



Interacting effects of size and prior injury in jumping spider conflicts

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An animal's ability to win intrasexual conflicts is often determined by the combined influence of several different traits, such as size, experience, residency and prior injury. When each of two (or more) asymmetries favours a different rival, the outcome of a conflict will reflect each asymmetry's contribution to overall status. We investigated the interacting effects of size difference and prior loss of forelegs (a common injury in nature) on the ability of males to win intrasexual conflicts in *Trite planiceps*, a New Zealand jumping spider (Salticidae). When both rivals were intact, the probability of the larger rival winning increased with the size difference between rivals. When rivals were of matching size, injury was a strong predictor of outcome; intact spiders beat rivals missing one or both forelegs and spiders missing one foreleg beat rivals missing both forelegs. During conflicts between spiders that differed both in size and in injury state, these two variables had combined effects on outcome. The tendency for larger rivals to win increased with size difference, but the probability of the larger rival winning diminished if the larger rival of the pair was the more injured. We used inverse prediction from logistic regression models to quantify the size advantage that is sufficient to offset the disadvantage of prior injury.

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Animals in conflicts typically differ in several different determinants of overall ability that may each, in part, predict outcome. Relevant asymmetries may include such diverse factors as body size (Riechert 1978; Pavey & Fielder 1996; Hack et al. 1997), residency (Jackson & Cooper 1991; Jennions & Backwell 1996; Hack et al. 1997), nutritional state (Plaistow & Siva-Jothy 1996; Hack 1997), badges of status (Dunham 1978), weapon size (Barki et al. 1997; Sneddon et al. 1997), experience at winning or losing (Beacham 1988; Chase et al. 1994; Whitehouse 1997), gonadal weight (Neat et al. 1998), body temperature (Stutt & Willmer 1998) and injury (Berzins & Caldwell 1983; Fox et al. 1990; Smith 1992). In laboratory experiments, researchers often boost the relative influence of investigated asymmetries by holding all other asymmetries as close as possible to some standard value. In nature, however, numerous conflicting asymmetries may exist (Parker & Rubenstein 1981; Leimar & Enquist 1984; Dugatkin & Biederman 1991; Jennions & Backwell 1996). In this study of *Trite planiceps* (Fig. 1), a New Zealand jumping spider (Araneae: Salticidae), we consider body size and prior injury (loss of

forelegs) as interacting influences on the ability of adult males to win conflicts.

Most invertebrates, and a few vertebrates (lizards, Arnold 1984; salamanders, Brodie 1983), are able to voluntarily discard ('autotomize') body parts that have been grasped or envenomated by enemies. An anti-predator role of leg autotomy has been directly confirmed in some spiders (Eisner & Camazine 1983; Roth & Roth 1984; Formanowicz 1990; Klawinski & Formanowicz 1994; Punzo 1997). Juvenile spiders are able to incrementally regenerate lost appendages at subsequent moults. But most spiders, including *T. planiceps*, cease moulting at adulthood and are hence unable to regenerate lost appendages (Foelix 1996). During field collections of adult *T. planiceps* spiders over 3 years (1991–1994), we noted that approximately 15% of males and 11% of females were missing one of their long and heavily built forelegs, and 2% of both sexes were missing both of these legs (P. W. Taylor, unpublished data). There have been reports of spiders autotomizing limbs that become trapped in exuviae during moults (Foelix 1996), but we have not observed this during laboratory rearing of several hundred *T. planiceps*. Hence, loss of legs in nature most likely occurs during encounters with predators. *Trite planiceps* shares its habitat with several species of large, aggressive, araneophagic spiders against which this defence might sometimes be necessary (Taylor 1997).

