ORIGINAL ARTICLE

Phillip W. Taylor · Oren Hasson · David L. Clark

Initiation and resolution of jumping spider contests: roles for size, proximity, and early detection of rivals

Abstract Animals are commonly expected to assess each other during contests in order to economically identify relative status. Escalated or long contests are expected to arise mainly when rivals have difficulty discriminating small differences. Results of the present study of male-male contests in *Plexippus paykulli*, a jumping spider (Salticidae) with acute vision, are not in accord with this widely held view. Despite the typical finding that size-advantaged rivals are more likely to win contests and that this tendency increases with size disparity, contest dynamics suggest that these tendencies are achieved in the absence of direct size assessment. In contests between different-sized spiders, maximum escalation and overall duration were predicted by the absolute size of the size-disadvantaged spider (usually the loser) rather than the size difference between the rivals. This result suggests that spiders base decisions of persistence on their own size, such that size-disadvantaged rivals usually reach their limits first, and then retreat. This interpretation is further supported by findings that maximum escalation and total duration were both positively related to size in contests between size-matched spiders. Spiders were more likely to win if they oriented and displayed first, and longer, more escalated, contests ensued if the size-disadvantaged spider was the first to orient and display. Proximity of rivals at contest outset also influenced contest dynamics, but not outcome.

P.W. Taylor (✉) · O. Hasson
Department of Entomology, The Hebrew University of Jerusalem, P.O. Box 12, Rehovot 76100, Israel

D.L. Clark
Biology Department, Alma College, Alma, MI 48801, USA

Present address:
P. Taylor, Department of Biological Sciences,
University of Cincinnati, Cincinnati, OH 45221-0006, USA
e-mail: taylorpp@email.uc.edu
Tel.:+1-513-5569753, Fax: +1-513-5565299

Introduction

In animal contests, rivals are in opposition over access to resources, but share the need to minimize the costs associated with deciding a winner. This common interest has lead to contests over minor resources most commonly taking the form of ritualized negotiations designed to economically expose asymmetries between rivals in resource holding potential (RHP; Parker 1974) or pay-offs (Parker and Rubenstein 1981; Enquist and Leimar 1983, 1987, 1990). To ascertain relative status, and thereby facilitate economic resolution, rivals may not only assess each other but may also aid each other's assessments by signaling (e.g., cichlid fish: Keeley and Grant 1993; Hurd 1997; thrips: Crespi 1986; horses: Rubenstein and Hack 1992; deer: Clutton-Brock and Albon 1979). Each rival may then use acquired information to predict its chances of winning and, in turn, to make decisions about whether and how to proceed.

If information-gathering and decision-making are central processes of ritualized contests, contest economies should depend on the ease with which decisive information can be obtained. Most theory predicts that contests between rivals of greatly disparate ability should be resolved quickly and cheaply, whereas contests between rivals of similar ability should be more protracted and costly. This is because rivals of similar ability are more likely to make mistakes about relative status and will both select the more costly tactics of expectant winners (Hammerstein and Parker 1982), or because more sampling is required to resolve small differences (Enquist and Leimar 1983; Leimar and Enquist 1984). Supporting this widely held view, negative relationships between RHP (usually as size) differences and contest costs have been identified in empirical studies of a diverse array of animals, including agelenid, linyphiid, and metid spiders (Riechert 1978; Austad 1983; Leimar

et al. 1991; Hack et al. 1997), cichlid fish (Enquist et al. 1990), crayfish (Pavey and Fielder 1996), dung flies (Sigurjónsdóttir and Parker 1981), caddis larvae (Englund and Olsson 1990), and crickets (Hack 1997).

There are, however, species in which this expected relationship between size difference and contest costs does not seem to hold true, or provides only a partial explanation of size effects. In *Uca annulipes* crabs and *Argyrodes antipodiana* spiders, victory tends to go to the larger rival and yet the escalation tendency of size-matched rivals is positively associated with body size (Jennions and Backwell 1996; Whitehouse 1997). Similarly, heavy weight-matched *Gryllus integer* crickets have longer contests than light weight-matched conspecifics (Dixon and Cade 1986). Glass and Huntingford (1988) found that total duration of contests in the swimming crab *Liocarcinus depurator* decreases with size disparity but also increases with the size of the smaller rival (usually the loser). In *Metellina mengei* orb-web spiders, both intensity and duration of contests increase with the loser's size, while the winner's size appears unimportant (Bridge et al. 2000). These trends are not consistent with the notion that effects of size on contest costs are solely explained by the ease with which differences can be discerned. Instead, they are consistent with the possibility that rivals persist simply in accord with their own size-associated ability or expected pay-offs. Under this hypothesis, contest costs may be best explained by the loser's persistence (typically the smaller rival), rather than differences between the rivals, as only the loser reaches its limit.

Most studies have, without analysis, dismissed the possibility of contest costs varying in relation to one rival's RHP, and considered only the expected relationships of RHP (size) difference (e.g., larger–smaller: Stokkebo and Hardy 2000; smaller/larger: Smith et al. 1994; Pavey and Fielder 1996; ln(rivalA)–ln(rival B): Leimar et al. 1991; Faber and Baylis 1993; absolute size difference/smaller size: Dowds and Elwood 1985; absolute size difference/larger size: Wells 1988; Dugatkin and Biederman 1991; absolute size difference/average size: Hack 1997). Analyses that only consider effects of size difference may produce misleading results. Size difference is correlated positively with size-advantaged (SA) rival size and is correlated negatively with size-disadvantaged (SD) rival size. This is because small size differences can involve any individual but large size dif-

ferences can only involve very big SA and very small SD individuals. Accordingly, contest escalation or duration that is biologically dependent on SD rival size may be detected coincidentally as negative effects of size difference. In this study, we consider whether costs of contests between males of a jumping spider, *Plexippus paykulli* Andouin (Araneae, Salticidae), diminish with size difference between rivals (implying assessment of size) or, instead, follow patterns consistent with each rival acting in accord with its own ability.

