



Fighting for harems: assessment strategies during male–male contests in the sexually dimorphic Wellington tree weta

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(Received 12 May 2005; initial acceptance 2 September 2005;
final acceptance 17 February 2006; published online 18 July 2006; MS. number: A10167R)

Females often aggregate at particular sites for feeding or shelter, thus giving adult males the opportunity to defend harems and increase male reproductive success. Rival males compete for control of harems via ritualized displays or direct combat using weaponry. Contests for harems or the resources required by females can be settled based on asymmetries in fighting ability or resource ownership. Males that accurately assess a rival's fighting ability prior to engaging in potentially costly combat should be favoured by selection. Game theory and optimality models provide three models to explain how individuals decide to persist in or flee from a fight. These models are the energetic war of attrition, the sequential assessment model and the cumulative assessment model. Using staged contests in the laboratory, I tested predictions of these models using the Wellington tree weta, *Hemideina crassidens*, a sexually dimorphic insect native to New Zealand. Male *H. crassidens* use their enlarged mandibles as weapons in fights for access to adult females that reside in cavities in trees. My results supported a prediction common to each assessment model: contest duration was negatively correlated with the asymmetry in opponent's weapon size. The sequential assessment model of contest settlement was partially supported but the strongest support was for the cumulative assessment model. Predictions of the latter model were supported because: (1) fights are apparently settled based on own-size assessment; (2) fights occur in a single phase and escalate; and (3) contests involve physical combat and injury. I suggest that, in nocturnal species, cumulative assessment will generally be most applicable.

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When a resource is of equal value to two animals, contests for it can be settled based on asymmetries in fighting ability (or resource holding potential, RHP; Parker 1974), which is typically influenced by body size or mass (reviewed in Huntingford & Turner 1987; Riechert 1998) and/or weapon size (reviewed in Huntingford & Turner 1987; Andersson 1994) or symmetry (Bateman 2000). That contests are often settled based on RHP is well documented (for examples see Andersson 1994; Bradbury & Vehrencamp 1998; Riechert 1998) but there are often other factors (e.g. Neat et al. 1998a; Jennings et al. 2004). In particular, an arbitrary or uncorrelated asymmetry such as resource ownership could be used to settle a dispute without recourse to escalated fighting (Maynard Smith & Parker 1976; Huntingford & Turner 1987; Riechert 1998). Some empirical research, for example in butterflies (reviewed by Kemp & Wiklund 2001) and skinks (Olsson & Shine 2000), supports the owner-wins

hypothesis of conflict resolution. This notion of contest settlement is often criticized because alternative hypotheses often are better at explaining why owners win fights (reviewed in Riechert 1998). Grafen (1987) pointed out that apparent support for an owner-wins hypothesis may instead involve intruders retreating after obtaining information about the resident; intruders appear to lose a fight when in fact a contest did not occur. Second, individuals with higher RHP tend to accumulate as residents (Leimar & Enquist 1984), which supports a positive feedback loop: if an individual wins an energy-based resource it will probably obtain more food, grow larger and be more successful at winning subsequent contests (Grafen 1987).

Fighting can be costly to combatants because of high energetic demands and the risk of injury or even mortality, either from opponents (Hack 1997a, b; Neat et al. 1998b; Sneddon et al. 1999; Schuett & Grober 2000; Briffa & Elwood 2004; but see Riechert 1988) or from predators (e.g. Jakobsson et al. 1995; Brick 1998; Kelly & Godin 2001). Therefore, males that accurately assess a rival's fighting ability before engaging in potentially costly combat should be favoured by selection (Maynard Smith

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& Parker 1976). Game theory and optimality modelling provide three models to explain how individuals gather information about RHP to allow them to decide to persist in or flee from a fight. These models are the energetic war of attrition (Mesterton-Gibbons et al. 1996), the cumulative assessment model (Payne 1998) and the sequential assessment model (Enquist & Leimar 1983; Enquist et al. 1990) (see Table 1). The former two models are considered self-assessment games because each rival persists in accord with its own RHP, whereas the sequential assessment game uses mutual assessment of own and rival RHP (Taylor & Elwood 2003; see also Gammell & Hardy 2003).

Each assessment model makes predictions regarding escalation (Payne 1998). Escalation can be defined as switching from one type of behaviour to another that is considered more aggressive or risky (e.g. sequential assessment model) or increasing the intensity (e.g. increase in rate of repetition of a behaviour) of a specific behaviour (e.g. cumulative assessment model). These forms of escalation are not mutually exclusive.

