



Fighting in fiddler crabs *Uca mjoebergi*: what determines duration?

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Contest duration in animals is often interpreted as being a consequence of mutual assessment of the difference in the competitors' resource-holding potential (RHP), allowing the inferior individual to avoid costly interactions it is likely to lose. Duration is thus predicted by the relative size of the competitors, and increases as the difference between them decreases. Alternatively, each individual may persist in accordance with thresholds determined by its own RHP, and weaker rivals retreat because they have lower thresholds. Contest duration depends on the RHP of the contestant that gives up first. Recent work suggests that even though duration is determined by the loser's size, this hypothesis also predicts a negative correlation between duration and the relative RHP of the contestants. However, it predicts (unlike the mutual assessment hypothesis) that contest duration should increase with the mean size of the contestants. We studied the determinants of fighting duration in the fiddler crab *Uca mjoebergi*. Fight duration increased with increasing size of the loser, and decreased, but to a lesser extent, with increasing size of the winner. Fights between size-matched individuals increased in duration with increasing mean size of the competitors. Neither the mutual assessment nor own-RHP-dependent persistence hypotheses can accurately explain the data. Instead, we present a modification of recent modelling work, and suggest that in *U. mjoebergi* individual cost thresholds may determine duration, but that larger opponents may inflict those costs more rapidly, consistent with the cumulative assessment game of animal conflict.

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Differences in resource-holding potential (RHP; Parker 1974) are important in determining the outcome of contests for territory ownership. Body size is often used as an indicator of RHP (e.g. Beaugrand et al. 1996; Jennions & Backwell 1996; Petersen & Hardy 1996; Johnsson et al. 1999), but other factors may contribute to an animal's ability to obtain or retain territories, including asymmetries in residency (Davies 1978; Jennions & Backwell 1996; Chellappa et al. 1999; Johnsson et al. 1999; Wenseleers et al. 2002), resource value (Krebs 1982; Alcock & Bailey 1997; Tobias 1997; Neat et al. 1998;

Johnsson & Forser 2002), energy reserves (Marden & Waage 1990; Marden & Rollins 1994), body condition (Fitzstephens & Getty 2000), age (Kemp 2003) and experience of winning or losing (Beaugrand et al. 1996; Hsu & Wolf 2001).

These factors may also be important in determining the duration of fights between individuals. Individuals may avoid extended and costly contests by assessing their own RHP relative to that of their rival, before deciding how to proceed (the mutual assessment hypothesis). The ability of rivals to assess their relative sizes has been incorporated into models of animal conflicts, including some war-of-attrition games (Maynard Smith & Parker 1976; Parker & Rubenstein 1981; Hammerstein & Parker 1982) and the sequential assessment game (Enquist & Leimar 1983; Leimar & Enquist 1984; Enquist et al. 1990). Asymmetries between individuals can lead to quick resolution of contests based on those asymmetries, but when competitors are evenly matched, escalated fighting results (Maynard Smith 1982; Enquist & Leimar

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1983). Many empirical studies have tested and found support for these models, finding that contest duration increases as some measure of the difference between competitors in RHP decreases (e.g. Englund & Olsson 1990; Enquist et al. 1990; Leimar et al. 1991; Faber & Baylis 1993; Marden & Rollins 1994; Smith et al. 1994; Dale & Slagsvold 1995; Jennions & Backwell 1996; Hack et al. 1997; Moya-Laraño & Wise 2000; Renison et al. 2002; Pratt et al. 2003).

More recent game theory approaches to modelling contest dynamics have included the possibility that contest duration and escalation could be determined by the size of one (usually the size-disadvantaged) of the competitors (war-of-attrition without assessment: Mesterton-Gibbons et al. 1996; energetic war-of-attrition: Payne & Pagel 1996, 1997; Payne 1998). If each individual involved in an energetically costly contest has a threshold level of costs that it is willing to accumulate, determined by that individual's RHP, a contest will persist until the individual with the lowest costs threshold reaches that level, and thus duration will be determined by the RHP of the eventual loser. Under the 'own-RHP-dependent persistence hypothesis', no assessment of the size of the opponent need take place. Support for these models includes situations where the escalation probability or duration of a contest between size-matched rivals is positively associated with body size (Dixon & Cade 1986; Glass & Huntingford 1988; Foster 1996; Jennions & Backwell 1996, Whitehouse 1997). Fight duration in contests of the orb web spider, *Metellina mengei* (Bridge et al. 2000) and jumping spider, *Plexippus paykulli* (Taylor et al. 2001) and escalation in fallow deer, *Dama dama* (Jennings et al. 2004) are better predicted by the size of the loser than by measures of relative size, supporting the own-RHP-dependent persistence hypothesis.

