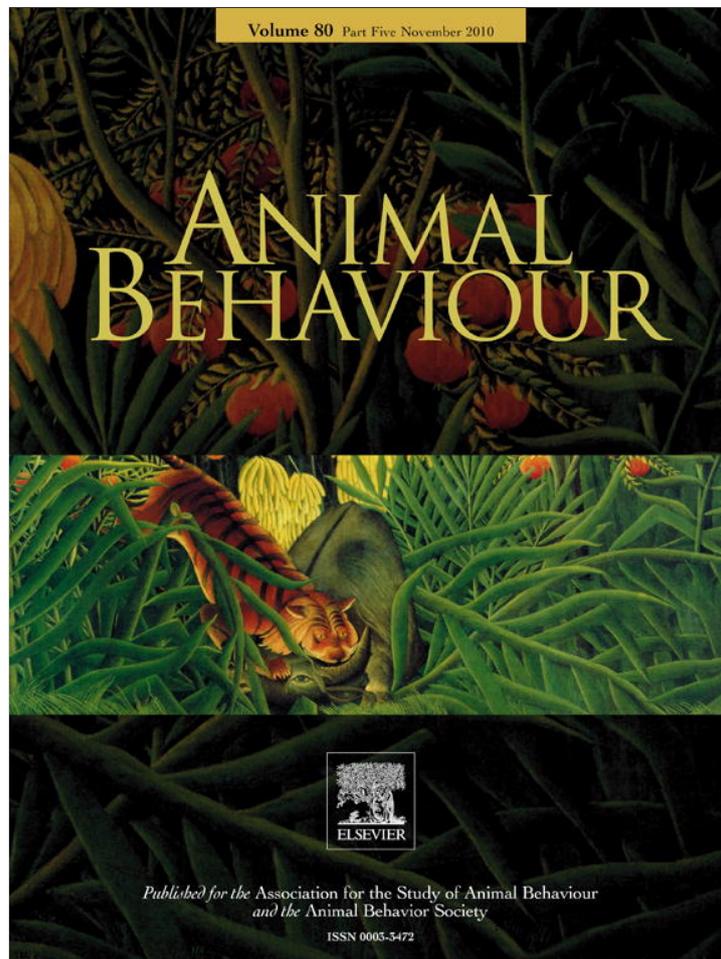


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Assessment of self, opponent and resource during male–male contests in the sierra dome spider, *Neriene litigiosa*: Linyphiidae

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Contestants in agonistic encounters may use assessments of self, opponent and resource quality as a basis for making behavioural decisions. Ritualized displays reduce risk and energy expenditure during assessments, but may lead to injurious fighting behaviour under certain circumstances. In this study, we examined the decision-making process of male sierra dome spiders (*Neriene* (= *Linyphia*) *litigiosa*: Linyphiidae) during 323 male–male contests using multivariate analysis. In contests over females, male ritualized displays include distinct phases by which males facultatively escalate fights: ritualized noncontact display, pedipalp wrestling, and unritualized biting and grappling. Amongst these phases we found evidence for all three types of assessment. Self-assessment was indicated by effects of the lighter male's mass and the metabolic effect of temperature. These factors influenced the duration of noncontact display, likelihood of escalation and energetic expenditures. Opponent assessment, indicated by the effects of the difference in mass between contestants, influenced all aspects of fight behaviour when differences in body mass were large. When differences in body mass were small, relative mass only affected the duration of the fight, primarily by lengthening noncontact display. Resource assessment, measured through effects of female reproductive value and the males' future reproductive opportunities, primarily influenced the decision to escalate to unritualized combat and the duration of the unritualized combat. Our multivariate analysis of behaviourally distinct phases of contests showed that contestants use diverse information to adjust investment in displays and potentially injurious fighting. We discuss the roles of information transfer versus raw attempts to influence outcomes in this complex contest system.

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Competition over resources routinely brings animals of many species into conflict with conspecifics (Huntingford & Turner 1987; Arnott & Elwood 2008). Males of many species compete for female reproductive capacity as a limiting resource (Andersson 1994). Each contestant must process multiple forms of information to weigh the economics of vying for the resource (Enquist & Leimar 1983, 1987). Rivals are also under selection to adaptively manipulate the opponent's perception of those costs and benefits (Johnstone 1998; Riechert 1998; Searcy & Nowicki 2005; Elwood et al. 2006; Szalai & Számadó 2009). The study of robust decision-making processes (i.e. those resistant to deception) should use multivariate data that represent the diverse information available to contestants in the real world (Kemp et al. 2006). Such studies should reflect the

fact that the kind and quality of information, and the assessment modes used by contestants, are likely to vary when assessment behaviours change qualitatively during a single contest (Morrell et al. 2005; Hsu et al. 2008; Triefenbach & Zakon 2008).

Three information sources are available during any contest: self, opponent and resource. Self-assessments estimate physiological capacities, residual reproductive value, energy reserves and accumulated fighting skill. Opponent assessments evaluate an individual's resource-holding potential (RHP) relative to their opponent's, and thus estimate the proportion of one's reserves that would have to be committed to prevail in continued and escalated displays, and in an all-out unritualized fight. Resource assessments estimate intrinsic qualities, such as the expected fertility, sexual receptivity, fecundity and genetic quality of potential mates. They could also estimate extrinsic factors affecting resource valuation, such as the expected costs of obtaining alternative reproductive opportunities of similar value (reviewed in Arnott & Elwood 2008).

Ritualized contest behaviours reduce the risk of injury and fatality associated with assessment compared to actual physical combat. Ritualization should also reduce the energy costs

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of assessment (deCarvalho et al. 2004) and reduce the risk of predation (Jakobsson et al. 1995). Proximity risk, from the potential for opponents to use physical strength and injurious weapons in escalated contests, is crucial to maintaining honesty in ritualized agonistic contests (Számádó 2008). It is thus clear why, across species, overt advertisement of strength and weaponry are common during ritualized displays (Számádó 2003). Regardless of proximity, the opportunity for cheating is higher when signals of lower cost are used. Thus, the quality of information concerning relative RHP is likely to be less accurate in a ritualized contest than in unritualized combat (Enquist et al. 1990), as well as in ritualized displays that are, on average, less energetically demanding. Time spent in ritualized behaviour may increase costs if an unritualized fight is warranted, such as when opponents have closely matched RHP (Reece et al. 2007), and the value of the contested resource is high or a contestant's residual reproductive value is low (Enquist & Leimar 1990). The likelihood of future conflicts with the same opponent also may contribute to occurrences of fatal fighting (Piper et al. 2008). Under these circumstances, cheaper ritualized modes of assessment should be more readily abandoned. Furthermore, the chance of winning an unritualized fight just by luck is likely to be higher. Therefore, 'underdogs' that would normally lose a resource by inflexibly using information on relative RHP gained during ritualized assessment may escalate to unritualized fighting more quickly and frequently than expected, especially under the circumstances mentioned above. Such escalations may be under-reported if contests in those circumstances cannot be followed from beginning to end (Piper et al. 2008).

Contestants should regulate the time and effort invested in ritualized displays to allow efficient management of their opponent's behaviour while estimating their opponent's RHP with a flexible degree of rigour (see Lailvaux & Irschick 2006). Many species have evolved multiple, usually sequentially deployed assessment behaviours (Enquist & Leimar 1983). These assessment behaviours help individuals adjust the costliness of assessment according to accuracy demands (Watson 1988; Wells 1988; Pratt et al. 2003; deCarvalho et al. 2004; Hsu et al. 2008; also see Arnott & Elwood 2009 for a discussion of switching assessment strategies). Each subsequent behaviour in a facultative series is expected to provide new or improved information acquisition or transfer because of its functional design or an associated increase in contest costliness.

