



Density dependence and fighting in species with indeterminate growth: a test in a fiddler crab



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Many forms of selection are density dependent. It is often assumed that all individuals of a given sex compete for the same resources, but in many species different types of individuals (e.g. morphs or body sizes) compete for different resources. Selection on competitive traits should be examined relative to the density of the relevant competitors (and contested resources) rather than total population density. Crucially, a predictable decline in effective competitor density with size might affect selection on fighting behaviour in species with indeterminate growth. We investigated whether male fighting behaviour over burrows in the fiddler crab *Uca annulipes* is consistent with size-dependent burrow usage that affects the density of relevant competitors and contested resources (burrow availability is limited). We show that larger males occupied larger burrows and occurred at lower densities, so they must travel further to locate new, suitably sized burrows. This should favour larger males investing more in each fight that they initiate. Indeed, larger males fought for significantly longer than smaller males, which increased their likelihood of winning a burrow. The observed increase in fight duration is not readily explained by ontogenetic changes in fighting costs (i.e. 'giving up' thresholds). It is worth testing whether increased fight duration with size/age occurs in the innumerable other species with indeterminate growth that compete for refugia (e.g. hermit crabs, reef fish) because a decline in density with body size is inevitable owing to cumulative mortality, and a physical constraint on the minimum-sized refugia that can be entered is commonplace.

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If all individuals compete for the same resources, then density-dependent selection depends on the total population density. Sometimes, however, individuals compete nonrandomly with each other for specific resources (e.g. one sex competes for access to the other). Here it is the density of relevant competitors relative to contested resources, rather than the total population density, that determines the selection that an individual will experience. Measuring the relevant density often requires detailed knowledge of the species' biology. For example, in Eurasian oystercatchers, *Haematopus ostralegus*, males and females subtly partition food resources and do not compete for every food item (van de Pol et al. 2009). The use of different resources by different types of individuals based on age or life history stage (Mouquet et al. 2005; Einum et al. 2006), sex (van de Pol et al. 2009), body condition (Curtis et al. 1995), morph type (reviewed in Smith & Skúlason 1996) and body size (Shine et al. 2001) is widespread in many taxa. If the ratio of the density of competitors to contested

resources shifts, then selection for competitive traits might vary among classes (but see Kokko et al. 2012). If there are consistent, predictable differences in competitor and/or resource density with age, size or sex, this should select for the evolution of levels of competitive behaviour that vary among different classes of individuals.

Sexual selection studies have long focused on how males and females compete for different resources (i.e. the opposite sex), and when this might lead to density-dependent selection (Kokko & Rankin 2006). For example, a higher density of males increases male–male encounter rate, which might select for greater investment in weaponry (Weir et al. 2011). By contrast, far fewer behavioural studies have investigated whether density-dependent selection varies among different types of individuals of the same sex. Ecological studies of within-class density-dependent selection are usually restricted to species with distinct cohorts that are at spatially segregated stages in the life cycle. For example, in the butterfly *Maculinea arion*, first-stage larvae live on host plants, where they show strong contest competition, whereas second-stage larvae occupy ant nests and experience severe scramble competition (Mouquet et al. 2005; see Einum et al. 2006 for another example).

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We suggest that the phenomenon of different classes of individuals experiencing different densities of competitors is not confined to species with distinct life history stages, and is actually widespread. It can arise even in continuously distributed populations of interacting individuals. Specifically, in species with indeterminate growth, cumulative mortality with age means that larger individuals are less common and occur at a lower density. This implies that competition will decline with size (i.e. fewer competitors) if fighting is size assortative. However, some of the resources that individuals require might also depend on their body size. For example, in fiddler crabs there is indeterminate growth and males compete for burrows. Fights between males are often size assortative, probably because larger males are physically incapable of entering smaller burrows (e.g. Jennions & Backwell 1996). There is also evidence that mating is size assortative, partly because a large female cannot enter a small male's burrow. This suggests that each male only competes with similar-sized males for access to burrows and females.

We investigated whether a size-based difference in competitor numbers and resource availability affects density-dependent selection on males in the fiddler crab, *Uca annulipes*. Male–male fights over burrows are strongly size assortative (Jennions & Backwell 1996). Males are unable to dig new burrows within the population, as there is no unchallenged surface space (territories about each other and residents fight off a male that attempts to dig a new burrow between existing territories). In addition, smaller intruders struggle to defeat a larger resident (Callander et al. 2012). *Uca annulipes* exhibits indeterminate growth, so larger males should be less common as a result of cumulative mortality. Given the body–burrow size correlation and the destruction of unoccupied burrows by tidal action (Hemmi & Zeil 2003), there should be a corresponding decline in the availability of larger burrows. Whether this leads to a lower density of suitable burrows for larger males depends on whether or not similar sized burrows are spatially clumped. If not, large males must travel greater distances to acquire a new burrow, which elevates their exposure to predators (Koga et al. 1998) and travel costs. Based on our previous work on *U. annulipes* we therefore predicted that larger males would value burrow ownership more highly. All else being equal, this should generate a positive correlation between male size and fight intensity/duration, because individuals are more persistent when fighting for a more valuable resource (Enquist & Leimar 1987).

Mutual Assessment

In order to use fight duration of size-matched fights to determine whether perceived resource value increases with male size, you need to test whether fights are resolved by mutual assessment or individual cost thresholds. Males may be more persistent because they have higher cost thresholds (Payne & Pagel 1996) rather than because of the effect of resource value on fight duration. Higher cost thresholds, however, are not expected to affect the relationship between fight duration and the mean size (i.e. strength) of size-matched rivals if fights are resolved by mutual assessment of strength.