Using simulation models Taylor & Elwood (2003) showed that a strong correlation exists between measures of relative size and duration of fights even when individual thresholds actually determine contest duration. In addition, there is a strong correlation between the size of the smaller rival and duration when mutual assessment determines duration. Thus, careful examination of data is needed to discover the true determinant of fighting duration (the loser's RHP or mutual assessment). The models suggest that by considering the direction of the correlation coefficients between the sizes of the smaller and larger rivals and the duration of fighting, it should be possible to distinguish between the two possibilities (Gammell & Hardy 2003; Taylor & Elwood 2003). In both cases, the loser's RHP will correlate positively with duration. When duration is determined by the loser's RHP, the winner's size will correlate positively but more weakly with duration. If mutual assessment occurs, and determines duration exclusively, the winner's size will correlate negatively with duration, but with approximately the same strength as the relation between the loser's size and duration (Gammell & Hardy 2003; Taylor & Elwood 2003).

We investigated whether contest duration in the Australian fiddler crab *Uca mjoebergi* is determined by individual thresholds or mutual assessment of fighting ability, and which type of game theory model is most

appropriate for this species. We used the framework for contest analysis suggested by Taylor & Elwood (2003), one of the first studies to do so (but see Jennings et al. 2004). In our study species, both males and females occupy and aggressively defend burrows, used as refugia from the high tide and for mating (Backwell & Jennions 2004). The surface area around the burrow entrance is used for feeding during diurnal low tides and courtship of wandering females (Backwell & Jennions 2004). In fiddler crabs, gravid females select males partly on the basis of burrow characteristics, and remain in the chosen male's burrow while the eggs develop (Backwell & Passmore 1996), and thus ownership of a burrow and surrounding area of the mudflat is important for both survival and reproduction. Burrow-holding males aggressively defend their burrows from wandering males (intruders). An intruder is a male that has lost his burrow, either because he forfeited it to a female whom he mated, or because he lost it in fighting with another male. Intruders wander through the population of territory-holders, and fight with several males before eventually winning a territory. In this study, we artificially created intruders in the population (see *Methods* for justification), and examined the duration of fights.

METHODS

We studied a population of *U. mjoebergi* at East Point Reserve, Darwin, Northern Territory, Australia, from October to December 2003. The study was conducted for 4–6 h per day during diurnal low tides. Within the areas of the mudflat occupied by *U. mjoebergi*, the population was divided into several smaller subpopulations, separated by unused areas (>1 m across), presumably unsuitable for the construction of burrows (personal observation). We examined fights between intruders and burrow-holding resident males. There were two ways to do this: either by following naturally occurring wandering males and documenting their fight with a resident; or by artificially creating wanderers by capturing, relocating and releasing resident males and following them until they fight with a resident. We chose the second method because it eliminates several potentially important problems. First, it prevents winner-loser effects since both males were burrow-holders and must therefore have won their last fights (see Hsu & Wolf 1999). Second, this method overcomes the possibility that wandering males are a class of weaker individuals that are unable to hold territories successfully (Bradbury & Vehrencamp 1998; Olsson & Shine 2000). Finally, it avoids the possibility of size-assortative fighting if individuals are distributed in a size-assortative pattern through the habitat (Christy 1980), as it ensures that males of all sizes could be introduced to each habitat patch.

We captured burrow-holding males ($N = 531$) and measured the carapace width and major claw length (pollex and manus; ± 0.1 mm) using dial callipers, a highly repeatable method (Backwell & Passmore 1996; Jennions & Backwell 1996). All measurements were carried out by a single observer (L.J.M.). We released each male at least

2 m away from his own burrow and observed him until he completed his first fight with a resident male defending another burrow. A fight was defined as any interaction in which the males touched claws, even briefly. We used a stopwatch to record the duration(s) of the fight (from first to last contact, $N = 173$ fights), and noted the winner (the male occupying the burrow when the interaction ended). For a subset of the data ($N = 109$ fights), we also recorded the level of fight escalation. Fights in *U. mjoebergi* escalate from pushing to grappling. Many fights are settled with 'pushing': while facing each other, males align their claws and push. If this does not end an encounter, they proceed to grapple by interlocking claws and twisting (Crane 1975). Once the fight was settled, we captured and measured the male that was originally resident.

We examined fights only between brachychelous (non-regenerated claw) males since regenerated claws are inferior weapons (Backwell et al. 2000). Brachychelous males were recognized by the presence of pronounced tubercles in the gape of the claw (Backwell et al. 2000). We included only those fights in which both males remained on the surface throughout the interaction, and excluded those that involved digging or fighting from within the burrow shaft ($N = 173$ fights recorded). Although males were not marked, we avoided recording the same males in observations on the same day. During each day of observations, we recorded fights in at least two locations on the mudflat (<2 m apart), and avoided using the same areas consecutively between days. Thus it is unlikely that the same males were observed repeatedly.