During intrasexual conflicts over females, males must update their estimate of the costs and benefits of competing for the current female versus moving on to search for an alternative mate. Core issues in the study of such intrasexual conflict include identifying the kinds of information that rivals gather during contests and how they do so, whether contest behaviours contain elements designed to influence contest outcome without transmission of useful information, and the conditions under which ritualized contest behaviours give way to injurious forms of fighting (Arnott & Elwood 2009; Randall et al. 2009; Briffa & Sneddon 2010). Game-theoretical models of contests purposely distil decision-making processes down to a few factors and assessment criteria (Kelly 2006; Arnott & Elwood 2008), and specifically test the predictions of alternative models (Briffa & Elwood 2009). When used as predictive tools, such models are able to explain some of the behaviours and contingencies seen in natural systems, but none provide full explanations (e.g. Jennings et al. 2005; Morrell et al. 2005).

To gain a more complete understanding of the decision-making process during a contest, researchers are increasingly using comprehensive multivariate approaches (e.g. Kemp et al. 2006; Jonart et al. 2007; Prenter et al. 2008; Ancona et al. 2010). In the present study, we used a multivariate approach to investigate assessment of self, opponent and resource in male sierra dome

spiders during contests over females. Over the course of several breeding seasons we staged male–male fights in a naturalistic context, where normal opportunities for retreat were available, resource values could be assessed as efficiently and accurately as allowed by evolved perceptual and cognitive mechanisms, and conditions were well suited for the execution of signalling adaptations designed to convey blends of honest and dishonest information and influence.

Here we present analyses of decision making during the fights of male sierra dome spiders competing for sexual access to females and their webs. Results presented here are condensed mainly from Keil (2007). Prior research on the female sierra dome spider's sexual selection system (Watson 1986, 1988, 1990, 1991a, b, 1993, 1998), and on the energetics of intersexual courtship (Watson & Lighton 1994; P. J. Watson, unpublished data) and male–male fighting (deCarvalho et al. 2004), provides the background for the present study.

Sierra dome males have a repertoire of three distinct contest behaviours, two ritualized and one unritualized, that they use facultatively, usually in sequence, during fights with conspecifics: noncontact display (=phase 1), pedipalp wrestling (=phase 2), and unritualized biting and grappling (=phase 3). Males make a series of decisions during a fight, such as how long to spend in any one of the three behavioural phases, how far to escalate, whether or not to engage in unritualized fighting, whether to take a break in fighting, and how long to continue fighting.

We performed a multivariate analysis of factors influencing the fighting behaviour of males based on observation of 323 fights: 268 staged in nature over free-living females and their webs and 55 staged in CO₂ respirometry flasks containing small webs without a female present. In addition to male behaviour and fight outcomes, we collected data on absolute and relative magnitudes of male RHP-related traits, several potential environmental influences, and two major dimensions of female reproductive value, namely, sexual receptivity and fertility. We examined the importance of assessment of self, opponent and resource to male decision-making processes during the three behavioural phases that characterize sierra dome spider contests. To find the qualities of the males that are operative in assessments of self and opponents, we first determined which traits influenced the likelihood of winning a fight. We then examined the influence of those traits, of environmental conditions and of resource quality on the duration and likelihood of escalation through the phases of assessment. We also used the behaviour of contestants to reveal which aspects of resource quality were important to males and when they became influential (as in Stocker & Huber 2001; Bergman & Moore 2003).

METHODS

Study System

Life cycle

Male sierra dome spiders mature within 2 weeks of one another at the beginning of the breeding season, while females mature more asynchronously over the next 6–7 weeks. Thus, in the present study, both virgin and nonvirgin females were available for use in staged fights well into the breeding season. Males become nomadic 2–3 days after maturation and then depend upon the webs of females for food and shelter. Male–male fights over exclusive access to a female and her web occur whenever there is an intrasexual encounter. All fights and matings occur within the dome portion of female webs and are readily observed.

Female reproductive value

Penultimate female sierra dome spiders communicate their nearness to sexual maturation through an easily observed set of

behaviours (Watson 1990). The female's signal of impending maturation entails maintaining close proximity to any visiting male within the dome portion of her web; this is termed 'associative' behaviour. Penultimate females begin associative behaviour 2–6 days (mean = 2.3 days) before maturation. Females further from maturation show 'avoidant' behaviour, shunning close contact with all visiting males. Associative behaviour is equivalent to a signal of reproductive value, because it reflects the time that a male can expect to guard the female in order to have sexual access to her as a newly mature virgin, and thereby profit from (1) her full receptivity to mating (2–3 h after her final moult) and (2) a 60–70% share in the fertilization of her eggs, a fertilization rate that, on average, is very high compared to that expected by subsequent mates (Watson 1991a). Males clearly recognize the greater reproductive value of associative females. While they guard avoidant females only for 1 day or less, they reliably attempt to guard an associative female for several consecutive days (i.e. until they are evicted by a rival male or the female matures and mates).

Nonvirgin or mated females reject most of their subsequent suitors (Watson 1990), but typically remate 1–2 times before oviposition. Males that mate with nonvirgin females share unevenly in the 30–40% of fertilizations that, on average, are not allocated to first mates (Watson 1991a, b). Regardless of the sexual receptivity of a previously mated female, males do not court or guard the female for more than 1 day.

We considered penultimate associative females and mature virgin females to provide a high-value first-mating opportunity for contesting males, and we considered penultimate avoidant females and mature mated females to be of relatively low reproductive value, because of the males' much lower chances of mating and fertilization success (Watson 1991a).

Females that have not mated 1 week or more after maturation will begin to apply a volatile pheromone to their web. The pheromone marks these females as a high-value mature virgins and helps males to find their webs from a distance. The pheromone elicits a distinct male behaviour termed 'web reduction', in which the male excises the scented silk from the dome of the female's web and packs into a tight ball or strand to prevent rivals from finding the female (Watson 1986; Schulz & Toft 1993). Because web reduction reduces the informational discrepancy between contestants, we excluded fights over pheromone-producing females from our analyses of fight duration, degree of escalation and intensity.

Male fighting behaviours

The fights of sierra dome males escalate facultatively through three distinct behavioural phases. The first two fighting phases, 'noncontact display' and 'pedipalp wrestling', are cooperative, noninjurious and stereotypical (Fig. 1). Escalation from noncontact display to pedipalp wrestling entails increased risk, however, as the latter is far more difficult to disengage from, especially if one male decides to escalate to the third, unritualized phase of fighting, 'biting and grappling', which always carries a high risk of injury or death. Energetic costs also increase nonlinearly with each phase; the greatest increase occurs between noncontact display and pedipalp wrestling (deCarvalho et al. 2004). Pedipalp wrestling is an apt name because it requires that the males lock themselves together, face to face (making bites impossible), by placing their palpi over one another's coxae ('shoulders'). However, the pushing, pulling and lifting forces generated once a lock is achieved, as in unritualized fighting, clearly involve use of all leg, pedicel and palpi musculature.

Data Collection

For each contest we measured three kinds of potential influences on fighting behaviour: (1) environmental factors, (2) traits

reflecting the quality of the female and her web and (3) characteristics of the two contestants relevant to their absolute and relative RHP. Table 1 defines the variables used in all analyses.

We recorded male behaviour as a narrative throughout each fight. We introduced both males to the female's web usually within a few minutes of each other and noted the timing and order of introduction. We recorded the time to the nearest second for each change in behaviour, including escalation from one phase to the next. When exact times could not be determined because of the rapidity of interactions, we estimated the times spent in each behaviour over 5 s intervals.