The energetic war of attrition without assessment (E-WOA) is a game of endurance in which individuals match each other's nondangerous (i.e. no physical contact) displays (Mesterton-Gibbons et al. 1996; Table 1). Escalation is possible and the contest ceases once the loser reaches its own absolute threshold based on accumulated time and energy costs (Payne & Pagel 1996). The E-WOA differs from the war of attrition (WOA) (Bishop & Cannings 1978; Maynard Smith 1982) in that the latter is based on time only and hence is often considered a limiting case of the E-WOA (Payne & Pagel 1996). Contests

between territorial male dragonflies exemplify energetic wars of attrition (Marden & Waage 1990; Marden & Rollins 1994; Mesterton-Gibbons et al. 1996).

The sequential assessment model applies to agonistic encounters in which ritualized behaviours are used to assess an opponent's RHP and relative fighting ability in an actual fight (Enquist & Leimar 1983, 1990; Enquist et al. 1990). Fighting ability is revealed through behaviours performed in a series of steps (phases) analogous to a statistical sampling process; each step contains random error and thus more 'sampling' provides a better estimate of combatant asymmetry (Enquist et al. 1990). Fights typically begin with low-cost/low-intensity elements that are unreliable and, if the asymmetry is small and more 'sampling' is required, will proceed to the use of high-cost/high-intensity elements that better indicate RHP (Enquist et al. 1990). The sequential assessment model makes several predictions (Enquist et al. 1990; see also Table 1): (1) an individual's probability of winning should increase as its relative fighting ability (RHP) increases; (2) fights won by the intruder should be longer than those won by the resident; (3) both contest duration and variance in duration should be negatively correlated with RHP asymmetry; (4) contest duration should be positively correlated with intensity (increasing cost of behaviour); and (5) contest intensity should be negatively correlated with RHP asymmetry (i.e. with larger RHP asymmetries, contestants should resolve conflicts with low-risk behaviours and not escalated fighting).

The cumulative assessment model is a game of both endurance and tolerance to damage inflicted by an

Table 1. Descriptions, characteristics and predictions of three assessment models for the settlement of agonistic encounters*

	Energetic war of attrition	Sequential assessment model	Cumulative assessment model
Characteristic	Nondangerous agonistic displays	Nondangerous agonistic displays	Dangerous and nondangerous agonistic displays
Decision based on:	Self-assessment (sum of own actions)	Mutual assessment (difference between averages)	Self-assessment (sum of opponent's actions)
Number of phases	One	Multiple	One
Escalation	Change in intensity (increase or decrease)	Intraphase with change in behaviour	Increase in intensity
Contest duration vs absolute RHP asymmetry	Negative	Negative	Negative
Contest intensity vs absolute RHP asymmetry	Positive or negative	Negative	Negative
Contest duration vs contest intensity	Positive or negative (de-escalation)	Positive	Positive
Contest duration vs loser (or smaller male) RHP	Strong positive	Positive	Positive
Contest duration vs winner (or larger male) RHP	Weak positive	Negative	Negative
Contest intensity vs loser (or smaller male) RHP	Positive or negative	Positive	Positive
Contest intensity vs winner (or larger male) RHP	Positive	Negative	Negative

RHP: resource holding potential.

*Modified from Table 2 in Payne (1998).

opponent (Payne 1998). In this model, individuals terminate the contest when accrued costs exceed an absolute individual threshold (Payne 1998). In addition to individuals suffering energetic costs (which is also assumed by other models of assessment), the cumulative assessment model requires individuals to incur costs that are beyond the control of the individual (Payne 1998). For example, time invested in the contest to the exclusion of other activities and physical or physiological damage as well as increased risk of predation or infection by parasites. The predictions of this model are similar to those for the sequential assessment game (Table 1). For example, in order to maintain the optimal balance between damage costs and costs associated with time and energy demands of their own actions, both contestants escalate as the contest proceeds. Contest duration should decrease with increasing asymmetry in fighting ability if individual thresholds are correlated with the rate at which they can inflict damage on opponents. However, there are features unique to each model that permit distinction. For example, both the cumulative assessment and energetic war of attrition models predict that contests occur as a single phase (recall that sequential assessment proceeds in a series of steps or phases) and, when dangerous displays are used, fights are expected to escalate (Payne 1998). Also, in a cumulative assessment game, individuals with larger RHP are expected to begin contests at higher intensity (Payne 1998).