For the analysis of fighting duration, we used the framework advocated by Taylor & Elwood (2003). We thus investigated the sizes of the winner and loser as distinct explanatory variables. If, in simple and multiple regression, these correlate positively with duration, then duration is determined by individual thresholds. If, however, the winner's size correlates negatively with duration, with an effect size approximately equal to that of the loser's size, then mutual size assessment is likely to be occurring, and the two variables can be replaced with a measure of relative size or size difference (Gammell & Hardy 2003; Taylor & Elwood 2003). Taylor & Elwood (2003) also suggested that when mutual assessment has been shown to occur, in a multiple regression involving the size of the loser and a measure of relative size as explanatory variables, only the measure of relative size should be significant. In addition, we investigated the duration of fights between size-matched competitors: mutual assessment predicts that contests between size-matched individuals should not vary with the absolute size of the competitors, as their size relative to each other is constant (Enquist & Leimar 1983, 1987). If fight duration is based on individual thresholds, fights between two larger size-matched individuals should be longer than those between two smaller size-matched individuals. Encounter duration was log transformed to normalize the data. All tests are two tailed and summary statistics are presented as mean \pm SE. Analyses were performed using SPSS for Windows, and adjusted r^2 values are reported to take account of the number of predictor variables and sample size (SPSS 2001).

RESULTS

The mean carapace size for crabs was 11.31 ± 0.046 mm and the mean claw size was 17.79 ± 0.124 mm ($N = 704$). Carapace width and claw length were highly correlated (Pearson correlation: $r_{702} = 0.958$, $P < 0.001$), so we present only the results of the analyses for claw size: the results using carapace width are qualitatively similar. There was no difference in mean size between intruders and the residents they chose to fight (residents: 17.82 ± 0.26 mm; intruders: 17.89 ± 0.24 mm; paired t test: $t_{172} = 0.269$, $P = 0.788$). Fighting was size-assortative (correlation between claw sizes of resident and intruder: $r^2 = 0.189$, $F_{1,171} = 41.167$, $P < 0.001$), but with much variation: the ratio of claw sizes (winner claw/loser claw) ranged from 0.741 to 1.852 (mean = 1.153 ± 0.016). To investigate the factors determining the outcome of fights, we followed the approach of Taylor & Jackson (2003) and used three independent predictors of outcome in a multiple logistic regression: size of the smaller rival, size of the larger rival, and whether the intruder was larger or smaller than the resident (intruder status). Overall, intruders won 33.4% of fights (exact binomial probability compared to the null expectation of 50%: $P < 0.001$). In the multiple logistic regression, the outcome of a fight was predicted by intruder status and the size of the smaller rival (status: $B_1 = 3.420$, $P < 0.001$; smaller rival size: $B_1 = -0.316$, $P = 0.003$). Stepwise multiple logistic regression revealed that only intruder status (larger or smaller) was important in determining outcome ($B_1 = 3.270$, $P < 0.001$). In cases where the intruder attacked a larger resident, intruders won only 5.7% of fights, and only the size of the larger (resident) individual was important ($B_1 = -2.673$, $P = 0.049$). Thus, smaller intruders had the best chance of winning when their opponent was not much larger. In cases where the intruder was larger than the resident, intruders won 38.4% of fights. The sizes of both rivals predicted fight outcome (larger rival: $B_1 = 0.552$, $P = 0.002$; smaller rival: $B_1 = -0.689$, $P < 0.001$; overall model: $P < 0.001$; Nagelkerke, $R^2 = 0.331$; the Nagelkerke R^2 is the logistic equivalent to the standard linear regression coefficient, SPSS 2001). As the effects are of approximately equal magnitude but opposite direction, the sizes of the larger and smaller rival can be more economically expressed as size difference ($B_1 = 0.637$, $P < 0.001$). Overall, both size and residency asymmetries were important in determining the outcome of fights in *U. mjoebergi*. The probability of a fight escalating from the push to the grapple stage was best predicted by the duration of the fight (stepwise logistic regression using smaller rival size, larger rival size, intruder status, fight outcome and fight duration as predictors: duration $B_1 = 7.60$, $P < 0.001$). Since many of the aspects of fighting follow patterns well documented in other species, we focus our discussion of fighting behaviour on the factors predicting the duration of fights.

What Determines the Duration of Fights?

The mean duration of fights was 7.48 ± 0.63 s (range 0.34–71.67 s). We began by investigating the relations

between measures of individual size and duration using simple regression. We investigated winner's size, loser's size and three measures of relative size (winner/loser, winner – loser and (winner – loser)/mean size) as predictors of fight duration (Table 1). There were significant bivariate relations between the predictor variables and the duration of fights (Table 1): all relations remained significant after correction for table-wide probability using the sequential Bonferroni procedure (Rice 1989, $N = 5$ correlations tested). The strongest single predictor of duration was the size of the loser, and duration correlated positively with both winner's and loser's size (Table 1, Fig. 1a, b), and negatively with measures of relative size (Table 1, Fig. 1c,d).