In our analyses, we used three semi-independent measures to characterize the level of investment that males made during each contest. Wells (1988) suggested that, in multistage contests, the degree of behavioural escalation, which he termed intensity, would often be a better measure of the cost of a fight than its duration. We include analyses of factors affecting degree of behavioural escalation and durations of fighting phases, but to obtain the best possible measure of fight costs, we also created an intensity variable incorporating both duration and degree of escalation. Moreover, our intensity measure was calculated using the empirical estimates of average energy expenditure for each fighting phase from deCarvalho et al. (2004). We multiplied the observed duration of each phase of fighting by the expected relative energetic expenditure for that phase, compared to male resting metabolic rate, so that $\text{intensity} = 3.5 \times (\text{phase 1 duration}) + 7.4 \times (\text{phase 2 duration}) + 11.5 \times (\text{phase 3 duration})$.

Staging of contests

Fights were conducted at The University of Montana's Flathead Lake Biological Station, Polson, MT, U.S.A., during the sierra dome breeding season (July–August). We collected data from 323 fights observed during eight breeding seasons between 1989 and 2001.

Males were either captured immediately after maturation (1995 and 1999–2001; $N = 204$ fights) or from the webs of females at an unknown time after maturation (1989–1992 and 1998; $N = 119$ fights). In most years, we captured males randomly, but in 1998, we captured one group of randomly selected males and one group of males from the webs of newly moulted females (i.e. assumed to be 'champions' of fights on the associative female's web). Most fights staged during 1998 were between a randomly selected male and a champion male ($N = 53$ fights). Data from these fights were included in analyses of behaviour but not in analyses of probability of winning.

During most years, behavioural observations of fighting were made on webs in the wild. In 1999, fights were staged in respirometric flasks containing web produced by a mature virgin female, but with no female present at the time of the fight (see deCarvalho et al. 2004). Energetic data were gathered during these fights along with behavioural observations ($N = 55$ fights). These 1999 data were used in analyses of probability of winning, which we felt confident could be determined, but not in analyses of fighting behaviours, because of concerns about how the limited space within the flasks and very small webs might lead to less natural fighting behaviour.

The average difference in body mass between contestants varied amongst years. In all years except 2001 we attempted to match the masses of opponents within 15% (mean = 7.9%, maximum = 30.8%), so that the influence of other factors could play a more detectable role in fight-related decision making. Most fights in 2001 involved opponents with more than a 25% mass difference (mean = 24.8%, maximum = 37.7%), and served as pretreatments for an experiment testing the effects of winning and losing experience on fighting behaviour (Keil 2007).

Between 1989 and 1991, males were captured and fought a single time before being released into their natural habitat.

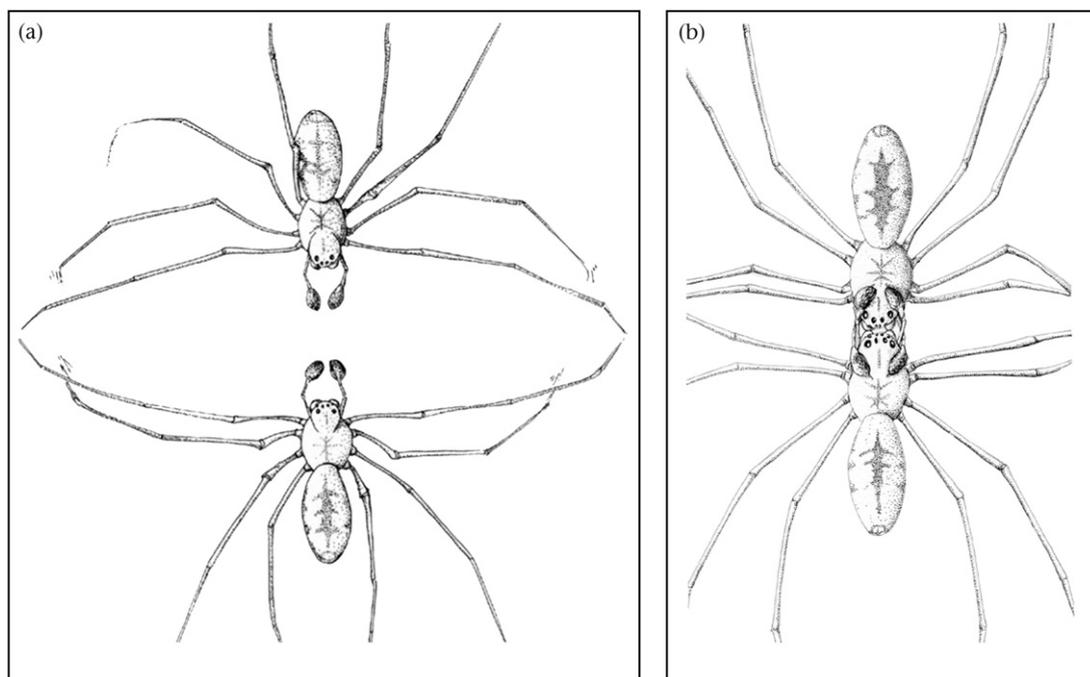


Figure 1. Ritualized fighting behaviours in male sierra dome spider contests. (a) Phase 1 noncontact display as seen from below. Both contestants spread their first pair of legs and may strum the web with the second pair. Males may tap one another with the tips of their legs but do not make further contact. (b) Phase 2 pedipalp wrestling as seen from below. Contestants place their pedipalps over their opponent's coxae and attempt to force their opponent through the dome of the web.

In later years, males were maintained in the laboratory for multiple fights, and for each fight we studied the effect of each male's recent win/loss record and duration of previous fighting experience. We did not include 2001 data in these analyses because in that year every male's win/loss record was experimentally determined by staging fights with a large mass difference between the opponents.

Animal Care

Captive males were housed individually, under roughly ambient conditions, in 600 cc containers, which provided ample fresh air and walking space. They received nightly misting with water and were fed freshly captured natural prey sometimes supplemented by laboratory-reared *Drosophila*. We fed captive males enough to maintain them at, or slightly above, their mass at the time of collection. We kept close track of each male's body mass, recording it before each fight trial or measure of metabolic rate, either alone at rest or during fight trials, in our CO₂ respirometry system (deCarvalho et al. 2004). Males that did not senesce while in the laboratory were released at the site at the conclusion of the study season.

Individual males generally were observed in multiple fights. To identify individuals, we used small amounts of thinned Testors® enamel paint, applied with the end of an insect pin, to mark each male with a unique set of colours on the tibia of the hindmost legs. The size and placement of these marks did not interfere with fighting. To ensure that other legs and mouthparts were not contaminated with paint, we waited for the spider to remain still voluntarily before quickly tapping their leg with a dab of paint. Most remained still or were allowed to crawl around until the paint dried, which takes about 45 s. If they showed signs of preparing to groom, then we used distraction (not restraint) to keep them from doing so by lightly shaking the petri dish they were in or poking them lightly with a finger or twig until the paint dried completely. No anaesthesia was used on any males.

During most years, we terminated a fight after more than 20 min of inactivity (10 min in 2001) or when one of the males left the web. When a male left the web he was declared the loser. When both males remained on the web, the declared winner was the male in the dome centre, the consistently favoured position on the web for foraging, predator protection and mating. If both males were in dome centre, or if the fight had ceased because of the presence of a predator, then the fight was declared a draw and was not used in any statistical analyses.

Statistical Analyses

We used SYSTAT version 11 (SYSTAT Software, Inc., Richmond, CA, U.S.A.) for all statistical analyses. We estimated univariate and multivariate linear models of factors influencing (1) the intensity of fights, (2) the total duration of fights and (3) the duration of each phase within fights. We tested residuals from the final multivariate linear models for normality using one-sample Kolmogorov–Smirnov–Lilliefors tests. The multivariate residuals for all these models were non-normally distributed. Therefore, we log transformed these dependent variables. All the models with log-transformed dependent variables had normally distributed multivariate residuals (all $P \geq 0.077$).

