



Residency and size affect fight duration and outcome in the fiddler crab *Uca annulipes*

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We performed a field experiment to investigate the effect of carapace width, major cheliped length and burrow ownership on the fighting success of male fiddler crabs (*Uca annulipes*). We removed males from their burrows and released them back into the colony ($n = 82$). Released males tended to initiate encounters with burrow owners slightly smaller than themselves. Several general predictions of Sequential Assessment Game models of contest behaviour were supported: (1) residents won more encounters; (2) intruders were more likely to win when larger than residents. When body size (carapace width) was controlled for, intruders with relatively large claws for their body size were more likely to win contests; (3) the duration of encounters was related to the size difference between males; (4) encounters won by the larger male were of shorter duration than those won by the smaller male; (5) encounters won by the resident tended to be of shorter duration than those won by intruders ($P = 0.07$); (6) on average, encounter duration was longer when the intruder was larger than the resident. However, the encounters we documented began with seemingly costly behaviour such as pushing and the inter-locking of claws and did not unambiguously escalate from initial low cost behaviours. Sequential assessment of relative fighting ability may therefore not have been occurring. Prior visual assessment of opponents' fighting ability, followed by 'all-out fights' during physical encounters may also provide a plausible explanation for our results.

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CONTENTS

Introduction	294
Methods	295
Results	296
Natural interactions	296
Experimental interactions	296

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Discussion	300
Male size and encounter duration	300
Handedness	301
Relative claw size	301
The sequential assessment model	302
Acknowledgements	305
References	305

INTRODUCTION

The outcome of agonistic encounters is usually determined by the relative fighting ability or resource-holding potential (RHP) of opponents (Parker, 1974). In many species, fights are costly because of high energetic demands and risk of injury or even mortality, either from opponents (Huntingford & Turner, 1987) or from predators (Jacobsson, Brick & Kullberg, 1995). Individuals that accurately assess the fighting ability of opponents before engaging in potentially costly fights should therefore be at a selective advantage (Maynard Smith & Parker, 1976). The most common correlate of fighting ability is body size. However, other factors such as resident-intruder status (Rosenberg & Enquist, 1991; Olssen, 1992; Turner, 1994), body condition (Thornhill & Sauer, 1992), weapon size and asymmetries in the perceived, or actual, value of a resource (reviewed in Keeley & Grant, 1993) may also influence fighting success.

Theoretical studies based on the sequential assessment game (Enquist & Leimar 1983; Leimar & Enquist, 1984; Enquist *et al.*, 1990) have led to a series of predictions about agonistic encounters. According to these models, agonistic encounters involve a series of interactions in which individuals attempt to assess their opponent's relative fighting ability. At the start of an encounter, low cost, low accuracy information is acquired. As the game proceeds, however, progressively more costly behaviour is employed. The more evenly matched the two opponents, the more costly the behaviour required to accurately assess relative fighting ability. It is thus predicted that the duration of the encounter should be inversely proportional to the difference in fighting ability between opponents. Moreover, when the difference in fighting ability is small, there is a greater likelihood that the individual with the greater fighting ability will make an error in assessment and give up first (Smith *et al.*, 1994). It is also predicted that owners will win more encounters, and are more likely to win when contestants are matched. The longest duration encounters should occur when the intruder is slightly stronger than the resident; and contests won by residents should be of shorter duration than those won by intruders (Leimar & Enquist, 1984).

Empirical studies support many of the key predictions of the sequential assessment game (Enquist *et al.*, 1990). A central question that remains, however, is the extent to which agonistic encounters should be viewed as opponents assessing relative fighting ability as opposed to 'all-out fights' (fight outcome determined by RHP) or 'limited fights' (the winner is the animal prepared to fight longer or harder) (reviewed in Harper, 1991). Similar predictions concerning fight duration and the effect of size are made in all cases. For example, in an 'all-out' boxing match the aim of each fighter is to emerge victorious: the greater the difference in fighting ability the shorter the fight: the smaller the difference in ability the greater the likelihood that a lucky punch will provide the underdog with a win. This is true even when boxers do not

assess each other, but simply 'come out swinging'. Fights are then settled by conventions — such as lying on the floor for 10 seconds.