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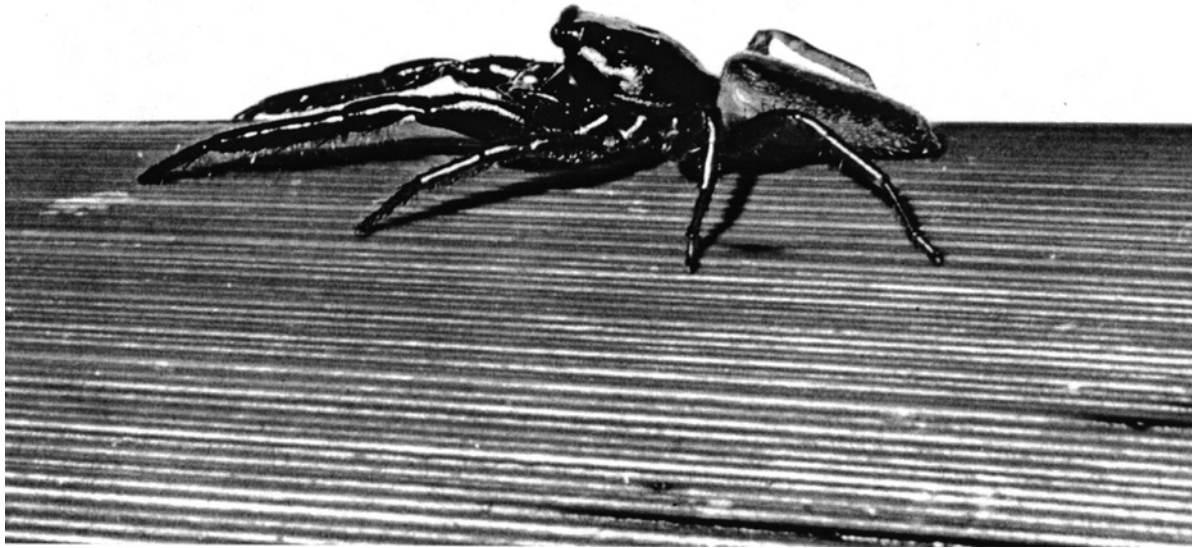


Figure 1. Adult *T. planiceps* male. Note the size, robustness and dark colour of the forelegs compared with the other legs. Forelegs play a prominent role in visual displays and physical exchanges during intrasexual conflicts.

Adults of *T. planiceps* have been observed autotomizing limbs when attacked by predators in the laboratory (P. W. Taylor, personal observation). Cannibalism by females on males and other females has been observed in this species (Taylor & Jackson 1999), and so autotomy might also serve as a defence against attacking conspecifics.

Although autotomy may offer an opportunity for escape, it is usually not without cost. After autotomizing tails, lizards may suffer reduced home range (Martin & Salvador 1997) and increased predation risk (Wilson 1992). Starfish may be rendered more prone to undernutrition and decreased gamete production (Lawrence & Larrain 1994). Damselfly larvae that autotomize caudal lamellae may be prone to increased intra- and interspecific predation and diminished hunting success (Stoks 1998). Decapod crustaceans may suffer reduced feeding efficiency, retarded growth, diminished mating success, increased predation risk and reduced competitive ability (Juanes & Smith 1995). Among wolf spiders (Lycosidae), autotomy may reduce locomotory speed (Amaya et al. 2001) or limit maximum prey size (Brueseke et al. 2001). Autotomy has been associated with the reduced ability of some spiders to win conflicts (Dodson & Beck 1993; Hammerstein & Riechert 1988), but this possibility has not been investigated in jumping spiders. Although infrequently reported in the literature (Jackson & Hallas 1986; Wells 1988), our personal observations indicate that autotomy is commonplace in jumping spiders. Yet this appears to be the first study attempting to characterize or quantify potential costs that might follow autotomy in these extraordinary spiders.

Jumping spiders are quite unlike other spiders in many of their abilities and habits. They have visual acuity that greatly exceeds the abilities of other spiders (Land 1985;

Blest et al. 1990; Harland et al. 1999) and rely primarily on visual displays to mediate interactions that take place in daylight (Jackson & Hallas 1986; Clark & Uetz 1993; Faber & Baylis 1993). *Trite planiceps* is most commonly found living in New Zealand flax (*Phormium tenax*) and similar monocotyledonous plants that have long narrow leaves with a tendency to roll up when they die and dry out, forming cavities exploited as retreats by spiders. On diurnal forays, during which they seek prey and mates, *T. planiceps* males often encounter each other on the long thin leaves that dominate their typical habitat (Taylor & Jackson 1999). As in many other jumping spiders (Crane 1949), various postures and waving of the elongate forelegs are common visual displays used by *T. planiceps* males during intrasexual conflicts (Forster 1982; Taylor & Jackson 1999). Male *T. planiceps* usually approach each other in a series of short indirect bouts of walking; each spider simultaneously steps towards the other and to one side. While walking towards conspecifics, spiders may wave their forelegs up and down or hold their forelegs in a raised posture. Between walking bouts, spiders may wave their forelegs up and down, posture, or stamp their forelegs on the substratum. Additionally, conflicts sometimes escalate to an 'embrace' during which the spiders step towards each other until contact is made and then push against each other while each uses its forelegs to grasp the other spider or to lift its legs off the substrate (see Taylor & Jackson 1999 for a detailed description of these behaviours). *Trite planiceps* males also use their forelegs to grasp and hold prey, and to repel the attacks of potentially cannibalistic females. Hence, absence of forelegs may be expected to impose a disadvantage on male spiders during intrasexual conflicts by diminishing their ability to display, grasp, mount attacks and defend against rivals.