Following Taylor & Elwood (2003) we compared the sizes of the winner's and loser's claws as independent predictors of duration in a stepwise multiple regression model (overall model $r^2 = 0.412$, $F_{2,170} = 61.299$, $P < 0.001$). Both factors remained significant (winner's claw: $F_{1,170} = 14.773$, $P < 0.001$; loser's claw: $F_{1,170} = 111.234$, $P < 0.001$). The standardized partial regression (β) coefficient for the loser's claw size ($\beta = 0.782$) is positive, while the β coefficient for the winner's size is negative ($\beta = -0.285$), opposite to the simple regression in Table 1. The results of the multiple regression suggest that duration increased with the size of the loser, and, for a given loser's size, duration decreased as the size of the winner increased. If duration is determined solely by mutual assessment, the effects of the winner's and loser's sizes in the multiple regression are expected to be of opposite direction and approximately equal magnitude (Taylor & Elwood 2003). The 95% confidence interval for the β coefficient of the winner's size (0.139–0.431; absolute values) does not overlap with the 95% confidence interval for the loser's size (0.636–0.928), and thus the magnitude of the effects differs at the $\alpha = 0.05$ level, and the size of the loser's claw has a stronger effect on contest duration than the size of the winner's claw. Thus, duration increased most strongly with the loser's size, and also increased as competitors became more size-matched. When the loser's size and a measure of relative size (winner size/loser size) are used as predictors in a multiple regression, both factors remain significant (overall model: $r^2 = 0.428$, $F_{2,170} = 65.368$, $P < 0.001$; loser's claw: $F_{1,170} = 24.773$, $\beta = 0.381$, $P < 0.001$; relative claw size: $F_{1,170} = 20.003$, $\beta = -0.343$, $P < 0.001$). The same is true if size difference (winner's size – loser's size) is used in

place of relative size (overall model: $r^2 = 0.412$, $F_{2,170} = 61.229$, $P < 0.001$; loser's claw: $F_{1,170} = 38.309$, $\beta = 0.445$, $P < 0.001$; size difference: $F_{1,170} = 14.773$, $\beta = -0.277$, $P < 0.001$).

When only fights between closely size-matched individuals ($0.9 < \text{winner's size/loser's size} < 1.1$, $N = 63$ fights) were considered, duration increased with increasing mean size of the competitors ($r^2 = 0.158$, $F_{1,62} = 12.651$, $P = 0.001$; Fig. 2).

DISCUSSION

Both the size of the loser and measures of relative size were related to the duration of the fight (Fig. 1). Is the decision of fiddler crabs to retreat in a contest (and lose the fight) based on individual thresholds (own-RHP-dependent persistence) or on the assessment of their relative inferiority (mutual assessment)? Our data provide evidence in support of both hypotheses.

Fighting in *U. mjobergi* is size-assortative: intruders tended to fight residents that were of a similar size to themselves, although there was considerable variation. Fights between very small and very large individuals tended not to occur. This suggests two possibilities. First, small individuals may be able to assess their relative inferiority before a fight with much larger individuals, and attempt to avoid the fight by retreating down the burrow (when the resident) or selecting a different opponent (when the intruder). Second, large individuals may choose not to challenge residents much smaller than themselves since their small size indicates a small burrow, which may be unsuitable (Jennions & Backwell 1996). Both possibilities suggest that the decision to begin a fight is based on the assessment of the potential opponent.

The mutual assessment hypothesis is also supported by the finding that winner's and loser's sizes had opposing effects in the multiple regression. Duration increased with increasing size of the loser but decreased with increasing winner's size for a given size of loser. As winners tended to be larger than losers, this implies that duration increased as the size of the winner approached that of the loser, i.e. as the competitors became more closely size-matched, or the smaller individual won the fight. More closely size-matched individuals fought for longer than pairs in which there was a large size discrepancy (Fig. 1c, d).

Taylor & Elwood (2003) predicted that if only mutual assessment is occurring, the effect sizes would be of approximately equal magnitude and opposite direction. However, we found that the loser's size had a significantly stronger effect on duration than the winner's size. This suggests that the loser's size has the greater influence on fighting duration, and that individual thresholds may be important in determining the duration for which an individual is willing to fight. The loser's size was also the single best predictor of contest duration (Table 1, Fig. 1a), and the winner's size correlated positively with duration (Fig. 1b). In addition, both the loser's size and measures of relative size remained significant predictors of duration in the multiple regression.

Table 1. Bivariate regression relations between claw size variables and duration (log transformed) of fights in *Uca mjobergi*

Predictor variable (claw sizes)	r^2	F	N	Sign of slope	P
Loser	0.365	99.658	173	+	<0.001
Winner	0.033	6.824	173	+	0.01
Winner/loser	0.349	93.030	173	–	<0.001
Winner–loser	0.284	69.077	173	–	<0.001
(Winner–loser)/mean size	0.333	87.045	173	–	<0.001

All relations are significant after sequential Bonferroni correction ($N = 5$ tests).