We approach the analysis of size effects from a perspective that recognizes effects due either to one rival's own size or to size difference. Rather than using the composite character of size difference, we instead include the sizes of both rivals as independent predictors in multivariate models. Using this approach of statistical control, effects of size difference are apparent as opposing effects of SA spider size and SD spider size in a single model. If spiders resolve contests by simple size-dependent persistence than there will be strong positive effects of SD spider size and no effects (or weak positive effects) of SA spider size. Additionally, we investigate how circumstances of proximity and which spider sees the other first influence contest outcome and dynamics.

Jumping spiders differ from other spiders by possession of highly developed acute vision (Land 1985; Blest et al. 1990) that allows them to discriminate different classes of conspecifics and prey from distances as great as 30 cm (Jackson and Blest 1982; Li and Jackson 1996; Harland and Jackson 1999). Instead of building webs, male jumping spiders roam about their habitats in search of prey and mates. When two males meet, they commonly enter into elaborate rituals that involve a highly stereotyped sequence of visual and tactile signaling, even when no obvious resource is at stake and when options of avoidance are available (Jacques and Dill 1980; Taylor and Jackson 1999). Our preliminary observations in the laboratory and in nature, and a qualitative study by Jackson and McNab (1989), indicate that contests between *P. paykulli* males broadly resemble those of salticids used in previous studies (see Wells 1988; Faber and Baylis 1993; Taylor and Jackson 1999), escalating through a series of distinct stages (Table 1). Contests begin with visual displays at a distance, which may be followed by spiders approaching each other, exchanges of highly active displays that include occasional contact, prolonged physical pushing matches, and a potentially

Table 1 Stages of escalation in male-male contests of *Plexippus paykulli*. For comprehensive descriptions of defining behaviors, see Jackson and McNab (1989)

(1) Orientation	The two spiders concurrently maintain orientation toward ('see') each other. Usually, the first spider to see the other adopts a 'hunch' display, with body raised far above the substrate, and standing still.
(2) Posing	Both spiders adopt hunch displays.
(3) Proximating	One or both spiders approach the other.
(4) Sparring	Having approached to within two to three body lengths apart, the spiders repeatedly lunge forward, flinging their legs upward. During these exchanges, spiders sometimes ram directly into their rival's face.
(5) Embracing	Spiders step forward until touching face-to-face, with front legs held out to the side, and attempt to push each other backwards.
(6) Struggling	Spiders grasp one another and roll about biting at each other.

injurious struggle. In other jumping spiders, the larger of two rivals tends to win contests (Jackson 1980; Wells 1988; Faber and Baylis 1993; Taylor and Jackson 1999). Wells (1988) and Faber and Baylis (1993) concluded that contests of the salticids *Euophrys parvula* and *Zygoballus rufipes* (respectively) follow the usual expectations of greater escalation or duration when rivals are of similar size. But neither of these studies considered the possibility that these trends might have actually arisen through spiders acting in accordance with their own size. Although Faber (1989) informally noted that pairs of large *Z. rufipes* males may be inherently more prone to escalated contests, the possibility that the behavior during contests of salticid spiders may depend on their own size, rather than on estimates of size difference, remains untested.

Methods

Collection and maintenance of spiders

Male *P. paykulli* spiders were collected as adults or subadults (penultimate instar) in the vicinity of Rehovot, Israel, between May and July of 1996 and 1997. They were housed in 500-ml translucent plastic cages and were fed three to four third-instar house fly *(Musca domestica* L.) maggots once each week. Each cage was provided with a folded piece of cardboard (10×30 mm) on the floor as a retreat. In the week prior to experiments and during the experimental period, spiders had at least one prey item available every day. Spiders were kept, and experiments carried out, in a laboratory maintained at 24–26°C, 60–70% relative humidity, and a 12:12 h light:dark photoperiod. All spiders had been in the laboratory as adults for 4–8 weeks when experiments began, this being a small portion of the typical 8- to 12-month adult lifespan in the laboratory (unpublished data).

Experiment 1: random size pairings

Arena design

The arena was an open-roofed box built using pale-gray formica glued to a composite board backing. The floor was 150×300 mm and the walls were 80 mm high. The bottom 15 mm of the walls was of glass, providing a window through which contests could be observed at floor level. A light coating of glycerol on the walls above the window prevented the spiders climbing out. Confining spiders to the floor facilitated observation and precluded asymmetries caused by differing altitude on a vertical surface. All contests were video-recorded from above using a camera that captured the whole arena, and close-up with a mobile camera from the side at floor level through the window. In addition to the fluorescent room lighting, illumination was provided by four 36-W fluorescent lights, two positioned 0.5 m above each side of the arena.

Pairing of rivals

Three hundred and thirty-six spiders were randomly paired (i.e., a total of 168 pairings) with rivals they had not encountered previously in the laboratory. For individual identification, each spider was marked with a small spot of non-toxic paint applied to the anterior-dorsal surface of the abdomen. Similar marking procedures have been used in studies of other salticids, with no apparent change in behavior (Wells 1988; Jackson and Cooper 1991).

Pre-test conditioning and staging of contests

To ensure that spiders had some recent experience of contests, all spiders took part in three preliminary contests with rivals from other pairings. Naive and experienced spiders may behave differently during contests (Whitehouse 1997). Most spiders in nature would have had some experience of contests and so ensuring recent experience increased the similarity between laboratory and wild populations. If size influences outcome, then these preliminary contests would mean that, as in nature, large spiders would gain more experience of winning than would small spiders. Selection of pairs for preliminary contests was random with the exclusion of spiders with the same color markings. These contests were staged 2 days apart during the week prior to assessed contests and there was a 2-day latency between the last preliminary contest and the first assessed contest. The procedures for staging preliminary and assessed contests were identical.

To stage a contest, the spiders were placed at opposite ends of the arena while a glycerol-coated formica barrier was in place at the arena mid-point. After a 5-min acclimation period, the barrier was removed and spiders were free to move around the arena and interact. Spiders were very active, walking and looking about almost constantly. When the first spider saw the other, it usually adopted a 'hunch' posture, raising its body off the substrate by extending its legs. A contest was defined as beginning when the second spider saw the other spider watching it, evident from both spiders standing still and maintaining orientation toward each other (i.e., 'orienting'; Table 1). Contests ended when one spider (the loser) retreated. Retreat was typically by walking backwards away from the rival and then turning to run away, but was also sometimes by leaping. Winners rarely chased retreating losers.

