



Hiding behaviour in fiddler crabs: how long should prey hide in response to a potential predator?

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Do predator–prey ‘waiting games’ where prey hide from potential predators have inherently unstable evolutionary outcomes, making it impossible to generate quantitative predictions about hiding times? Fiddler crabs, *Uca lactea perplexa*, respond to potential predators by retreating into their burrows. Time inside the burrow during unprovoked retreats during normal activity provides a ‘null model’ to test whether sex, tidal cycle and body size affect hiding time from potential predators. Using experimentally created predator-like stimuli we found that males hid for significantly longer than females, and larger crabs of both sexes also hid for longer. This differs from burrow use during unprovoked retreats, suggesting hiding time varies depending on the potential risk of predation on re-emergence. If risk prior to hiding predicts risk on emergence, the closer the proximity of a predator-like stimulus when first encountered the longer crabs should hide. We confirmed this experimentally (stimuli at 0.5 versus 2.5 m). Finally, we tested whether males hide for longer when a predator-like stimulus approaches them directly rather than tangentially. None of three pairwise comparisons was statistically significant, but crabs hid less as the angle of approach became more tangential. These results suggest prey can use stimuli prior to hiding to predict predation risk on re-emergence, but studies on predators are required to test this claim. Finally, theoretical models must explain why hiding time has a lognormal distribution and low variance such that a predator can predict when most prey will re-emerge. For example, 95% of crabs re-emerged within 2.3 min of hiding.

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A common behavioural response to predators is hiding in a refuge. Most researchers have asked when prey should seek refuge (reviewed by Lima & Dill 1990). For example, at what distance from a predator should they flee (Kramer & Bonenfant 1997)? Or how does a predator’s angle of approach affect the timing of flight (Cooper 1997)? Far fewer studies have asked how long prey should hide (Scarratt & Godin 1992; Dill & Fraser 1997; Martín & López 1999).

Animals in hiding must balance the benefit of predator avoidance against several potential costs. These include reduced foraging time (Koivula et al. 1995; Dill & Fraser 1997; Houtman et al. 1997), lost mating opportunities (Kålås et al. 1995; Cooper 1999), greater risk of territorial

intrusion (Elwood et al. 1998; Díaz-Uriate 1999), and physiological costs arising from suboptimal conditions inside refuges (Wolf & Kramer 1987; Martín & López 1999). These costs and predation risk often depend on factors such as body size and sex (e.g. Backwell et al. 1998; Shine et al. 2000) that may influence optimal hiding duration. Surprisingly, there are few theoretical models of hiding duration (Lima 2002). In a partial analysis, Johansson & Englund (1995) argued that the predator–prey ‘waiting game’ is a war of attrition with role asymmetry and an inherently unstable evolutionary outcome. If true, this makes it difficult to generate quantitative predictions about optimal hiding times (but see Hugie, *in press*).

Fiddler crabs, *Uca lactea perplexa*, live in individual burrows in mixed-sex colonies on intertidal mudflats. They are surface active for 6–8 h around the diurnal low tide when they feed, court and mate (Nakasone & Murai 1998). When crabs detect a potential predator they usually hide in their burrow. Crabs also enter their burrow to replenish gill water, repair the burrow and

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reduce their heat load (Smith & Miller 1973). *Uca l. perplexa* is ideal for investigations of refuge use. First, studies can be conducted in the field. Second, the fiddler crab visual system is acutely sensitive to large objects moving above their visual horizon (i.e. potential predators); these stimuli induce flight or hiding (Layne et al. 1997), and are easy to create experimentally. Third, diurnal shorebirds are major predators on fiddler crabs (Backwell et al. 1998; Koga et al. 1998, 2001). Fourth, unprovoked refuge use occurs, which allows for a 'null model'. Few studies test whether refuge use in the absence of predators varies predictably between prey (e.g. males versus females) or in relation to other factors (e.g. time of day). If prey use refuges for other purposes then, while hiding from predators, they may also engage in normal within-refuge activities. Variation in hiding time could therefore be erroneously (or less parsimoniously) attributed to specific effects of factors such as predation risk or hiding costs.