Here we investigate agonistic behaviour in the fiddler *Uca annulipes*, a small (1–2 g), sexually dimorphic crustacean that lives at high densities in mixed-sex colonies on inter-tidal mud flats (Gordon, 1958; Crane, 1975). Individuals of both sexes defend burrows and there are frequent aggressive interactions between neighbouring males. However, individuals occasionally move away from their burrows to forage along the edge of the receding tidal water. Wandering males fight resident males to acquire new burrows. Males rarely fight females for burrows. Burrows are important both as refugia during high tide, and for mating. Wandering gravid females choose males partly on the basis of burrow features, and remain in the chosen male's burrow while their eggs develop (Backwell & Passmore, in press).

We examined two main aspects of agonistic behaviour:

- (1) The influence of size and resident-intruder status on the outcome of fights and contest duration.
- (2) The effect of major claw size on fighting success once body size is controlled for. Although claw size and carapace size are closely related ($r > 0.95$), major cheliped size is more likely to be the key determinant of fighting ability. Previous work on *U. annulipes* has also shown that relative major claw size is condition-dependent (Jennions & Blackwell, unpublished data).

We also looked for an effect of handedness on fight initiation. It may be easier for opposite handed males to accurately assess each other's size. Their claws are mirror images when they face each other during an agonistic encounter. We therefore predicted that heteroclawed fights should be more common than homoclawed fights.

METHODS

We studied a population of *U. annulipes* in Durban Harbour, KwaZulu-Natal, South Africa (25° 48' S 15° 10' E) from October 1992 to March 1994. We captured males that were defending burrows and then released them several meters from their own burrows. We then observed these males through 8 × 30 binoculars as they wandered across the mud flat. We recorded the details of the first agonistic encounter they initiated with a burrow owner that involved intense major claw contact such as pushing and grappling. Any physical encounters prior to this were a few seconds (1–3 s) in duration and, at most, only involved a brief touching of claws.

Males were captured by placing a sharpened stick at the burrow entrance and waiting several minutes until the male emerged. The stick was then pushed into the substrate such that it blocked the burrow entrance and prevented the male from retreating back into the burrow. The male was then moved several meters from his burrow. From capture to release only took a few seconds and did not appear to have an adverse effect on the male. (The pattern of size-based fight initiation did not differ between natural and male-release fights; see Results.) After an encounter, we captured both the released male and the resident male and measured major claw length and carapace width to the nearest 0.1 mm using dial callipers. Linear measurements were significantly and highly repeatable (intra-class correlation coefficients; Carapace width: $r = 1.00$, $F > 1000$, d.f. = 14,15, $P < 0.0001$; Claw

length; $r = 1.00$, $F > 1000$, d.f. = 14,15, $P < 0.0001$). The duration of the encounter and the identity of the winner were also recorded. Duration was not recorded in one encounter due to stopwatch malfunction. We also collected data on the size and handedness of pairs of opportunistically captured, naturally fighting males. 'Relative claw size' is a measure that corrects for carapace size. It is defined as the standardized residuals from the regression of major claw length on carapace width. Residuals were normally distributed and homoscedastic (Jennions & Backwell, unpublished data).

The carapace width ratio of pairs was calculated as the smaller width divided by the larger width (range = 0.77–1.00). Comparisons of observed and expected frequencies were made using two-tailed exact binomial probabilities or Chi-square tests with Yates correction. The frequency of same-handed to opposite-handed pairs of fighting males should be 1:1 as the ratio of left to right handed males is equal (102:98, $n = 200$, binomial exact, $P > 0.8$). Comparisons of two observed proportions were made using Fisher's exact test (two-tailed). Where possible we transformed data and used parametric statistics. Encounter duration was log-transformed and carapace width ratio was arcsine transformed. Data that were not transformable were analysed using standard non-parametric tests. Unless otherwise stated all tests are two-tailed, and summary statistics are presented as mean \pm SD. Analysis was performed using SYSTAT for Windows.

RESULTS

Natural interactions

We captured 200 pairs of males naturally engaged in agonistic encounters. There was a strong positive correlation between both major claw length and carapace width of pairs of fighting males (claw: $r_s = 0.746$, $P < 0.0001$; carapace: $r_s = 0.725$, $P < 0.0001$, $n = 200$ pairs). There was no significant trend towards more encounters between opposite-handed males (54.7%) than same-handed males ($\chi^2 = 1.31$, d.f. = 1, $n = 150$ pairs, $P > 0.5$).