Between contests, the arena was thoroughly washed with warm soapy water and then ethanol (95%) to remove the glycerol, chemical cues, and silken draglines deposited by spiders (see Jackson 1987). Contests were not staged within 3 h of the beginning or end of the 12-h laboratory light phase.

Measuring spider size and distances between rivals

After interactions were completed, all spiders were measured so that we could determine the influence of spider size on contest outcome, contest costs, and fighting tactics. The distance between the outer margins of the posterior-medial eyes was selected as an index of spider size. To measure spider size, the dorsal carapace was video-recorded while the spider was gently pressed against a glass cover slip fastened to the end of a syringe. These video images were transferred to a computer for scaling and measurement to the nearest 0.01 mm using NIH Image (a public domain program from U.S. National Institutes of Health). The video record of the entire arena from above was used to measure the distance between rivals when contests began ('proximity').

Statistical procedures

Proportional representation in frequency data sets involving only two classes (e.g., SA wins, SD wins) were analyzed using binomial tests approximated to the normal distribution, corrected for continuity. Effects of linear (SA spider size, SD spider size, and proximity) and categorical predictors (orientation order) on probabilities of events with categorical outcomes were analyzed using logistic regression, a generalized linear model specifically appropriate for data of these types (see Hardy and Field 1998; Thompson et al. 1998). Statistical significance of each predictor and the overall model were tested using log-likelihood ratio χ^2. Predictors of continuous outcomes (e.g., contest duration) were analyzed by least-squares regression, using transformations when necessary to ensure that residuals were normally distributed and homoscedastic. To describe partial effects in linear regression models, we present partial regression coefficients (b±SE) for all predictors and least-square means (LSM±SE) for categorical predictors. We used

backwards elimination of highly non-significant ($P>0.1$) predictors until left with the most parsimonious suite of significant predictors (Sokal and Rohlf 1981). The significance level of each eliminated predictor is presented in order of removal. For each multiple-regression model, we present statistics for overall significance of the full model as well as lack of fit (LOF), a test for inappropriate functional form of predictors. Final model statistics refer only to retained predictors. All regression analyses were carried out using JMP 4.0 (SAS Institute). We elected to use SA and SD size, rather than winner and loser size as predictors so that we could use the same predictors for models of contest outcome and contest dynamics. However, models of contest escalation and duration were repeated using winner and loser size in lieu of SA and SD spider size, respectively, and in all cases returned the same final predictors with similar slopes and significance levels.

Experiment 2: equal-size pairings

This experiment was carried out to test whether experimental control of spider size produces the same result for contest escalation and duration as the procedures of statistical control outlined above. If persistence tendencies are associated with size difference between the rivals, there should be no effects of size on escalation or duration of these contests. Alternatively, a tendency toward greater escalation or longer contests when same-sized pairs are large would be consistent with spiders persisting in accord with their own size rather than estimates of size difference. We selected 48 pairs of size-matched spiders that were not involved in experiment 1. They were individually marked and subjected to the same preliminary and testing protocol as in experiment 1.

Results

Body size and contest outcome

In experiment 1, size advantage was a strong predictor of contest outcome, with the SA spider winning 135 (83%) of 163 contests in which a size difference was detected ($z=8.30$, $P<0.001$). This tendency for the SA spider to win contests was positively related to SA spider size ($\chi^2=16.073$, 1 df, $P<0.001$), negatively related to size disadvantaged (SD) spider size ($\chi^2=13.847$, 1 df, $P=0.002$), and was diminished when the SD spider saw the SA spider first ($\chi^2=6.261$, 1 df, $P=0.012$) (Fig. 1). Outcome did not vary significantly with proximity of rivals at the outset of contests ($\chi^2=1.171$, 1 df, $P=0.279$; $n=163$, overall $\chi^2=25.964$, 3 df, $P<0.001$; LOF $\chi^2=123.571$, 153 df, $P=0.961$). The effects of SA and SD spider size clearly express tendencies of size difference; for an SA spider of any given size, the tendency to win diminished as rival size increased (size difference decreased); for an SD spider of any given size, the tendency to lose increased as rival size increased (size difference increased) (Fig. 1).

Maximum escalation

To identify variables influencing costs of resolution, we modeled maximum escalation as an ordinal response, ranking contests from 1 if they were resolved while orienting to 6 if they reached the maximum rank of struggling (see Table 1, Fig. 2). Maximum escalation rank
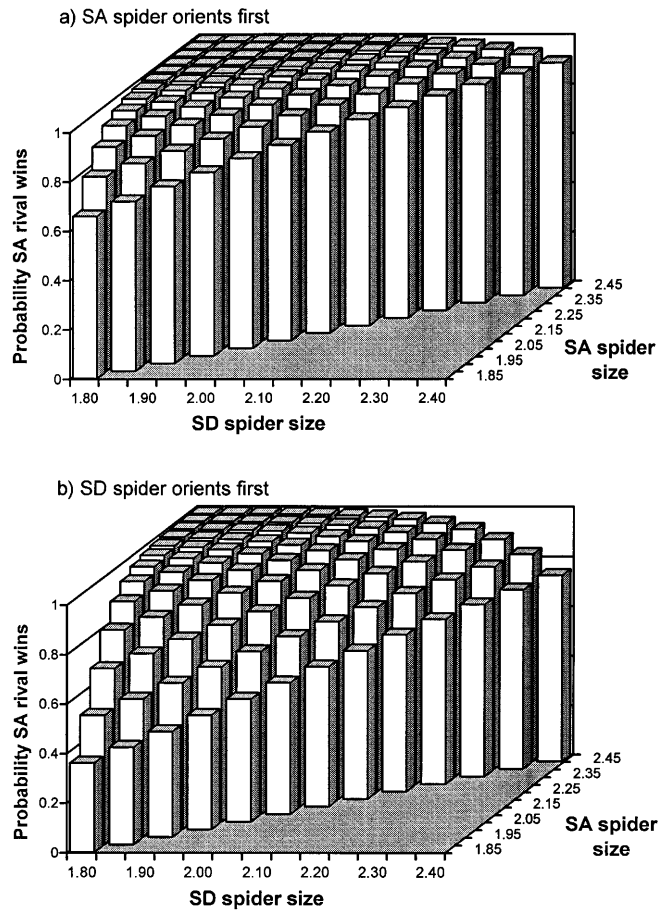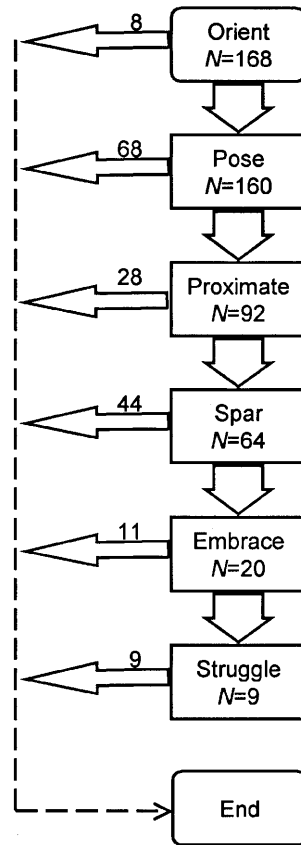