Precise predictions about an individual's optimal hiding time are difficult, perhaps impossible, to make (Johansson & Englund 1995). Even so, some tests are possible. Here we assume that the risk a crab perceives prior to hiding is correlated with the risk on re-emergence (see Discussion). If correct, we then predict that stimuli indicating a high predation risk before hiding will result in greater hiding duration. Studies of flight distance generally show that prey respond sooner to a predator moving directly, rather than tangentially, towards them (e.g. Burger & Gochfield 1990; Bulova 1994; Cooper 1997; Martín & López 1999; for fiddler crabs see Koga et al. 2001); and that the closer a predator the more likely prey are to flee (Ydenberg & Dill 1986; Kramer & Bonenfant 1997). Directly approaching and closer predators therefore indicate a greater immediate threat of predation. We therefore predicted: (1) a longer hiding time when a predator moves directly rather than tangentially towards a crab; (2) the closer the predator initially is to the burrow the longer the hiding time. We also predicted that: (3) larger individuals will hide for longer because they are preferred prey items (Koga et al. 2001); (4) crabs hide for longer later in the daily tidal cycle because they have already had some opportunity to gather food from the substrate, so lost feeding time is less important.

METHODS

We conducted fieldwork from June to September 2000 on an intertidal mud flat on the Okukubi River, Okinawa, Japan. Because moulting influences burrow use (Thorpe et al. 1994), we collected data only from crabs with hardened exoskeletons (usually determined by direct inspection of captured crabs). No licence was required for this study.

Unprovoked Burrow Use

We observed 15 sets of crabs each at a different location. We marked 8–20 burrows per set with tooth-picks and then observed the occupants for 35 min or

more, starting observations at 1422 hours \pm 21 min ($\bar{X} \pm$ SE, $N=15$). We measured the time spent in the burrow following a retreat where predatory stimuli were absent ($\bar{X} \pm$ SE = 1.8 ± 0.1 retreats/crab, range 1–5, $N=209$ crabs). Re-emergence was defined as the moment when the entire dorsal carapace was visible. Because we remained motionless, crabs immediately resumed normal feeding and courting behaviour. (Burrow use in response to predator-like stimuli is readily apparent because several crabs all move rapidly towards their burrows simultaneously. Hereafter we refer to a slower retreat that is unsynchronized between neighbours as 'unprovoked'.) We measured the repeatability of time spent in the burrow by testing for an effect of crab identity in a general linear model (GLM) with crab identity nested within set identity (both random factors). This controlled for variation between crabs attributable to general location or time of observation (which varied between, but not within, sets). We then calculated the intraclass correlation coefficient (Lessells & Boag 1987). Finally, we captured crabs (by jabbing a stick just beneath the burrow entrance to trap the crab as it emerged) and used dial callipers to measure carapace width (± 0.1 mm) as an index of body size. We analysed the effects of sex and body size on retreat time, using the mean value per crab in a GLM (sex: fixed factor; body size and 'time relative to low tide': covariates). We excluded set identity as a random factor because it obscured the biologically more interesting effect of time relative to low tide (i.e. variation between sets was primarily due to differences in the time relative to low tide).

Hiding After Predator-like Stimulus

We examined the effects of sex, body size and time relative to low tide on hiding duration when crabs were exposed to a predator-like stimulus (i.e. one eliciting rapid flight). This stimulus came from a seated observer, 0.5–1.0 m from the focal crabs, who stood and sat rapidly once. A large object moving above the crabs' visual horizon elicits antipredator behaviour (Layne et al. 1997). Although the decision of crabs to retreat into a burrow could well be influenced by the movements of their neighbours, we know of no evidence that the time until re-emergence is influenced by when neighbours re-emerge. We measured the duration from the time of descent until: (1) re-emergence; (2) the crab's legs no longer touched the burrow entrance. Unless otherwise stated 'hiding duration' refers to the first measure. The difference between (1) and (2) indicates how long crabs took from re-emergence until they resumed feeding. We collected data on 279 different sets of four crabs. Each set comprised a small, medium and large male and a female within 50 cm of each other. We measured carapace widths in 119 sets ($\bar{X} \pm$ SD; female: 10.88 ± 1.64 mm, $N=111$; large: 16.25 ± 1.20 mm, $N=116$; medium: 13.05 ± 1.24 mm, $N=113$; small: 9.71 ± 1.17 mm, $N=115$). We excluded from our analyses 10 sets where hiding duration was more than 600 s for one crab. Over all, 1072 of 1116 crabs (96.1%) emerged within 300 s. We then performed a fully balanced ANCOVA using 98 sets with