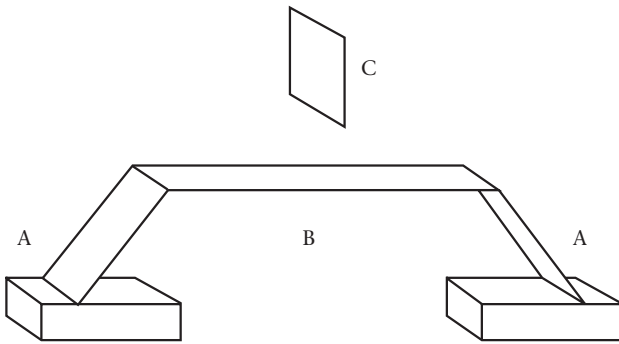


Figure 2. Arena on which conflicts between *T. planiceps* males were staged. (A) Ramp and base. (B) Platform. (C) Screen (raised).

Size asymmetry is an important predictor of outcome in the conflicts of many jumping spider species (Jackson 1980; Wells 1988; Jackson & Cooper 1991; Faber & Baylis 1993; Taylor et al. 2001), including *T. planiceps* (Forster 1982; Taylor & Jackson 1999). If both size and prior injury (loss of forelegs) are important asymmetries, then we predict that the more injured rival of a size-matched pair will tend to lose but that there will be some size advantage that is sufficient to offset an injury disadvantage. In the present study, we confirm size and prior injury (loss of forelegs) as important influences on the ability of *T. planiceps* males to win intrasexual conflicts and also quantify the impact of prior injury in terms of an equivalent size currency.

METHODS

Collection and Maintenance of Spiders

We collected adult male *T. planiceps* from a population living in New Zealand flax (*Phormium tenax*) near Christchurch, New Zealand. Spiders were maintained in isolation from each other using standard methods (see Jackson & Hallas 1986) and were provided ad libitum access to water in cotton wool and house flies (*Musca domestica*) as prey. As a size index, we measured prosoma width to the nearest 0.025 mm using an ocular micrometer in all analyses involving autotomy (experiments 2 and 3 below). We collected data for analysis of conflicts between intact spiders (experiment 1 below) during an earlier study (Taylor & Jackson 1999) in which prosoma width was measured to the nearest 0.05 mm.

Testing Procedures

The testing arena comprised a thin, green, plastic platform (300 mm long, 70 mm wide) that was supported at each end by a glass ramp (150 mm long, 70 mm wide) mounted on a wooden base (Fig. 2). This arena simulated a section of the long, narrow, flax leaves on which *T. planiceps* usually encounter each other in nature (Taylor & Jackson 1999).

We released one spider onto the ramp at each end of the platform while holding an opaque screen in place at

the midpoint of the platform. After both spiders had walked up onto the platform, we removed the screen so that the spiders could see each other and interact. All trials were videotaped and analysed later. We thoroughly washed the arena between trials with warm water and then 80% ethanol to remove chemical cues that might have been left by spiders in the previous trial (Jackson 1987).

A trial ended when one spider (loser) ran away from the other (winner). To investigate variation in the probability that the size-advantaged rival won, we first ran logistic regression models using the sizes of the size-advantaged (SA) and size-disadvantaged (SD) rivals as covariates along with the categorical predictor 'SA or SD rival missing more legs' when both asymmetries were involved (for a useful primer on logistic regression, see Hardy & Field 1998). By this approach, effects of size difference are expressed as equal and opposite effects of SA rival size and SD rival size (Taylor et al. 2001; Taylor & Elwood, in press). Upon finding such effects, we opted for the equivalent, but more economical, predictor of size difference (SA rival size – SD rival size). All statistical analyses were carried out using JMP 4.0.2 (SAS Institute). Significance of predictors in logistic regressions was tested by log-likelihood ratio (*G*). In addition to overall model significance, we present lack of fit statistics, which test for inappropriate functional form of predictors in the model.