Fig. 1 The effects of size-advantaged (*SA*) and size-disadvantaged (*SD*) spider size on the tendency of SA spiders to win contests when the SA spider (**a**) or the SD spider (**b**) oriented and displayed first. Trends are predicted probabilities at 0.05-mm size increments derived from multiple logistic regression including SA spider size, SD spider size, and orientation order as effects

was greater if the SD spider was large or saw the SA spider first (Table 2, Fig. 3). Escalation was slightly greater if the spiders were in close proximity when they oriented (Table 2, Fig. 3), but the size of the SA spider was not important ($\chi^2=0.797$, 1 df, $P=0.372$). This result suggests that decisions of maximum contest escalation are not based to any great extent on SA spider size or size difference but instead reflect only the persistence of SD spiders (usually losers). This tendency was also apparent in the size of SA and SD spiders remaining in contests at each stage. Whereas the size of SD spiders persisting varied through escalation (ANOVA: $F_{5,495}=2.758$, $P=0.018$), tending to increase as contests progressed, there was no change in SA spider size persisting at each stage (ANOVA: $F_{5,495}=0.520$, $P=0.761$; Fig. 4). This is consistent with hypotheses of SD spiders retreating once they reach their size-characteristic persistence limits but is not consistent with hypotheses of spiders basing persistence and escalation rules on estimates of size difference. Although we did not observe limb loss or death, injuries did sometimes occur in the most intense con-

Fig. 2 Flow chart describing the sequence of events in contests between *Plexippus paykulli* males

Table 2 Predictors of maximum escalation reached in contests between spiders of different sizes (experiment 1) and spiders of the same size (experiment 2). For graphical representation of trends, see Figs 3, 4, and 5

	df	χ^2	P
Experiment 1 (*n*=163)			
SD spider size	1	11.859	<0.001
Orientation order	1	7.712	0.006
Proximity	1	3.677	0.055
Overall	3	28.496	<0.001
LOF	802	460.918	>0.999
Experiment 2 (*n*=48)			
Spider size	1	5.445	0.020
Proximity	1	7.521	0.006
Overall	2	13.105	0.001
LOF	228	143.519	>0.999

Table 3 Predictors of total duration of contests between spiders of different sizes (experiment 1) and spiders of the same size (experiment 2)

	b	F	P
Experiment 1 (*n*=163, R^2=0.21)			
SD spider size	4.17±0.80	27.093	<0.001
Orientation order	0.24±0.10	6.285	0.013
Overall (*df* 2,160)		18.535	<0.001
LOF (*df* 71,89)		0.926	0.630
Experiment 2 (*n*=48, R^2=0.18)			
Spider size	4.42±1.90	5.383	0.025
Proximity	−0.14±0.07	4.106	0.049
Overall (*df* 2,45)		5.091	0.010
LOF (*df* 44,1)		68.267	0.096

tests; losers bled from bite wounds to their legs as they fled after two struggles, 22% of contests that reached this escalation rank.

If escalation decisions were based on estimates of size difference, we would not expect to find any effects of size in experiment 2, in which spiders were closely size-matched. However, maximum escalation was greater if the size-matched spiders were large or in close proximity when they oriented (Table 2, Fig. 5). Supporting the results of experiment 1, this finding suggests that spiders base decisions of persistence on their own ability, paying little heed to their rival's size.

Contest duration

Contests in experiment 1 ranged in duration from 1 to 874 s and in experiment 2, from 1 to 894 s. There was a strong positive correlation between total duration and maximum escalation rank reached in the contest both in experiment 1 (*n*=168, Spearman's *r*=0.74, *P*< 0.001) and in experiment 2 (*n*=48, Spearman's *r*=0.65, *P*<0.001). Accordingly, like maximum escalation, total duration of contests (ln transformed) in experiment 1 was greater if the SD spider was large or saw the SA spider first (LSM: SA saw SD first 2.85±0.14, SD saw SA first 3.34±0.13; Table 3), whereas the weak effects of proximity on maximum escalation did not translate to significant effects on duration ($F_{1,158}$=0.910, *P*=0.342), and the SA spider's

size was also not of significant importance ($F_{1,159}$=1.769, *P*=0.185). In experiment 2, contests lasted longer (ln transformed) if size-matched pairs were large or were in close proximity when they oriented (Table 3). As with maximum escalation, these trends are all consistent with spiders basing decisions of persistence simply on their own ability, rather than taking their rival's size into account.