Experimental interactions

Initiation

We released and successfully recorded agonistic behaviour for 82 males. Released males initiated fights with burrow-owning males of smaller carapace widths in 63% of encounters (Exact binomial probability, $P < 0.02$). However, both the major claw length of pairs and carapace width of pairs were highly correlated (claw: $r = 0.812$, $P < 0.001$; carapace: $r = 0.756$, $P < 0.001$, $n = 82$ pairs) (Fig. 1). The mean carapace width ratio was 0.93 ± 0.06 .

The larger of the pair won significantly more than 50% of the encounters (carapace width: $n = 48$ of 79, $P = 0.035$; claw length: $n = 49$ of 82, $P < 0.05$, both Exact binomial probabilities, one-tailed). There was, however, a significant interaction between claw size and resident-intruder status (Fisher exact, two-tailed, $P < 0.003$) (Table 1). When the resident won, the proportion of cases in which the male with the larger carapace width (or claw length) won was not significantly

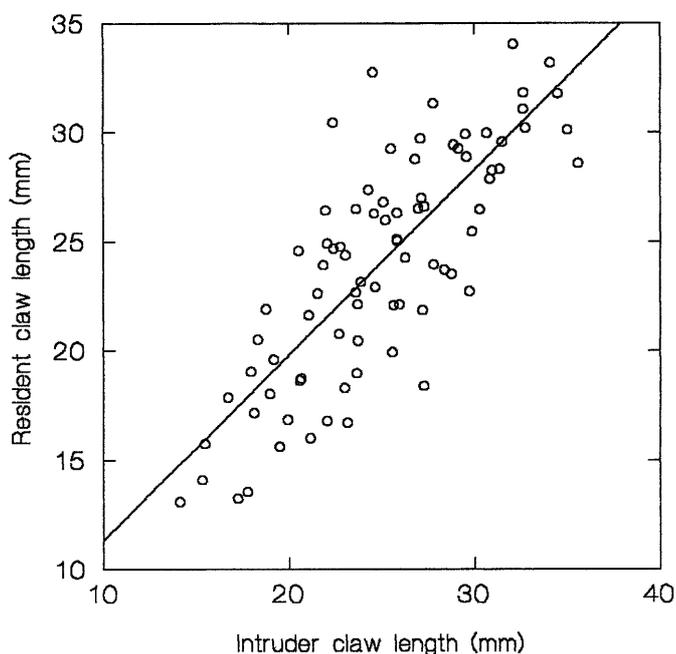


Figure 1. Relationship between intruder and resident major claw length in the experimental release trials. The line is the least squares regression ($Y = 2.853 + 0.849X$; $F = 154.57$, d.f. = 1,80, $P < 0.001$, $r^2 = 65.5\%$, $n = 82$).

different from 50%. However, when an intruder won, he was larger than the resident in 88% of cases (exact binomial probability, $P < 0.0001$). In total, the resident male won 70% ($n = 57$ of 82) of the encounters (exact binomial probability, $P < 0.0005$).

We divided the pairs into five classes based on carapace width ratio. The number of pairs in each class was approximately the same ($n = 16-17$). There was no trend for the proportion of encounters won by the smaller crab to increase as the carapace width of contestants became more evenly matched. The percentage won by the smaller male in each class, listed from smallest to largest carapace ratio was: 41.2%, 25%, 31.3%, 37.5%, 64.7% ($t_S = 0.40$, $n = 5$, $P > 0.50$). The absence of a trend held even when the effects of residency were taken into consideration.

Duration

TABLE 1. Male major claw size in relation to fighting success. I = Intruder R = Resident. Exact binomial probabilities are for the proportion of fights won by larger and smaller individuals.

	Major claw length		Probability
	Intruder > Resident	Resident > Intruder	
Intruder wins (<i>n</i>)	22	3	<0.0001*
Resident wins (<i>n</i>)	30	27	0.81*

*Comparison of proportion of fights won by larger and smaller individuals.