Experiment 1: Effects of Size

Taylor & Jackson (1999) reported that size-advantaged *T. planiceps* won 44 (83%) of 53 conflicts between intact rivals. However, no attempt was made to investigate whether or how this general tendency varies with the size of rivals. The present study addresses these questions using data from interactions described in Taylor & Jackson (1999). Spider source, maintenance and experimental procedures in the present study were identical to those used by Taylor & Jackson (1999), except that in our earlier study we used a wider range of spider ages and some of the spiders tested were collected as subadults and matured in the laboratory.

Experiment 2: Effects of Prior Injury

If loss of forelegs reduces the ability of spiders to win conflicts, then the expected tendency would be for spiders that have lost one or both forelegs to lose against intact rivals that are equal in other respects. Also, if loss of forelegs is a graded injury (i.e. more legs missing means greater loss of ability), then spiders missing both forelegs should tend to lose when matched against rivals that are missing only one foreleg, but are equal in all other respects. To test these hypotheses, we staged conflicts between size-matched spiders (<0.025 mm size difference) that differed in the number of forelegs that had been lost.

After collecting adult spiders from nature and measuring their size, we assorted the spiders into same-sized

pairs. Each member of each pair was placed into a different one of three treatments; 'intact', 'missing one foreleg' and 'missing both forelegs'. To ensure that spiders were in healthy condition, they were maintained in the laboratory for 10–14 days before legs were removed. To remove a spider's foreleg, the femur of the leg being removed was held with forceps until the spider voluntarily autotomized the leg to escape (almost always within 10 s). Spiders always autotomized legs at the coxa-trochanter joint, the point at which legs had also been detached by spiders observed in nature. For spiders in the missing one foreleg treatment, we randomly selected a leg for removal. For spiders in the missing both forelegs treatment, we removed the second foreleg between 1–2 h after removing the first leg. All spiders were then maintained for a further 10–14 days with ad libitum access to food and water, allowing them to recover before being used in experiments. We used binomial tests to assess whether the frequency of wins by spiders from each injury class differed from the 1:1 ratio expected if there were no effects of injury (Zar 1984).

Experiment 3: Interacting Effects of Size and Prior Injury

We selected spiders of various sizes at random for each of the three classes of prior injury (intact, missing one foreleg and missing both forelegs). Between 10 and 15 days after removal of legs, we paired spiders of different injury status and size at random.

We first used logistic regression to test for effects of size and injury on the SA spider's probability of winning for each of the three possible types of injury asymmetry (intact versus missing one foreleg, intact versus missing both forelegs, missing one foreleg versus missing both forelegs). We then used inverse prediction from these logistic regression models to estimate the size difference at which the two spiders had an equal probability of winning when the SA rival was injured. Deviation of this size difference from zero represents the disadvantage imposed by this prior injury in terms of a size currency.

Ethical note

Two aspects of the present study require some ethical consideration: removal of spiders' legs and staging of potentially injurious conflicts. Autotomy is very common in spiders in nature and appears to function primarily as an adaptive antipredator device. Spiders have special muscular mechanisms used to voluntarily detach limbs that have been grasped, and the wound seals naturally with negligible loss of body fluids (Roth & Roth 1984; Foelix 1996). In this study, the legs were not surgically excised. Instead, we simply invoked the natural autotomy response by grasping a spider's leg. All spiders survived this treatment and resumed locomotory activity immediately. Spiders missing legs also appeared to have little difficulty catching prey. To test this, after staging conflicts we left a group of spiders representing each of the