Tactical roles in contests

Taking the first step

The matching displays during posing, during which spiders stood still and faced each other with their bodies raised in the 'hunch' display, could end by four possible outcomes for contests in which rivals were of different sizes (*n*=156): the SA spider retreated in 15 (10%), the SD spider retreated in 51 (33%), the SA spider initiated proximation in 59 (38%), and the SD spider initiated proximation in 31 (19%). Which of the four outcomes ended posing depended on which spider oriented first (χ^2=24.676, 3 *df*, *P*<0.001), SA spider size (χ^2=14.610,

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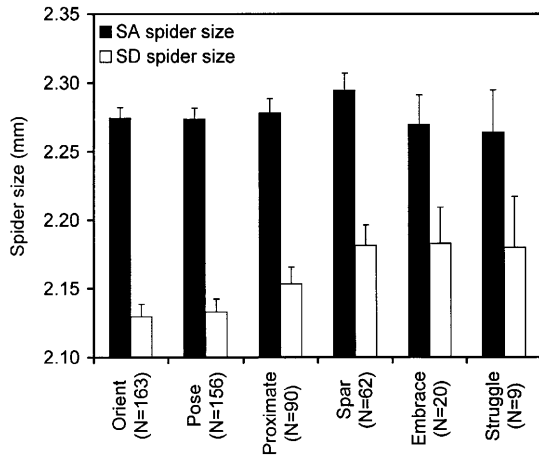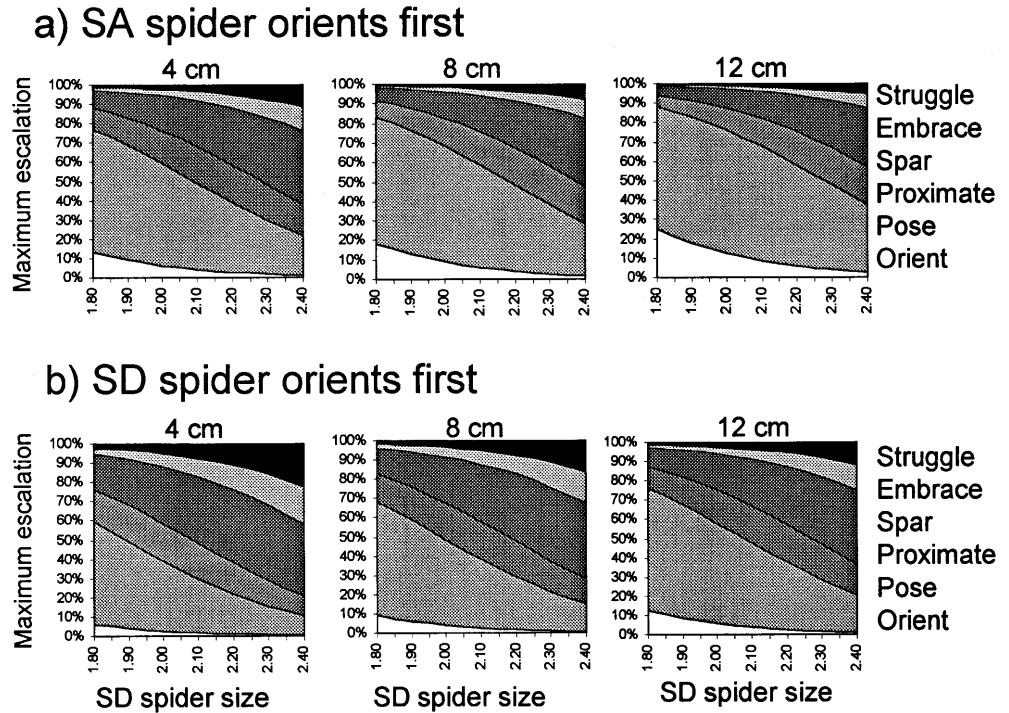## a) SA spider orients first

b) SD spider orients first

Fig. 4 Average sizes (±SE) of SA and SD spiders persisting in contests at each stage of escalation. The absence of a decrease in SA spider size as escalation increases is inconsistent with decisions based on size difference but is consistent with decisions based on own size

3 *df*, *P*=0.002), and SD spider size (χ^2=17.202, 3 *df*, *P*<0.001), but there were no effects of proximity (χ^2=0.261, 3 *df*, *P*=0.967) (*n*=156, overall χ^2=48.751, 9 *df*, *P*<0.001; LOF χ^2=347.688, 438 *df*, *P*=0.999). The effects of SA and SD spider size acted largely in opposition and may be construed as effects of size difference in some cases (Figs. 6, 7, 8, and 9). For contests escalating beyond posing, the probability that the SA spider initiated proximation increased with SA spider size but effects of SD spider size were slight and varied with SA spider size (Fig. 6). However, the probability that the SD spider initiated proximation was more clearly related to size

difference, increasing with SD spider size and decreasing with SA spider size (Fig. 7). For contests resolved at this stage, the probability that the SA spider retreated decreased with SA spider size and increased with SD spider size (Fig. 8). Finally, the probability that the SD spider retreated decreased with SD spider size and increased with SA spider size (Fig.9).

Spiders were less likely to take the active roles of initiating proximation or retreating if they were first to orient (Figs. 6, 7, 8, and 9). Of the 90 contests progressing beyond posing in which a size difference was detected, the SA spider more often initiated proximation (SA in 59, SD in 31; *z*=2.85, *P*=0.004).

Leading the way

The way in which posing terminated was an important turning point in contests and to a large extent predicted each spider's future actions. After one spider (the 'escalator') initiated proximation by stepping toward its rival, the other spider (the 'hesitator') almost always stood still either until one of the spiders retreated or the contest proceeded to sparring. There was only one contest in which both spiders stepped toward the other during proximating. Both spiders always maintained the hunch posture throughout proximating.