We estimated univariate and multivariate logistic regression models of (1) the probability of winning a given fight, based on the relative characteristics of the males, and (2) the probability of escalation or deritualization, based on the quality of the resource and the characteristics of the males. Significance tests for individual predictors in the multivariate logistic regression models were based on Wald tests.

The core model for all behavioural analyses included the following covariates: date, time, temperature, mass difference and lighter male's mass. These covariates were kept in the model on theoretical grounds, regardless of their statistical significance, for their conditioning effect on model estimation. Other characteristics

Table 1
Dependent and independent variables analysed in this study

Variable	Description
Fight outcome	
Analysed in relation to the relative characteristics of the contestants	
<i>Dependent variable</i>	
Probability of winning	For the multivariate analyses one of the two contestants was chosen randomly for each fight, and the advantages were calculated as (focal individual–opponent). For univariate analyses, all calculations were (winner–loser)
<i>Independent variables</i>	
Mass	Mass of the males recorded to the nearest 0.001 mg
Age	The number of days since male sexual maturation; only when final moult observed
Resting metabolic rate	Resting metabolic rate on or near the date of the fight, standardized for temperature
Mass-adjusted win/loss record	A male's prior win/loss record, adjusted for the asymmetry in mass he had with opponents in those fights (for details see Keil 2007, Chapter 1, Methods)
Fighting experience	Summation of the time that a male spent fighting in prior won and lost fights
Behavioural decisions	
Analysed in relation to environmental factors, characteristics of the opponents and characteristics of the resource	
<i>Dependent variables</i>	
Escalation	Differentiating fights that included only noncontact display from those that escalated at least to pedipalp wrestling (excludes fights with out-of-phase escalations directly from phase 1 to phase 3)
Deritualization	Differentiating fights that contained only pedipalp wrestling from those that became unritualized (excludes fights that did not escalate beyond phase 1)
Breaks	Denotes fights in which males took one or more breaks from fighting for other behaviours
Out-of-phase deritualization	Denotes fights with an instance of direct escalation to unritualized fighting, either from no fighting behaviour, or from noncontact display (regardless of whether phase 2 occurred previously during the fight)
Total duration	Length of time actually spent fighting (combination of the 3 behavioural phases).
Phase duration	Length of time spent in each of the 3 phases, tested separately
Intensity	Estimate of the energetic cost of the fight (see deCarvalho et al. 2004) incorporating both the degree of escalation and the duration of the fight (see Methods)
<i>Independent variables</i>	
Date	Day of the breeding season (recorded as number of days since 1 June)
Time of day	Time when the second introduced male entered the dome of the web
Temperature	Ambient temperature (in °C) at the start of each fight
Mass difference	Mass difference between the opponents: (heavy male mass)–(light male mass)
Lighter male's mass	Mass of the lighter of the two contestants
Female reproductive value	Female's virgin versus nonvirgin status, denoting whether she afforded the contestants an opportunity to be her first mate ('yes', for associative penultimate and mature-virgin females; 'no', for avoidant penultimate or mature mated females)
Web diameter	Diameter of the web's dome: an estimate of the web's value as a foraging resource
Female presence	A female was considered present during the fight if she was in the dome at the end of the fight and at dome centre at some point after the second male entered the web

of the males, the resource and the environment were removed from the model in a stepwise fashion if they had a $P > 0.15$, with the largest P values being removed first.

Our experimental design in 2001 resulted in a strong positive relationship between female reproductive value (virgin versus nonvirgin status) and body mass difference between males in all

staged fights (two-sample t test: $t_{241} = 9.028$, $P < 0.001$). Mass differences between contestants greater than 20% occurred almost entirely on the webs of relatively low-value mated females. Therefore, we examined the behavioural effect of mass differences using only fights staged on webs of low-value females, and we included only independent variables of the core model as covariates. We then examined the behavioural effects of other variables using only fights between males differing in mass by less than 20%.

We examined correlations between predictors in multivariate models. Temperature and date were significantly positively correlated (e.g. Pearson correlation: $r_{141} = 0.432$, $P < 0.001$) for the data used to estimate the final multivariate model of fight intensity. Date also was negatively associated with the frequency of observations involving females of high reproductive value (separate variances: $t_{140.7} = 7.63$, $P < 0.001$). Moderate tolerance statistics (well above 0.5) and the stability of betas when variables were included or excluded suggest, however, that multicollinearity did not have degrading effects on our model estimates.

In our study, the lighter male's mass and the relative mass difference between contestants were not correlated, because we paired males at specific mass differences regardless of their absolute mass (Pearson correlation: $r_{167} = -0.064$, $P = 0.412$). We found no significant interactions in our regression models between lighter male mass and heavier male mass. Heavy male mass was never the stronger predictor of the winning male. Thus, for our purposes the occurrence of self-assessment was indicated by a correlation between the lighter contestant's mass and fighting behaviour, while opponent assessment was supported by fighting behaviours correlated with the mass difference between contestants (Taylor & Elwood 2003; Arnott & Elwood 2009).

RESULTS

Probability of Winning

Fights were more likely to be won by the heavier contestant ($t_{313} = 12.243$, $P < 0.001$). The advantage conferred by greater mass was especially dramatic when contestants differed by more than 15–20%, with the lighter male winning only 5% of fights staged between males with more than 20% mass difference compared to 37% in fights staged between males with less than a 15% mass difference (Fig. 2).

In fights with mass differences less than 15%, males with a history of winning previous fights (against different opponents) had a greater probability of winning their current fight in analyses controlling for the small residual mass difference ($t_{41} = 2.429$, $P = 0.015$). We found no evidence of associations between a male's

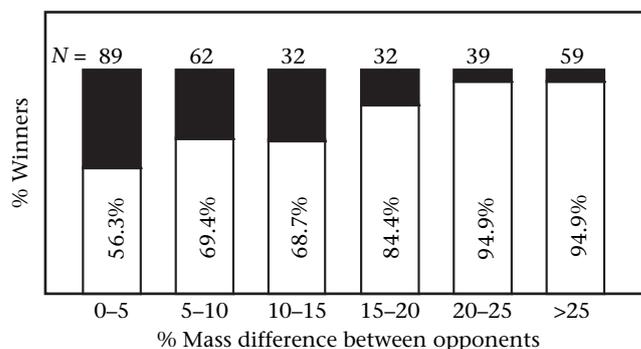


Figure 2. Percentage of fights in which the lighter male won based on the percentage mass difference between opponents. ■: lighter male; □: heavier male.

Table 2
Logistic regression models of factors influencing contest behaviours for fights with ≤20% relative mass difference

Variable	Dependent variable: Wald <i>t</i> statistic (<i>P</i> value)*			
	Escalation	Deritualization	Out-of-phase deritualization	Occurrence of breaks
N of final model †	132	108	146	152
Time	-1.393 (0.163)	-0.111 (0.912)	-0.731 (0.465)	-0.710 (0.477)
Temperature	0.501 (0.616)	0.217 (0.828)	0.249 (0.804)	-0.528 (0.597)
Date	-0.253 (0.801)	3.782 (<0.001)	2.832 (0.005)	0.983 (0.326)
Mass difference	0.747 (0.455)	-0.542 (0.587)	-0.253 (0.800)	1.470 (0.142)
Lighter male's mass	2.544 (0.011)	-1.451 (0.147)	-1.987 (0.047)	0.193 (0.847)
Female reproductive value	1.712 (0.087)	2.208 (0.027)	1.847 (0.065)	-0.100 (0.920)
Web diameter	-0.629 (0.529)	0.073 (0.941)	1.166 (0.244)	0.751 (0.452)
Female presence	-0.002 (0.998)	-0.026 (0.979)	-0.129 (0.898)	-0.803 (0.422)
McFadden's r^2 of final model	0.094	0.189	0.105	0.025

* Values in bold were significant at $P < 0.05$. Values in italic denote variables that were removed during stepwise elimination (i.e. the effect of each variable when it was included in the final model, and not necessarily the value at the time of elimination).