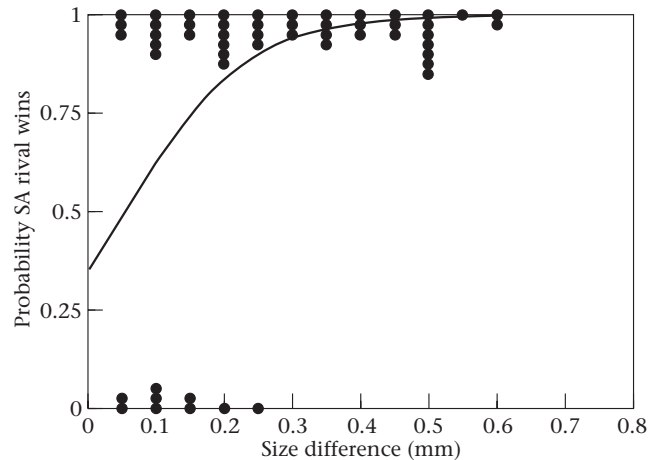


Figure 3. Relationship between the size difference between intact *T. planiceps* male rivals and the probability that the size-advantaged (SA) male would win conflicts (data from Taylor & Jackson 1999, $N=53$). The line represents the predicted probabilities derived from a logistic regression ($Y=1/(1+(\exp(0.62-11.25X)))$). Points above indicate wins by size-advantaged spiders; points below indicate wins by size-disadvantaged spiders.

three injury states without prey for 6 days and then introduced a house fly to each of their maintenance cages. Success at catching the house fly during the following 10 min was similar for spiders in the three injury states (54 of 62 intact spiders, 44 of 57 spiders missing one foreleg and 40 of 48 spiders missing both forelegs; log-likelihood test: $G_2=2.037$, $P=0.361$).

Conflicts between *T. planiceps* males are highly ritualized and no injuries were observed in any of the trials reported here, including those of Taylor & Jackson (1999). The arena used in the present study (Fig. 2) was designed to simulate the conditions under which spiders would encounter each other in nature. Spiders could readily avoid each other simply by moving to the opposite surface of the platform, by running down one of the ramps or by leaping off the arena.

RESULTS

Experiment 1: Effects of Size

In multiple logistic regression, using data collected during the study of Taylor & Jackson (1999), the tendency of SA rivals to win agonistic interactions was positively associated with the SA rival's size ($b=11.246$, $G_1=10.697$, $P=0.001$) and was negatively associated with the SD rival's size ($b=-11.277$, $G_1=9.724$, $P=0.002$) ($N=53$, overall model: $r^2=0.23$, $G_2=11.323$, $P=0.004$; lack of fit: $G_{40}=24.832$, $P=0.971$). These approximately equal and opposite-signed effects of SA and SD rival size can be more economically expressed as a positive effect of size difference ($N=53$, $b=11.251$, $r^2=0.23$, $G_1=11.323$, $P<0.001$; lack of fit: $G_{13}=8.036$, $P=0.841$; Fig. 3). Escalation to embracing was observed in only seven conflicts (13%). All other conflicts were resolved at a distance.

Table 1. Effects of male *T. planiceps* size and injury status (number of missing forelegs) on the probability that size-advantaged (SA) males would win in conflicts with size-disadvantaged (SD) rivals (all predictors carry 1 degree of freedom)

	Intact–Missing one leg (N=40)		Intact–Missing both legs (N=49)		Missing one leg–Missing both legs (N=57)	
	G	P	G	P	G	P
Model 1: using each rival's absolute size						
SA rival size	5.591 (<i>b</i> =11.36)	0.018	10.746 (<i>b</i> =8.02)	0.001	8.979 (<i>b</i> =9.84)	0.003
SD rival size	4.018 (<i>b</i> =−9.99)	0.045	8.226 (<i>b</i> =−7.08)	0.004	9.927 (<i>b</i> =−10.48)	0.002
Injury status	14.875	<0.001	25.325	<0.001	4.874	0.027
Model (<i>df</i> =3)	18.934 (<i>r</i> ² =0.36)	<0.001	34.324 (<i>r</i> ² =0.57)	0.001	12.427 (<i>r</i> ² =0.21)	0.006
Lack of fit	30.089 (<i>df</i> =32)	0.564	26.041 (<i>df</i> =44)	0.986	36.879 (<i>df</i> =46)	0.829
Model 2: using size difference between rivals (i.e. SA rival size −SD rival size)						
Size difference	5.385	0.020	10.757	0.001	9.901	0.002
Injury status	14.122	0.001	25.126	<0.001	4.729	0.030
Model (<i>df</i> =2)	18.081 (<i>r</i> ² =0.35)	0.001	34.025 (<i>r</i> ² =0.56)	<0.001	12.201 (<i>r</i> ² =0.21)	0.002
Lack of fit	17.758 (<i>df</i> =23)	0.771	23.566 (<i>df</i> =35)	0.929	22.057 (<i>df</i> =38)	0.982