The three assessment models all predict a negative relationship between contest duration and RHP asymmetry (Taylor & Elwood 2003; Table 1). The underlying mechanisms driving this relationship, however, are different for each model and can be understood only through careful examination of contest dynamics. Taylor & Elwood (2003) developed an analytical approach to differentiate between the two types of model, self- and mutual-assessment, based on aspects of contest intensity such as duration. They show that, in the sequential assessment model, contestants mutually assess RHP, resulting in correlations between contest duration and winner and loser RHP that are approximately equal in magnitude but opposite in sign. The cumulative assessment model also predicts these relationships but the mechanism driving them is the sum of an opponent's actions on the recipient, not mutual assessment (Taylor & Elwood 2003). The self-assessment model, which supports the energetic war of attrition settlement game, predicts a positive relationship between loser RHP and contest duration and a positive, but weaker, correlation between winner RHP and contest duration. In the present study I test predictions of these assessment models by staging contests between males for control of resources attractive to females in the sexually dimorphic Wellington tree weta, *Hemideina crassidens* (Orthoptera: Tettigonioidea: Anostostomatidae), a flightless and nocturnal orthopteran insect endemic to New Zealand (Gibbs 2001).

Hemideina crassidens is a male-dominance polygynandrous (sensu Shuster & Wade 2003) insect in which the positively allometric heads of males (Kelly 2005) possess enlarged mandibles that have been long considered weapons used during fights for possession of harems (groups of one to several adult females) residing in tree

cavities, known as galleries (Hudson 1892, 1920; Sandlant 1981; Kelly 2005). Galleries are used year-round by both sexes as diurnal shelters and mating sites (Kelly, 2006b). Experimental evidence suggests that competition for larger harems (or larger galleries) should be more intense, so males with larger mandibles should reside with larger harems (Kelly 2006a). However, field studies in two *Hemideina* species have shown that cavities in trees or under rocks are often controlled by some of the smallest males in a population (*H. maori*: Gwynne & Jamieson 1998; Jamieson 2002; *H. crassidens*: Kelly 2005). This pattern could arise either if smaller males acquire unoccupied galleries that have yet to be usurped by a larger male or, as Jamieson (2002) suggested for *H. maori*, if an uncorrelated asymmetry operates in *H. crassidens* and contests are settled based on gallery ownership. Field & Sandlant (1983; see also Field 2001) showed that male *H. femorata* with greater RHP (i.e. larger mandibles) are more likely to win fights; however, hypotheses addressing the role of other asymmetries have not been tested for this or any other *Hemideina* species.

I experimentally tested the prediction that males with larger weapons (larger head size) are more successful in fights irrespective of residency status. Second, I tested the predictions of the three game theoretic assessment models (Enquist & Leimar 1983; Enquist et al. 1990). Quantifying the costs accrued by individuals during agonistic encounters is the best approach for teasing apart which assessment game combatants play and the decision rules they use to settle contests (Jennions & Backwell 1996; Hack 1997a, b; Neat et al. 1998b; Payne 1998). Unfortunately, this is often difficult to do experimentally. Recognizing this limitation, Payne (1998) argued that while support for some predictions of a model does not necessarily confirm its validity, a mismatch is a powerful refutation.

METHODS

Study Site

I conducted all experiments in the laboratory on Te Hoiere/Maud Island, New Zealand (41°02'S, 173°54'E), a 309-ha scientific reserve free of alien predators (e.g. rodents, *Mus* and *Rattus* spp., and stoats, *Mustela erminea*).

Male Head Length and Male–Male Contests

I collected experimental animals from the wild 3–4 days before a trial and isolated each in a large plastic container fitted with a perforated lid. By using digital callipers (Mitutoyo Digimatic, Toronto, Ontario, Canada) I measured male head length (top of head capsule to tip of right mandible; Fig. 1). Head length is an excellent predictor of mandible length ($r = 0.99$; Kelly 2005), the structure used in combat. For individual identification, I glued a uniquely numbered bee tag (H. Thorne Ltd., Market Rason, U.K.) to each individual's pronotum. All males were provided with food (carrot and apple ad libitum) and water each night and kept on a natural light cycle (10:14 h light:dark) and temperature regime (10–20°C, night:day).



Figure 1. Photograph of heads from dried specimens of adult male Wellington tree weta, *Hemideina crassidens*, showing the variation in head length (weapon size).

The experimental test arena was a five-sided glass cage ($23 \times 23 \times 45$ cm) with an artificial gallery made of wood attached to plywood backing on the open (sixth) side. The plywood backing was held in place using two bungee cords. The cavity diameter (including the entrance hole) was 20 mm and the cavity was 200 mm long and was bisected by a removable piece of perforated metal, to make two separate chambers. The gallery was capped by a removable unperforated piece of metal. The perforated and unperforated gates permitted the tree weta to be easily added to and removed from the experimental gallery. The bottom of the arena was covered with 20 mm of vermiculite. Test males were put into the arena through a hole above the artificial gallery; the hole was fitted with a cork stopper to prevent escape. Entrance to the gallery from the ground was facilitated by a small stick glued to the plywood backing. Two such cages were used.