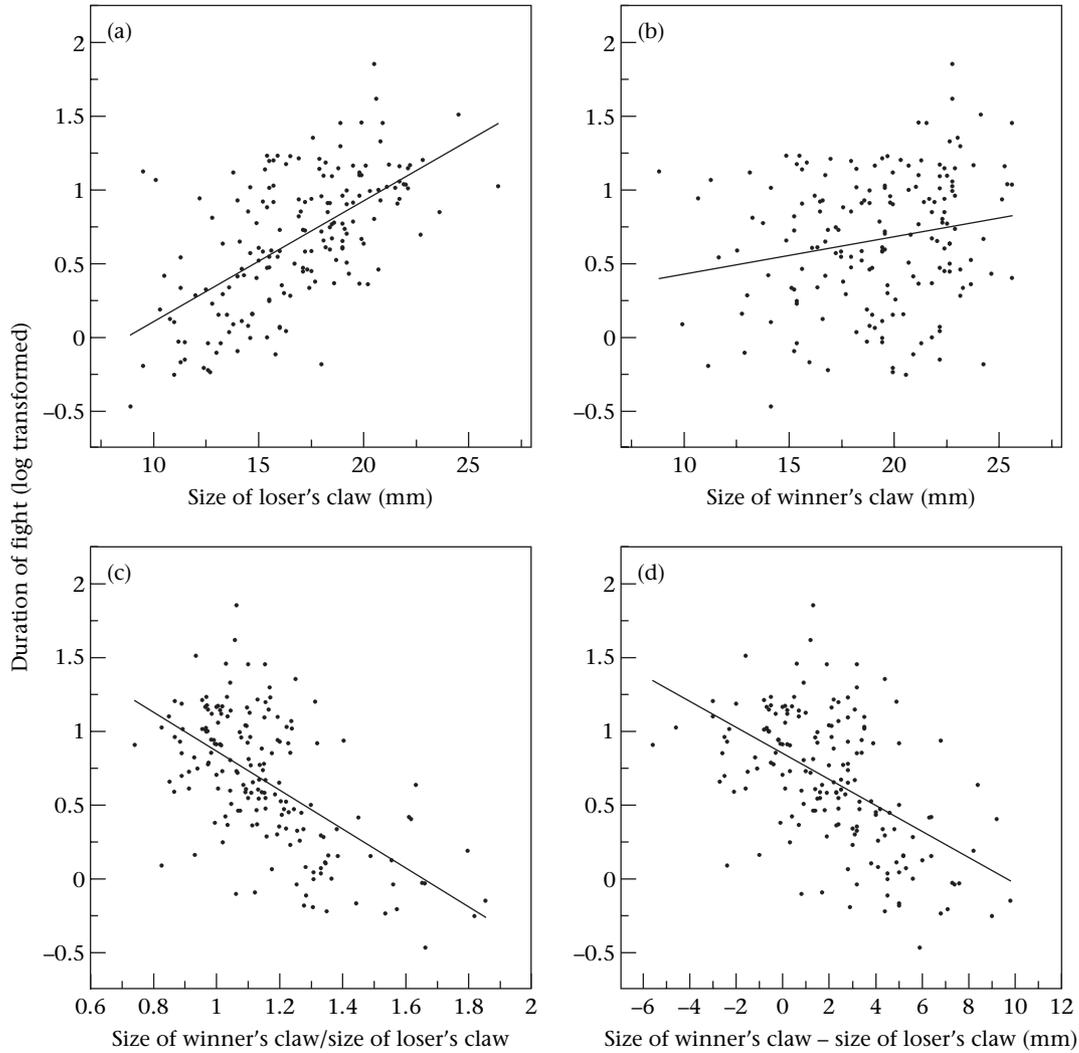


Figure 1. Relation between fight duration in *Uca mjoebergi* and (a) the claw size of the loser, (b) the claw size of the winner, (c) the relative claw sizes (winner/loser) and (d) the difference in claw sizes (winner – loser). The regression lines are (a) $Y = 0.082X - 0.712$, (b) $Y = 0.031X + 0.0725$, (c) $Y = -1.319X + 2.184$, (d) $Y = -0.081X + 0.894$ (see text for full statistical analysis).

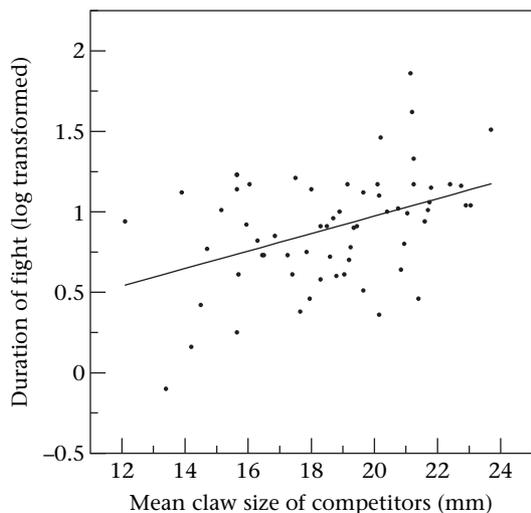


Figure 2. Relation between the mean claw size of two size-matched competitors and the duration of the fight. The regression line is $Y = 0.054X - 0.107$ (see text for statistical analysis).