† 'Escalation' excludes fights that became unritualized but did not cooperatively escalate to phase 2 at some stage; 'Deritualization' excludes fights that did not escalate beyond phase 1; 'Occurrence of breaks' includes fights in which all of the variables in the final model were measured.

probability of winning and resting metabolic rates, age, or overall (i.e. winning and losing) fighting experience (all $P > 0.9$).

In fights where we imposed small mass differences and statistically controlled for residual effects of mass difference, we found an association between male residency status and the probability of winning that depended on female reproductive value (i.e. virgin or nonvirgin status). The first male placed on the web (the resident) tended to win more often than expected in fights staged on webs of females with high reproductive value (univariate logistic regression, Wald test: $t_{61} = 1.843$, $P = 0.065$). The resident male lost significantly more often than expected on the webs of females with low reproductive value (Wald test: $t_{37} = -2.795$, $P = 0.005$). In a multivariate logistic regression, an interaction term between female value and male residency was a significant predictor of winning (Wald test: $t_{97} = 3.345$, $P < 0.001$). This result was not affected by the time elapsed between the introduction of the second (nonresident) male and the onset fighting, or by the number or length of breaks during fighting, the length of residency prior to the second male's introduction, or the size of the web.

Behavioural Patterns: Effects of Relative Mass

ANCOVAs examining various influences on male behavioural patterns during contests are detailed in Tables 2 and 3. Table 2 gives results of logistic regression models looking at influences on categorical dependent variables, namely, escalation, deritualization, and the occurrence of out-of-phase deritualization and breaks.

Table 3 shows results from our linear regression models of factors influencing the continuous dependent variables intensity, duration, and phase duration. Table 4 then summarizes statistically significant results from Tables 2 and 3, organized to make clear how each significant factor indicated the presence of one of the three types of assessment: self, opponent and resource.

Mass difference between opponents was a predictor of key behavioural decisions, and an indication that opponent assessment influences sierra dome spider contests. In fights on webs of nonvirgin low-value females, those involving a male–male mass difference of more than 20% were more likely to end in noncontact display (≥20% mass difference: 64.9% of 74 fights, <20% mass difference: 41.5% of 65 fights; Pearson chi-square test: $\chi^2_{37} = 8.818$, $P = 0.003$). Fight intensity decreased with increasing mass asymmetry in multivariate models ($t_{122} = -5.713$, $P < 0.001$). This result is attributable to more closely matched males being more likely to (1) escalate to pedipalp wrestling (Wald test: $t_{117} = -2.459$, $P = 0.014$) and (2) fight longer ($t_{122} = -5.313$, $P < 0.001$), especially in noncontact display ($t_{122} = -4.534$, $P < 0.001$) and pedipalp wrestling ($t_{58} = -3.054$, $P = 0.003$).

On these nonvirgin females' webs, relative mass of closely matched contestants was not significantly related to the occurrence ($t_{66} = -1.787$, $P = 0.074$) or duration ($t_{17} = 0.128$, $P = 0.900$) of unritualized fighting. However, out-of-phase deritualization (i.e. the direct transition from noncontact display to biting and grappling, without pedipalp wrestling) was more likely between more closely matched males ($t_{125} = -2.838$, $P = 0.005$). Breaks in fighting

Table 3
Linear regression models of factors influencing contest behaviours for fights with ≤20% mass difference between contestants

Variable	Dependent variable: <i>t</i> statistic (<i>P</i> value)*				
	Log total duration	Log phase 1 duration	Log phase 2 duration	Log phase 3 duration	Log fight intensity
N of final model †	143	149	95	48	143
Time	0.392 (0.696)	0.824 (0.411)	-0.368 (0.713)	1.949 (0.058)	0.019 (0.985)
Temperature	-3.253 (0.001)	-4.142 (<0.001)	-1.297 (0.198)	-0.834 (0.409)	-2.467 (0.015)
Date	2.492 (0.014)	2.003 (0.047)	0.604 (0.547)	2.644 (0.011)	2.730 (0.007)
Mass difference	-2.082 (0.039)	-2.228 (0.027)	-1.385 (0.170)	0.111 (0.912)	-1.885 (0.061)
Lighter male's mass	2.974 (0.003)	2.142 (0.034)	1.501 (0.137)	-0.133 (0.895)	2.870 (0.005)
Female reproductive value	1.547 (0.124)	0.177 (0.860)	1.107 (0.272)	0.249 (0.805)	2.260 (0.025)
Web diameter	0.803 (0.423)	1.258 (0.210)	-1.497 (0.138)	0.788 (0.435)	0.380 (0.704)
Female presence	-0.226 (0.822)	-0.749 (0.455)	2.242 (0.028)	-0.052 (0.958)	-0.108 (0.914)
R² of final model	0.186	0.163	0.130	0.180	0.180

* Values in bold were significant at $P < 0.05$. Values in italic denote variables that were removed during stepwise elimination (i.e. the effect of each variable when it was included in the final model, and not necessarily the value at the time of elimination).

† 'Total duration', 'Phase 1 duration' and 'Phase 1 intensity' exclude fights with >1000 s ($N = 3$); 'Phase 2 duration' and 'Phase 3 duration' exclude fights in which the dependent variable was equal to zero.

Table 4
Influence ($P \leq 0.150$) of factors indicating types of assessment used for decision making throughout a fight

Decision type	Self-assessment		Assessment of opponent*		Assessment of resource		
	Lighter male's mass	Temperature (metabolic rate effect)	Mass difference (full range)	Mass difference (<20%)	Female reproductive value	Date	Female presence
Intensity	+(0.005)	–(0.015)	–(<0.001)	–(0.061)	+(0.025)	+(0.007)	NS
Escalation	+(0.011)	NS	–(0.014)	NS	+(0.087)	NS	NS
Deritualization	–(0.147)	NS	–(0.074)	NS	+(0.027)	+(<0.001)	NS
Out-of-phase deritualization	–(0.047)	NS	–(0.005)	NS	+(0.065)	+(0.005)	NS
Total duration	+(0.003)	–(0.001)	–(<0.001)	–(0.039)	+(0.124)	+(0.014)	NS
Phase 1 duration	+(0.034)	–(<0.001)	–(<0.001)	–(0.027)	NS	+(0.047)	NS
Phase 2 duration	+(0.137)	NS	–(0.003)	NS	NS	NS	+(0.028)
Phase 3 duration	NS	NS	NS	NS	NS	+(0.011)	NS
Breaks	NS	NS	–(0.007)	+(0.142)	NS	NS	NS

Significant values are shown in bold.

* 'Mass difference (full range)' = multivariate analysis for all fights staged on webs of females with low reproductive value, which provide no first-mate opportunity, in a model including only the core variables; 'Mass difference (<20%)' = multivariate analysis for all fights with less than 20% mass difference between the males, in the final model for each decision type. The results for all other assessment variables were also taken from the final model for fights with less than 20% relative mass difference between the males.

also occurred more often when males were more closely matched in body mass ($t_{125} = -2.700$, $N = 127$, $P = 0.007$).

Behavioural Patterns: Escalation and Deritualization

Female reproductive value was not a significant predictor of any dependent variable in univariate analyses (all $P > 0.15$), but was predictive in several multivariate models. In fights where the males differed in mass by less than 20%, escalation to pedipalp wrestling occurred more when the lighter male was of greater absolute mass and when the female represented a high-value first-mate opportunity for the males (Table 2). Fights over high-value virgin females were more likely to escalate and deritualize (Table 2). Although the probability of escalation beyond noncontact display varied little throughout the season (pooled variance: $t_{148} = -1.280$, $P = 0.214$), fights that did escalate were more likely to become unritualized later in the season (Tukey HSD multiple comparison: $P = 0.006$; Fig. 3).