In addition to making the first move from posing and almost always being responsible for the following transition to sparring (unless contests terminated first), the escalator lunged and rammed more frequently than did the hesitator during sparring in 52 (81%) of the 64 contests that reached this stage. In 5 contests (8%), frequency of lunging and ramming was equal and in the remaining 7

Fig. 5 Predicted probability (from logistic regression in Table 2) of a contest between size-matched spiders in experiment 2 terminating at each contest stage in relation to spider size and proximity (4, 8, and 12 cm). Escalation was greater if the spiders were large and if they were close when they oriented
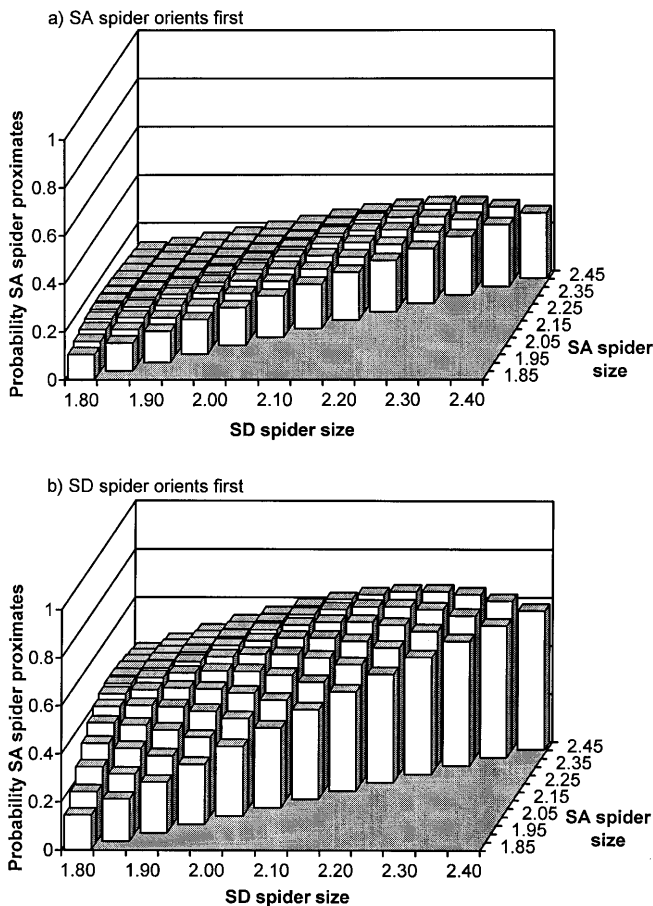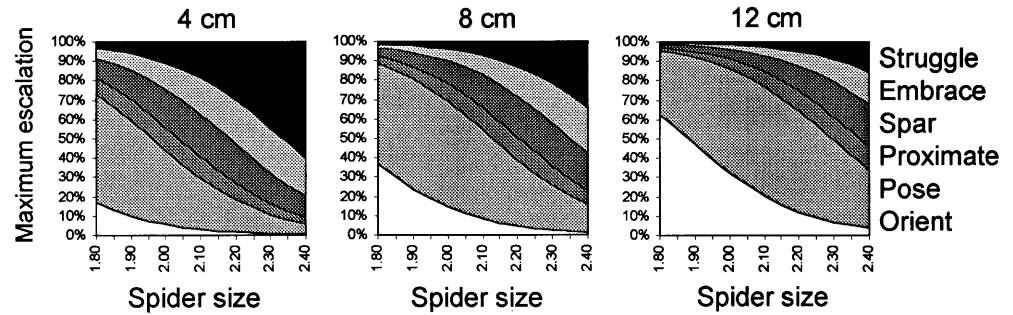

Fig. 6 Predicted probability that the SA spider terminated posing by initiating proximation if the SA spider oriented first (**a**) and if the SD spider oriented first (**b**)
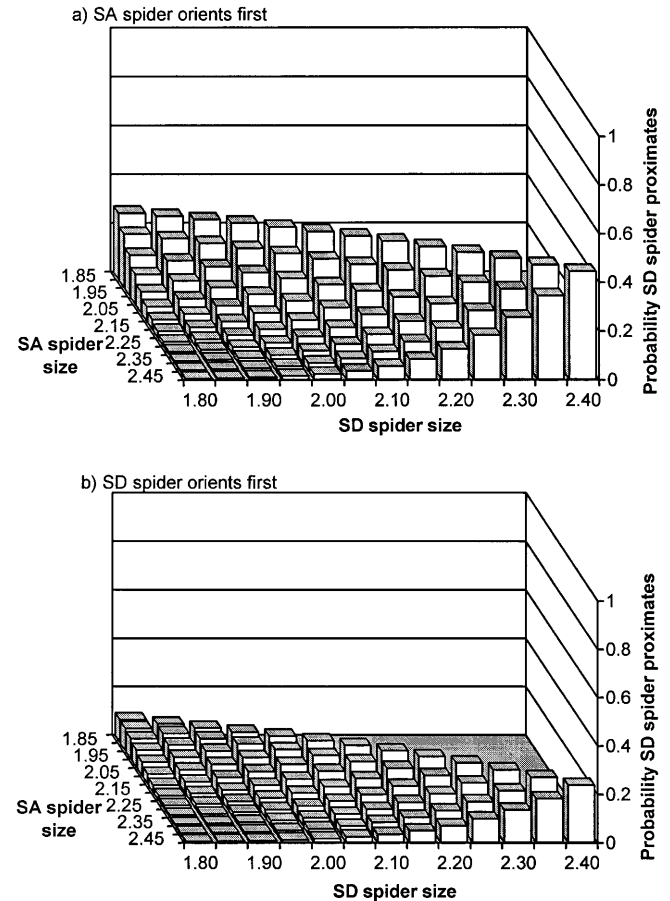
Fig. 7 Predicted probability that the SD spider terminated posing by initiating proximation if the SA spider oriented first (**a**) and if the SD spider oriented first (**b**)

(11%), the hesitator lunged and rammed more frequently than the escalator. Escalators were more likely than hesitators to dominate activity during sparring ($z=5.73$, $P<0.001$). In 34 contests (53%), lunging and ramming were carried out exclusively by the escalator; in just 2 contests (3%), these activities were carried out exclusively by the hesitator. Associated with their greater tendency to take the role of escalator, SA spiders were more likely to maintain greater activity during sparring (SA spider in 37, SD spider in 21; $z=1.97$, $P=0.049$).

