The assessment game in sand fiddler crab contests for breeding burrows

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The single enlarged claw of male sand fiddler crabs, *Uca pugilator*, is used in contests for control of breeding burrows. The larger of the two contestants has the larger claw and usually wins. Males use one or more of 10 agonistic elements that vary in intensity from a no-contact extension of the claw to the flip of an opponent. We used the sequence of elements employed and the duration of unstaged, naturally occurring contests in a South Carolina salt marsh to evaluate three models of extended contests: (1) energetic war of attrition, (2) cumulative assessment and (3) sequential assessment. Contests usually began with elements of low action intensity and often proceeded to elements of high intensity. Elements of higher intensity were correlated with both contest duration and the number of contest elements. Contest duration increased as opponents became more evenly matched in size, a result consistent with both cumulative and sequential assessment models. Variation in duration increased as the relative sizes of opponents increased, also in accordance with sequential assessment. The absolute size of the smaller contestant had no effect on contest duration, in contrast to predictions based on cumulative assessment or energetic war of attrition models. Contestants that lost a fight were more likely to engage immediately in another fight without loss of contest intensity, if their previous fight had been long and intense. This result is inconsistent with contests of endurance, such as the energetic war of attrition or the cumulative assessment game, but it is consistent with the ritualized display of strength and fighting skill. Thus, sequential assessment appears to best explain ritualized fiddler crab contests. Cumulative assessment, however, may be the appropriate model for extended, nonritualized, all-out fights. Cumulative assessment may also explain the tenure of individuals on breeding grounds where multiple engagements are likely to test endurance and tolerance to damage over a period of days.

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Various game theory models have been proposed to account for contests in which animals compete through the exchange of a series of actions (Enquist & Leimar 1983; Leimar & Enquist 1984; Payne & Pagel 1997; Payne 1998). In each model, actions are evaluated through the application of a simple, unique assessment rule that yields a series of testable predictions. However, it can be difficult in practice to distinguish between models with field observations of natural, unstaged contests. Any actual contest may not conform to just one model and one assessment rule. Moreover, there can be difficulties of interpretation that are relevant to the models under consideration. For instance, a series of behavioural elements might represent a contest occurring in phases as each new element is used. Alternatively, each such series or similar series might represent a single action, the intensity of which depends on the exact set of subelements constituting the action.

We evaluated three models pertinent to contests in which animals may engage in a series of exchanges and in which they may employ a variety of behavioural elements. These are the energetic war of attrition (Payne & Pagel 1996, 1997), the cumulative assessment model (Payne 1998), and the sequential assessment model (Enquist & Leimar 1983; Leimar & Enquist 1984). We based our evaluation of models on natural, unstaged contests between male sand fiddler crabs, *Uca pugilator*, for control of breeding burrows.

The energetic war of attrition (Payne & Pagel 1996, 1997) is a game of endurance. The assessment rule is to give up when accumulated time and energy costs reach an absolute individual threshold. Escalation is expected when time costs rise at a greater-than-linear rate with contest duration. De-escalation is expected when time costs rise at a less-than-linear rate with contest duration. Contest duration is expected to reflect the endurance of

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the weaker of two contestants. In fiddler crab contests, this is typically the smaller individual (Hyatt & Salmon 1978; Jennions & Backwell 1996).

Cumulative assessment is a game of both endurance and tolerance to damage inflicted by the opponent (Payne 1998). Thus, costs include the energy invested in performance of behaviours, time invested in the contest to the exclusion of other pursuits, and physical or physiological damage. The assessment rule is to give up when accrued costs reach an absolute individual threshold. In contests where dangerous displays are used, such as fiddler crab contests (Crane 1975), escalation is expected but not de-escalation. In contests between male sand fiddler crabs, the time for escalation is similar to fight duration (Hyatt et al. 1979). In such contests, individuals of higher quality are expected to begin contests at higher intensity (Payne 1998). Both contestants escalate as the contest proceeds to maintain the optimal balance between damage costs and costs associated with time and energy demands of their own actions (Payne 1998). Contest duration should decrease with asymmetry in fighting ability if individual thresholds are correlated with the rate at which they can inflict damage on opponents.

The sequential assessment game applies to contests in which ritualized behaviours are used to reveal relative ability in nonritualized, all-out fights (Enquist & Leimar 1983, 1987; Leimar & Enquist 1984). The predictive accuracy of behavioural elements increases with their intensity. Thus, elements of low intensity are unreliable indicators of asymmetry in fighting ability and are, consequently, likely to resolve only contests in which the asymmetry is large. Sequential assessment games are expected to occur in phases, proceeding to the use of more expensive but more reliable indicators of relative ability as opponents become more evenly matched (Enquist & Leimar 1983; Leimar & Enquist 1984). However, there may be a return to elements of lower intensity due to the variance associated with the information they convey. Contest duration and the number of elements used is expected to increase as the asymmetry in ability of opponents decreases (Enquist & Leimar 1983; Leimar & Enquist 1984). Variance in duration should also increase with decreasing opponent asymmetry, reflecting both the error associated with assessment and the difficulty of relative assessment when opponents are evenly matched in ability (Enquist & Leimar 1983; Leimar & Enquist 1984). With sequential assessment, the sequence of contest elements should be similar regardless of ability or asymmetry in ability (Enquist et al. 1990).