How fight duration changes with the size of two competitors depends on how they determine whether to continue or abandon a fight. There are two main categories of fighting models: 'mutual assessment' and 'individual cost threshold' (or self-assessment) models. The best-known mutual assessment models are 'asymmetric war of attrition' (Maynard Smith & Parker 1976; Parker & Rubenstein 1981; Hammerstein & Parker 1982) and 'sequential assessment' models (Enquist & Leimar 1983). Here, individuals assess their own and their rival's resource-holding potential (RHP; sensu Parker 1974) to decide whether to escalate, prolong or abandon a contest. The greater the similarity in RHP, the more

difficult it is for each contestant to assess who is the weaker individual. It is assumed that contestants continue to fight and escalate the fight's intensity to gain additional information about their rival's RHP. The best-known 'individual cost threshold' models are the 'war of attrition without assessment' (Mesterton-Gibbons et al. 1996), the 'energetic war of attrition' (Payne & Pagel 1996, 1997) and the 'cumulative assessment' models (CAM; Payne 1998). Here, there is no assessment of a rival's RHP. Instead, a fight ends when the cost threshold of the weaker individual (lower RHP) is reached. Costs accumulate as the fight continues and increase with the intensity of the fighting and/or the opponent's RHP.

Mutual assessment and individual cost threshold models are distinguished by investigating natural fights between males that differ in size. If fight duration is determined by an individual's cost threshold, only the weaker rival's RHP will positively correlate with contest duration in a multiple regression (Taylor & Elwood 2003). Although there may be a weak relationship between the winner's RHP and contest duration (Gammell & Hardy 2003; Briffa & Elwood 2009), the fight is thought to end once the weaker rival's cost threshold is reached. If, however, there is a positive effect of the weaker contestant's RHP and a negative effect of similar magnitude for the stronger contestant's RHP, then fight duration is determined by the contestants' relative RHP. This suggests there is mutual assessment of RHP. An effect of relative male size is, however, also possible for one individual cost threshold model: the CAM model of Payne (1998). Here, fight duration is determined by the weaker individual's cost threshold, but rivals impose costs on each other that are proportional to their RHP. Consequently, the greater the RHP of the stronger contestant, the sooner the weaker contestant will abandon the fight. Distinguishing between CAM and mutual assessment models is, however, still possible if we have direct information about how costs are imposed (i.e. are the models' assumptions upheld?).

Assuming size is indicative of RHP, the 'mutual assessment' and 'individual cost threshold' models make different predictions about the relationship between fight duration and the mean size of males in size-matched fights. If fight termination depends on the weaker male's individual cost threshold there should be a positive correlation between mean male size and duration (i.e. because the weaker male's size and the mean size are synonymous). If mutual assessment occurs, however, fight duration should be independent of mean size because the relative size difference is unchanged (Enquist & Leimar 1983). Two small males should take as long as two large males to determine the inferior competitor. If, however, larger males place greater value on gaining a burrow, then fight duration should increase with mean size in size-matched fights, even with mutual assessment (Fig. 1).

We used fight duration in size-matched fights to determine whether perceived resource value increases with male size. We therefore tested whether fights are resolved based on mutual assessment or individual cost thresholds (see Morrell et al. 2005). Specifically, if mutual assessment occurs, then a positive relationship can plausibly be attributed to selection for greater investment in fighting by larger males (although, of course, as in any observational study additional unknown variables might also be responsible). Alternatively, if males simply fight until the weaker one reaches his individual cost threshold, then a positive relationship is predicted given an increase in the cost threshold with size. It is then difficult to 'remove' this underlying relationship to test for a residual positive correlation between mean size and fight duration owing to an increase in resource value (Fig. 1).

Testing the Predictions

To test our prediction, we documented the size distributions of burrow owners and burrow-seeking males that fight residents for

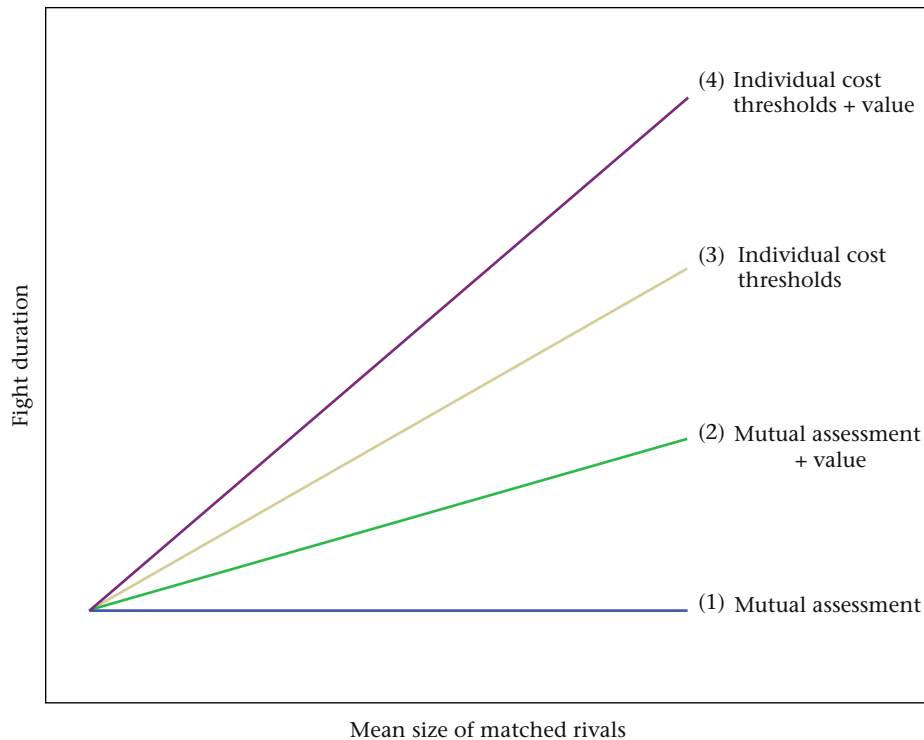


Figure 1. The predicted duration of fights between size-matched rivals. (1) Under mutual assessment models, fight duration is unrelated to body size. (2) Taking into account a size-dependent increase in resource value, however, fight duration should increase with body size. (3) Under individual cost-threshold models, fight duration is expected to increase with body size. Therefore, (4) any increase in fight duration as a result of a size-dependent change in resource value will be difficult to detect based solely on a positive correlation.

their burrows ('wanderers'). We determined the availability of suitably sized burrows by experimentally determining the smallest diameter of burrow that a male of a given size can enter. We then measured the minimum distance between suitable burrows for a set of males that covered the size range in the population. Next we experimentally released males and recorded the distance they travelled to acquire a new burrow. Finally, we documented the relationship between fight duration and escalation and male body size. To interpret this relationship, we regarded fight duration (correcting for any size difference between contestants) as providing information about the value of the resource to contestants. That is, fights between similar-sized competitors will last longer when a resource is more valuable. In fiddler crabs, a 'valuable' burrow is one that females will select for incubation: a narrower entrance, a more vertical shaft, a smaller chamber volume and surrounded by firmer sediment (Backwell & Passmore 1996).