Further support for the hypothesis that fight duration is determined by individual thresholds is seen when fights occurred between closely size-matched individuals. In this situation, fight duration increased with increasing mean size of the competitors, suggesting that larger individuals are able to fight for longer than smaller ones. Models based on relative size assessment (e.g. the sequential assessment game, Enquist & Leimar 1983; Leimar & Enquist 1984; Enquist et al. 1990) predict that the duration of fights between size-matched individuals should be constant regardless of the size of the competitors, since their relative size to each other is constant. Increasing duration with increasing size of size-matched competitors has been noted before (e.g. Dixon & Cade 1986; Glass & Huntingford 1988; Jennions & Backwell 1996; Whitehouse 1997; Taylor et al. 2001), but the implications of this for the applicability of models of fighting behaviour may not have always been recognized (Taylor & Elwood 2003).

Which models of animal contests provide the most appropriate description of fighting behaviour in this particular system? Our results provide partial support for both the own-RHP-dependent persistence hypothesis and the mutual assessment hypothesis, but also provide evidence against these hypotheses. Size-assortative fighting and opposite effects of the winner's and loser's sizes provide support for models based on mutual assessment, such as the war-of-attrition (Maynard Smith & Parker 1976; Parker & Rubenstein 1981; Hammerstein & Parker 1982) and the sequential assessment game (Enquist & Leimar 1983; Leimar & Enquist 1984; Enquist et al. 1990), but not for models based on individual thresholds (Mesterton-Gibbons et al. 1996; Payne & Pagel 1996, 1997; Payne 1998). Increasing duration with increasing mean size of size-matched rivals and a stronger effect of the loser's size suggest the importance of individual thresholds and support models based on own-RHP-dependent persistence, such as the war-of attrition without assessment (Mesterton-Gibbons et al. 1996) and the energetic war-of-attrition (Payne & Pagel 1996, 1997; Payne 1998), but not models based on mutual assessment (Maynard Smith & Parker 1976; Parker & Rubenstein 1981; Hammerstein & Parker 1982; Enquist & Leimar 1983; Leimar & Enquist 1984; Enquist et al. 1990).

Size-assortative Fighting?

How can we reconcile these differences? First, can the observed size-assortative fighting explain the differences we see between the predictions of Taylor & Elwood (2003) and the findings of the current study? To investigate this effect on the duration of contests, we provide a modification of the Taylor & Elwood (2003) model, where we consider size-assortative fighting. Following Taylor & Elwood (2003), we consider an animal population in which size is normally distributed about a mean \pm SD of 30 ± 6 mm. Population characteristics presented are arbitrary and serve as illustration only (as in Taylor & Elwood 2003). All simulations were performed using MatLab (Mathworks 2002). We set up 150 random pairings and select only those where the ratio of the sizes of the two individuals lies between 0.7 and 1.3. These pairs compete to simulate size-assortative fighting ($N = 121$ fights). We assume that other pairs do not compete, perhaps because rough mutual assessment causes one to retreat. As in Taylor & Elwood (2003), where fight duration was based on individual thresholds, persistence times are randomly dispersed to an approximately normal distribution centred on duration equal to own size with a standard deviation of 5 s. A fight continues until the individual with the lowest threshold reaches that level. This individual loses the fight, and the threshold is recorded as the fight duration. When duration is determined by individual thresholds, duration of size-assortative fights is positively related to the sizes of the winner and loser in a multiple regression (overall model: $r^2 = 0.563$, $F_{2,118} = 78.368$, $P < 0.001$; winner's size: $F_{1,118} = 53.000$, $\beta = 0.523$, $P < 0.001$; loser's size: $F_{1,118} = 21.139$, $\beta = 0.330$, $P < 0.001$).

Where mutual assessment occurs, and size difference determines the duration of fights, contest duration is equal to 30 s minus the absolute size difference between the contestants, randomly dispersed to a normal distribution with a standard deviation of 5 s, and we investigate duration in relation to the size of the larger and smaller contestants. When mutual assessment operates, duration is positively related to the size of the smaller contestant, but negatively related to the size of the larger contestant (overall model: $r^2 = 0.281$, $F_{2,118} = 24.423$, $P < 0.001$; larger individual size: $F_{1,118} = 47.290$, $\beta = -0.847$, $P < 0.001$; smaller individual size: $F_{1,118} = 37.599$, $\beta = 0.755$, $P < 0.001$). Comparison of the 95% confidence intervals of the β coefficients (larger size: 0.6047–1.0893; smaller size: 0.5127–0.9973) shows that the effect sizes of the larger and smaller individuals on the duration of contests are of equal magnitude, as in the original Taylor & Elwood (2003) model. Thus, size-assortative fighting alone cannot explain the patterns seen in *U. mjoebergi*, whether fights are decided by mutual assessment or individual thresholds.

Cumulative Assessment?

A potential solution can be found in the cumulative assessment game (Payne 1998). This game resembles the individual threshold models, in that each individual has a threshold level of costs it is willing to bear before retreating in a contest, and costs accrue as the result of the actions of the rival. However, superior rivals (of higher RHP) may inflict higher costs, and/or costs may accrue faster for weaker rivals (Payne 1998; Briffa et al. 2003; Taylor & Elwood 2003). To investigate such effects on the duration of contests, we provide a second modification to the Taylor & Elwood (2003) model, in which fighting is size-assortative, and persistence is based on individual, size-determined, costs thresholds, but larger rivals inflict costs at a higher rate.