Most empirical tests of assessment models have tested the predictions of sequential assessment (e.g. Enquist & Jakobsson 1986; Englund & Olsson 1990; Enquist et al. 1990; Jennions & Backwell 1996; Jensen & Yngvesson 1998; Molina-Borja et al. 1998; Bridge et al. 2000; Hofmann & Schildberger 2001; López & Martín 2001). Relatively few tests have considered other models such as the energetic war of attrition or the cumulative assessment game (e.g. Briffa et al. 1998; Briffa & Elwood 2000a, b, c; 2001a, b). Moreover, the majority of these tests, whether in the laboratory or the field, involved manipulation of contests or staging of fights. Contests were also often simple, with few potential contest elements. In contrast, over 20 behavioural elements have been identified in contests among fiddler crabs (Crane 1967, 1975).

This study of the sand fiddler crab represents the first test of predictions of the different assessment games through analysis of the diverse array of fiddler crab behaviours used in naturally occurring contests that were observed from beginning to end.

Fiddler Crabs

In *U. pugilator*, burrow-holding males (residents) are challenged by nonburrow holders (intruders) for burrow possession. Ovigerous females choose males by the quality of the breeding burrow, which is where both mating and subsequent brooding of fertilized eggs occur (Christy 1982, 1983; Salmon & Hyatt 1983).

Contests consist of a series of behavioural elements in which the single enlarged claw of males plays a major role (Crane 1967, 1975; Hyatt & Salmon 1978). Although some contest elements appear dangerous, death or serious injury seldom result. Fighting ability is correlated with carapace width (a measure of body size) and the size of the claw (Hyatt & Salmon 1978; Jennions & Backwell 1996), which increases almost with the square of carapace width (Pratt & McLain 2002).

METHODS

Study Site

The study site was in the high intertidal zone of a large salt marsh along the banks of the Beaufort River at Cat Island, South Carolina, U.S.A. It consisted of a 4 × 12-m mud flat bordered on its upslope side by sand mounds covering an area of 2 × 12 m. *Spartina alterniflora* bounded the lower edge of the site, and needlerush, *Juncus roemerianus*, and glasswort, *Salicornia virginica*, grew on the supratidal edge.

Breeding burrows, recognizable by the presence of mud 'hoods' at their entrance (Crane 1975; Christy 1982) were abundant at the study site. Based on measured densities of breeding burrows, we estimate that the study site supported at least 1800 resident males. Based on video-taped observations, we estimate that each day during the study several thousand intruders moved through the breeding area on their way from feeding sites in the lower marsh. Consequently, contests between intruders and residents for possession of burrows occurred frequently. We made observations at different locations in the study site over the course of the study and did not revisit a location. Thus, although we did not mark individuals, it is highly unlikely that we observed the same individual, much less the same dyad, on different days.

The study was conducted for 2–4 h a day during 10–21 May 1999 and on 4, 11, 25 June and 11 July 1999. Observations were made from low stools adjacent to the study area. Contests were recorded in their entirety. Once an observer was seated and stationary, crabs returned to

Table 1. Agonistic and nonagonistic behavioural elements observed in contests

Behavioural elements	Description
Agonistic	
Extend	Claw is swept toward opponent; no contact.
Jump	One opponent lunges at the other; no contact.
Manus align	Opponents face each other with manus of one claw held adjacent to the other; no shoving.
Manus push	Opponents face each other; each opponent pushes the claw of the other with his claw held level to the substrate.
Dactyl slide	Pollex and dactyl of the claw of each opponent are intercrossed and slid back and forth near their distal ends.
Heel and ridge	Intercrossed pollex and dactyl slide proximally to the manus; some shoving occurs.
Tap	Rapping of dactyl or pollex during Heel and ridge.
Downpush	After a Burrow retreat by one, the other opponent reaches in with his claw; claws often interlock with pinching.
Interlace	Intercrossed pollex and dactyl are clamped tight on opponents claw; vigorous shoving and pinching occurs.
Flip	With interlaced claws, one opponent is lifted from the substrate and tossed.
Nonagonistic	
Burrow retreat	One opponent retreats into the burrow, often with at least part of the claw visible.
Motionless	One opponent freezes, with the claw held aloft.
Leave	One opponent walks away.

Agonistic elements are those in which claw use is directed towards the opponent and are listed in order of increasing of contact.

normal activities. In addition to direct observation, some crabs in the study were videotaped for later analysis of contests. The area videotaped varied from day to day. Because videotapes focused on only 0.10-m² area for an hour, examination of videotape allowed us to observe 25 intruding males engaging in successive contests. We compared the duration and intensity of successive contests and determined whether duration or intensity varied with the time elapsed between successive contests.

Body Size

Because measuring crabs would have caused undue disturbance, we visually assigned contestants to one of three size categories based on carapace width: small (<14 mm), medium (14–16 mm) or large (>16 mm). Preliminary investigations revealed that assignment of an individual to a size category was correct 98% of the time. When contestants were in the same size category, we noted whether one was obviously larger than the other.

Four relative size designations permitted us to use the size differential between contestants as a categorical or ordinal variable in statistical tests: (1) 0: both contestants were in the same size category and neither was obviously larger than the other; (2) 0.5: both contestants were in the same size category, but one was obviously larger than the other; (3) 1: contestants were in different size categories, either small and medium or medium and large; and (4) 2: contestants were in different size categories, small and large.

Estimates of the density of resident males by size category were made on 21 May, 4 June and 11 June. On each date, we randomly selected six 1-m² quadrats along two transects that bisected the study area.
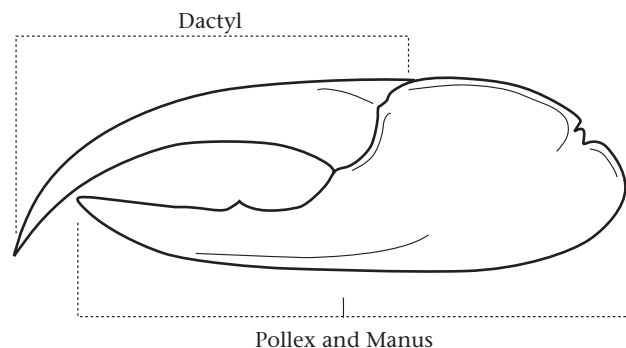

Figure 1. Claw of the fiddler crab, *Uca pugilator*.