Out-of-phase deritualization occurred more often as the season progressed and in the presence of high-value females. The probability of out-of-phase deritualization also increased in fights where the lighter contestant also was of lower absolute mass (Table 2). Of the 21 fights in which the male that initiated the first out-of-phase deritualization was known, 13 were initiated by the heavier male (chi-square test: $\chi^2_{19} = 1.190$, $P = 0.275$).

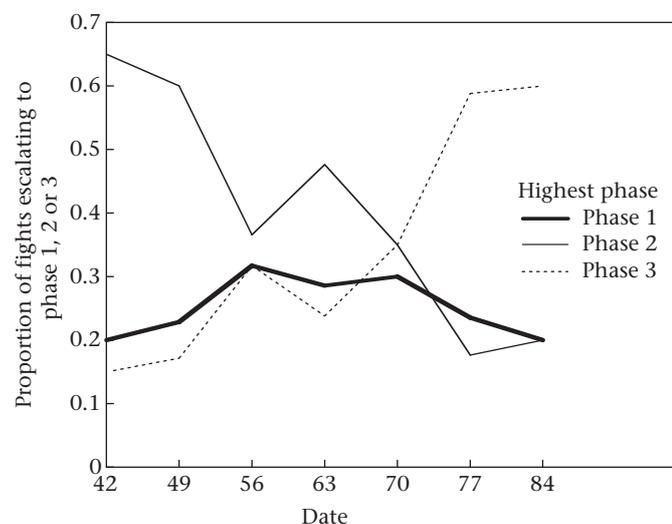


Figure 3. Proportion of fights that escalated to phase 1, 2 or 3 as a function of date (days since 1 June). Fights were compiled over 7-day periods to obtain proportions.

Behavioural Patterns: Duration and Intensity

In univariate analyses, fight duration and intensity both significantly increased with web diameter ($t_{153} = 2.539$, $P = 0.012$ and $t_{143} = 2.939$, $P = 0.004$, respectively), but web diameter was not a significant predictor of any dependent variable in multivariate analyses (Table 3).

Even amongst fights with less than 20% mass difference between the males, fights lasted longer when males were more closely matched in mass. Total fight duration also was greater, on average, in contests where the lighter contestant was of greater absolute mass, later in the breeding season, and at lower temperatures (Table 3). The increased duration of fights between closely matched males and at cooler temperatures appeared to be associated mainly with longer durations for noncontact displays.

The duration of noncontact display also increased as the season progressed (Table 3). In fights that included some pedipalp wrestling, the duration of wrestling was only influenced by the presence of the female in the dome portion of the web; longer bouts of pedipalp wrestling occurred when the female was in the dome at some time during the fight (Table 3). In fights that included some biting and grappling, the unritualized fighting lasted longer both later in the day and later in the season (Table 3).

The duration of noncontact display and pedipalp wrestling can be decided by either escalation to the next phase, or termination of the fight. Fights that escalated to pedipalp wrestling or unritualized biting and grappling lasted longer overall than fights that ended in noncontact display in a one-way ANOVA model of fight duration versus the highest fighting phase reached ($F_{2,252} = 30.296$, $P < 0.001$; Tukey pairwise comparisons: phase 1 versus 2: $P < 0.001$; phase 1 versus 3: $P < 0.001$; phase 2 versus 3: $P = 0.653$). When a variable indicating whether escalation beyond noncontact display occurred was added to the final multivariate model of noncontact display duration (see Table 3), we found that noncontact displays were longer in fights that escalated than in those that did not (standardized $\beta = 0.238$, $P = 0.002$). When a variable indicating whether biting and grappling occurred was added to the final multivariate model of the duration of pedipalp wrestling (Table 3), we found that wrestling lasted longer in fights that subsequently became unritualized (standardized $\beta = 0.356$, $P = 0.001$).

Multiplying phase duration by the relative energetic cost of each phase allowed us to examine factors affecting fight intensity. Intensity decreased as temperature increased and was higher in fights in which the lighter male was of greater absolute mass. Fights also were more intense on the webs of high-value females and if they occurred later in the season (Table 3).

DISCUSSION

Recent reviews of game-theoretical models of contests are provided by *Arnott & Elwood (2009)* and *Briffa & Sneddon (2010)*. Sierra dome spider fights entail a complex system of assessment, with key assessment modes varying amongst the three distinct fighting phases. As such, these contests are an exemplar of the kind of signalling system that begs for development of 'variable assessment models' (*Briffa & Sneddon 2010*).

Several aspects of the sierra dome spider's ecology and life history underpin selection for multifaceted decision making about the duration and intensity of fights. The high density of typical sierra dome spider populations (*Comstock 1912*) leads to several weeks of high male–male and male–female encounter rates during the breeding season (*Watson 1990, 1991a, b, 1993*). An adaptive context for continuous monitoring of self and opponent RHP is provided by high variance in male size, an important determinant of fighting ability. Such monitoring should also cover males' changing performance capacities within contests as they tire, and between contests as they age (*P. J. Watson, unpublished data*) or experience shifts in their nutritional status.

Moreover, the asynchronous sexual maturation of females and high variance in female reproductive value, especially before and after their first matings (*Watson 1990, 1993*), causes males to face frequent high contrast trade-offs between current versus future reproductive opportunities throughout the breeding season. This selects for active resource assessment. Taken together, these pressures have predictably selected for modulation of contest behaviour on the basis of information on self, opponent and resource.

Our analyses indicate that in the overall course of their three-phased, sequential assessment style contests (*Enquist & Leimar 1983; Enquist et al. 1990*), male sierra dome spiders assess aspects of self, opponent and resource (i.e. female) value. Cumulative assessment (*Payne 1998*) or various war-of-attrition types of decision-making algorithms (*Parker & Rubenstein 1981; Hammerstein & Parker 1982; Mesterton-Gibbons et al. 1996; Payne & Pagel 1996, 1997*) may be in play within contest phases. Male sierra domes with very different levels of RHP routinely meet on female webs, so there will be selection for opponent assessment, especially during noncontact display. On average, however, males display at roughly similar rates and intensities, especially during pedipalp wrestling and biting and grappling (but, see discussion of information versus influence, below), so it would be important during these phases to self-monitor reserve performance capacities.

Categories of Assessment

Taking stock of one's own capacities is essential for any organism needing to survive or reproduce (see *Lailvaux & Irschick 2006*). Intrinsic capacities self-assessed before and during contests over resources should include size, commonly a strong influence on contest outcome (see *Huntingford & Turner 1987; Andersson 1994; Riechert 1998; Briffa & Sneddon 2007*). But, size is an imperfect predictor of competitive ability, as seen in sierra dome spiders and other systems (e.g. *Prenter et al. 2008*). Other objects of self-assessment could include the limits of aerobic and anaerobic metabolism (*Briffa & Sneddon 2007; Mowles et al. 2009*), energetic reserves (*Jennings et al. 2005; Ancona et al. 2010*), experience and skill (*Khazraie & Campan 1999; Pratt et al. 2003*), and alternative future reproductive opportunities (*Grafen 1987; Enquist & Leimar 1990; West et al. 2001; Piper et al. 2008*).