Larger males might, however, have greater inherent fighting persistence because the costs they incur per unit time when fighting are lower (Payne & Pagel 1996). Game theory models of fighting behaviour suggest, however, that when fights are resolved via mutual assessment, as opposed to self-assessment, an increase in fighting persistence by large males can plausibly be attributed to an increase in resource value (Arnott & Elwood 2008). We therefore determined whether fights are resolved by mutual assessment in this species.

METHODS

Study Species

We studied *U. annulipes* on Inhaça Island, Mozambique (26° 01' 51'' S 32° 55' 00'' E) from September to October 2008. Crabs live in mixed-sex colonies on mudflats with both sexes defending territories centred on a burrow. Males have an enlarged major claw that is used as a weapon during fights (Allen & Levinton 2007).

Burrows are an essential resource. They are a refuge against predators and inundation at high tide (Koga et al. 2001), and contain water that prevents dehydration and reduces the heat load when crabs are feeding and courting on the surface (Smith & Miller 1973). During the breeding period, ovigerous females leave their own burrow and select a male based partly on his burrow's properties (Backwell & Passmore 1996). Mating occurs in the burrow, after which the male relinquishes it to the female (Backwell & Passmore 1996). Wandering males have either lost their burrow after a fight with another male (Jennions & Backwell 1996; Callander et al. 2012) or forfeited it to a female (Backwell & Passmore 1996). Wandering males obtain a new burrow by evicting a resident crab or locating an empty burrow (Milner et al. 2010). Males are unable to dig new burrows owing to space constraints. The surface area around the burrow entrance is used for feeding and displaying and is strongly defended by the burrow owner. Territories abut one another, and if a male attempts to dig a burrow between existing territories, the neighbours immediately challenge him (P. Backwell, personal observations). New burrows are only built on the edges of the population and are generally built by small males that presumably are unable to fight for a burrow (P. Backwell, unpublished data). Burrows within the main area of the population are modified and repaired by successive owners on a daily basis and are only destroyed when they are unoccupied as a result of changes in the sediment structure caused by altered patterns of water flow.

Population Size Distribution: Resident Males and Occupied Burrows

We randomly placed 0.25 m² plots throughout the study population ($N = 26$). We captured all adult residents (carapace width > 10.5 mm), noted their sex (presence/absence of large claw) and measured male carapace width ('body size') and major claw length using dial callipers (± 0.1 mm; $N = 135$ males). In 22 of the

plots, we also measured each resident's burrow diameter ($N = 117$ males; 98 females).

Population Size Distribution: Wandering Males

We monitored randomly placed 3 m² plots for 40 min each during the 3 h period before low tide (four to six plots/day over 14 days). All wandering males (carapace width >10.5 mm) that entered plots were caught and measured ($N = 178$ males). Crabs were classified as wanderers if they fought a resident male.

Burrow Availability: Empty Burrows

We determined the availability of unoccupied burrows by randomly placing small flags at 813 burrow entrances. We observed each burrow for 10 min and noted whether a crab emerged. If not, we placed a light bottle cap over the entrance and again examined the burrow 30 min before tidal inundation. If the cap had been shifted this indicated that a resident crab had emerged: if not, the burrow was classified as unoccupied. Pilot tests showed that all crabs ≥ 10.5 mm could move a cap.

Burrow Distribution

We captured, measured and released 98 males into a series of small (approximately 15 cm diameter) enclosures (clear plastic collar pushed into the sediment), each containing a differently sized burrow. We started with a small burrow and moved the male to enclosures with progressively larger burrows until he entered one. Each male was offered a completely new set of burrows. We recorded the diameter of the first burrow that he entered and the preceding (slightly smaller) burrow that he did not enter. The mean of the two diameters was our estimate of the smallest burrow that the male could enter. To determine the minimum distance a resident male would have to travel from his burrow to another burrow of a suitable size, we selected a focal burrow ($N = 186$) and measured its diameter. We then determined the average size of a male that would occupy such a burrow (using the relationship previously estimated from the 117 resident males), and the minimum burrow diameter that such a male could enter. Finally, we measured the distance between the focal burrow and the nearest burrow that he could potentially enter.

Wandering Males: Behaviour

We tracked 99 burrowless males (10.7–18.4 mm) during the 3 h period before low tide. We experimentally created wandering males by catching a resident, measuring him, marking him with white paint and releasing him >2 m from his burrow. Release points were all well within the population boundaries and among suitable burrows (fiddler crab populations are highly homogeneous). We created experimental wanderers to: (1) exclude the possibility that natural wanderers are a subset of poor fighters; (2) ensure an appropriate number of wanderers of all sizes; (3) ensure that the wanderer was observed from the start of his burrow-searching behaviour. For each male, we recorded: how many burrows he approached (touched the entrance with his walking legs); the number of fights he had; the time taken to acquire a new burrow; the method of burrow acquisition (fought resident male, evicted female, occupied empty burrow, dug new burrow); and the linear distance between his release point and the new burrow.

Fight Outcome and Duration

We recorded the duration (first to last contact) of 104 natural resident–wanderer fights. Encounters that did not escalate beyond a

brief touching of claws were not considered fights. Fight escalation was 'low' (opponents align claws and push); 'medium' (claws interlocked, followed by grappling) or 'high' (resident retreats into the burrow entrance and the intruder drums on the surface and/or digs out the burrow entrance). We included drumming and digging in the fight duration, because we believe that the most accurate measure of 'giving up' is when the defeated male leaves the burrow. When the intruder is drumming or digging at the burrow entrance, the resident is just below him in the burrow shaft. At some point, the resident pushes out past the intruder and leaves. We consider this the point at which the resident 'gives up'. We also consider drumming and digging as the most highly escalated phase of the fight, as it is when most injuries are likely to occur (P. Backwell, personal observations). Grappling very seldom results in injury to either male, but we have witnessed a male being impaled on the large claw of an intruder when he tried to push past him to leave the burrow during a fight (P. Backwell, personal observations). We noted the winner and measured both males. We only used fights between original clawed males, as regenerated claws are inferior weapons (Backwell et al. 2000).