Behavioural Elements

We recorded contest elements in sequence and the length of time each was used. Assignment of contest elements largely followed that of Hyatt & Salmon (1978). We observed 13 contest elements (Table 1, Fig. 1).

We observed or videotaped 152 contests between burrow residents and intruders where the sizes of opponents and the outcome (i.e. won by resident or intruder) were visible. Of these, we timed 128 from beginning to end. For 122 of these, we were able to record all behavioural elements used and the sequence in which they occurred. Another 13 fights were fully observed but, because these involved either two residents or two intruders, they are not included in our analyses.

Agonistic elements are those in which the claw is directed towards the opponent. We ranked these from least to greatest intensity of contact and apparent potential to inflict injury (Table 1), such that higher rank

implies greater intensity. Crane (1967) categorized behaviours as either low- or high-intensity components of combat. Our ranking matches that of Hyatt et al. (1979) and Hyatt & Salmon (1979) with the exception that we viewed Downpush as part of an ongoing fight while they regarded its use as the beginning of a different contest or subgame akin to a war of attrition. Moreover, we recognized Downpush only when a contestant reached forcibly into the burrow with his major claw. Hyatt et al. (1979) recognized the use of walking legs to contact an opponent in a burrow and excavation of the burrow while the opponent still occupied it as forms of Downpush (neither observed in our study). Some elements of contests do not appear agonistic (Table 1), and were not ranked for intensity even if common (e.g. Burrow retreat).

Statistical Analysis

The nonparametric Kruskal–Wallis test was used instead of one-way analysis of variance (ANOVA) in a number of tests because distributions were not normal for contest duration and number of elements used. With one exception (where $N_i = 5$ and $P < 0.001$), the sample size exceeded five for any given group of the categorical variable in Kruskal–Wallis tests (Mundry & Fischer 1998).

We used the Page test for ordered alternatives (Siegel & Castellan 1988) to test whether an a priori ranking of behavioural elements predicted when in a contest sequence they were first used. For every fight, each of the six common agonistic elements ($N > 20$; Extend, Manus push, Dactyl slide, Heel and ridge, Downpush and Interlace) was assigned a rank from 1 (used first) to 6. Elements not used in a given fight were assigned the same average rank, which depended on the number of the other six elements used. The value of the test statistic depended on the sum of ranks for each element. For our large sample sizes, the test statistic, Z_L, was approximately normally distributed ($\bar{X} + SD = 0 + 1$).

We also used another test to assess whether interaction elements of lower intensity were used early while elements of greater intensity were used late because, with the Page test, rarer elements get ranked as though used late in a fight, and no consideration is given to the reuse of a contest element. Here, a sequence index is assigned each time an element is used in a contest, but only if it is used. The sequence index is $m - n$, where m is the number of agonistic elements (including repeats) preceding the given occurrence of the element, and n is the number of agonistic elements following that occurrence. The index is negative for elements occurring early and positive for those occurring late. We used Spearman rank correlation to test whether the sequence index was correlated with the ranking on intensity of interaction.

Log-linear and probit analyses were used to model the categorical response variable, contest outcome, as a function of, respectively, categorical or categorical and ordinal variables (Fingleton 1984; Demaris 1992). Both log-linear and probit analyses used size and outcome (win or lose)

data from the perspective of only one contestant per fight (resident, $N = 76$; intruder, $N = 76$) because outcome and relative size are negatively symmetrical between contestants. That is, if one contestant is larger by +0.5, the other is smaller by -0.5; if the outcome is win (+1) for one opponent, it is lose (-1) for the other.

Relative variation (e.g. in contest duration as a function of the size differential) was tested with Levene's test, which compares the mean sizes of residuals among groups (Schultz 1985).

To control for type I error and maintain a study-wide $\alpha = 0.05$, we applied the sequential Bonferroni adjustment across all tests for which there was an a priori expectation of effect or association (post hoc tests excluded; Chandler 1995). For no test was the assessment of significance changed by this application.

Terminology

The order in which behavioural elements were used in a contest constitutes the contest sequence. The sequence is subject to two interpretations. It may be composed of subsequences that represent different phases, each characterized by entirely different elements. This interpretation is consistent with sequential assessment. Alternatively, each element of a contest may represent a separate action within a single phase. This interpretation is consistent with cumulative assessment or an energetic war of attrition.

A phase in a contest is all behavioural elements of similar intensity and form that occur in a subsequence that is not interrupted by use of any element of very dissimilar intensity and form. Phase category 1 includes elements in which the dactyl and/or pollex of opponents are not crossed or overlapped (Extend, Jump, Manus align and Manus push). Phase category 2 includes elements where the dactyl and/or pollex of opponents are crossed or overlapped, but without pinching and twisting (Dactyl slide, Heel and ridge and Tap). Phase category 3 includes elements in which dactyl and/or pollex of opponents are crossed or overlapped while pinching and twisting occurs (Downpush, Interlace and Flip). Interphase escalation is switching from one phase category to another of greater intensity of contact (Payne & Pagel 1996) and is a characteristic of a sequential assessment game (Enquist et al. 1990). Interphase escalation includes switching from phase 1 to phase 2 or 3 or from phase 2 to phase 3. De-escalation or even the absence of escalation would be contrary to sequential assessment.