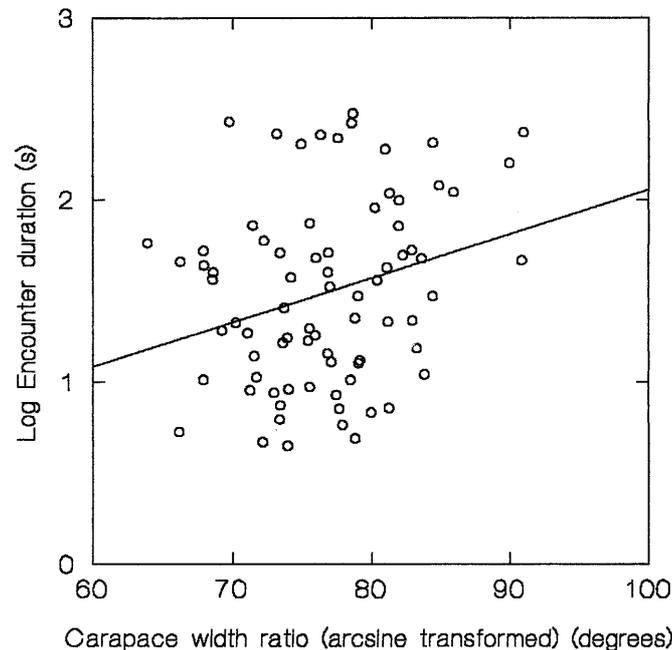


Figure 2. Relationship between carapace ratio of the fighting males and encounter duration. The line is the least squares regression of the transformed variables excluding cases where the carapace ratio was less than 0.80 ($Y = -0.371 + 0.024X$; $F = 6.03$, d.f. = 1,79, $P = 0.016$, $r_{\text{adj}}^2 = 6.2\%$, $n = 77$).

The mean duration of encounters was 63.4 ± 9.0 s (mean \pm SE). There was a non-significant relationship between carapace width ratio and encounter duration ($r = 0.175$, $n = 81$, $P = 0.118$). However, when four outliers (all involving males that differed greatly in carapace width) were excluded there was a significant correlation between carapace width ratio and duration (carapace width ratio range 0.80–1.00, $r = 0.273$, $n = 77$, $P < 0.02$) (Fig. 2) The smaller the size difference between males, the longer the encounter lasted. There was no significant correlation between carapace width ratio and variability in encounter duration ($r_S = 0.452$, $n = 8$, $P > 0.20$). Pairs were placed into eight size ratio classes with approximately equal numbers of pairs per class ($n = 9$ –11); variability was measured as the coefficient of variation in duration.

Fight duration differed significantly between the four encounter types (larger or smaller male/resident or intruder won) (one-way ANOVA, $F = 4.158$, d.f. = 3,77, $P = 0.009$). We then performed a two-way ANOVA on encounter duration to determine the relative effect of the status of the winner (resident or intruder) and the size of the winner (larger or smaller). Encounter duration was significantly shorter when the winner was larger than the loser ($F = 7.00$, d.f. = 1,77, $P = 0.010$; Winner larger: 47.4 ± 70.0 s, Winner smaller: 88.1 ± 90.4 s). There was also a trend towards a significant effect of the status of the winner ($F = 3.352$, d.f. = 1,77, $P = 0.071$). Encounters tended to be shorter when the resident won. There was no significant interaction between the two factors (interaction: $F = 0.379$, d.f. = 1,77, $P = 0.540$) (Table 2).

The data were also analysed in a slightly different way, whereby the second factor was the relative claw size of the intruder and resident (i.e. which was larger). When

TABLE 2. Male major claw size and fighting duration in seconds (mean \pm SD). Comparisons were made using post-hoc Tukey tests.

	Major claw length of winner		<i>P</i>
	Larger	Smaller	
Intruder wins	66.8 \pm 86.5	139.5 \pm 51.6	0.314§
Resident wins	31.5 \pm 49.3	84.6 \pm 91.8	0.019§
<i>P</i>	0.352*	0.557*	
Total	47.4 \pm 70.0	88.1 \pm 90.4	

*Tukey test between row means.

§Tukey test between column means.

the resident won, encounters were significantly shorter when resident claw length was greater than intruder claw length (Tukey, $P = 0.019$). When the resident was larger than the intruder, there was a trend towards longer encounters when the intruder won (Tukey, $P = 0.086$). None of the other pairwise comparisons approached statistical significance ($P > 0.30$). Disregarding fight outcome, fights were significantly longer when the resident was smaller than the intruder (Intruder larger: 77.1 ± 89.2 s; Intruder smaller: 39.0 ± 56.0 s; Mann-Whitney, $U = 522$, $n = 29,52$, $P = 0.022$).