Statistical Analysis

Male carapace width and claw length were highly correlated ($r_{306} = 0.978$, $P < 0.001$), so we only present results using carapace width as the measure of male size. We compared size distributions between groups (e.g. resident versus wandering males) with chi-square tests. If necessary, size classes (1 mm bins) were pooled to ensure that all expected counts exceeded five. We used parametric tests where possible and transformed data if required. Sequential Bonferroni correction was applied for multiple testing. We had clear a priori predictions (previous work on this species allowed us to predict that larger males would value burrow ownership more highly; this should generate a positive correlation between male size and fight intensity/duration), so we used one-tailed tests for the relationship between male size and distance travelled or time taken to acquire a burrow. All other tests were two tailed. Summary statistics are presented as mean \pm SD. Analyses were run using SPSS 17.0 (SPSS Inc., Chicago, IL, U.S.A.).

We ran two logistic regressions with the size of the wanderer and resident males as predictor variables and the dependent variable being whether or not the wandering males won the fight, or whether or not the fight reached the drum/dig stage. We also ran a general linear model with fight duration as the dependent variable and the size of the wanderer and resident males as predictor variables. Note that we ran our analysis with males classified as being the wanderer or resident rather than the larger or smaller male. This classification was used because the resident male has a positional advantage that gives him greater RHP (see Discussion) so that resident/wanderer dichotomy is loosely equivalent to the larger/smaller or winner/loser male dichotomy (which is a surrogate for RHP) usually seen in tests of whether fights are resolved based on mutual assessment or individual cost thresholds (Taylor & Elwood 2003).

RESULTS

Population Size Distribution: Resident Males and Wandering Males

The average carapace width of resident males was 12.6 ± 1.6 mm (range 10.5–16.9 mm, $N = 135$) and 13.2 ± 1.7 mm (range 10.5–16.4 mm, $N = 178$) for wandering males. The size distribution of resident and wandering males differed significantly ($\chi^2_5 = 12.95$, $P = 0.024$; Fig. 2). There were disproportionately more large males (≥ 13.5 mm) among wanderers. As expected with cumulative mortality, the population distribution of both resident and wandering males was heavily skewed towards smaller individuals.

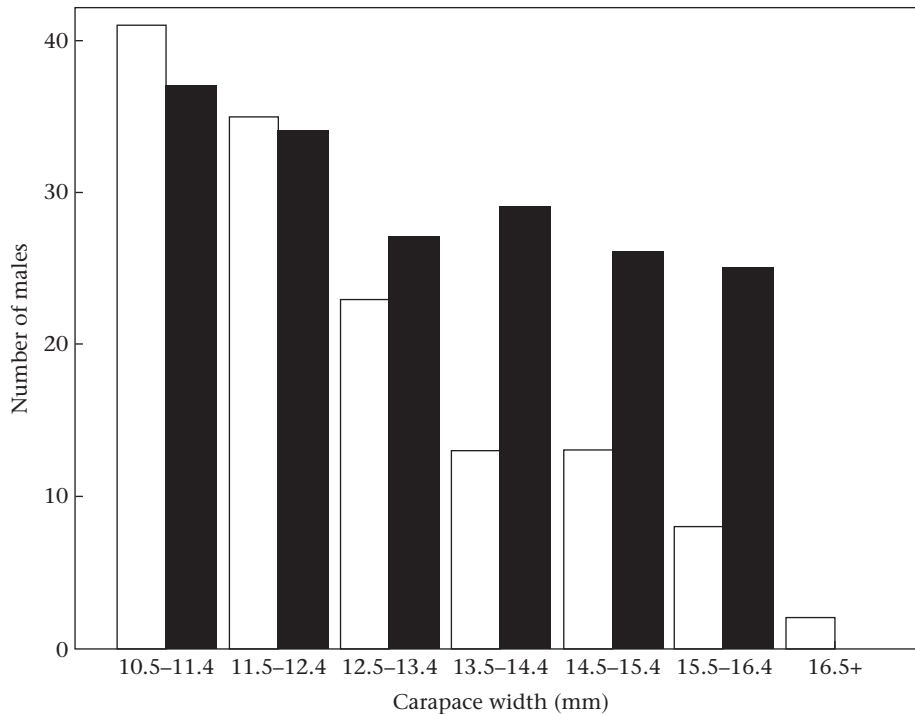


Figure 2. Male size. The size distribution of resident (open bars, $N = 135$) and burrowless wandering (solid bars, $N = 178$) males.

Burrow Availability: Occupied and Empty Burrows

Burrows with a wide entrance were rare. This was true for both male- and female-owned burrows (Fig. 3), although the size distributions differed significantly between the sexes ($\chi^2_4 = 15.13$, $P = 0.004$). This was mainly due to there being proportionately fewer large female- than male-owned burrows. Only 30 of 813 burrows were unoccupied (3.7%). There was no size difference between occupied and empty burrows (Mann–Whitney U test: $Z = 1.30$, $N_1 = 30$, $N_2 = 783$, $P = 0.193$).

Burrow Distribution

Large resident males occupied burrows with a wider entrance (burrow diameter = $0.698 \times$ carapace width + 0.117 , $r^2 = 0.641$, $N = 87$, $P < 0.001$), and the narrowest burrow that they could physically enter was also wider than for smaller males (minimum burrow diameter = $0.575 \times$ carapace width + 0.735 , $r^2 = 0.853$, $N = 98$, $P < 0.001$; Fig. 4). The regression slopes of male body size against occupied or minimal burrow diameter were significantly different ($F_{1,181} = 4.69$, $P = 0.032$). Compared with smaller males, larger males could fit into relatively smaller burrows than those they usually occupied (Fig. 4). The distance from a burrow that a male of a given size would, on average, occupy to the nearest burrow that he could physically enter increased significantly with male size. The relationship was best explained by an exponential function (distance = $0.125e^{0.343 \times \text{carapace width}}$, $r^2 = 0.61$, $N = 186$, $P < 0.001$). Larger burrows were further apart (i.e. no evidence for spatial clumping). Larger males therefore live at a lower effective population density, and must presumably travel further to obtain a new burrow.