Unlike the sequential assessment game, the energetic war of attrition and cumulative assessment permit escalation, de-escalation or no change in intensity, depending on how time costs accumulate with contest duration (Payne 1998). Intraphase escalation or de-escalation is, respectively, the general increase or decrease in the proportion of elements of greater intensity from the beginning to the end of the single phase that constitutes a contest. Escalation is predicted, however, in a cumulative assessment game that uses ritualized elements that are potentially dangerous (Payne 1998).
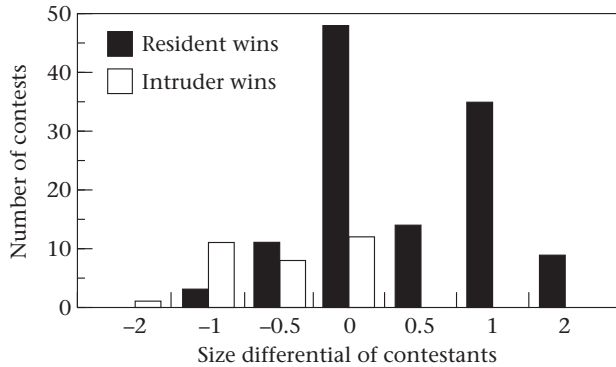
Figure 2. Number of contests won as a function of the signed size differential, resident size category–intruder size category (0=same size category, no obvious difference in size; ±0.5=same size category, one contestant obviously larger; ±1=one contestant medium in size, the other either large or small; ±2=one contestant small, the other large).

RESULTS

Demographics

The range of densities of obviously hooded breeding burrows was 13–41/m². This is probably an underestimate, because hoods destroyed by rain and tides were not reconstructed immediately. Based on counts of waving males, 24.1% of burrows were occupied by small males, 32.5% by medium-sized males and 43.4% by large males. Burrow residents in close proximity occasionally engaged in contests (8 of 165, 4.8%). Intruders that were simultaneously drawn to the same burrow sometimes also engaged in contests with each other (5 of 165, 3.0%). Most contests (152 of 165, 92.1%) were between a resident and an intruder.

The average size of the subpopulation of intruders was smaller than that of the subpopulation of challenged residents (Kruskal–Wallis test: $\chi^2_{1 \text{ (approx.)}}=6.148$, $P=0.013$).

Residents retained their burrows in 78.9% of 152 contests (chi-square test: $\chi^2_1=51.089$, $P<0.001$). Log-linear models revealed that both male type (resident or intruder) and relative size (0, 0.5, 1 or 2) explained a significant portion of the variation in contest outcome (effect for male type: $\chi^2_1=40.63$, $P<0.001$; effect for relative size: $\chi^2_9=54.86$, $P<0.001$; Fig. 2). Nonlinear probit (maximum likelihood) analysis predicted that residents would win over 80% of contests if they were in the same or larger size category relative to that of the intruder (Fig. 3).

Contest duration was positively correlated with both the number of elements used (Spearman rank correlation: $r_S=0.760$; Student's t test: $t_{121}=12.756$, $P<0.001$) and the intensity of agonistic elements ($r_S=0.439$, $t_{280}=8.147$, $P<0.001$). The average ± SD length of contests won was 21 ± 39.984 s for residents ($N=120$) and 51 ± 73.077 s for intruders ($N=32$). The longest contest (307 s) was won by an intruder. Overall, contests won by intruders were longer (Kruskal–Wallis test: $\chi^2_{1 \text{ (approx.)}}=9.235$, $P=0.002$) and used more behavioural elements (Kruskal–Wallis test: $\chi^2_{1 \text{ (approx.)}}=16.811$, $P<0.001$).

Handedness (right- or left-clawed) did not influence contests. Contestants had claws on the same side ($N=65$) or on opposite sides ($N=75$) in expected frequencies (chi-square test: $\chi^2_1=0.714$, $P=0.305$). Residents were equally likely to win when opponent claw sides matched (53 of 65 contests, 81.5%) as when claw sides differed (58 of 75 contests, 77.3%) ($\chi^2_1=0.375$, $P=0.619$).
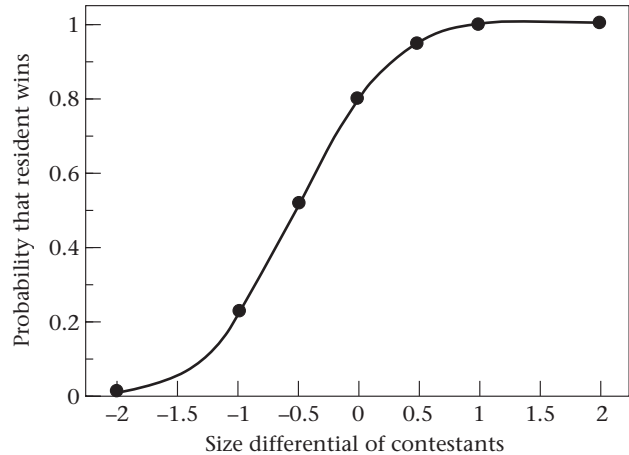

Figure 3. Maximum likelihood estimate of the probability the resident wins a contest as a function of the signed size differential, resident size–intruder size (0=same size category, no obvious difference in size; ±0.5=same size category, one contestant obviously larger; ±1=one contestant medium in size, the other either large or small; ±2=one contestant small, the other large).