Experiment 2: Effects of Prior Injury on Conflict Outcome

Intact spiders won 20 (77%) of 26 conflicts against same-sized rivals that were missing one foreleg (binomial test: $Z=2.55$, $N=26$, $P=0.012$) and 18 (90%) of 20 conflicts against same-sized rivals that were missing both forelegs ($Z=3.35$, $N=20$, $P<0.001$). Spiders that were missing one foreleg won 18 (75%) of 24 conflicts against same-sized rivals that were missing both forelegs ($Z=2.25$, $N=24$, $P=0.025$) consistent with the absence of these legs being a graded injury, depending on the number of legs lost. Escalation to embracing was similarly uncommon in the three interactions types: 4/26 intact versus missing one foreleg (15%); 3/20 intact versus missing both forelegs (15%); 2/24 missing one foreleg versus missing both forelegs (8%) (log-likelihood test: $G_2=0.711$, $P=0.701$).

Experiment 3: Interacting Effects of Size and Prior Injury

For each of the three combinations of injury status, SA rival size, SD rival size and injury status were significant predictors of outcome (Table 1). As all initial models detected approximately opposing effects of SA and SD rival sizes, we reformulated the models using the more economical predictor of size difference (Table 1, Figs 4, 5, 6).

Using inverse prediction from the logistic regression models, we estimated the disadvantage of autotomy in terms of the equivalent size advantage required to place the two spiders on equal terms. For conflicts between intact spiders and spiders missing one foreleg, the two rivals had an equal chance of winning when the injured spider was 0.20 mm larger (7% of average spider size; Fig. 4). For conflicts between intact spiders and spiders missing both forelegs, the two rivals had an equal chance of winning when the injured spider was 0.34 mm larger (12% of average spider size; Fig. 5). For conflicts between

spiders missing one foreleg and spiders missing both forelegs, the two rivals had an equal chance of winning when the spider missing both legs was 0.11 mm larger (5% of average spider size; Fig. 6).

As in other experiments, most interactions were resolved without physical contact between the spiders. Escalation to embracing was observed in 7/40 interactions between intact spiders and spiders missing one foreleg (18%), 4/49 interactions between intact spiders and spiders missing both forelegs (8%), and 6/57 interactions between spiders missing one foreleg and spiders missing both forelegs (11%) (log-likelihood test: $G_2=1.885$, $P=0.390$).

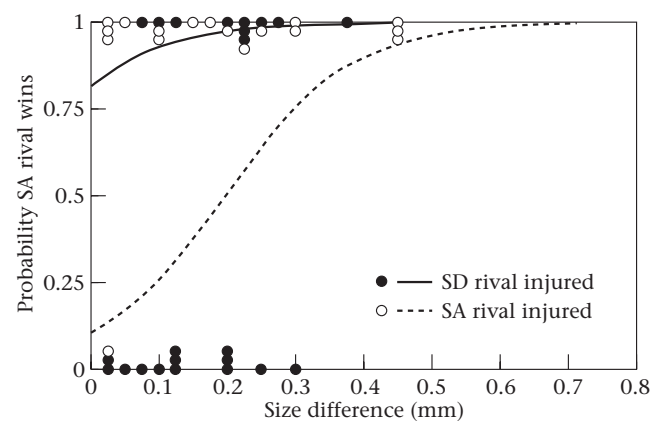


Figure 4. Relationship between the size difference between *T. planiceps* male rivals and the probability that the size-advantaged male would win conflicts when one rival was intact and the other rival was missing one foreleg ($N=40$). The lines represent predicted probabilities derived from logistic regression for each of two conditions tested; when the size-advantaged (SA) spider was missing a leg ($Y=1/(1+(\exp(2.14-10.85X))))$ and when the size-disadvantaged (SD) spider was missing a leg ($Y=1/(1+(\exp(-1.49-10.85X))))$ (Table 1). Points above indicate wins by size-advantaged spiders; points below indicate wins by size-disadvantaged spiders.