I controlled for resource value because it can influence contest duration, intensity and outcome (reviewed in Riechert 1998). Studies have shown that the presence of a female increases contest intensity (e.g. Clutton-Brock et al. 1979; Verrell 1986; Wells 1988). Consequently, it is likely that galleries housing a female have greater value than an empty gallery. Pilot studies showed that males appeared less motivated to fight for or remain in experimental cavities that did not have a female. Therefore, for each trial, an adult female was placed in the upper section of the gallery and denied exit by the perforated gate. Eight such stimulus females were used.

In the early afternoon on the day of a trial, I haphazardly chose two males from a pool of males and randomly assigned one male to the role of 'resident'. Each male was used once. After placing the stimulus female in the upper chamber of the gallery, the resident male was placed in the bottom chamber below the stimulus female. The exit hole was plugged to prevent the male from leaving the gallery. The other male was assigned to the 'intruder' role and set aside in a plastic container until the trial began. Trials were

started a minimum of 2 h after sunset and were conducted in the dark. I videotaped each trial using the 'nightvision' option on a Sony Digital 8 video camera (DCR-TRV330). Trials were videotaped for a maximum of 4 h or until an interaction between the experimental males was observed.

My criterion for trial success was that the intruder placed at least a part of his head into the cavity entrance. I assumed that this behaviour was sufficient to inform the intruder that a gallery was present and to provide information as to its occupancy status. A trial was terminated if the resident exited the cavity before a contest.

Components of Fighting Behaviour

The behaviours monitored during agonistic male–male encounters in this study were described for the congeneric tree weta *H. femorata* by Sandlant (1981; see also Field 2001). I describe each element in Table 2. Each element comprises subelements typically occurring together as a 'unit' (i.e. males will typically perform the elements kick, push and grapple at the same time). I defined contest duration as the period between the first aggressive action after antennation or palpation (typically kicking or grappling) and retreat. Contest intensity was a per-contest measure based on the highest perceived degree of harm an element or action was thought to inflict. For example, antennate-palpatate should be less dangerous than lock jaws-bite, so a contest showing only the former was considered less intense than one showing the latter. A phase in a contest consists of all behaviours of similar intensity and form that are not interrupted by behaviours of dissimilar intensity or form (see Table 1). Male *H. crassidens* will often stridulate after winning a contest but pre-fight stridulation is rare, so I did not record it in this study.

Statistical Analysis

I recorded the level of escalation of all agonistic actions performed by each contestant and the duration and eventual winner of each contest (small versus large male and resident versus intruder). Intruders can evict residents either by biting, holding and pulling the resident by the hind tibia or by entering the cavity and manoeuvring above the resident to push him out using their hind legs.

The difference in weapon size of opponents was calculated in two ways: (1) percentage size difference in head length: $((\text{resident} - \text{intruder}/\text{intruder}) \times 100)$ and (2) absolute size difference in head length: $|\text{resident} - \text{intruder}|$. By using logistic regression (Hardy & Field 1998), I calculated the probability of a resident winning a contest over a gallery as a function of the percentage size difference between male head length. The sequential assessment and energetic war of attrition models predict that the variability in contest duration increases as size asymmetry decreases. Testing this prediction requires that data be grouped into bins of similar contest duration with calculation of the standard deviation of each group. The standard deviations are then correlated with absolute size asymmetry. I categorized the data into eight bins that provided

Table 2. Behaviours performed by male *H. crassidens* in contests and their associated level of escalation

Actions	Element	Level of escalation	Description*
Agonistic			
Antennate-palpate	1	Low	Males contact each other with alternating movements of antennae and maxillary and mandibular palps.
Kick-push-grapple	2	Medium	Male kicks and pushes opponent with his hind legs (often performed by intruder that has manoeuvred above resident); grappling involves males pushing against each other with mid- and forelegs.
Grapple-lunge-bite	3	High	One or both males will use their forelegs to push opponent and/or to get positioning to flip/throw, bite the head of or to block attack from the opponent. Males will lunge at opponent with mandibles gaped and will typically spread and close mandibles repeatedly while grappling apparently in preparation to bite.
Lock jaws and wrestle	4	High	Males interlock mandibles and twist their heads and bodies while they push-pull each other. This behaviour often results in an opponent being flipped over and thrown from tree. Males can also bite the head capsule of opponent. Typically terminates the contest.
Enter gallery and stridulate			Victor enters gallery after loser retreats. Victor stridulates outside and inside gallery.
Nonagonistic†			
Retreat			Loser abruptly turns from opponent and leaves immediate area.
Apply genitalia			Male curls abdomen forward and makes contact with another male. Resembles male-female copulation behaviour.
Touch mandibles			Male touches the outside tips of mandibles of opponent. Typically terminates contest without wrestling.