Interphase Escalation

Interphase escalation characterized fiddler crab contests. The mean ± SD position of a behavioural element in a contest sequence varied with its phase category (phase 1: 1.829 ± 1.496; phase 2: 2.636 ± 1.488; phase 3: 3.980 ± 1.824; Kruskal–Wallis test: $\chi^2_{2 \text{ (approx.)}}=83.14$, $P<0.001$). Contests usually began with low-intensity agonistic elements of phase category 1 (85 of 122, 70%). In 68 contests, one or more interphase transitions occurred. In 61.8% (42 of 68) of these contests, the only transitions were from a lower- to higher-phase category. Thus, as the contests proceeded, opponents used elements of ever greater intensity of contact. In 19.1% (13 of 68) of contests, there was a transition to low-intensity elements of another phase without return to a phase with high-intensity elements. In nine of these 13 contests, a phase 1 element concluded the contest following a nonagonistic element that constituted a pause in the agonistic interaction. In another 13 contests, transitions from lower- to higher-intensity elements were repeated. In 12 of these cases, nonagonistic elements separated each set of transitions from low- to high-intensity elements.

Transitions from one phase to another were most likely to involve a change from phase 1 elements and least likely to involve a change from phase 3 (chi-square test: $\chi^2_4=64.542$, $P<0.001$). Transitions from phase 1 to 2 or from phase 2 to 3 (71 of 107 phase transitions) were twice as likely as all other phase transitions (36 of 107; t test for proportions: $t_{107}=3.820$, $P<0.001$).
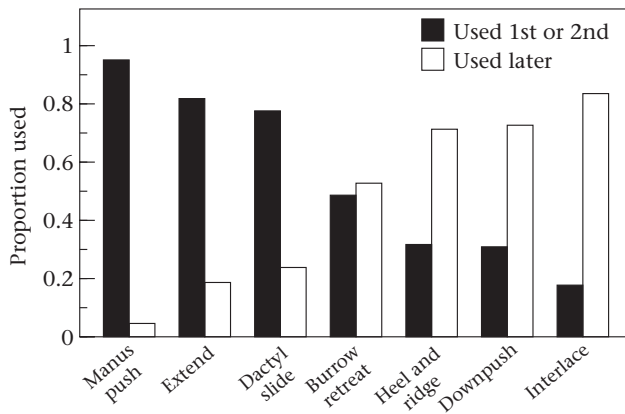
Figure 4. Proportion of use of common agonistic and nonagonistic (Burrow retreat) elements early (first or second element used) versus late (third or later element used) in contests. Arrangement of elements on the horizontal axis emphasizes the difference in use of common elements within contest sequences. Burrow retreat is used equally early versus late, but Downpush, which must follow Burrow retreat if it occurs, is primarily used late.

Intraphase Escalation

Intraphase escalation occurs when the intensity of elements increases over the course of a contest. The rank by intensity of interaction of the six common agonistic elements predicts when in a fight sequence they are first used (Page test for ordered alternatives: $Z_L=7.415$, $N=122$ contests, $K=6$ behavioural elements, $P<0.001$; Fig. 4). The sequence index was also significantly associated with the rank by intensity of interaction of all 10 observed agonistic elements (Kruskal–Wallis test: $\chi^2_{12\ (approx.)}=43.599$, $P<0.001$). Thus, elements of high intensity were only infrequently followed by other elements, but those of low intensity were often followed by others. Elements of greater intensity of interaction were used later in contest sequences (Spearman rank correlation: $r_S=0.578$; Student's t test: $t_{301}=12.289$, $P<0.001$).

Contest Duration and Relative Size of Opponents

Contest duration was positively correlated with the size category of the smaller contestant ($r_S=0.341$, $t_{127}=4.088$, $P<0.001$). Contest duration was also negatively correlated with the difference in size (i.e. relative size designation) between contestants ($r_S=-0.378$, $t_{127}=4.601$, $P<0.001$). When both the size difference and the size of the smaller contestant were modelled as categorical predictors of contest duration (log-transformed), only the effect for the size difference was significant (ANCOVA: effect for size difference: $F_{3,122}=4.637$, $P=0.004$; effect for size of smaller contestant: $F_{2,122}=0.191$, $P=0.827$). Thus, when contestants were both small, both medium-sized, or both large, there was no variation by size category for either duration (Kruskal–Wallis test: $\chi^2_{2\ (approx.)}=2.802$, $P=0.246$) or number of behavioural elements ($\chi^2_{2\ (approx.)}=1.026$, $P=0.599$).

As the size differential decreased, the mean size of the residual for contest length increased (Levene's test:

Table 2. Mean±SD sizes of the residuals for contest duration (s) and number of behavioural elements used as functions of the size differential for contestants

Size differential*	Duration		Number of elements	
	$\bar{X}\pm SD$	N	$\bar{X}\pm SD$	N
0	31.364±46.266	51	1.497±1.408	52
0.5	35.263±51.976	29	1.449±1.207	31
1	7.842±10.162	38	0.940±0.851	40
2	4.840±3.889	10	0.988±0.717	9

*0=same size category, no obvious difference in size; 0.5=same size category, one contestant obviously larger; 1=one contestant medium in size, the other either large or small; 2=one contestant small, the other large.

$F_{3,124}=14.746$, $P<0.001$; Table 2). Variation in the number of elements employed did not covary with the size differential ($F_{3,128}=2.100$, $P=0.103$; Table 2). Neither the size category of the larger contestant (Kruskal–Wallis test: $\chi^2_{1\ (approx.)}=2.842$, $P=0.092$) nor that of the smaller contestant ($\chi^2_{2\ (approx.)}=1.065$, $P=0.587$) affected the time for a contest to proceed to higher-intensity elements of phase 2 or 3 ($\chi^2_{2\ (approx.)}=3.345$, $P=0.188$). However, the difference in size between opponents was negatively correlated (Spearman rank correlation: $r_S=-0.317$) with the time until higher intensity elements were used ($\chi^2_{2\ (approx.)}=3.345$, $P=0.188$).