The probability that an individual's energy budget or risk thresholds will be exceeded during a contest or after recovery from a contest also is predictable on the basis of an opponent's intrinsic

RHP and motivation (*Parker 1974*). These may be revealed by their size, ornaments, weaponry and actions (e.g. *Rillich et al. 2007; Prenter et al. 2008*). It may be inefficient to rely solely on knowledge of one's own RHP to determine how much to invest in a given contest. Thus, in some systems, qualities of the opponent (e.g. *Pratt et al. 2003*), or even potential opponents (e.g. *Höjesjö et al. 2007; Zulantz et al. 2008*), may be compared to corresponding aspects of the self's RHP, although detecting such mutual assessment processes can be tricky (*Taylor & Elwood 2003; Briffa & Elwood 2009*).

Assessments of resource quality can be viewed as refining the limits to energetic expenditures and risk taking (i.e. motivation) set by an individual during self- or mutual assessment (*Arnott & Elwood 2008*).

Self-assessment

Body mass and energy

We used body mass as an index of each male contestant's energetic reserves and his self-assessed contest-specific limit for energy expenditure. All else equal, the lighter contestant in any given fight should be the first to reach his limit, and so be the individual less willing to continue or escalate (*Briffa & Elwood 2009*). In accord with this prediction, we found a positive association between fight intensity and the absolute mass of the lighter contestant. Furthermore, as the absolute mass of lighter contestants increased, contest duration increased and escalations became more frequent. We also found that contests were more intense between larger males, again suggesting that an upper energy limit may exist for each fight based on self-assessment.

Temperature and energy

Metabolic capacities of individuals, especially ectotherms, also are affected by their 'thermal condition'. Thus, individuals should assess how close their body temperature is to the one that maximizes the effectiveness and efficiency of their behaviours (*Huey 1991*). The resting metabolic rate of sierra dome spiders increases by a factor of 2.21 with each 10 °C increase in temperature (*Watson & Lighton 1994; deCarvalho et al. 2004*), a level of temperature sensitivity (Q_{10}) typical for arthropods (*Weinstein 1998; Nespolo et al. 2003*). The few empirical data available on the temperature sensitivity of costly behaviour (*Herreid et al. 1981; Full & Tullis 1990; Weinstein 1998*) suggest that the costs per unit time of a given fighting behaviour in the sierra dome spider is likely to increase with temperature, even after controlling for body mass and behavioural intensity. Thus, at higher temperatures, energy reserves are likely to be depleted more quickly and any investment thresholds met sooner. However, the metabolic effects of more intense behaviours, like pedipalp wrestling and biting and grappling, may be less sensitive to temperature (*Herreid et al. 1981*).

In our study, observed temperature effects also suggest that self-assessment influences contest decision making. Temperature was negatively correlated with the duration and intensity of noncontact display. Individuals were willing to engage longer in this least-intense form of display when rates of energy depletion were slower. Because noncontact displays were longer at lower temperatures, decisions about pedipalp wrestling and unritualized fighting may be influenced more by factors other than rate of energy expenditure, such as relative RHP and resource quality.

We considered whether lower temperatures may have led to longer noncontact displays because they slow collection of information about opponent's and thus relative RHP. However, the associated prediction that lower temperatures should be more strongly associated with longer noncontact displays when males

are more closely matched in body mass was not supported by our data.

Deritualization and energy

Fights involving light contestants of greater absolute mass were less likely to switch directly from noncontact display to unritualized fighting, bypassing pedipalp wrestling. Although it increases risk of injury, bypassing this more rigorous ritualized assessment could help smaller or senescing males with low energy reserves or reduced future mating opportunities more efficiently intimidate a rival having greater RHP. Because a quick single bite delivered to any but the most distal parts of a rival's body results in an almost instant sharp reduction in a male's RHP, males that are underdogs by body mass or energy reserves sometimes may bypass ritualized displays and choose unritualized fighting, which probably favours agility more strongly and offers the possibility of delivering a lucky bite. These factors could reduce a heavier opponent's advantage, on average, relative to that of sustained ritualized fighting.

Assessment of Opponent

We used the difference in body mass between contestants as our index of relative RHP. The heavier males almost always won contests when their mass advantage was greater than 20%. Heavier males were more likely to win even when the mass difference between contestants was below 20%. If one includes both the mass difference between contestants and the lighter male's mass in any multivariate analysis of fight behaviour, then a significant correlation with mass difference indicates an influence of opponent assessment on the behaviour being tested (Taylor & Elwood 2003; Arnott & Elwood 2009). Our analyses all included the difference in mass between contestants and the mass of the lighter contestant. When both factors were incorporated in our multivariate regressions, we sometimes found a significant effect of mass difference, indicating the existence of opponent assessment.

Sierra dome spider males appear capable of predicting when a mass difference is large enough to accurately predict the winner of an unritualized fight. Opponent assessment in sierra domes appears to occur mostly during noncontact displays. On the webs of mated females, fights that entailed more than a 20% mass difference between males escalated beyond noncontact display about 38% of the time, as compared to 69% in fights where the mass difference was less than 20%. When we limited analyses to fights in which the lighter male had an appreciable chance of winning (those with less than 20% mass asymmetry), we only found evidence that mass difference, and thus some form of opponent assessment, influenced the duration of noncontact display (Table 4). Opponent assessment showed broader influence in analyses that included fights with the full range of mass differences, although there still was no evidence for an effect on the frequency or duration of unritualized fighting.

In fiddler crab, *Uca mjoebergi*, contests, the duration of low-intensity displays also decreases when the size difference between the contestants is greater (Pratt et al. 2003). In contrast to sierra dome contests, the degree of escalation in fiddler crab encounters appears not to be influenced by size disparity. Each male in a fiddler crab contest can be performing different displays, so it is possible for the larger male to escalate without waiting for a consensual escalation, when he perceives that his chances of winning are high. Other systems in which the relative size of contestants may not predict fight intensity include those, such as the freshwater amphipod *Gammarus pulex*, in which the resident male can gain such a grip on the female that it overrides a size disadvantage (Prenter et al. 2006). In species like the sierra dome, residents enjoy

no such positional advantage. Moreover, the sierra dome's most frequent and clear form of escalation, the switch from noncontact display to pedipalp wrestling, requires complete cooperation. In contests with these features, the degree of escalation is more likely to be influenced by the difference in RHP.

Assessment of Resource

Wells (1988) used presence or absence of female models during multistage fights of male jumping spiders to show that resource value positively affects fight intensity. Dowds & Elwood (1983) found that in the European marine hermit crab *Pagurus bernhardus*, males are more likely to escalate and win contests when the potential gain in resource value is high. Ancona et al. (2010) found that male whiptail lizards adjust energy investments in mate guarding according to the accompanying female's fecundity, as predicted by the female's size. The present study indicates that fighting investments by male sierra dome spiders are affected by the reproductive status (virgin versus nonvirgin) of the female owner of the web where the fight is taking place.

Female fertility and receptivity to mating

In contests between male sierra dome spiders, males compete for sexual access to the female and the use of her web, both for foraging and as a refuge from predators. However, we found that the female's reproductive value, specifically, her virgin versus mated status, was the main resource influencing the males' decision-making process during contests with rivals. Females that afforded males a first-mating opportunity, which is associated with high fertility and complete sexual receptivity (Watson 1986, 1990, 1991a, b), evoked more intense fights. Much of this effect was attributable to an increased probability of contests becoming unritualized in the presence of virgins (Table 4). High-value virgin females gradually become scarce as the breeding season progresses. At the same time, residual male reproductive value is in decline via ageing. Together, these factors probably combine to select for more risk-prone fighting later in the season.

Our measure of web quality was its diameter, which is positively and nonlinearly correlated with its efficacy in prey capture (P. J. Watson, unpublished data), but it bore no relation to male fighting behaviour. The majority of males in our staged fights were provided with regular food and water in the laboratory, which may have artificially reduced the value of females' webs as a foraging resource compared to that expected for free-living males.