*Descriptions are based on those given in Field (2001).
 †Nonagonistic actions can occur at any time during male-male interaction.

a minimum of five data points within each. Bivariate correlations were performed using Spearman rank correlation because variables were not normal. For each correlation predicted by Taylor & Elwood (2003) that was statistically nonsignificant, I calculated the sample size required to achieve significance (0.05 α level and power = 0.80) given my observed effect size (r). Tests were one tailed in accordance with the predictions of Taylor & Elwood (2003) and were calculated using StudySize 1.0.8 (Olofsson 2004).

Statistical analyses were conducted using SPSS 11.0 (SPSS, Inc., Chicago, Illinois, U.S.A.) for Mac OSX.

RESULTS AND DISCUSSION

Weapon Size and Contest Outcome

Fifty-nine trials were successful, with 36 and 23 trials, respectively, having the smaller and larger male as the resident. In two trials, the conflict ended in a tie (neither male took over the cavity after the resident was displaced) and these trials are removed from some analyses.

The outcome of a contest was dependent upon role and weapon size (role \times size interaction: $G^2_1 = 5.43, P = 0.02$) with small intruders winning fewer contests than expected (2 of 23 contests; standardized residual = -1.4) and small residents winning more than expected (8 of 36 contests; standardized residual = 1.5). In general, larger males tended to win contests (resident: 19 of 23 contests; intruder: 28 of 36 contests). This result supports the sequential and cumulative assessment models because bigger males can inflict more damage (sequential assessment) and withstand more punishment (cumulative

assessment). It supports the energetic war of attrition if larger males incur fewer energetic costs than smaller males. In line with the sequential and cumulative assessment models, the probability that the resident maintained control of a gallery increased as his RHP increased relative to the intruder's (binary logistic regression: $\beta_1 = -0.096 \pm 0.027$; Wald statistic: $W_1 = 12.30, N = 57, P < 0.0001$; Fig. 2).

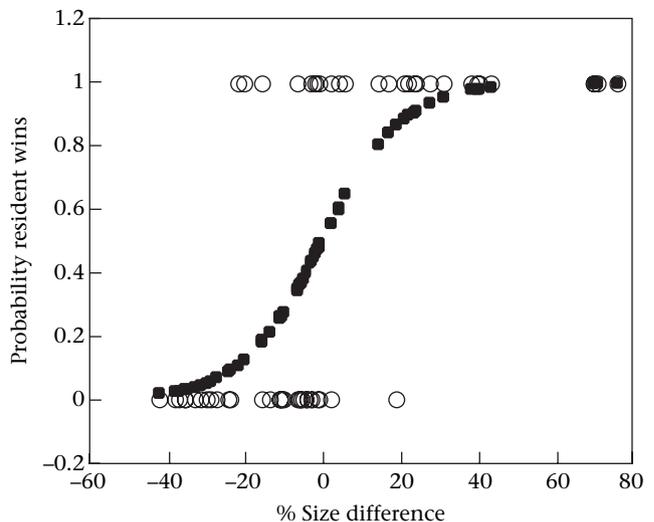


Figure 2. The outcome of 57 tree weta contests (O) and estimated probabilities of the resident male winning (■) as a function of the percentage size difference of the two contestants. Smaller negative values on the X axis indicates that intruders had larger weaponry and vice versa for larger positive values.

Rival Assessment and Contest Duration

Fights were longer and more intense when the intruder had larger RHP than the resident (Table 3) but outcome depended more on RHP than role (see above). As predicted by the sequential assessment game (Enquist et al. 1990), fights in which the intruder won were significantly longer (mean \pm SD = 74.97 ± 146.38 s, $N = 30$) than those in which the resident won (12.37 ± 19.35 , $N = 30$; independent t test for unequal variances: $t_{30.13} = 2.32$, $P = 0.027$). Smaller-RHP residents would often leave the gallery following an opportunity to inspect a larger intruder (see below).