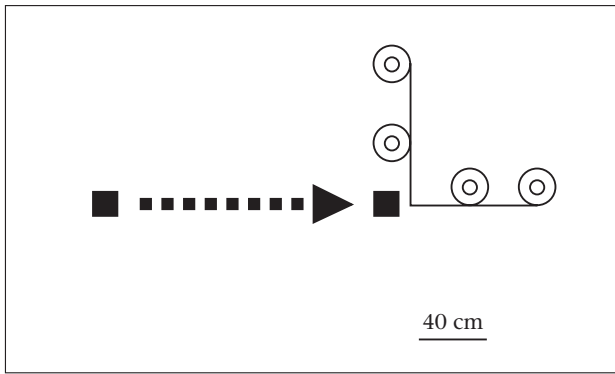


Figure 1. Diagram of the set-up for assessing how approach angle affects retreat duration. One burrow was located in each of the four smaller circles (radius=3 cm; the larger circle is used for clarity to locate burrows on the scaled diagram) located either 40 or 80 cm from the intersection of two lines of string indicated by thin lines. The predator-like stimulus (vertical cylinder: diameter 7 cm, height 23 cm) was moved 2.0 m as indicated by the arrow. Black squares represent the start and end position of the stimulus.

complete information on body size and hiding duration (sex: fixed factor; time relative to low tide, body size: covariates). Again we excluded set identity as a factor. Because the sexes differed in their responses to predator-like stimuli (see Results), in subsequent experiments we used only males.

Hiding and Stimulus Distance

To test whether the distance between a crab and a predator-like stimulus affected hiding duration, we marked the burrows of four males (two dyads). In each dyad, males were less than 20 cm apart, and the dyads were ± 2.0 m apart ($N=50$ sets, 200 males). An observer sat about 0.5 m from the first dyad and 2.5 m from the second. After the crabs resumed normal activities, the observer stood and sat rapidly and we measured hiding duration. We then repeated this procedure with the observer 0.5 m from the second dyad and 2.5 m from the first. Each crab therefore perceived a predator-like stimulus twice: once from each distance. To analyse the data we used a linear mixed-model approach using restricted maximum likelihood to estimate parameters for random factors and Wald's F tests for fixed factors (trial identity and male identity nested within trial identity: random factors; initial stimulus distance and stimulus number: fixed factors; body size: covariate).

Hiding and Stimulus Approach Angle

To test whether predator approach angle influences hiding duration, we moved a stimulus either directly or tangentially towards four males. We marked four males' burrows, each less than 3 cm from two lines of string placed at 90° to each other such that each line had a burrow ± 40 and ± 80 cm from their intersection (Fig. 1). The predator-like stimulus was a black vertical cylinder (diameter 7 cm, height 23 cm) mounted on a 1.8-m-long

stick. A seated observer moved it ± 2.0 m directly towards two burrows until it reached the line's intersection. Crabs were therefore on-axis or off-axis with respect to the approaching cylinder, which was moved as close to the ground as possible. We recorded hiding duration and body size in 50 trials ($N=200$ males). For pairwise comparisons we regressed hiding time difference against size difference. A nonzero regression slope indicates an effect of body size, and a nonzero intercept shows an effect of location (tested with one-sample t tests). Finally, we repeated the experiment with two males per trial with burrows ± 60 cm from the line's intersection ($N=60$ trials/120 males). This intermediate distance was selected because at 80 cm some off-axis males did not retreat into their burrows (see Discussion).