Wandering Male Behaviour

On average a wandering male visited 6.1 ± 4.9 burrows (range 1–23; $N = 99$ wanderers) and engaged in 2.6 ± 2.6 fights (range 0–10). Neither the number of burrows visited nor fights engaged in was correlated with male body size ($r_5 = 0.077$, $P = 0.447$ and

$r_5 = 0.174$, $P = 0.084$, respectively; both $N = 99$). It took 655 ± 650 s (range 5–2839 s) to obtain a new burrow that was 4.24 ± 5.61 m (range 0.03–38.5 m) from the male's previous burrow. There was a nonsignificant trend for larger males to take longer to acquire a burrow ($r_{97} = 0.139$, $P = 0.086$) even though they travelled significantly further to acquire a new burrow (Fig. 5).

Males obtained new burrows by: (1) evicting resident males ($N = 52$; 52.5%); (2) locating an unoccupied burrow ($N = 37$; 37.4%); or (3) evicting a resident female ($N = 10$; 10.1%). No males dug a new burrow. The size of males using the three methods differed significantly (Kruskal–Wallis test: $\chi^2_2 = 15.89$, $P < 0.001$). Males that evicted a resident female (median size = 12.1 mm) were significantly smaller than those that evicted a resident male (median size = 15.3 mm; $Z = 3.94$, $P < 0.001$) or acquired an empty burrow (median size = 15.1 mm; $Z = 3.55$, $P < 0.001$). There was no significant size difference between males that acquired an empty burrow or evicted a resident male ($Z = 0.316$, $P = 0.753$).

Fight Outcome

Fighting was positively size assortative ($r_{102} = 0.81$, $P < 0.001$). Nevertheless, wandering males fought resident males with a slightly smaller carapace width in 63 of 101 encounters (62.4%; binomial test: $P = 0.017$). On average, wanderers were slightly larger than the residents they fought (13.4 ± 1.9 mm versus 13.0 ± 1.8 mm; paired t test: $t_{103} = 4.308$, $P < 0.001$). The mean carapace width ratio of wanderers to residents was 1.04 ± 0.09 (range 0.87–1.29).

Prior residency was a key determinant of fighting success (see Fayed et al. 2008). Residents won 72 of 104 fights (69.2%; $P < 0.001$). For size-matched fights (<5% size difference) the resident's success was even higher (36 of 43 fights; 83.7%; binomial test: $P < 0.001$). However, relative male size remained a predictor of fight outcome: the larger male won 61 of 101 fights (60.4%; binomial test: $P = 0.046$). The probability the wandering male won increased with his size and decreased with the size of the resident (Table 1). The approximately equal and opposite effect of wanderer

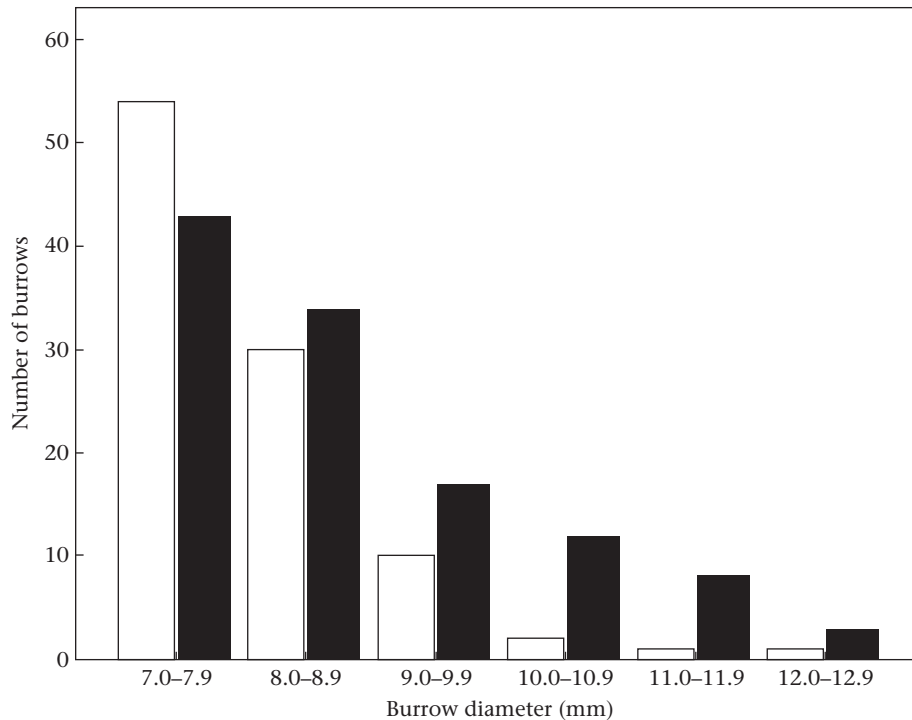


Figure 3. The relative availability of burrows owned by males (solid bars, $N = 117$) and females (open bars, $N = 98$).

and resident size allows for the substitution of a single predictor of fight outcome, namely relative size (wanderer/resident; $r^2 = 0.167$, $\beta = 8.672 \pm 2.577$, $\chi^2_1 = 11.33$, $P = 0.001$). In sum, the probability the wanderer won increased when he was larger than the resident.

Fight Duration

The mean fight duration was 48.7 ± 80.5 s. Fights won by wanderers (111.3 ± 114.5 s, $N = 32$) were significantly longer than

those won by residents (20.8 ± 33.6 s, $N = 72$; Mann–Whitney U test: $Z = 6.03$, $P < 0.001$). Fights that progressed to the drum/dig stage were significantly longer (125.8 ± 110.6 s, $N = 25$) than those that ended at the push/grapple stage (24.2 ± 47.9 s, $N = 79$; $Z = 6.13$, $P < 0.001$). The size of both the resident and wanderer predicted whether the fight progressed to the drum/dig stage (Table 2). The equal and opposite effect of wanderer and resident size allows substitution of the single term 'relative size' ($r^2 = 0.294$, $\beta = 12.965 \pm 3.139$, $\chi^2_1 = 17.06$, $P < 0.001$). The probability of the fight progressing to the drum/dig stage increased when the wanderer was relatively larger than the resident.