My data met some predictions of each assessment model (Table 1). First, the relationship between mean contest duration and mean RHP difference was significantly negative (Spearman rank correlation: $r_s = -0.690$, $N = 8$, $P = 0.029$; Fig. 3); however, the relationship between mean standard deviation of contest duration and mean RHP difference was not significant ($r_s = 0.381$, $N = 8$, $P = 0.176$; Fig. 3). Second, conflict intensity (elements 1–4) was significantly positively correlated with contest duration ($r_s = 0.653$, $N = 57$, $P < 0.001$; Fig. 4). Third, contest duration was negatively correlated with both the absolute and percentage size difference in opponents (Table 3). Fourth, contest intensity was significantly negatively related to the absolute difference in RHP and showed a negative trend with percentage size difference (Table 3).

Contest dynamics in *H. crassidens* tentatively support some of the predictions of Taylor & Elwood (2003). That loser RHP and smaller male RHP were strongly positively correlated with both contest duration and intensity strongly supports self-assessment (energetic war of attrition and cumulative assessment models). That both winner RHP and larger male RHP were not significantly correlated with contest duration or intensity, as predicted, could be due to small sample size. The effect size for many of the relationships reported in Table 3 were very small and so required much larger sample sizes than I obtained.

Table 3. Spearman rank correlations between contest duration and contest intensity and eight measures of resource holding potential, RHP (head length)

Measure	N	Contest duration	Contest intensity
Resident	57	-0.104 (571)	-0.058 (1837)
Intruder	57	0.219* (128)	0.242**
Winner	57	-0.136 (333)	-0.083 (897)
Loser	57	0.298**	0.276**
Larger	57	-0.121 (421)	-0.033 (5678)
Smaller	57	0.284**	0.287**
% Size difference	57	-0.216* (131)	-0.202 (158)
Absolute size difference	57	-0.330**	-0.230**

All tests were one-tailed as per the predictions of Taylor & Elwood (2003). Numbers in parentheses were the required sample size to achieve statistical significance at $\alpha = 0.05$. * $P < 0.06$; ** $P < 0.05$.

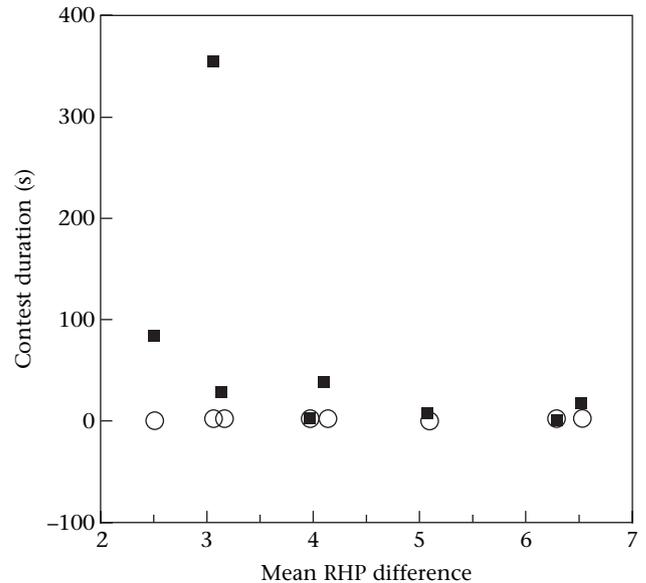


Figure 3. Mean (■) and mean standard deviation (○) of contest duration in eight different size asymmetry classes.

Agonistic Behaviour and Description of Contests

In 77.9% of all trials (46 of 59), the intruder entered the gallery and extracted the resident male using his mandibles to grip the hind tibia of the resident and pull him from the cavity. In seven trials, the resident backed out of the cavity without direct removal; these instances involved a very large resident male (head length > 24 mm) and a much smaller intruder male. In 10.2% of trials, the smaller intruder entered and left the gallery without extracting the larger resident. In 47.5% of trials (28 of 59), the loser either left the immediate vicinity without further contest or he antennated-palpated the opponent and then retreated (element 1). Contests escalated to

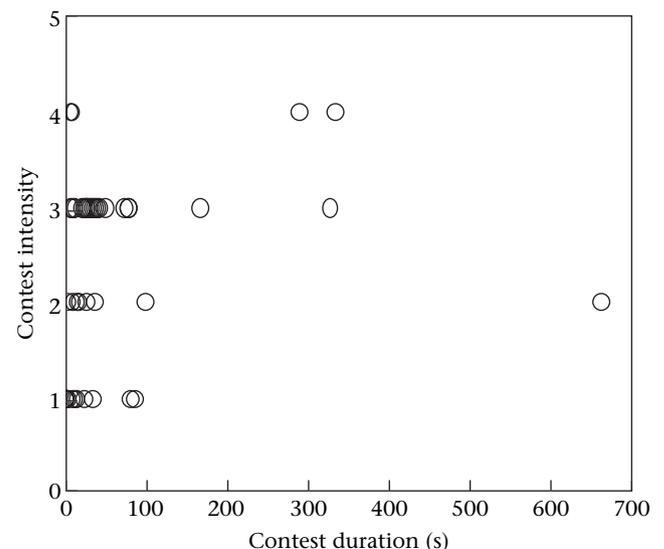


Figure 4. Relationship between contest intensity and contest duration.

element 2 in 13.6%, to element 3 in 32.2%, and to element 4 in 6.8% cases.