General Statistical Analysis

The durations of unprovoked retreats were measured later (16–19 August) than stimulus-induced retreats (14 June–15 July), but in the same general area of the mudflat and over a similar period with respect to low tides. We therefore included date as a covariate in an ANCOVA when comparing time in the burrow between the two retreat types. Carapace width and hiding duration were log transformed to normalize distributions. Summary data are presented as $\bar{X} \pm SE$ and $\alpha=0.05$ (two tailed). GLMs were run in Systat 8.0 or SPSS Version 11. Models were fitted using type I sum of squares and we removed nonsignificant interaction terms from final models. Type III sum of squares were then used to calculate the probabilities associated with the terms in the final model. The linear mixed model using REML was run in SPSS Version 11. To aid interpretation, we report the effect size (Pearson r) for each test (Cooper & Hedges 1994; Stoehr 1999). For nonsignificant tests we present the statistical power to detect an effect of $r=0.3$ ('medium strength') following Cohen (1988) or Erdfelder et al. (1996).

RESULTS

Unprovoked Burrow Use

Log-transformed retreat duration was normally distributed for males and females (Lilliefors' tests: males: $N=157$, $P=0.42$; females: $N=52$, $P=0.12$). Retreat duration varied significantly between sets for both males (GLM: $F_{12,74}=2.69$, $P<0.005$) and females ($F_{8,17}=3.11$, $P=0.024$). This indicates an effect of location/time of testing on retreat duration. When this effect was removed, individuals' retreat duration was still strongly repeatable for both males ($r=0.55$, $F_{74,129}=3.47$, $P<0.0001$) and females ($r=0.58$, $F_{17,28}=4.42$, $P=0.0003$).

Ignoring body size, there was no difference in mean retreat duration between the sexes (GLM: $F_{1,201}=0.014$, $P=0.91$, $r=0$, power: $>99\%$). However, the effect of body size on retreat duration differed between the sexes ($F_{1,201}=4.92$, $P=0.028$, $r=0.15$). Duration increased with body size for males ($F_{1,155}=18.16$, $P<0.0001$, $R_{adj}^2=9.9\%$) but not for females ($F_{1,50}=0.05$, $P=0.83$, $R_{adj}^2=0.0\%$,