In our second modification of the Taylor & Elwood (2003) approach, the sizes of 150 pairs are again normally distributed about a mean \pm SD of 30 ± 6 mm, and we again select only those fights where the ratio of the sizes of the two individuals lies between 0.7 and 1.3 ($N = 119$ fights). Again, fighting is size-assortative. In the cumulative assessment game, each rival is willing to accumulate a level of costs proportional to its size (Payne 1998), and we express this in terms of the maximum number of seconds for which the individual would be willing to fight. We incorporate random variation in the relation between size and cost threshold such that thresholds are randomly dispersed to an approximately normal distribution centred on size with a standard deviation of 3 s. Opponents inflict costs at a rate proportional to their size: larger individuals inflict costs more rapidly, and cause their opponents to reach their threshold more quickly. We define the duration persistence of an individual as (own threshold $- 1/3 \times$ size of opponent); thus, individuals are willing to fight for a shorter duration when competing against a larger opponent. A fight between two individuals continues until the lower of the two persistence levels has

been reached; this individual is designated the loser, and the fight duration recorded. Investigation of the simulated population using simple regression (Table 2, Fig. 3) reveals similar patterns of relations to those obtained from our study of fighting in fiddler crabs (Table 1, Fig. 1). Duration increases with the size of both the winner and the loser, and decreases as the difference in size between the opponents increases. We compared winner's and loser's sizes as predictors in a stepwise multiple regression (overall model: $r^2 = 0.554$, $F_{2,116} = 61.229$, $P < 0.001$), and both factors remained significant (winner's size: $F_{1,116} = 7.498$, $P = 0.007$; loser's size: $F_{1,116} = 118.033$, $P < 0.001$). As we found in *U. mjoebergi*, the standardized partial regression coefficient for the loser's size ($\beta = 0.871$) is positive, whereas the β coefficient for the winner's size is negative ($\beta = -0.219$). The 95% confidence intervals for the β coefficients do not overlap (loser's size: 0.712–1.030;

Table 2. Bivariate regression relations between size variables and duration in a simulated population of individuals, where the duration for which an individual is willing to fight depends on individual thresholds, but costs are inflicted more quickly by larger rivals

Predictor variable	r^2	F	N	Sign of slope	P
Loser	0.529	133.513	119	+	<0.001
Winner	0.107	15.195	119	+	<0.001
Winner/loser	0.169	24.983	119	-	<0.001
Winner-loser	0.251	40.440	119	-	<0.001
(Winner-loser)/mean size	0.244	38.991	119	-	<0.001

All relations are significant after sequential Bonferroni correction ($N = 5$ tests).