Contests between male *H. crassidens* appear to occur in a single phase; fights did not proceed in an ordered manner (i.e. all behavioural elements performed in an order) with subsequences (different phases with different elements) of repeated displays. Instead, after a bout of brief and mutual antennation, males would fight ($N = 31$). Fights could quickly escalate and did not always include all the behavioural elements listed in Table 2.

Thirteen fights (22%) were settled after males faced each other and opposed their spread mandibles. The male with mandibles on the inside (typically narrowest gape) immediately retreated in 100% of such interactions and in all but two cases the larger male (widest gape) won the contest. In the interactions in which the smaller male won, the difference in weapon size was very small between the opponents (i.e. 0.79 and 0.59 mm, respectively). Field & Sandlant (1983) argue that mandible gaping by male *H. femorata* is a visual signal of RHP to opponents. However, because tree weta fights occur in near complete darkness, a visual signal is probably useless. I suggest that gaping is used as a tactile signal of RHP. Additionally, gaping could represent a male readying his jaws for fighting or protection. Fights only increased in intensity and did not de-escalate (i.e. contests did not go from lock jaws to antennate/palpatate).

GENERAL DISCUSSION

The Role of Asymmetries in Contest Outcome

Male Wellington tree weta can take over and control galleries through combat, using their enlarged mandibles as weapons. My results show that males with larger weapons (head length) have greater resource holding potential (RHP) and that this factor affects contest outcome more than does resource ownership. Similarly, Sandlant (1981) reported that male *H. femorata* with a wider mandible gape, which is positively related to head length, were more likely to win contests.

I found a weak residency effect: resident males with smaller RHP won more contests than expected (sensu Maynard Smith & Parker 1976). Sandlant (1981) found that resident male *H. femorata* were more successful than intruders at winning contests; however, weapon size of the experimental males was not controlled for in his study. Perhaps male *H. femorata* with larger weapons accumulated as residents (sensu Leimar & Enquist 1984) and the observed fights were settled based on RHP. Jamieson (2002) suggested that a residency advantage may be operating in a third species, *H. maori*, thus explaining why males with small mandibles controlled harems in cavities (under rocks in this species).

Assessment Strategies

Fights between Wellington tree weta, similar to fights in other animal species (Jennings et al. 2005; Morrell et al. 2005), agree with several shared predictions of the

energetic war of attrition and the cumulative and sequential assessment models. First, contest intensity was positively correlated with fight duration. Second, contest duration was negatively correlated with asymmetry in weapon size. In the sequential assessment model, closely matched opponents require more time to detect smaller differences in RHP (Enquist & Leimar 1983), and in the cumulative assessment model, individual thresholds depend upon the rate at which they can inflict damage on rivals, where larger RHP males can inflict greater damage on a smaller RHP male than can two evenly matched opponents (Payne 1998).

If a negative relationship exists between RHP asymmetry and contest duration or intensity, as predicted by each of the three assessment models, Taylor & Elwood (2003; see also Gammell & Hardy 2003) recommend examining contest dynamics in order to determine whether individuals are self- or mutually assessing. Determining how animals assess is important because it sheds light on which assessment model explains contest settlement in that species. My results showed the predicted negative relationship between RHP asymmetry and both contest duration and intensity; therefore, I examined the underlying mechanism driving such a negative correlation. Self-assessment (own RHP-dependent persistence; Taylor & Elwood 2003) is supported because contest duration strongly increased with smaller rival RHP (or loser RHP). This finding excludes the sequential assessment model, which requires mutual assessment of combatants, but supports the energetic war of attrition model and the cumulative assessment model (Taylor & Elwood 2003). Taylor & Elwood (2003) showed that when contest settlement is based on own-RHP persistence, contest duration depends primarily on the weaker (loser) rival's RHP rather than RHP difference between contestants. This is because costs accrue through each combatant's own actions and stronger rivals are more persistent; hence, a positive relationship exists between smaller male RHP (or loser RHP) and contest duration (Taylor & Elwood 2003).

Taylor & Elwood (2003) also recommend evaluating assessment models by examining the relationship between larger male RHP (or winner RHP) and contest duration; a positive relationship suggests self-assessment is operating whereas a negative relationship suggests mutual assessment. Tree weta fights showed a negative trend for the relationship between contest duration (and intensity) and larger male RHP (and winner RHP) (Table 3). These trends suggest mutual assessment, however, the results are inconclusive.