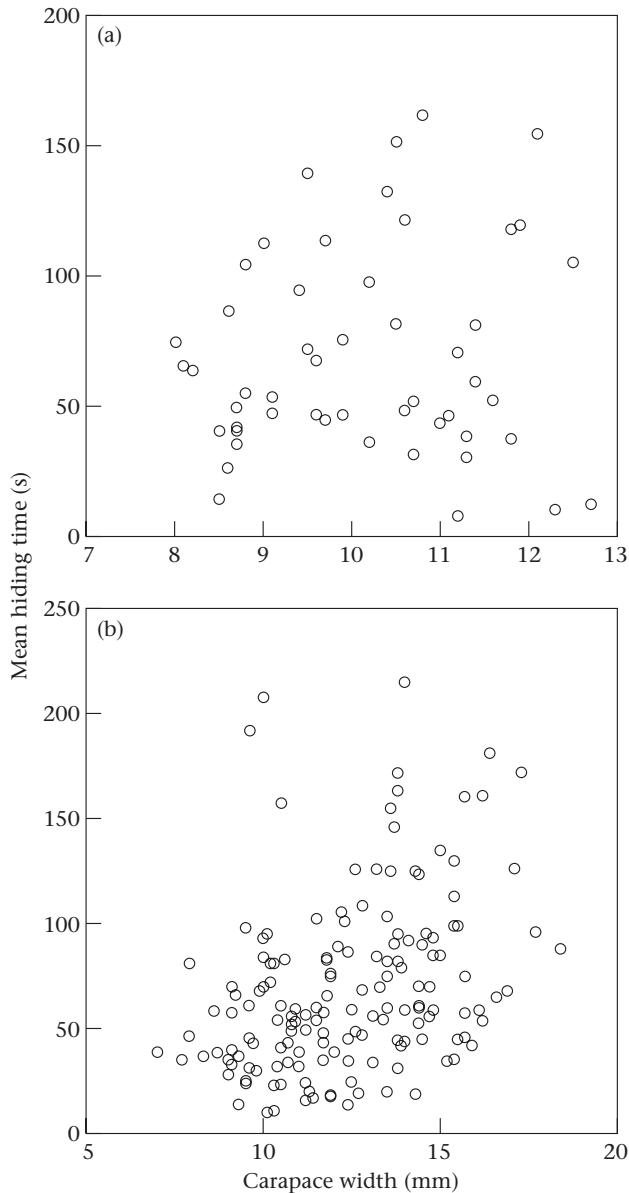


Figure 2. The relation between unprovoked retreat duration and carapace width for (a) females ($N=52$) and (b) males ($N=157$). One outlier was removed from each graph. Regressions in the text were based on log-transformed data.

power: 73%; Fig. 2). Retreat duration also increased later in the daily tidal cycle ($F_{1,203}=52.51$, $P<0.0001$, $r=0.45$). There was a significant interaction between sex and time relative to low tide ($F_{1,203}=6.88$, $P=0.009$, $r=0.18$), because the increase in hiding time later in the cycle was greater for females than males. The three-way interaction between sex, body size and time relative to low tide was not significant ($F_{1,201}=1.67$, $P=0.191$, $r=0.091$; power: >99%).

Hiding After Predator-like Stimulus

For the 98 sets with complete data on body size, log-transformed hiding duration was normally

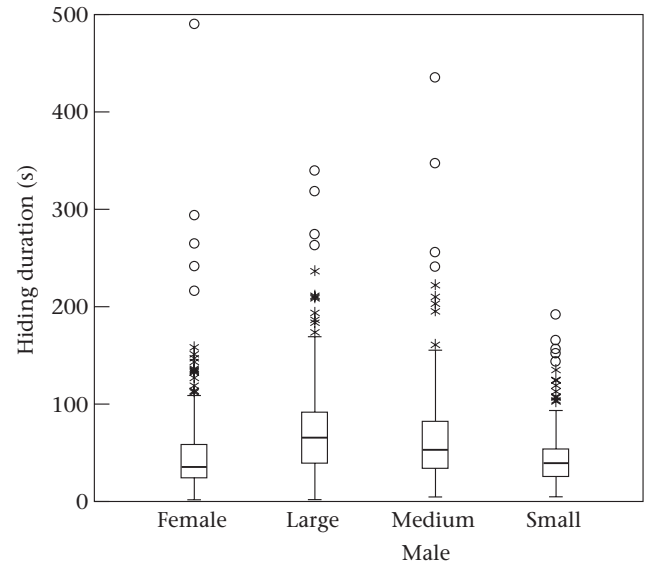


Figure 3. Box plots of time spent in the burrow after a predator-like stimulus for four classes of individuals: females and large, medium or small males ($N=269$ sets; see text for definitions of male size classes). The line inside the box is the median; box edges are at the first and third quartiles (Q_1 and Q_3); whiskers show the range of values that fall between $Q_1-1.5\times(\text{median}-Q_1)$ and $Q_3+1.5\times(Q_3-\text{median})$. Asterisks indicate data points falling outside the whiskers but between $[Q_1-3\times(\text{median}-Q_1)]$ and $[Q_3+3\times(Q_3-\text{median})]$. \circ : Extreme data points (Systat 1998).

distributed for females and small, medium and large males (all: Lilliefors' tests: $N=98$, $P>0.13$). There were no significant two-way or three-way interactions between sex, body size and time relative to low tide (GLM: all: $F_{1,384}<0.224$, $N=392$, $P>0.64$, $r\leq 0.01$; power: >99%). Hiding duration increased later in the daily tidal cycle ($F_{1,388}=9.57$, $P=0.002$, $r=0.16$), and was greater for larger crabs ($F_{1,388}=27.28$, $P<0.0001$, $r=0.26$; Fig. 3). Females spent less time hiding than males (42.2 s versus 48.8 s; $F_{1,388}=3.86$, $P=0.050$, $r=0.10$). Finally, crabs that hid for longer took more time after re-emergence before they moved away from the burrow entrance ($r_{1074}=0.169$, $P<0.001$). Of 1134 crabs, 90% re-emerged within 115 s and 95% within 138 s.