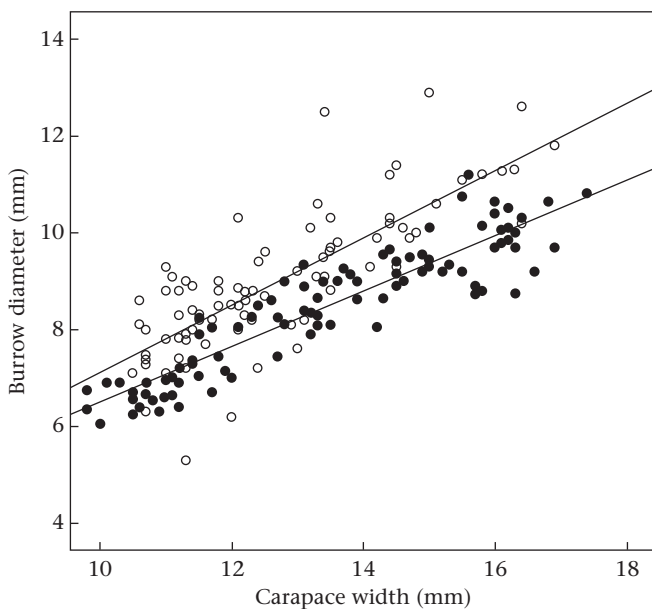


Figure 4. The average burrow diameter of resident males (open symbols) and the average minimum burrow opening males could physically enter (filled symbols). See text for regression equations.

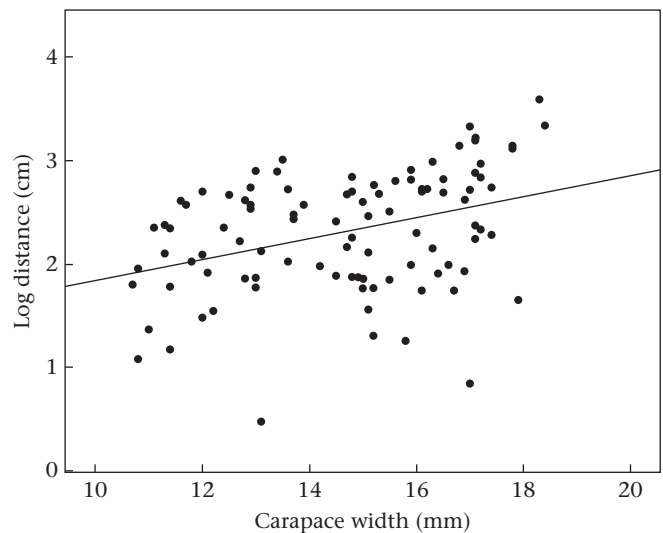


Figure 5. Relationship between the size of a wandering male and the distance (log transformed) from his release point to his newly acquired burrow ($r^2 = 0.366$, $N = 99$, $P < 0.001$).

Table 1
Logistic regression analysis of the effect of rival size on fight outcome

Predictor	β	SE	Wald's χ^2	df	P
Wanderer carapace	0.078	0.022	12.149	1	<0.001
Resident carapace	-0.065	0.023	8.419	1	0.004
Constant	-2.906	1.694	2.941	1	0.086

Overall model fit: $r^2 = 0.187$, $\chi^2_2 = 14.832$, $P = 0.001$.

Fight duration was also significantly influenced by the size of both the wanderer and resident. It increased significantly with the size of the wanderer and decreased significantly with the size of the resident (Table 3). Although the estimate of the effect of the size of the wanderer is greater than that of the size of the resident (Table 3), the difference is not significant, as the absolute values for the 95% confidence intervals for the effect of wanderer size (0.011–0.028) broadly overlap those for resident size (0.003–0.022). Contest duration is therefore parsimoniously described as being driven by the relative size of the two contestants. Relative size is a significant predictor of contest duration in a linear regression ($r^2 = 0.127$, $\beta = 2.180 \pm 0.565$, $t = 3.86$, $P < 0.001$). Fight duration increased as the relative size of the rivals increased (Fig. 6).

Finally, to test for an effect of absolute male size on fight duration, we analysed only fights between closely size-matched rivals (<5% size difference; i.e. wanderer/resident size ratio: 0.95–1.05). As predicted, fight duration increased significantly with the mean size of rivals ($r_s = 0.453$, $N = 43$, $P = 0.002$; Fig. 7).

DISCUSSION

Key Prediction and Testing Assumptions

We predicted that in the fiddler crab *U. annulipes*, males mainly compete with similar-sized males for a key resource: namely a burrow. If there is a size-dependent decline in male density and the density of suitably sized burrows, this should increase the value of gaining a burrow for larger males. This might increase the strength of selection on male fighting ability as males grow, and favour the evolution of greater male investment in weaponry and fighting persistence in older males. We therefore made the key prediction that fight duration will increase with male body size. To test our prediction we initially had to confirm our underlying assumptions.

First, as expected given indeterminate growth and cumulative mortality, smaller males were more common than large males in our study population. Second, the density of burrows declined as burrow entrance width increased. This is because of a strong correlation between male size and burrow diameter, and unoccupied burrows being rare. Third, we showed experimentally that larger males are incapable of entering narrow burrows. Compared with smaller males, larger males could, however, fit into a relatively narrower burrow than the one that they naturally occupied (based on the slope for the regression of minimum burrow diameter on male size being flatter than that for naturally occupied burrow diameter on male size). Even so, the absolute density of suitably sized burrows still declined as male size increased. Fourth, when males were experimentally forced to seek a new burrow they preferentially fought with similar-sized males to acquire a burrow.

Table 2
Logistic regression analysis of the effect of rival size on whether a fight progresses to the dig stage

Predictor	β	SE	Wald's χ^2	df	P
Wanderer carapace	0.106	0.027	15.670	1	<0.001
Resident carapace	-0.101	0.027	13.641	1	<0.001
Constant	-2.658	1.869	2.022	1	0.155

Overall model fit: $r^2 = 0.287$, $\chi^2_2 = 22.171$, $P < 0.001$.