Why did tree weta show a significantly positive effect for correlations involving smaller RHP males (and loser RHP) but not for those involving larger males (or winners)? Perhaps this is a consequence of the nature of tree weta fights. Because fights occur at night and often involve males pulling other males out of galleries, males rarely have the opportunity to evaluate rivals visually before or during a contest (occasionally males will be able to match mandibles). Perhaps when two contestants are more closely matched for RHP, and thus evaluation of the rival is made more difficult, the larger male occasionally retreats. Examination of Figure 3 in Taylor & Elwood (2003)

shows that this situation would change little the positive relationship between smaller rival size and contest duration compared with its tendency to reduce the effect of larger rival size on contest duration. To detect potentially smaller effects involving larger male RHP in tree weta, and possibly in other nocturnal species (or species in which reliable information is difficult to acquire), larger sample sizes are required to increase statistical power.

Despite a lack of clear differentiation of the assessment models using statistical methods, there are several key characteristics that can discriminate the models (Payne 1998; Taylor & Elwood 2003). For example, fights in tree weta do not agree with the energetic war of attrition because contests involve physical contact and are probably not based on endurance; nor do they agree with sequential assessment because contests do not involve ritualized displays. On the other hand, tree weta contests agree with the assumptions of the cumulative assessment model in that they involve dangerous displays. All models of assessment assume some energetic costs to fighting; however, Payne (1998) argues that only the cumulative assessment model is applicable to situations in which there are significant physical costs, arising as a direct result of an opponent's actions. Fights between male tree weta are probably costly in terms of energy and time expenditure. However, potentially more significant costs are probably physical in nature; fighting male tree weta can incur substantial injury including loss of antennae, legs and mandibles. In one case, an opponent died after his head capsule was crushed by his rival. Male tree weta can also suffer costs beyond their control, what Payne (1998) calls 'external costs'. For example, because fights are often terminated when one opponent throws the other off a tree trunk, loser males may expose themselves to increased predation risk and lost mating opportunities.

Wellington tree weta contests agree with the cumulative assessment model in that they showed intraphase (contests occur in one phase) escalation; sequential assessment predicts interphase escalation (more than one phase with each phase being more intense than the previous) (Pratt et al. 2003). This distinction largely hinges upon whether contests are properly viewed as occurring in one phase (i.e. as predicted by cumulative assessment and energetic war of attrition) or in discrete phases (i.e. sequential assessment) and relies on the degree to which elements are mixed across phase categories within a contest sequence. That contests between male *H. crassidens* appear to proceed in one phase with dangerous and costly elements (i.e. without ritualized displays) and elements could be mixed offers further support for the cumulative assessment model in this species. All models of assessment rely on investigators accurately identifying costly versus noncostly behaviours in their species. Jennions & Backwell (1996) warn that ranking different behavioural acts on a scale of costliness can be very difficult and relying on our perceptions of what is costly can be unreliable. Therefore, the costs of agonistic behaviours should be better quantified in *H. crassidens* to offer a less subjective appraisal of costs.

Finally, the sequential assessment model predicts that contests will begin with low-intensity elements and

proceed to the use of high-intensity elements. On the other hand, the cumulative assessment model predicts that individuals of higher quality will begin contests at higher intensity and individuals of lower quality will escalate faster. All 59 contests in this study began with antennation-palpation and did not de-escalate if high-intensity elements were used. Although contests never began with two males locking jaws, they could quickly escalate to this element without using the other elements. These observations lend support to the cumulative assessment model.

In conclusion, contest resolution in *H. crassidens* appears to conform to the cumulative assessment model. Perhaps the cumulative assessment model is generally applicable to nocturnal species and species in which information about the rival (gathered visually, acoustically or otherwise) is unreliable. More study is required in tree weta and other nocturnal species to determine whether there is a consistent interspecific pattern to contest resolution.

Acknowledgments

I thank Darryl Gwynne, Michael Jennions, Robert Payne and two anonymous referees for comments and advice that improved the manuscript. I am grateful to Steve Ward and Karen Mayhew of the New Zealand Department of Conservation for logistical support and haircuts while this work was conducted on Maud Island. This study was supported by grants from the Natural Sciences and Engineering Research Council of Canada and the National Geographic Society to Darryl Gwynne and an Orthopterists' Society Research Grant to the author.

Supplementary Material

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.anbehav.2006.02.007](https://doi.org/10.1016/j.anbehav.2006.02.007).

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