Contest Sequence and Contestant Size

The intensity ranking of the first element of a contest sequence did not vary with the size category of the smaller opponent (Kruskal–Wallis test: $\chi^2_{2\ (approx.)}=1.904$, $P=0.386$), the difference in size between opponents ($\chi^2_{3\ (approx.)}=5.425$, $P=0.143$), the size of contestants when both were in the same size category ($\chi^2_{2\ (approx.)}=0.557$, $P=0.757$) or the size category of the larger contestant ($\chi^2_{2\ (approx.)}=0.170$, $P=0.919$).

We found the same nonsignificant effects for size and relative size of contestants for every subsequent position in fight sequences. Consequently, the relative size of contestants had no effect as a covariate (ANCOVA: $F_{3,284}=0.630$, $P=0.596$) on the significant variation in the sequence index as a function of element intensity rank ($F_{5,284}=9.056$, $P<0.001$). Only the element Extend varied in use with the relative size of contestants. Extend was more likely to be used in contests where the resident was at least as large as the intruder (Kruskal–Wallis test: $\chi^2_{1\ (approx.)}=8.694$, $P=0.003$).

Multiple Engagements

The mean ± SD time between successive videotaped contests was 10.160 ± 10.757 s (range 1–37 s), which was short compared with the mean duration of the initial contest (28.880 ± 28.793 s; range 2–106 s; Kruskal–Wallis test comparing durations: $\chi^2_{1\ (approx.)}=9.139$, $P=0.003$).

The duration of first ($\chi^2_{2\ (approx.)}=19.047$, $P<0.001$) and second contests ($\chi^2_{2\ (approx.)}=17.519$, $P<0.001$) increased with the phase category of the most intense element used. There was no significant difference between first and second contests in the log-transformed duration (paired-difference t test: $\bar{X} \pm SD = -0.064 \pm 1.559$: $t_{24}=0.201$, NS) or intensity (by phase category: $t_{24}<0.001$, NS).

The time that elapsed between successive engagements was not correlated with the duration of the first (Spearman rank correlation: $r_S = -0.108$; Student's t test: $t_{23}=-0.521$, NS) or second contest ($r_S = -0.196$, $t_{23} = -0.959$, NS), nor did it vary with the phase category of the most intense element used in first (Kruskal–Wallis test: $\chi^2_{2\ (approx.)}=0.669$, $P=0.716$) or second contests ($\chi^2_{2\ (approx.)}=2.351$, $P=0.309$). Males that used more intense elements in their first contest were more likely than other males to use more intense elements in their second contest ($\chi^2_{2\ (approx.)}=8.448$, $P=0.015$). There was also a tendency for successive contests to be of similar duration, although the correlation between them was not significant ($r_S=0.323$, $t_{23}=1.637$, NS).

Ten of the 25 intruders engaging in successive contests won their second contest. The mean duration of these contests was longer than the mean for second contests in which intruders lost (Kruskal–Wallis test: $\chi^2_{1\ (approx.)}=6.687$, $P=0.010$).

DISCUSSION

Male Size and Quality

Assessment of asymmetry in fighting ability is selectively favoured to the extents that substantial costs might be incurred if a contest proceeds to dangerous fighting (Enquist & Leimar 1990) and resources could be controlled or co-opted through dangerous fights. Models of extended, potentially escalating contests make predictions with respect to the quality of combatants. Therefore, assumptions must be made to permit assessments of quality. We assume that the size of male fiddler crabs is positively correlated with quality. Larger males have larger, more powerful claws that can deliver substantial closing force (Levinton & Judge 1993; Levinton et al. 1995), are better able to endure prolonged mating competition (Pratt & McLain 2002) and, as we found, are more likely to control and win contests for control of breeding burrows (see also Hyatt & Salmon 1978; Christy 1982; Jennions & Backwell 1996). Larger males are also less vulnerable to some predators (Bildstein et al. 1989; Pratt et al. 2002). Thus, small-, medium- and large-sized males are assumed to be of low, intermediate and high quality, respectively.

Residents were larger than intruders, on average, and won over 78% of encounters. Residents also have larger claws for a given body size than do intruders (Pratt & McLain 2002), which suggests that breeding areas accumulate males of greater fighting ability. An accumulation effect occurs when a limited resource, such as quality breeding burrows (Hyatt & Salmon 1978; Christy 1982, 1983), can be co-opted for exclusive use.

Contest Duration

The model of the energetic war of attrition predicts that contest duration will be determined by the individual of lower quality (Payne & Pagel 1996). For fiddler crab contests, this leads to the prediction that duration will be proportional to the size of the smaller contestant. Indeed, this was the case for contests overall in our study. However, when contestants were matched for size, size did not correlate with contest duration. This result suggests that the correlation between size and duration is driven by the very short duration of contests between small and large individuals. In fact, when duration was modelled as a function of both the size of the smaller contestant and the difference in size of contestants, only the size difference was a significant predictor of duration. Thus, the energetic war of attrition is not supported by contest duration.

Contest duration and variation in contest duration were negatively correlated with the difference in size of contestants, as predicted by the sequential assessment model (Enquist & Leimar 1983; Leimar & Enquist 1984; Enquist et al. 1990). These relationships may also be consistent with cumulative assessment, if individuals of higher quality have higher thresholds to accumulated damage and inflict damage on opponents at a higher rate. When contestants are evenly matched, variation in the duration of a sequential assessment game arises from the premature termination of some contests due to imperfect information provided by low-intensity elements. In a cumulative assessment game, such variation could reflect the occasional lucky strike that severely damages an opponent.