Table 3
Linear regression analysis of the effect of rival size on fight duration

Predictor	β	SE	t	df	P
Wanderer carapace	0.021	0.004	23.306	1101	<0.001
Resident carapace	-0.013	0.005	7.294	1101	0.008
Intercept	0.50	0.375	0.133	1101	0.895

Overall model fit: $r^2 = 0.214$, $F_{2,104} = 13.716$, $P < 0.001$.

The strong relationship between male body size and the diameter of the burrows they competed for, combined with the fact that unoccupied burrows are destroyed by the tide, suggests that the ratio of competitors to burrows is fairly constant in *U. annulipes*. There might, however, be more burrows available for smaller males. Female burrows tend to be fairly narrow as a result of sexual size dimorphism (Christy & Salmon 1991). We found smaller males were more likely to evict a female, while larger males did not evict females as they could not fit into their burrows. This implies that smaller males have access to more burrows than larger males. These lines of evidence suggest that larger males should place greater value on burrow ownership because of burrows being a scarcer resource. However, even if there is no body size effect on the ratio of male competitors to suitable burrows, the lower density of wider burrows is still potentially important in increasing the level of competition over burrows for larger males because a lower density increases travel costs. Indeed, we found that the distance between suitably sized burrows was greater for larger males. This need not have been the case. For example, there might have been spatial clumping of similar-sized males, as occurs in some fiddler crabs (Croll & McClintock 2000). Crucially, we then confirmed that larger males travelled significantly further to acquire a new burrow.

In sum, we obtained strong evidence that a male's size determines with whom he will compete (similar-sized males) and for what (suitably sized burrows that depend on male body size). Larger males must acquire an increasingly rare resource that occurs at a low density in the population. There is a fitness cost to being without a

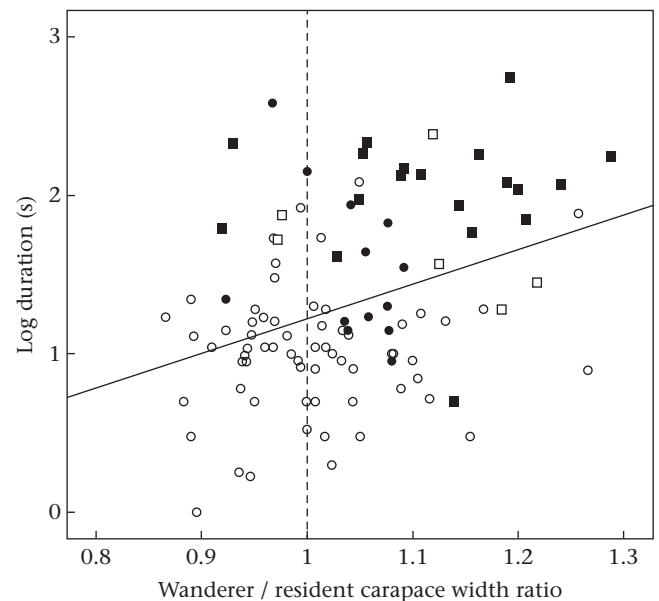


Figure 6. The relationship between fight duration and the relative size of rivals. Open symbols indicate fights won by residents ($N = 72$), closed symbols fights won by wanderers ($N = 32$); circles indicate fights that escalated to the push/grapple stage ($N = 79$); squares indicate fights that escalated to the drum/dig stage ($N = 25$). The vertical dashed line indicates whether the resident was the larger rival. Fights in which the resident was larger were predominantly won by the resident (89.5%, 34 of 38).

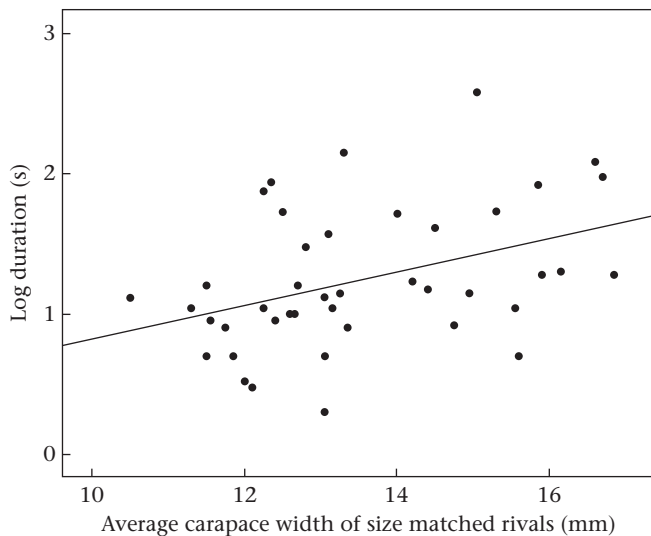


Figure 7. Relationship between fight duration and the mean size of males in size-matched fights ($0.95 \leq \text{wanderer/resident carapace} \leq 1.05$; $r^2 = 0.165$).

burrow, primarily because of an increased exposure to predators for crabs that cannot retreat into their own burrow when threatened (Koga et al. 1998). Although larger males travelled further to find a new burrow, they did not take significantly longer to do so. This suggests that larger males moved faster, either to reduce the time spent on the surface or because they took longer strides.

Mutual Assessment?

To test our prediction that a greater travel distance would lead to larger males valuing burrow ownership more highly than smaller males, we investigated male fighting behaviour. When fights are resolved based on mutual assessment, there should be no relationship between mean male size and fight duration when size-matched males fight. This is because there is no size-dependent variation in the speed with which males can assess a rival's relative strength.