Weapon size

The length of the major cheliped was significantly and closely correlated with carapace width for males in the experimental study ($r = 0.94$, $n = 164$, $P < 0.0001$). The use of major claw length or carapace width as the measure of size thus produced similar results in all the tests performed. The proportion of fights won by the males with the larger carapace width ($n = 58$ of 79) did not differ significantly from that won by the male with the larger major cheliped ($n = 59$ of 82).

We attempted to control for differences in carapace width by considering only pairs closely matched ($< 5\%$ difference) for carapace width (carapace width ratio greater than 0.95). The relative major claw size (standardized residuals from a least squares regression of major claw length on carapace width) of intruders that won was significantly greater than that of intruders that lost (Mann-Whitney U-test, $U = 66$, $n = 10,26$, $P = 0.024$) (Fig. 3). This was not due to covariance of relative claw size and carapace width. The carapace width of winning and losing intruders did not differ (Mann-Whitney U-test, $U = 142$, $n = 10,26$, $P = 0.67$). Intruders with relatively large claws for their body size are thus more successful during agonistic encounters between males of similar carapace size.

Absolute size

Males that won fights were significantly larger than those that lost (Wilcoxon matched-pair tests, $n = 82$ pairs: carapace width: $Z = 2.351$, $P = 0.019$; claw length: $Z = 2.203$, $P = 0.028$). To distinguish the effects of difference in size from absolute size, we considered only pairs of males that were closely matched for size (carapace width ratio > 0.95 ; $n = 38$). In this range there was no correlation between carapace width ratio and mean male carapace width ($r_s = 0.09$, $n = 38$, $P > 0.5$). There was a trend towards a significant correlation between mean male size and encounter duration ($r = 0.279$, $n = 38$, $P = 0.126$). This trend was significant when the sample size was increased by extending the ratio range to 0.92

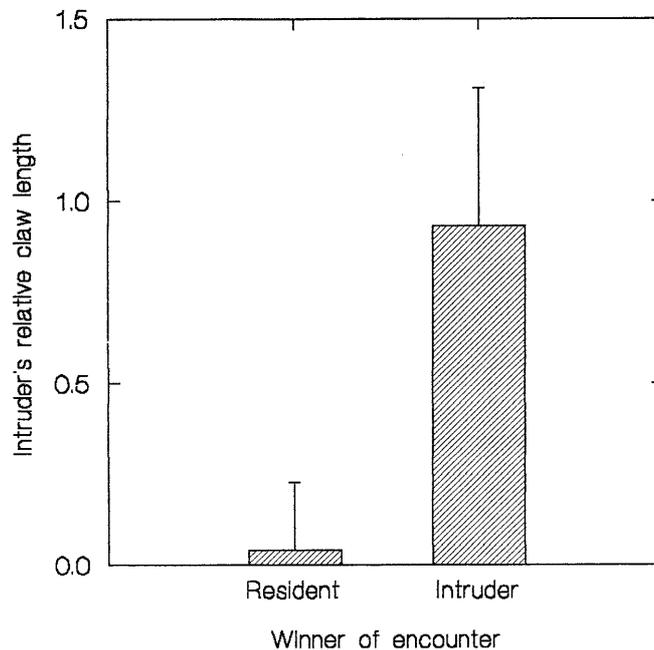


Figure 3. Relative claw length (see text) of intruding males that won and lost encounters when the carapace ratio of the pair of males was greater than 0.95. ($n = 10$ winners, 26 losers). The difference is significant (see text). Mean \pm SE are shown.

($r = 0.282$, $N = 53$, $P < 0.05$) (Fig. 4) In this extended range there was also no correlation between mean male size and carapace width ratio ($r = 0.186$, $n = 54$, $P > 0.10$). Encounters between larger males were of a longer duration.