Phases and Interphase Escalation

Interphase escalation is a unique prediction of the sequential assessment model (Enquist et al. 1990; Payne 1998). With respect to fiddler crab contests, sequential assessment games should be characterized by use of ever more intense behavioural elements, with increases in either contest duration or the number of elements used. Most contests begin with low-intensity elements in which claws are not overlapped or interlaced. Use of elements of greater intensity is restricted mainly to late use in long contests. Phase changes are characterized by procession from low-intensity elements in which claws are not overlapped to higher intensity elements in which claws are overlapped, sometimes with twisting and pinching. Transitions from pinching and claw-twisting elements to those of lower intensity are relatively rare.

As is predicted in sequential assessment games, our results are consistent with interphase escalation. Based on observations of which specific element was likely to follow any given element, Hyatt & Salmon (1978) described four levels in contests between *U. pugilator* males: (1) initiation, beginning with Extend and usually proceeding to Manus push, (2) testing, entailing use of Manus push and Dactyl slide, after which most contests end, (3) escalation, where forceful tactics such as Heel and ridge and Interlace are used, and (4) terminal phase,

characterized by Burrow retreat, then Downpush. The successive use of elements described in these levels matches the rank of elements by sequence index (which describes the likelihood that an element is preceded or succeeded by another element) and is closely approximated by the progression of elements that would be used in contests with transitions from phase category 1 (Extend, Manus push) to phase category 2 (Dactyl slide, Heel and ridge) and from phase category 2 to phase category 3 (Forceful interlace, Downpush).

Escalation or De-escalation

Intraphase escalation or de-escalation may occur through changes in the intensity with which an action is performed or changes in the proportion of high-intensity elements across a contest sequence. The latter form of escalation is potentially relevant to fiddler crab contests where a variety of distinct elements are used. Cumulative assessment games and energetic wars of attrition may exhibit intraphase escalation or de-escalation. In general, our results are consistent with intraphase escalation, which is a prediction of the cumulative assessment model when contests use dangerous displays (Payne 1998). However, whether contests are more properly viewed as occurring in one phase (consistent with cumulative assessment or the energetic war of attrition) versus discrete phases (consistent with sequential assessment) depends on the degree to which elements are mixed across phase categories within a contest sequence.

The termination of contests with phase category 1 elements after the contests had proceeded to elements of phase category 2 or 3 is contrary to the prediction of interphase escalation in a sequential assessment game. Because this was observed in 13 of 68 contests using elements of different phase categories, examination is warranted. In nine contests, the late use of a low-intensity phase category 1 element followed a nonagonistic element such as Leave. Nonagonistic elements constitute a pause in the agonistic interaction. In these cases, the better interpretation may be that the contests had begun anew and not that the prior contests were continuing. In three other contests, the concluding element was a Jump that followed a high-intensity phase category 3 element. Jump is a no-contact element, but its use after a high-intensity element suggests the willingness of the victor to continue the engagement at a high level of intensity. In the other contest concluding with a phase category 1 element, the victor used the no-contact element Extend. Again, this element, which is not reciprocated, may really serve to reveal the willingness of the victor to continue a contest. Thus, all 13 engagements that appear to contra-indicate contests occurring in phases may in fact be consistent with this interpretation.

In another 13 of the 68 contests using elements from different phase categories, there was a return to elements of lower intensity that was followed by reuse of elements of high intensity. Thus, the contests occurred in two stages. In 12 of these 13 cases, the two stages were punctuated by a nonagonistic element, either Burrow retreat or Leave. Again, it may be more appropriate to view each two-stage contest as two separate contests and not as one contest without consistent escalation.

Size, Relative Size and Contest Intensity

The cumulative assessment model predicts that males of higher quality will initiate contests at higher intensity and that contestants of lower quality will increase the intensity of their actions more quickly (Payne 1998). However, the intensity of the element with which fiddler crab contests began was not correlated with the size of the contestant and neither was the time taken for a contest to proceed to more intense elements of later phases. The size difference between fiddler crab males was significantly negatively correlated with the time to proceed to more intense elements. This result is consistent with a sequential assessment game, because once a contestant perceives that an opponent is weaker, escalation is favoured (Enquist & Leimar 1983; Enquist et al. 1990).

The sequential assessment model predicts that the size difference between contestants will not affect the sequence in which elements are used, although fewer elements are expected as the size disparity increases (Enquist et al. 1990). In the present study, the overall sequence of elements in contests for burrows did not vary with the size of either contestant or with the difference in size. Thus, the intensity of elements used in fiddler crab contests did not vary with the size of either contestant nor with the difference in size at any point along a fight sequence.

One element, Extend, was more likely to be used in contests where residents were at least as large as intruders. Extend is an unusual agonistic element in that no contact is made with the opponent and there is no reciprocal agonistic response by the opponent. Thus, it is a non-dangerous display (Payne 1998), unlike other agonistic elements used in fiddler crab contests. This observation suggests that Extend is not properly a component of the assessment game. Rather, Extend may be favoured as a signal of resident size when that signal may dissuade a potential opponent from a challenge. None of our results would change qualitatively by failure to consider Extend.

The energetic war of attrition requires that contestants match each other with regard to both the behavioural element used and the intensity with which it is used (Mesterton-Gibbons et al. 1996; Payne 1998). These requirements do not apply to fiddler crab contests, where the force of application can vary between opponents (e.g. Interlace that leads to a Flip; Manus push that sends one opponent backwards).

