$).

Context 1: aggressiveness

Bold ($n = 26$) and shy ($n = 25$) males that were released into the population to acquire a new burrow did not differ in carapace width ($t_{1,49} = 0.62$, $P = 0.54$; bold males: 10.4 ± 1.2 mm; shy males: 10.2 ± 1.4 mm) or major claw length ($t_{1,49} = 0.30$, $P = 0.78$; bold males: 15.2 ± 3.32 mm; shy males: 14.9 ± 3.3 mm). There was no difference in the amount of time bold and shy males took to gain a new burrow ($t_{1,49} = 1.52$, $P = 0.14$; bold males: 811.0 ± 815.9 s; shy males: 534.3 ± 437.8 s) or the distance traveled before gaining a new burrow ($t_{1,49} = 1.8$, $P = 0.08$; bold males: 118.4 ± 123.6 cm; shy males: 84.0 ± 92.5 cm). Bold males, however, had significantly more fights with territorial males ($F_{1,48} = 5.03$, $P_1 = 0.02$; bold males: 5.4 ± 6.3 ; shy males: 3.0 ± 4.1), when controlling for major claw size ($F_{1,48} = 5.46$, $P = 0.02$). There was also a significant difference in the way bold and shy males gained a new burrow when released into the population (*G*-test: $G = 6.13$, degrees of freedom = 1, $P_1 = 0.01$). Bold males were more likely to evict a territorial male from his burrow compared with shy males, who evicted more females or occupied empty burrows (Figure 2).

Context 2: daily activity

The average proportion of bold and shy males that emerged from their burrows daily did not differ (Wilcoxon signed ranks test: $Z = 1.33$, $P_1 = 0.09$, $n = 12$ enclosures; bold males: 0.84 ± 0.19 ; shy males: 0.75 ± 0.18). However, of those males that were surface active, bold males spent significantly more time on the surface than shy males (Wilcoxon signed ranks test: $Z = 1.71$, $P_1 = 0.04$, $n = 14$ enclosures; bold males: 0.83 ± 0.12 ; shy males: 0.72 ± 0.18).

Context 3: courtship effort and mating success

Although there was no difference in the wave rates between bold and shy males when they were actively courting a female ($F_{1,22} = 0.43$, $P_1 = 0.26$; bold males: 0.41 ± 0.14 waves/s, $n = 14$; shy males: 0.38 ± 0.14 waves/s, $n = 10$), bold males spent

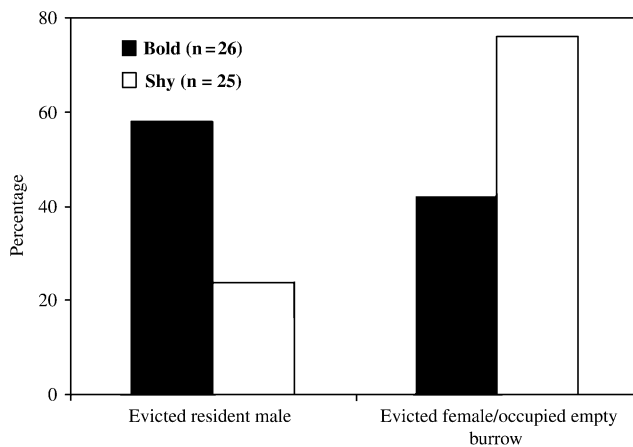


Figure 2

The percentage of bold and shy males that either fought a territorial male for a new burrow or avoided fights by evicting a female or occupying an empty burrow.

significantly more time engaging in courtship (Wilcoxon signed ranks test: $Z = 2.14$, $P_1 = 0.02$, $n = 12$ enclosures; bold males: 0.16 ± 0.14 ; shy males: 0.07 ± 0.12).

We released a total of 42 sampling females into the enclosures. Of the 18 females that actively sampled males within an enclosure, 9 selected a mate. There was no difference in the number of bold and shy males that received a visit by a female (5 bold vs. 5 shy). Bold males, however, received significantly more matings than shy males. Eight bold males successfully mated with a female compared with only one shy male (binomial test: $P_1 = 0.02$). This result still held after controlling for the number of bold and shy males that were surface active while the female was sampling ($P_1 = 0.02$).