In sierra dome spiders, female fertility and sexual receptivity, as opposed to genetic quality, probably are the main components of female reproductive value that limit male reproductive success and thus control decision making during fights. We studied these female traits, as opposed to measures of fecundity or genetic quality, because prior work has shown that (1) sexual receptivity and fertility vary drastically amongst females during the entire breeding season according to each female's virgin versus mated status and (2) this variation is highly detectable by males. Penultimate female sierra dome spiders behaviourally signal to males when they are 1–5 days from sexual maturity (Watson 1990). Males that receive these signals consistently behave as though the high fertility and guaranteed receptivity to mating immediately after the final moult of virgin females swamps all other aspects of variation in female value (Watson 1990, 1991a, b).

We do not argue that male sierra dome spiders ignore female fecundity or genetic quality when they decide how heavily to invest in a fight. For example, although we did not measure female body mass in this study, it must be easily assessed by males via the magnitude of web vibrations, even from a distance. Moreover, female mass is known to be closely related to lifetime fecundity

even when measured in penultimate females 4–8 weeks before they oviposit (P. J. Watson, unpublished data). This component of variance in female quality and more subtle ones may influence male contests and warrant further study.

Effects of residency on resource valuation

Resident males were more likely to lose fights on webs of low-value females and more likely to win on webs of high-value females. This residency effect seems to be an informational advantage concerning resource quality. Resident males in our staged fights, defined as the first males to be placed on the web, seemed better informed about female value because their willingness to fight was more strongly correlated with virgin status, even when introduction of the second male occurred only 5–15 min later. More effective assessment of female quality may occur when a male is alone with the female. To focus on this informational advantage in our analyses of residency effects, we excluded fights over females producing male attractant pheromone, which immediately reveals the high-value mature-virgin status of the female to any male present, even to those males that are still en route to the web (Watson 1986).

There is no strategic positional advantage for residents in this system either with regard to fighting or information gathering. Both residents and intruders have equally high mobility across the web and neither have good control over female movements. But, since we found effects of female reproductive value on both fight intensity and the probability of deritualization, intruding males must obtain some information. This could occur in a variety of nonpheromonal ways, such as through the associative behaviour of penultimate females (Watson 1990), the receptivity-related behaviours of adult females (Watson 1993), or the degree of agonism or tenacity of the resident male. Nevertheless, the effect of female value on a resident's probability of winning a fight indicates that intruders are under-informed compared to the residents. This result is in accord with findings concerning informational asymmetry and resident advantage in house crickets, *Acheta domesticus* (Buena & Walker 2008).

Effects of male residual reproductive value on resource valuation

Maturation in the female sierra dome spider population occurs asynchronously over a 6–7-week period. The majority of females mature relatively early in this time window (Watson 1988). Thus, a male's probability of finding females that offer a first-mating opportunity decreases with time, especially across the second half of the breeding season. Male senescence also continuously decreases the probability of negotiating the gauntlet of predators to discover additional female webs, winning possession of them, and successfully courting less receptive nonvirgin females to become a secondary mate and sire (Watson 1991b, 1993). In accord with the 'desperado effect' proposed by Grafen (1987), the date on which a given fight occurs should reflect the residual reproductive value of sierra dome males and thus their assessments of current resource value.

Indeed, we found that fights were more intense later in the season. Noncontact display duration was significantly longer later in the season, but the strongest effect of date was on deritualization. The probability of deritualization, the frequency of out-of-phase deritualizations, and the duration of biting and grappling all increased later in the season (Table 4). Males evidently became more risk tolerant as the season progressed.

Information versus Influence

Organisms must process information to support behavioural adaptations that deal with the dynamic fabric of positive and negative fitness affordances in the environment. To continuously reprioritize execution of such behavioural adaptations, organisms

must self-monitor their capacities and needs and integrate those data with information gleaned from extrinsic sources.

Randall et al. (2009) questioned whether the transfer of such valuable information is the best way to construe what happens during animal communication. We agree that where individuals have a conflict of interest, overly emphasizing the idea of information exchange may not lead to the best understanding of the detailed functional design of display behaviours. We suggest that encounters typically interpreted as exchanges of information could even contain elements that interfere with self-assessment or evaluation of the resource. In high-stakes contests with long histories of antagonistic coevolution between Darwinian algorithms for signalling and receiving (i.e. deciphering), the demands of processing extrinsic and intrinsic information perhaps are highest.

In contests, accurate information about the environment can be strategically mixed with inaccurate information. Moreover, some contest behaviours may serve specifically to interfere with an opponent's timely accurate processing of informative signals or cues contained in other aspects of the display. By blending honest information with dishonest signals or purely distracting stimuli, contest opponents may make it more difficult for their adversary to ignore display components that serve as 'propaganda' or 'jamming devices', behaviours designed purely to influence contest outcome.

Sierra dome spider noncontact displays and pedipalp wrestling, while 'ritualized' and 'stereotypical' compared to all-out fighting, are loaded with subtle improvisational elements that may not be designed to convey real information so much as to exert raw influence. For example, noncontact displays often include quick nips or slow stealthy moves obviously designed to sneak in a quick bite on one of the opponent's front legs. Pedipalp wrestling, although almost certainly more honest and data rich than the noncontact display that precedes it, is not a 'pure' informational display either. Instead, there is a great deal of leg movement as opponents jockey for superior footholds and leverage. In addition, each contestant's exertion during pedipalp wrestling is highly variable, with each male seemingly trying to take the other by surprise, perhaps at a moment when some positional advantage is obtained, or just to confuse the opponent by being less predictable.

An extreme example of design for influence over information transfer comes from our result that the less massive the lighter contestant is, the more likely the pair is to exhibit an unconventional out-of-phase escalation where they skip pedipalp wrestling and escalate straight from noncontact display to unritualized fighting. This is possibly a tactic by the less massive male to avoid an energetically costly display that most likely would lead to exhaustion and defeat. It seems strained to portray this striking 'breach of protocol', like the more subtle moves mentioned above, as an attempt to convey information about skill or motivation. It may be more logical to look at these behaviours as attempts to influence the risk or RHP assessments of an opponent before he fully assesses the 'truth', namely, that he would have the best chance of winning an unritualized fight, especially if it follows the two energetically demanding and motivationally influential ritualized phases of assessment.

Having observed many hundreds of sierra dome spider contests since 1980, in addition to the 323 formally recorded here, we could not help notice that while virtually all such encounters entail well choreographed core behavioural elements, they also are all wildly variable on the margins. Such pervasively 'borderline' ritualized structure strikes us as evidence for an ongoing arms race for influence over contest outcomes. Game-theoretical models of contests have produced a useful array of hypotheses and predictions to guide empirical work on contest design, but the evolutionary race for influence evident in this system and others demands movement towards dynamical models of signaller and receiver strategies (see Enquist et al. 2010).

The two ritualized elements of sierra dome spider contests may have reached a degree of evolutionary stability due to the value of information transfer for both contestants. But their use seems 'set' at a vulnerable quasi-equilibrium. Ritualization often breaks down in individual high-stakes contests, usually between well-matched opponents. The ritualized elements typical in today's sierra dome spider populations probably could vanish altogether as an evolutionary response to minor changes in life history or ecological parameters, such as greater extrinsic male mortality rates or reduced population densities.

Many previous studies of communication indicate that information transfer is basic to many, if not all, animal signalling systems (Seyfarth et al. 2010). We think that our study supports this view. At its core, however, interacting is all about exerting influence: an individual can never have too much influence exactly because it can never have too much fitness. Influence is attained by adaptively managing an opponent's (or a partner's) perceptions, computations and resultant behaviours. Selection should favour individuals that use strategic combinations of honest information sharing, deception and tactics that interfere with information processing. It therefore should be common to find contests with moderately stable ritualized elements that are riddled with adjunct behaviours that may seem minor, but nevertheless highlight the race for and the primacy of influence in animal communication.

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