Multiple Engagements

Intruders may engage in successive contests with different residents where the time between contests is short relative to contest duration. If each contest proceeded until the weaker contestant had reached an endurance threshold, as in an energetic war of attrition or a cumulative assessment game, then either duration or intensity should be negatively correlated between successive contests that are separated by an average of only 10 s, unless

the recovery time is comparably short. Alternatively, a general decrease in duration or intensity might be expected. In our study, new contests were as long and intense as the contests that immediately preceded them. Furthermore, males engaging in more intense initial contests were more likely than others to engage in more intense second contests.

Videotapes revealed that some residents were challenged numerous times. For instance, one resident was engaged in 13 contests over 12.25 min. Another was engaged seven times in 9.25 min before beginning an eighth contest that lasted 11.50 min. These observations and the failure of successive contests to decline in intensity or duration suggest that most fiddler crab contests are demonstrations of strength and fighting skill that are resolved before becoming contests of endurance. However, endurance and the ability to tolerate damage may be critical to the outcome of unusually long contests and those rare contests that proceed to wild fighting as opposed to ritualized fighting. Thus, both sequential assessment and cumulative assessment games may be necessary to encompass the full range of potential conflicts.

The tendency for fiddler crab males to engage in successive contests suggests the possible appropriateness of viewing the multiple contests of a single male as one energetic war of attrition or cumulative assessment game in which the male plays the field over time. All males may eventually lose stamina due to energy use or accumulated damage as they continue to engage in contests, but high-quality males should be more likely to acquire burrows and then maintain them for longer periods due to their greater tolerance to stress and damage. Eventually, any given male must abandon his breeding area to feed and, perhaps, to recover when his energetic or tolerance threshold has been reached. However, the subpopulation of burrow residents will be of higher quality than will the subpopulations of either intruders or the males feeding at sand flats away from breeding areas (Pratt & McLain 2002), if tenure at breeding grounds is a consequence of a prolonged cumulative assessment game.

Other Extended Contests

Empirical tests of game theory models show that animal fights in nature may not conform perfectly to a single model. Predictions of the sequential assessment model have been tested both in the field and the laboratory on a variety of organisms including fish (Enquist & Jakobsson 1986; Enquist et al. 1990; Johnsson & Forser 2002), lizards (Molina-Borja et al. 1998; López & Martín 2001), pigs (Jensen & Yngvesson 1998), insects (Englund & Olsson 1990; Hofmann & Schildberger 2001), crustaceans (Jennions & Backwell 1996; Briffa & Elwood 2000a, b, c, 2001a, b), and spiders (Leimar et al. 1991; Bridge et al. 2000). In most cases, some tested predictions are upheld but others are not. For example, contests of cichlid fish, *Nannacara anomala*, provide mixed support for sequential assessment (Enquist & Jakobsson 1986; Enquist et al. 1990). Rates of behaviours vary with size of the individual, and sometimes winners and losers show different behaviours in later stages of a contest. These contest characteristics suggest cumulative assessment.

Factors not considered in the original model, such as the threat of increased predation, result in greater variability in use of agonistic elements in cichlid fish (Brick 1999). In contests between male crickets, the best indicator of resource holding power is not size asymmetry but a set of behaviours such as antennal fencing and mandible spreading (Hofmann & Schilderberger 2001). Thus, unique aspects of the ecology and natural history of animals may be reflected in contests that fail to confirm all the predictions of generally applicable models.

Most predictions of the sequential assessment model have been supported by contests in the bowl-and-doily spider, *Frontinella pyramitela* (Leimar et al. 1991). On the other hand, contests of the orb-weaving spider, *Metellina mengei*, are more consistent with the energetic war of attrition, because contest duration is correlated with absolute size of the loser rather than with relative size of contestants (Bridge et al. 2000).

Contests in the hermit crab, *Pagus bernhardus*, do not conform to any one game theory model (Briffa et al. 1998; Briffa & Elwood 2000a, b, c, 2001a, b). In this species, an 'attacker' performs rapping bouts on the shell of a 'defender'. A successful attack results in an exchange of shells between the combatants. Some contest outcomes are consistent with sequential assessment. For example, fight duration is longer when the intruder wins, and the intensity of shell rapping is indicative of resource holding power. However, stamina and fatigue appear to determine outcomes of contests, which is consistent with either the energetic war of attrition or cumulative assessment. The fact that the opponents do not match behaviours (one raps, one receives), however, is inconsistent with an energetic war of attrition.

Jennions & Backwell (1996) interpreted contests in another fiddler crab, *U. annulipes*, to provide only weak support for sequential assessment. For example, no correlation was found between contest duration and the difference in size of opponents. However, their study departs from ours in several important respects. First, their analyses did not include brief contests using only low-intensity elements. Second, they did not note element sequences. Consequently, some predictions of the model could not be tested. Third, contests were staged by removing burrow holders and placing them, as intruders, in the vicinity of other burrow holders. Thus, the resource holding potential (Parker 1974) of intruders was probably higher than for unstaged contests (e.g. Leimar & Enquist 1984; Englund & Olsson 1990).

In our study, contests between male *U. pugilator* conformed to sequential assessment games with respect to variation in duration by relative size of contestants, presence of interphase escalation and the failure of element sequences to vary by the size of contestants. Variation in contest duration was also consistent with cumulative assessment games. The failure of initial element sequences to vary by contestant size is not consistent with cumulative assessment unless the intensity with which an element is performed varies. Contests did not

conform to the energetic war of attrition because duration was not determined by the size of the smaller contestant and because opponents did not match each other for intensity. The fact that contest duration was not determined by the size of the smaller contestant is also contrary to cumulative assessment. We conclude that single contests between male sand fiddler crabs for possession of breeding burrows are generally resolved by sequential assessment games. However, cumulative assessment may explain the outcome of wild fights or the tenure of individuals on breeding grounds where multiple engagements are likely.

Acknowledgments

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