DISCUSSION

Fiddler crabs are repeatedly faced with risk-taking decisions because they retreat in response to virtually all overhead movements, including predatory birds and harmless butterflies (Reaney LT, personal observation). We found that individual male *U. mjoebergi* were highly consistent in the level of risk they took when confronted with a potential predator, both when tested repeatedly on the same day and when retested over the 2-week activity cycle. Reemergence times of males were unrelated to body or claw size. The variation in reemergence times were also not a consequence of age differences among males because fiddler crabs have indeterminate growth (Crane 1975).

The level of risk a male took when threatened by a predator was a good predictor of his behavior in other contexts, including aggressiveness, activity levels, and mating success. Males that took greater risks in the predation context (bold males) were more likely to act aggressively toward other males. When searching for a new territory, bold males fought more territory holders than did shy males (low-risk takers), who avoided fights by evicting females or occupying empty burrows. The willingness of bold males to engage in fights could have consequences in terms of both territory quality and territory defense. Bold males may be more successful at gaining good-quality territories irrespective of who owned them, as well as being more likely to engage in fights with potential usurpers when defending a burrow. The willingness to behave aggressively may therefore have important fitness consequences in both of these fighting contexts in *U. mjoebergi*.

This unlikely link between risk-taking behavior and aggressiveness has also been found in other species, including fun-

nel web spiders (*Agelenopsis aperta*, Riechert and Hedrick 1993), the Eurasian perch (*Perca fluviatilis*, Westerberg et al. 2004), and three-spined sticklebacks (Huntingford 1976; Bell 2005). Although there is a limited understanding of the causal mechanism behind these behavioral correlations, there is growing evidence that hormonal levels may be involved. Testosterone, for example, can influence an individual's phenotype and behavior in different contexts (Ketterson and Nolan 1999). Japanese quail chicks (*Coturnix japonica*) that received additional exogenous testosterone into their yolk were less fearful during an isolation period and more likely to approach a novel object (Daisley et al. 2005). Work on funnel web spiders (*A. aperta*) further suggests that both fearfulness and aggressiveness might be under the control of only 2 hormones (Riechert and Hedrick 1993).

We also found a correlation between risk-taking behavior and mating success in *U. mjoebergi*. When given the choice between bold and shy males of similar sizes, females more often chose to mate with bold males. There may be several reasons for this. Bold males spent significantly more time active on the surface, whereas shy males spent longer periods of time in their burrows. Females would therefore be more likely to encounter bold males. Bold males also spent significantly more time courting females, which is likely to give them a mating advantage (Backwell et al. 1999). Furthermore, the behavior of mate-searching females may influence their selection of bold males: when receptive females move through the population in search of mates, they are constantly scared into nearby burrows by perceived threats (either predator approaches or other overhead movements, or even the rapid movements of nearby crabs). Unlike most males, females reemerge very rapidly from the burrow (14.1 ± 7.9 s SD; $n = 20$, Reaney LT, unpublished data; also see Pratt et al. 2005). Bold males will therefore be the first potential mates that a female detects when she continues to search. Finally, a rapid reemergence time could reflect a male's ability to escape predators and may be an honest signal of quality that females could use in selecting mates (Kalas et al. 1995; Zahavi A and Zahavi A 1997). Any or all these factors may be responsible for the increased mating success of bold *U. mjoebergi* males.

Risk-taking behavior therefore accurately predicted mating success in *U. mjoebergi*. A similar correlation between risk taking and mating success has been found in the great snipe (*Gallinago media*), where males that are the quickest to reemerge after a scare have the highest probability of receiving a visit from a female (Kalas et al. 1995). Risk-taking tendencies also have the potential to predict key behavioral dichotomies that may ultimately affect reproductive success. For example, in the water skink (*Eulamprus heatwolei*), territorial and floater lizards differ in their antipredation and exploration behavior independently of any morphological traits (Stapley and Keogh 2004). It is common to find that individuals will adjust their response to predators depending on the risks and benefits involved (reviewed by Lima and Dill 1990; Lima 1998). Bold males accept a higher level of risk in order to maximize the benefits of early reemergence. Although a high level of risk taking in the presence of a predator may appear maladaptive, bold males appear to gain profound fitness benefits due to the suite of correlated behaviors in other contexts.

There is increasing evidence that behavioral correlations are widespread and have the potential to create differences in social and reproductive success among individuals. Although the evolutionary origin and maintenance of behavioral correlations are still poorly understood, the predictive power of consistent individual variation in a nonsexually selected trait, such as risk taking, may prove to be as useful as other fundamental phenotypic or sexually selected traits in many species.

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