Unprovoked and Stimulus-induced Durations

For males, date had a weak but significant effect on retreat duration (GLM: $F_{1,1006}=3.87$, $P=0.049$, $r=0.06$). There was, however, no difference in the time males spent inside the burrow for the two types of retreats (stimulus versus unprovoked: 60.8 ± 1.6 s versus 72.4 ± 4.5 s, $N=852, 157$; $F_{1,1006}=0.44$, $P=0.51$, $r=0.02$; power: >99%). For females, date was a nonsignificant covariate ($F_{1,328}=0.56$, $P=0.45$, $r=0.04$; power: >99%). Females stayed in the burrow for less time after a predator-like stimulus than during an unprovoked retreat (48.7 ± 3.0 s versus 72.8 ± 6.9 s, $N=279, 52$; $F_{1,329}=17.68$, $P<0.0001$, $r=0.23$).

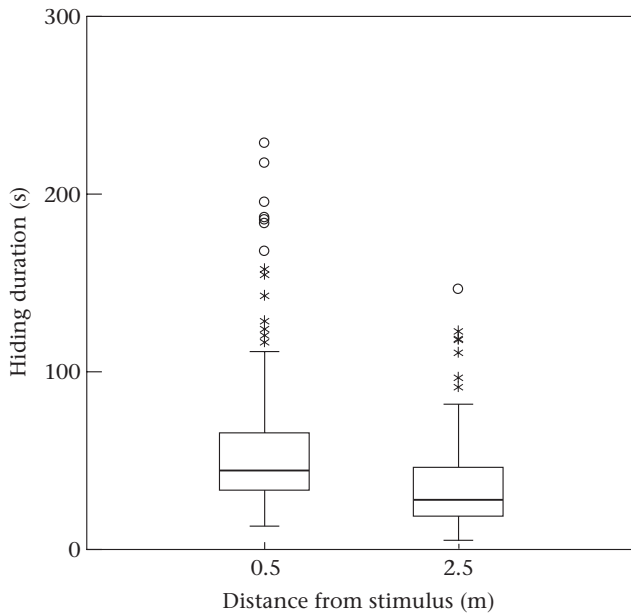


Figure 4. Box plots of the time spent underground by males after a predatory stimulus at 0.5 and 2.5 m ($N=200, 200$). Details of the box plot are given in Fig. 3.

Hiding and Stimulus Distance

Males hid significantly longer when the predator-like stimulus was at 0.5 m rather than 2.5 m (56.4 ± 2.7 s versus 36.9 ± 1.7 s, $N=200, 200$; linear mixed model: $F_{1,63}=7.26$, $P=0.009$, $r=0.32$; Fig. 4). Mean hiding duration was positively related to body size ($F_{1,74}=16.2$, $P<0.001$, $r=0.42$), but the effect of distance did not depend on body size ($F_{1,72}=0.41$, $P=0.38$, $r=0.08$; power: $>90\%$). There was a nonsignificant trend towards males hiding for longer after the second stimulus ($F_{1,198}=2.59$, $P=0.109$, $r=0.114$; power: $>95\%$). There was also a carry-over effect of the initial stimulus distance, because mean hiding duration was greater for males first presented with a stimulus at 0.5 m than at 2.5 m (49.5 ± 3.0 s versus 43.8 ± 2.3 s, $N=100, 100$; $F_{1,198}=99.13$, $P<0.001$, $r=0.578$).