Discussion

The winner of contests between *P. paykulli* males can be readily predicted by size advantage (Fig. 1). This result indicates a robust relationship between size and RHP in the spider population used. Body size is commonly expected to correlate with ability to inflict injury in unrestrained fights and ability to defend against attacks, and this result is no surprise given the similar results of previous salticid studies (Jackson 1980; Wells 1988; Faber and Baylis 1993; Taylor and Jackson 1999). Further-
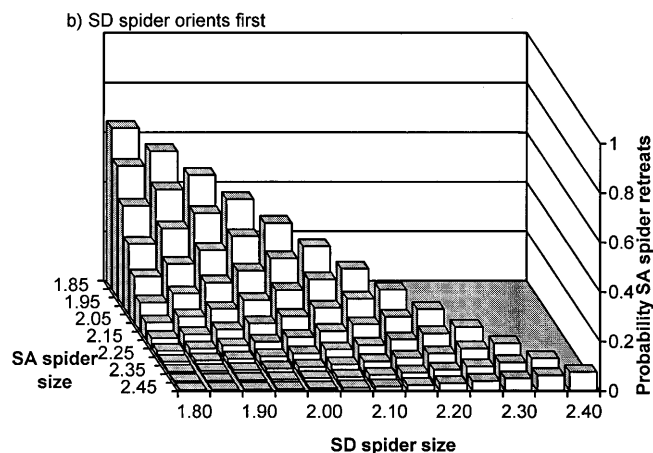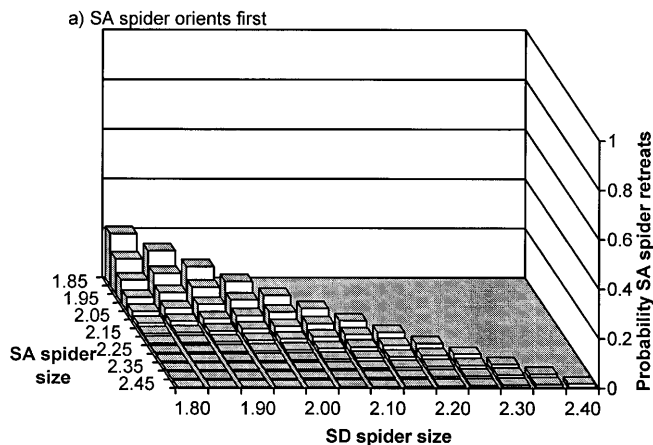
Fig. 8 Predicted probability that the SA spider terminated posing by retreating if the SA spider oriented first (**a**) and if the SD spider oriented first (**b**)

Fig. 9 Predicted probability that the SD spider terminated posing by retreating if the SA spider oriented first (**a**) and if the SD spider oriented first (**b**)

more, the gradual stepwise progression of these contests (Table 1, Fig. 2) is rather typical of interactions between male salticids. Nevertheless, other aspects of our study differ markedly from previous accounts.

Contest resolution using size-dependent persistence

Salticids are unique among spiders both in their visual acuity and in their reliance on visual cues when navigating, hunting, and communicating. However, we did not detect any evidence that *P. paykulli* males use information gained by visual assessment of rival size when making decisions in contests. If decisions of persistence were based on estimated size differences, we would expect contest escalation and duration in a multiple regression to be positively related to SD spider size and negatively related to SA spider size (i.e., negatively related to size difference). Instead, escalation tendencies and overall duration were both predicted by SD spider (usually the loser) size alone (Tables 2, 3, Figs. 3, 4), a result more consistent with rivals basing these decisions on their own ability (Mesterton-Gibbons et al. 1996). This idea is
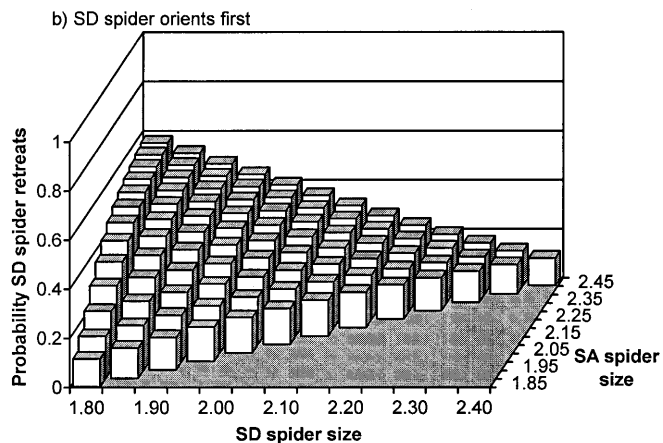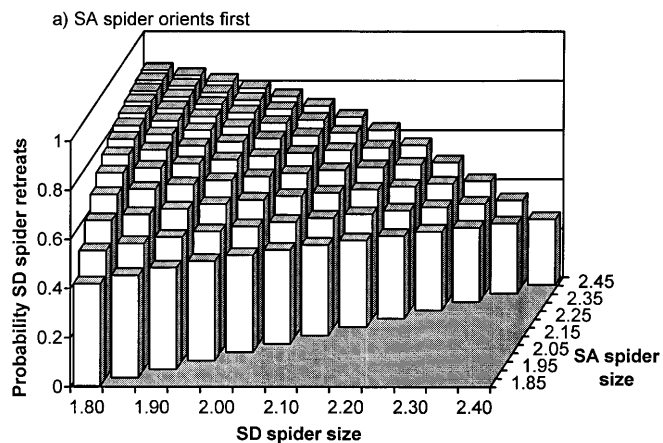
further supported by the tendency for large size-matched pairs to have more escalated and longer contests than small size-matched pairs (Tables 2, 3, Fig. 5). Contests are ended by the retreat of losers, typically the size-disadvantaged rival when such an asymmetry exists; rival *P. paykulli* males seem to persist in a size-characteristic manner, and then retreat. A limited ability to directly assess rivals might lead rivals to adopt rules based on individual ability or estimated probability of superiority (Mesterton-Gibbons et al. 1996; Whitehouse 1997). The combined demands of spatial resolution and correction for distance to accurately assess rival salticids may be beyond the ability of these spiders.