DISCUSSION

Male size and encounter duration

Fights were significantly longer between larger males. In contrast, in swimming crabs (*Necora puber*) encounters between larger males are resolved more rapidly (Smith *et al.*, 1994). Similarly, Crespi (1986) found that fights between larger individuals were shorter in a thrip (*Elaphrothrips tuberculatus*). Our result may be attributed to the fact that large males are less common in the population. Hence the burrow of a large male is a more valuable resource increasing the benefits of winning an encounter. Small males, because they often lose fights, are actually far more likely to excavate their own burrow than fight for one (Backwell, unpublished data). The correlation between the size of opponents in *U. annulipes* may be related to the need for larger males to acquire burrows with larger entrances. Some modification of burrow dimensions is necessary when larger males acquire burrows from smaller males. The costs of burrow modification may be sufficiently large that males choose to initiate fights with similar-sized opponents even though this increases fight duration and search costs and decreases the likelihood that they will win an encounter (J.H. Christy, personal communication). Englund & Olsson (1990) have also suggested

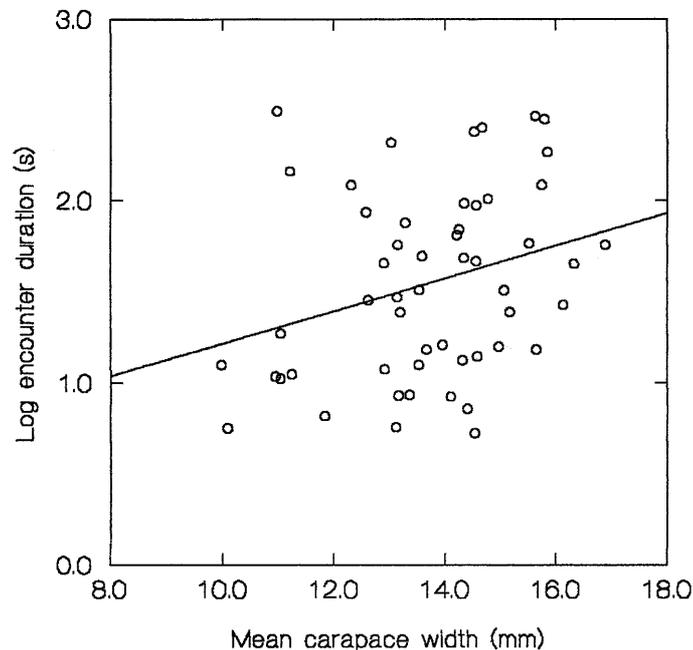


Figure 4. Relationship between mean carapace width of fighting males and encounter duration (carapace width ratio ≥ 0.92). The line is the least squares regression ($Y = 0.324 + 0.089X$; $F = 4.42$, d.f. = 1,51, $P = 0.041$, $r_{\text{adj}}^2 = 6.2\%$, $n = 53$).

that if males can assess their own size, then larger males may 'know' that, on average, they have a greater fighting ability and adjust their behaviour accordingly.

Handedness

Handedness of opponents had no effect on a male's decision to initiate fights. Similar findings have also been reported for the ghost crab *Ocypode ceratophthalmus* (Brooke, 1981) and several species of fiddler crab (Crane, 1975; Hyatt & Salmon, 1978). Perhaps any benefits derived from 'specialization' on attacking heteroclawed or homoclawed opponents are outweighed by the doubling in search costs involved in finding a male of a specific handedness (J.H. Christy, personal communication).

Relative claw size

We controlled for carapace size by considering only pairs closely matched for this variable and found that intruders with relatively large claws were more likely to win encounters. This strongly suggests that claw size is a more important indicator of fighting ability than carapace size. However, relative claw size is positively correlated with body condition (Jennions & Backwell unpublished data), so fighting success may also be related to body condition as well as being a direct consequence of larger claw size. Males with greater fat reserves have been shown to win significantly more fights

in the damselfly *Calopteryx maculata* (Marden & Waage, 1990; Marden & Rollins, 1994).

The sequential assessment model

Our results are in accordance with several predictions of sequential assessment models of conflicts (see Enquist & Leimar, 1983; Leimar & Enquist, 1984; Enquist *et al.*, 1990).