Hiding and Stimulus Approach Angle

Body size was positively related to hiding duration in both experiments (GLM: experiment 1: $F_{1,48}=6.98$, $P=0.011$, $r=0.36$; $N=50$ trials; experiment 2: t test: $t_{58}=3.73$, $P=0.0004$, $r=0.44$, $N=60$ trials). There was no significant difference in hiding duration for off-axis and on-axis males at 40 cm ($t_{48}=0.72$, $P=0.47$; power: 92%). In fact, off-axis males had a slightly longer hiding duration (50.3 ± 4.6 s versus 44.6 ± 3.7 s). At 80 cm there was a marginally significant trend for off-axis males to hide for less time (41.3 ± 3.9 s versus 47.5 ± 4.3 s; $t_{47}=1.87$, $P=0.067$; one outlier removed; power: 92%). In experiment 2, there was a nonsignificant trend for off-axis males at 60 cm to have a shorter hiding duration (46.0 ± 3.7 s versus 54.1 ± 4.3 s; $t_{58}=1.40$, $P=0.17$; $N=60$ trials; power: 96%). The magnitude of the effect of axis type (where a positive value of r indicates a shorter hiding

duration for off-axis males) increased from $r=-0.08$ to $+0.18$ to $+0.26$ as the difference in the approach angle increased.

DISCUSSION

A 'Null Model' of Refuge Use

It is generally assumed that variation in hiding duration is due to prey differing in the costs or benefits of avoiding predators. This could be incorrect if, once in a refuge, prey use this time to complete tasks unrelated to predation (e.g. thermoregulation, burrow cleaning), and the time needed to complete these activities generally exceeds the optimal timing of emergence based purely on predator avoidance considerations. We therefore compared unprovoked retreat duration and hiding duration after predator-like stimuli in *U. l. perplexa*. Retreat time was highly repeatable for individuals of both sexes. Time spent underground after a predatory threat was significantly shorter than unprovoked retreat time for females, and shorter, albeit nonsignificantly so, for males. Thus variation in hiding duration after a predatory threat is unlikely to be confounded by prey engaging in time-consuming activities associated with unprovoked retreats (e.g. thermoregulation; Smith & Miller 1973), because crabs do not stay underground long enough to complete any activities occurring during unprovoked retreats. This conclusion is bolstered by other differences between the two retreat types. There was a positive effect of body size on unprovoked retreat time for males, but not for females, and hiding time after a predatory threat increased with body size for both sexes. A comparison of a random sample of crabs showed that unprovoked retreat time was almost identical for males and females, but time spent underground after a predatory threat was significantly shorter for females than males. This difference remained even after we statistically controlled for the effect of body size. Finally, after a predatory threat, *U. perplexa* often retreat into the upper part of the burrow (i.e. they remain visible from directly overhead) and do not fully descend into the burrow, as usually occurs during unprovoked retreats (M. Murai, personal observation).

The time spent hiding after predatory stimuli was normally distributed when log transformed. The low variance means that a predator can fairly accurately predict how long to wait for a crab, as half the males emerged after a minute, and 95% of crabs emerged with 138 s. Johansson & Englund (1995) have suggested that there is no evolutionarily stable strategy for predator-prey waiting games, because they are asymmetric wars of attrition (Lima 2002, page 74). Prey hiding and predator waiting time should therefore shift over evolutionary time. It is certainly surprising that crabs hide for such a short time, making them vulnerable to a sit-and-wait predator. We successfully used this technique to catch crabs (see Methods) and we could just as easily have killed the crab as it re-emerged.

In *U. perplexa* males may hide for longer than females because they are more vulnerable to predation. Male-

biased predation has been shown in some fiddler crabs (e.g. *U. beebei*, Koga et al. 2001), but not others (*U. pugillator*, Bildstein et al. 1989). Walker (1972) found no sexual difference in hiding duration in *U. annulipes* but failed to correct for smaller female body size. In *U. perplexa*, larger crabs of both sexes may stay underground longer because predators preferentially target larger potential prey. Detailed foraging studies on avian predators of *U. perplexa* are now required to test the validity of these explanations. However, sexual and size-based differences in crab behaviour need to be considered when examining predators' feeding preferences, because antipredator behaviour will itself influence prey availability and profitability (e.g. Backwell et al. 1998).