For persistence alone to yield reliable outcomes, it must be constrained either by physical limits or tactical trade-offs. Otherwise, small cheats would be free to choose persistence typically associated with large spiders. Energy is an important currency in the contests of many animals, including house crickets (Hack 1997), damselflies (Marden and Waage 1990; Marden and Rollins 1994), and cichlid fish (Neat et al. 1998). Because stamina may be closely associated with performance in unrestrained combat, energetically expensive

displays may provide a very direct and reliable assessment of RHP. Perhaps agonistic displays are energetically expensive and spiders desist once they reach a certain threshold of energy reserves or harmful metabolites of anaerobic respiration. Under this hypothesis, small spiders are more likely to retreat because, compared with large spiders, they are less able to bear the time-dependent energetic costs of interaction. The relatively great propensity of SA spiders to initiate proximation and later, as 'escalators,' maintain higher levels of activity while sparring might also be explained by decisions based on size-associated energetic budgets.

One alternative hypothesis to energetic costs as a limit on display performance is that spiders simply respond to risk associated with their position in the population distribution of fighting abilities, with smaller individuals taking a more cautious approach in accord with the low probability of superiority over a rival they cannot assess accurately. Under this hypothesis, small spiders may be reluctant to persist because it is dangerous to be caught out in an escalated contest with a much larger rival. Cautiousness of small spiders, and boldness of large spiders, might well have been further promoted by experiences during preliminary experiments (Whitehouse 1997). As would be the case in nature, smaller spiders would have had more experience of losing contests.

Roles for orienting order and proximity

Which spider saw the other first had important consequences for contest outcome, tendency to take the active role of 'escalator,' as well as maximum escalation and duration of contests. Spiders that oriented second were more prone to retreat overall (Fig. 1) and during posing (Figs. 8, 9), indicating an advantage to being the first rival to orient and begin display. This advantage may be related to asymmetries of information and preparation. Spiders that orient first might have more opportunity to assess the terrain and prepare for the interaction (e.g., modify physiological state, take positional advantage). Spiders that orient second might then consider themselves disadvantaged by this asymmetry and be more prone to avoiding further interaction. Jacques and Dill (1980) reported a similar tendency in another salticid, *Salticus scenicus*, in which wandering spiders tended to retreat first during contests with stationary spiders occupying a space on an artificial wall. They present this as a likely case of an arbitrary 'uncorrelated asymmetry' (asymmetry not related to ability or pay-offs to rivals) being used to settle conflict. However, the stationary 'residents' seem likely to have more often seen the approaching wanderer first. Because salticids rely largely on motion sensors to detect each other, stationary salticids readily detect mobile conspecifics, but mobile salticids have difficulty detecting stationary conspecifics (Forster 1982). Hence, the stationary spiders probably had time to prepare before being noticed by the wanderer, providing opportunity for asymmetry correlated with a real advantage in contests. For example, they might have taken a positional advantage by maintaining a higher position on the wall, such that gravity would aid their attacks and impair those of the encroaching rival.

In addition to a greater propensity for retreat, spiders that oriented second were more prone to initiating escalation (Figs. 6, 7). This might be a means of overcoming the rival's timing advantage. The tendency for spiders to initiate escalation more frequently if they orient second might also be explained by energetic considerations. If hunching displays used during posing are energetically costly, limiting future actions, then, having already expended more energy in display, the spider that orients first might be reluctant to adopt the more active role of escalator. In contrast, the spider that orients second would be less constrained energetically and would hence be more capable of maintaining the more active role. Alternatively, they may have simply been left little option by their rival's reluctance to act.

Contests tended to reach higher levels of escalation, and last longer, if the SD spider oriented first. Although SA spiders were somewhat disadvantaged if they oriented second, some losing contests that they would have won had they oriented first (compare Fig. 1a, b), most SA spiders prevailed in the end (Fig. 1). SA spiders may need a longer more intense effort to overcome whatever advantage the SD rival gains by orienting first. SA spiders with insufficient size advantage failed to overcome the asymmetry of orientation order.

Tactical differences between rivals

Contests in *P. paykulli* resembled those of some crayfish (Pavey and Fielder 1996) and crabs (Dowds and Elwood 1985; Smith et al. 1994) in that the SA rival, who has a better than even chance of winning, tended to initiate escalation. The decision to increase rates of cost accrual persist into the contest as the escalator was almost always the rival responsible for the subsequent transition to sparring and was usually more active with lunging and ramming at that stage. Other tactical differences bearing an association with relative RHP have been reported in fish (Turner and Huntingford 1986; Ribowski and Franck 1993), crabs (Dowds and Elwood 1985; Glass and Huntingford 1988), and anolis lizards (Tokarz 1985). In each case, the rival with the greater chance of winning acts more boldly. It is tempting to interpret such trends as indicating that some direct assessment of relative status has taken place. However, such trends may also derive from absolute size-dependent tendencies (see Whitehouse 1997). Spiders of high RHP may have a greater inherent tendency to both initiate escalation and choose costly tactics as a means of intimidating rivals.

Effects of size in other studies

The conclusions of this study differ considerably from other studies of salticid spider contests. Whereas both

Wells (1988) and Faber and Baylis (1993) concluded that escalation tendency depends on size difference between the rivals and direct size assessment we instead conclude that escalation tendency more closely follows the SD (or losing) rival's persistence. However, looking closely at the relationship between size difference and maximum escalation in these previous studies reveals evidence that their results may also be better explained by SD spider size alone. Both Wells (1988) and Faber and Baylis (1993) reported that contests between spiders of large size difference were resolved only at low intensity whereas contests between spiders of small size difference might be resolved at any intensity. This is precisely the distribution that would be expected when effects of SD spider size are investigated only through their contribution to measures of size difference. Small size differences may involve any sized SA or SD spider and hence resolve at any level of escalation but large size differences involve only small SD spiders (and large SA spiders) and therefore tend to resolve more often at low levels of escalation. Similar results have been reported for duration of contests in cichlid fish (Enquist and Jakobsson 1986), butterflies (Rosenberg and Enquist 1991), and in other measures of contest cost in swordtail fish (Ribowski and Franck 1993; Morris et al. 1995). The possibility that effects of size difference are due simply to association with one rival's absolute size should be tested in studies showing such relationships between size difference and contest costs.

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