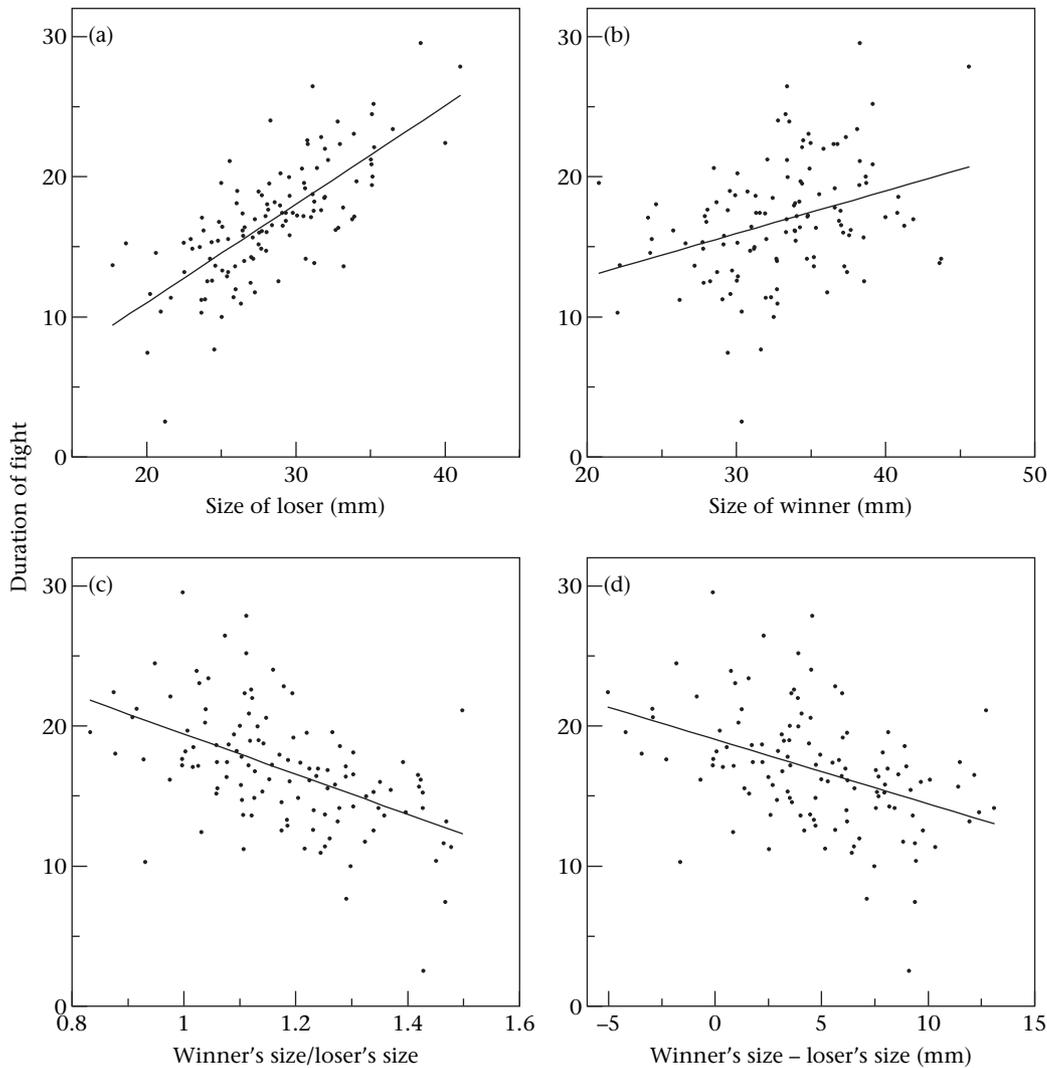


Figure 3. In a modification of the Taylor & Elwood (2003) model, individual cost thresholds determine duration, but larger individuals inflict costs more rapidly than smaller ones. When this is the case, in a simulated population, contest duration is predicted by (a) loser's size, (b) winner's size, (c) relative size (winner/loser) and (d) size difference (winner - loser). The patterns seen are qualitatively similar to those in Fig. 1. The regression lines are (a) $Y = 0.703X - 3.055$, (b) $Y = 0.306X + 6.759$, (c) $Y = -16.58X + 36.651$, (d) $Y = -0.57X + 19.59$ (see text for full statistical analysis).

winner's size: 0.060–0.378), and thus the magnitude of the effects differs at the $\alpha = 0.05$ level, and the loser's size in this simulation has a stronger effect on contest duration than the winner's size, as it did in our empirical results.

The simulation provides a reasonable match to the observed data, and suggests that in *U. mjoebergi*, the persistence of individuals in fights could be determined by individual thresholds, but that fighting a large opponent causes those thresholds to be reached more quickly, suggesting that no assessment of the opponent need occur. The cumulative assessment game (Payne 1998) may therefore be a more appropriate description of fighting behaviour in this species than the games involving mutual assessment (sequential assessment game: Enquist & Leimar 1983; Leimar & Enquist 1984; Enquist et al. 1990; war-of-attrition: Maynard Smith & Parker 1976; Parker & Rubenstein 1981; Hammerstein & Parker 1982) or based entirely on individual size (energetic war-of-attrition, Payne & Pagel 1996, 1997; Payne 1998; war-of-attrition without assessment, Mesterton-Gibbons et al. 1996). Careful consideration of the dynamics of contests can help distinguish between the true assessment of rival sizes (in the sequential assessment game) and the effect of size on the infliction and accumulation of costs (in the cumulative assessment model, Payne & Pagel 1997; Payne 1998; Briffa & Elwood 2000; Taylor & Elwood 2003). For example, the rate and sequence of actions used by the contestants within a fight can be studied.

Another possibility is that different assessment mechanisms are used during different phases of the contest. Our data on size-assortative fighting suggest that some assessment of the opponent occurs before an individual decides to engage in an interaction. Assessment of opponents may occur during one phase of an escalated fight, while individual thresholds are important in another. To investigate different assessment mechanisms during different phases, data on the duration of the different phases of the fight (e.g. the push and grapple phases in fiddler crab fights) would be needed.

Different models may be applicable to fighting behaviour in different species. In sand fiddler crabs, *Uca pugilator*, relative size is a better predictor of contest duration than the loser's size, providing support for the sequential assessment game (Pratt et al. 2003). In fights for shells in the hermit crab, *Pagurus bernhardus*, stamina and fatigue levels determine the duration and outcome of contests, supporting the energetic war-of-attrition and the cumulative assessment games (Briffa et al. 1998; Briffa & Elwood 2000). Finally, factors not considered in the original models may also influence fighting behaviour (Pratt et al. 2003), such as the risk of predation (Brick 1999).

Together with recent studies concluding that the duration of fights is determined by individual thresholds (Bridge et al. 2000; Taylor et al. 2001), our result supports the request for reanalysis of much fighting data to take the possibility of individual thresholds into account (Gammell & Hardy 2003). The results of our and other studies suggest that different models may be appropriate to different species and situations, but the differences between the models need to be tested, and further analysis of the structure of contests may be needed in

addition to studies of duration. This is especially true in cases where previous investigation has shown only some support for the model being tested. Alternative models need to be considered where the predictions of only one model have been tested, as data might have been incorrectly interpreted (Gammell & Hardy 2003).

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