Males exposed to predator-like stimuli spent longer underground later in the daily tidal cycle. This fits with our initial prediction that crabs should be more risk averse after they have had an opportunity to feed. However, unprovoked retreat time also increased after low tide. It is therefore more parsimonious to assume that the increased time spent underground after low tide by males exposed to predator-like stimuli is not directly related to the presence of these stimuli. This finding illustrates the potential importance of acquiring information on factors associated with burrow use in the absence of predatory stimuli. A possible explanation for the time of tide effect is that it takes longer to 'dump' body heat when the air/soil temperature is elevated, and temperature varies with time of day.

Assessing Future Predation Risk

As with many species, *U. perplexa* appear to adjust hiding time in relation to the net benefits (Ydenberg & Dill 1986; Lima & Dill 1990). This requires that prey can assess the costs and benefits of hiding. Most studies test whether prey can assess the cost of hiding attributable to lost opportunities or feeding requirement. This requires that prey can assess, for example, past feeding rates (e.g. Dill & Fraser 1997; Houtman et al. 1997), rate of mate attraction (e.g. Kålås et al. 1995) or the risk of starvation (Koivula et al. 1995) and use these to predict the benefits of re-emergence. Few studies have tested which cues prey can use to predict predation risk on re-emergence. We tested two potential cues: predator proximity and approach angle.

First, male *U. perplexa* stayed underground significantly longer when a predatory stimulus was initially presented closer to the burrow (0.5 versus 2.5 m). A similar response occurs in the African fiddler crab, *U. annulipes* (Walker 1972). Close proximity of a predator is associated with a greater immediate risk of death, as indicated by studies measuring when prey initiate flight with respect to their distance from a refuge (e.g. Bonenfant & Kramer 1996). Given that closer predator proximity increased hiding duration, and assuming this is adaptive, predator proximity before retreating must predict the risk of predation on re-emergence. Although trivially true on short time scales, we are unaware of data designed specifically to test this prediction. We predict that prey will

adjust emergence time in relation to how sedentary the predatory species is. A comparison of hiding duration of fiddler crabs presented with models of sit-and-wait versus wandering avian predators provides one obvious test. Male *U. perplexa* also showed a 'carry-over' effect because they stayed underground significantly longer after a second stimulus if the initial predator-like stimulus was closer to the burrow. This suggests that the proximity of predators may act as a general index of local predator density (which would correlate with predation risk). This 'carry-over' effect is unlikely to persist in the long term though. Fiddler crabs habituate to repetitive stimuli and reduce hiding duration, or even fail to retreat, when repeatedly disturbed (Walker 1972; personal observations).

Second, based on the timing of flight, a predator directly approaching its prey is more dangerous than one moving tangentially by (Bulova 1994; Cooper 1997). In *U. beebei* males more often hide in their burrows when a model predator approaches them directly (Koga et al. 2001). In *U. perplexa*, however, none of three pairwise comparisons of hiding duration of on-axis and off-axis males was significant. One explanation is simply that approach angle does not predict predation risk on re-emergence. However, an examination of a standardized measure of the influence of approach angle on hiding duration showed that, as the difference in the angle of approach increased, the effect became stronger ($r = -0.08$ to $+0.18$ to $+0.26$). In addition, when males were 80 cm off-axis (the greatest difference in the angle of approach), in several trials the male did not descend into his burrow after the predatory model was run (personal observation). This may have weakened the treatment effect because no hiding duration data were obtained from these trials. If, for example, these had been scored as a hiding time of zero, a highly significant difference between on and off-axis males would probably have emerged. The failure of off-axis males to retreat into their burrows is clearly consistent with approach angle influencing a crab's perception of predation risk.

Conclusions

Our data suggest that fiddler crabs can use the proximity and possibly the approach angle of predators to predict both their immediate and future risk of predation. However, the effects of sex and size on hiding duration indicate that the net benefit of hiding is smaller for females than males, and for smaller than larger crabs. Finally, the lognormal distribution of hiding time, combined with low variance, shows that 91.4% of crabs emerge within 2 min of hiding. This raises several questions for future studies. Is hiding a successful tactic because predators are 'unaware' of the distribution of re-emergence times? Or is the average time predators can afford to wait less than that for which crabs hide? Or is crab hiding time usually sufficient to avoid common predators that move through an area but not to avoid sit-and-wait predators?

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