When we controlled for a strong residency advantage, relative male size was the best predictor of fighting success. Male size and residency are both good measures of RHP. Fights between closely matched males lasted longer and were more likely to involve drumming and digging. Similarly, after we controlled for the residency effect, relative male size was a good predictor of fight duration. Consequently *U. annulipes* fights do not fit the assumption of 'individual cost threshold' models of a 'war of attrition without assessment' (Mesterton-Gibbons et al. 1996) or an 'energetic war of attrition' (Payne & Pagel 1996, 1997). Instead, relative male size strongly predicted fight duration, which is consistent with 'mutual assessment' models such as asymmetric 'war of attrition' (Maynard Smith & Parker 1976; Parker & Rubenstein 1981; Hammerstein & Parker 1982) or 'sequential assessment' models (Enquist & Leimar 1983). If a mutual assessment model applies, we can use the relationship between fight duration and mean male size in size-matched fights to draw inferences about size-dependent change in burrow value. First, however, we need to consider the possibility that a third individual cost-threshold model, namely the CAM of Payne (1998), applies in *U. annulipes*. CAM can also account for an effect of relative male size on fight duration if larger males impose greater costs per unit time so that the smaller male reaches his own individual cost threshold sooner.

To assess the applicability of the CAM model, it is important to note that the greater RHP of residents is primarily attributable to a

positional advantage. Resident males can partially or fully retreat into their burrow during a fight. Fayed et al. (2008) have shown in a related species of fiddler crab (*Uca mjoebergi*) that resident males with the option of retreating won 88% of fights, but only 38% of fights when the burrow entrance was experimentally blocked. This indicates that the greater RHP of resident males is not due to their being inherently stronger individuals. It is therefore unlikely that resident males (our definition of the male with the higher RHP in our analysis) inflict greater direct physical costs upon their rivals, especially as wanderers tended to fight residents that were slightly smaller than themselves. Payne (1998) did, however, argue that the greater costs inflicted by the individual with the greater RHP could be indirect (e.g. loss of feeding time). This leads to the prediction that, as the size of the rival with the stronger RHP (residents) increases, greater time costs will accrue for the rival with the weaker RHP (wanderers). This is the opposite of what we observed. The longest fights (i.e. greatest time-related costs) were those that escalated to the drum/dig stage because the resident retreats into the burrow. The size of both rivals predicted whether a fight progressed to this stage. Finally, there is a second line of evidence for mutual assessment, which is how males initially choose their opponents. Males chose to fight similar-sized opponents, but ones that were slightly smaller than themselves. To do this, males must be able to assess their size relative to that of potential rivals. We therefore assume, as has been shown in many other species, that mutual assessment is the most parsimonious mechanism that males use to decide when to abandon a fight.

Cumulative Assessment?

It is usually difficult to differentiate between different modes of assessment in animal contests (Briffa & Elwood 2009). It is particularly difficult to differentiate between mutual assessment and cumulative assessment (CAM) in this study system. Although we argue that there is mutual assessment in this system, the data are also potentially consistent with CAM. The CAM model is unique in that it allows for escalation or de-escalation within each phase of the fight (Briffa & Elwood 2009), and it would be necessary to examine closely the behaviour of rivals within each stage of the contest in order to eliminate/include CAM as a possible mode of assessment. However, in this particular case, it was not necessary to differentiate between these alternatives because the CAM model makes the same predictions as the mutual assessment models about contest duration and opponent size during RHP-matched fights: no relationship is predicted between fight duration and RHP (Briffa & Elwood 2009). We are therefore confident that, whether there is mutual assessment or CAM, the finding of increased duration with increasing opponent size requires an explanation that is unrelated to rival assessment methods.

Resource Value

Fight duration increased significantly with mean male size. Given mutual assessment, a probable explanation, invoking a factor frequently included in game theory models of fighting, is that resource value increases with absolute male size (Lindström & Pampouli 2005). Specifically, the lower density of suitable burrows for larger males means that they should be prepared to invest more in each fight, which increases the average fight duration. In the longer term, selection should also favour greater investment into weaponry by older, larger males. Indeed, claw size is positively allometric in most fiddler crabs, including *U. annulipes* (Rosenberg 2002).

The fighting behaviour of another fiddler crab, *Uca pugilator*, fits with our claim that selection for fighting persistence is partly driven

by the density of suitable burrows, rather than being an inherent feature of fiddler crab fights. In *U. pugilator*, males either feed at the water's edge and return to a temporary burrow at high tide or occupy and defend a breeding burrow (Christy 1983). In areas with breeding burrows, larger males accrue as owners (Pratt et al. 2003) and the largest males occupy preferred high-elevation burrows (Christy & Salmon 1984). Large burrows are therefore spatially clumped. In contests for breeding burrows, rivals appeared to engage in mutual assessment of strength (Pratt et al. 2003), but in fights between closely size-matched individuals, unlike in *U. annulipes*, fight duration did not increase with mean male body size. The latter result is expected given no size-dependent change in effective local burrow density so that there is no elevated density-dependent selection for greater fighting persistence by larger males.

Conclusions

We have identified a population in which competitor and resource density change predictably with size/age. Consequently different types of individuals effectively experience consistently different levels of any selection that is density dependent. We suggest that the occurrence of within-population variation in density is commonplace. There are two particularly important situations. First, in species with indeterminate growth, there is always a decline in effective density with age/size. There is the potential for large shifts in the intensity of competition as the ratio of competitors to resources changes. Larger individuals often require larger resources (e.g. owing to physical constraints or changes in feeding requirements) that tend to be less common. More importantly, it is a simple truism that a decline in resource density will always increase time/travel costs to get access to resources. This should lead to greater investment in acquiring encountered resources, be they food, shelter or mates (e.g. 'marginal value theorem: optimal staying time in patches increases as resource density declines and "travel time" increases'). Second, sexual selection often leads to size-assortative mating and/or fighting. In some cases this is the result of mechanical constraints, but in others it could be the result of prudent choice of opponents (e.g. Jennions & Backwell 1996) or mates (Härdling & Kokko 2005; Servedio & Lande 2006). The immediate outcome is that any study of density-dependent sexual selection (reviewed in Kokko & Rankin 2006) needs to consider what the density of effective opponents and resources really is. Is it the density of individuals with whom a male will actually fight or mate (i.e. ignore those that are 'excluded' through prudent choice)? Or should one consider every adult male a potential rival and every female a potential mate, and measure density accordingly (Klug et al. 2010)? Species with indeterminate growth and a wide range in adult body size are ideal to address both situations (e.g. many crustaceans, fish and marine invertebrates), especially when resource use is also size dependent (e.g. Ménard et al. 2012).

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