(1) *Residents won more encounters.* This was not due to the accumulation of males with greater fighting ability as burrow owners. The experimental design meant that intruders were formerly burrow owners. It is also unlikely to be due to difference in the perceived value of the resource (Keeley & Grant, 1993). Males do not appear to be able to assess the attractiveness of burrows to females. Females show a strong preference for certain burrow types; however, there is no correlation between male size and burrow features even though larger males should be able to win more 'attractive' burrows (Backwell & Passmore, in press). The 'bourgeois' strategy of owner wins does not seem to be applicable either (Grafen, 1987). The most likely explanation is that owners have a positional advantage (Christy, 1982). First, owners may have a better 'foothold' during fights, as they can anchor onto the entrance of the burrow (Adams & Caldwell, 1990). Second, owners can also partially retreat into the burrow. If the intruder wishes to continue the fight he must therefore remove some of the soil from the burrow entrance to reach the owner (see the discussion of 'down-pushing' behaviour in Hyatt & Salmon, 1978, 1979). This may make the costs of fights greater for intruders than residents leading to an asymmetry in the cost to benefit ratio for intruders and residents (Hammerstein & Parker, 1982). Hyatt & Salmon (1978) also found that residents won more fights in *Uca pugilator* and *U. pugnax*.

(2) *Residents won significantly more encounters when contestants were matched.* Intruders only won 10% of the encounters where they were smaller than the resident, but residents won more than 58% of the encounters when smaller than the intruder. Similar results were recorded for *Uca pugilator* and *U. pugnax* (Hyatt & Salmon, 1978).

(3) *Encounters won by the intruder tended to be longer than those won by the resident* ($P = 0.07$).

(4) *There was a correlation between difference in fighting ability and encounter duration.* Carapace width is assumed to be a measure of fighting ability and the carapace width ratio of fighting pairs was correlated with the duration of the encounter. However, this was only true when four fights involving males that differed greatly in size were excluded (carapace width ratio < 0.80).

(5) *Encounters were significantly longer when the intruder was larger than the resident.* It should also be noted, however, that the longest encounters occurred when a smaller intruder won.

Two predictions were not fulfilled. First, there was no relationship between variability in fight duration and the size difference between males (for justification of this prediction see Englund & Olsson, 1990). Second, there was no trend for smaller males to win more fights as the difference in carapace width decreased. It could,

however, be argued that fight assessment is so accurate (and size so closely correlated with RHP) that this trend need not occur, even if the contest is structured as a series of sequential assessments. Likewise, if fighting ability is extremely closely related to size and fighting ability strongly predicts fight outcome then no trend will emerge if encounters are 'all-out fights'.

The work presented here differs from most other studies in two important respects. First, fights were not staged and males were free to choose opponents. Most studies involve staged fights in captivity (e.g. Englund & Olsson, 1990; Enquist *et al.*, 1990; Lindström, 1992; Faber & Baylis, 1993; Smith *et al.*, 1994; Turner, 1994). By allowing males to choose opponents, the potential for males to visually assess opponents is enhanced; because males are free-ranging there is also no risk of unnaturally prolonged encounters as may occur in captive studies. Second, intruders were former residents. Simple observation of natural fights cannot control for the possibility that natural intruders are inferior males of lower fighting ability (e.g. Hyatt & Salmon, 1978, 1979; Rosenberg & Enquist, 1991; Olsson, 1992) or possibly even superior competitors, if most males wander because they have relinquished their own burrow to a female with whom they mated (J.H. Christy, personal communication). Together these two factors may account for some of the minor discrepancies between our results and those from other studies.

In contrast to the conclusions most authors draw from similar data sets, we question whether our confirmatory results validate the sequential assessment model. We intentionally only documented encounters that began with pushing, claw locking and grappling. We believe these are the most costly behaviours engaged in by fighting males. Natural occurrence of encounters involving these types of behaviour can lead to severe injury and even mortality (personal observations).

We suggest that the close correlation between the size of opponents, combined with the tendency for intruders to initiate encounters with males slightly smaller than themselves indicated that males visually assess fighting ability on the basis of size prior to physical encounters (see also Enquist, Ljungberg & Zandor, 1987). Hence we argue that the encounters we monitored were already at the stage designated 'dangerous fighting' by Enquist *et al.* (1990), or 'all-out fights' by Harper (1991) and had little to do with assessment. In *Uca pugilator* wandering males also tend to initiate fights with males smaller than themselves (Hyatt & Salmon, 1978). However, in *U. pugnax* there is no bias in the relative size of burrow-owning males with which wandering males initiate fights (Hyatt & Salmon, 1978); and wandering male *U. rapax* initiate fights with males larger than themselves (Crane, 1967).

If the agonistic encounters we documented were not assessment interactions, but rather 'all-out' or 'limited' fights (see Harper, 1991), what determines when a male decides to terminate an encounter? A 'war of attrition' between males is unlikely to account for our results. Fights were comparatively short, and males did not appear to use up substantial energy reserves (c.f. Marden & Waage, 1990; but see Marden & Rollins 1994). Losers often initiated a new fight within a minute of a previous encounter. There is one obvious 'convention' that may apply. An encounter ends if the intruder enters the burrow while the resident is still on the surface. Former burrow owners always relinquished their burrow if this happened. It is less clear what influences the termination of a fight when the intruder retreats. We suspect, however, that something as simple as being flicked away by the resident is usually sufficient. Males that were flicked a few centimetres from the burrow rarely returned to continue the encounter. A threshold response during any specific aspect of fighting

(such as being pushed over, or flipped away) may act as a clear indicator that an opponent is stronger. Although this response can be viewed as an act of assessment; up to that point males may simply have been fighting as hard as possible.

Of course, it is possible to view agonistic interactions in *U. annulipes* as fitting the sequential assessment game model. If we had included very brief encounters (< 3 s) in our analysis we would have *definitely* documented highly significant relationships whereby: (1) encounters won by residents are shorter in duration. In all the brief encounters (< 3 s), intruders moved away from residents. (2) Fights between unevenly matched opponents are shorter. The wandering male frequently approaching burrow owners that were considerably larger or smaller during brief encounters. (3) The occurrence of costly 'assessment' behaviour increases as encounter duration increases. Brief encounters involved males approached and waving at each other, and possibly a brief touching of claws. These encounters clearly influence a male's choice of opponent when initiating a physical fight (see Grafen, 1987).

The main point we wish to make, however, is that even if these brief encounters are excluded, the outcome and duration of the physical fights we documented still fit most predictions of the sequential assessment game, even though they may not involve a series of escalated signals used to assess fighting ability. Interestingly, Enquist *et al.* (1990) also reported a negative relationship between fight duration and size asymmetry in the dangerous fighting phase of encounters in a cichlid fish. We therefore suggest that the use of data on encounter duration and the status of winners cannot discriminate between the various models of fighting behaviour.

Detailed analysis of fighting behaviour may resolve the problem of whether or not assessment occurs during contests. The sequential assessment model predicts the use of increasingly costly behaviour as an encounter progresses. However, to test this prediction we must be able to rank different behavioural acts on a scale of costliness. We are not confident in our ability to do this for *Uca annulipes*. For example, is grappling more or less costly than pushing? Is 'downpushing' which occurs towards the end of some encounters more costly than the grappling which precedes it? We suspect that similar problems arise in many other species, although authors may downplay the difficulties by appealing to 'common-sense' estimates of relative costliness.

Some studies have attempted to quantitatively assess costs by determining the probability of injury associated with different behavioural elements. Ironically, in one of the most thorough studies Waas (1991) found that the rate of attack was greater for 'submissive' displays than for 'aggressive' displays in the blue penguin *Eudyptula minor*. Although he stated that attacks during 'submissive' displays were less likely to result in injury, this was a subjective assessment and no data were directly presented to support this view. Detailed studies of the elements of fighting behaviour in two fiddler crabs (*Uca pugilator* and *U. pugnax*) have shown that there is usually a regular sequence of behaviours involved (Hyatt & Salmon, 1978, 1979). We do not dispute that similar behavioural sequences may well occur in *U. annulipes* (Crane, 1975). However, it is a leap in logic to assume that the presence of a regular sequence of behaviours indicates sequential assessment of fighting ability.

In conclusion, the sequential assessment model is only weakly tested by studies of encounter duration and contest outcome. 'All-out fights' can lead to similar trends. The strongest evidence is provided by studies showing that the behaviours used during encounters become increasingly costly as they progress. Detailed quantitative data on the risks of injury, metabolic costs and even predation (see Jacobsson *et al.*,

1995) associated with different behavioural elements are needed rather than simple 'common sense' ranking of relative costliness.

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