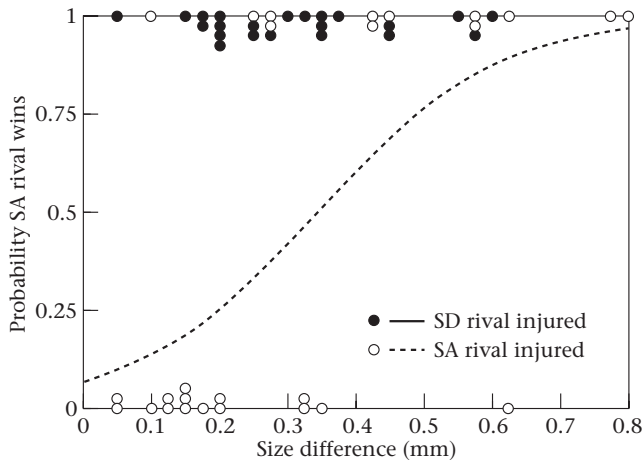


Figure 5. Relationship between the size difference between *T. planiceps* male rivals and the probability that the size-advantaged male would win conflicts when one rival was intact and the other rival was missing both forelegs ($N=49$). The lines represent the predicted probabilities derived from logistic regression for each of two conditions tested: when the size-advantaged (SA) spider was missing legs ($Y=1/(1+(\exp(2.60-7.57X)))$) and when the size-disadvantaged (SD) spider was missing legs ($Y=1/(1+(\exp(-11.27-7.57X)))$) (Table 1). Points above indicate wins by size-advantaged spiders; points below indicate wins by size-disadvantaged spiders. Injured size-disadvantaged spiders always lost these conflicts and the predicted line is superimposed on the line along the top of the figure.

DISCUSSION

Our results clearly show that asymmetries of size and prior injury (loss of forelegs) are both important predictors of outcome in conflicts between *T. planiceps* males. When each asymmetry was held at a constant value, either experimentally (experiments 1, 2) or statistically (experiment 3), the other asymmetry was a strong predictor of outcome. Furthermore, by use of inverse prediction, we quantified the impact of foreleg loss on the tendency to win conflicts in terms of an equivalent size disparity. This approach renders the effects of different asymmetries in a single currency, thereby aiding comparisons.

Loss of appendages is also associated with a reduction in ability during conflicts of some stomatopods (Berzins & Caldwell 1983), crabs (Smith 1992), snapping shrimps (Conover & Miller 1978), thomisid spiders (Dodson & Beck 1993; but see Dodson & Schwaab 2001) and agelenid spiders (Hammerstein & Riechert 1988). After losing a leg, juvenile males of *Schizocosa ocreata*, a wolf spider (Lycosidae), regenerate the limb, but often fail to regenerate ornamental tufts. When lacking these tufts, adult males tend to lose conflicts against tufted rivals (Uetz et al. 1996). Prior loss of legs is associated with a reduced ability to win escalated, but not nonescalated, conflicts of pholcid spiders (Johnson & Jakob 1999). Jackson & Hallas (1986) suggest that *Portia* spp. (Salticidae) that have lost legs might be disadvantaged during conflicts, but no experiments have been carried out on these jumping spiders. The present study of *T. planiceps* is the first experimental demonstration that prior autotomy of

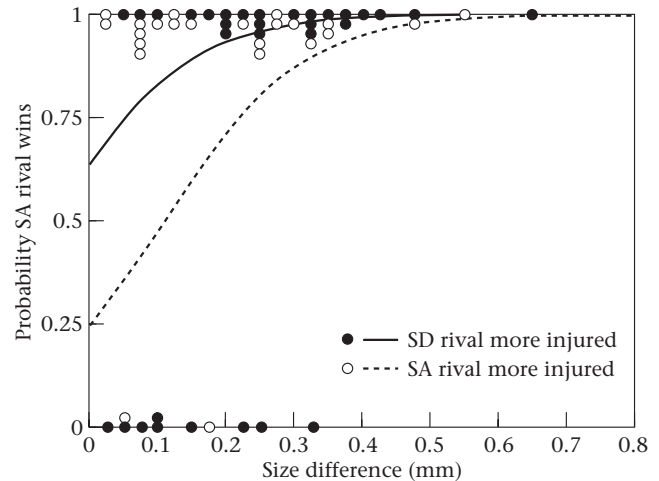


Figure 6. Relationship between the size difference between *T. planiceps* male rivals and the probability that the size-advantaged male would win conflicts when one rival was missing one foreleg and the other rival was missing both forelegs ($N=57$). The lines represent the predicted probabilities derived from logistic regressions for each of two conditions tested: when the size-advantaged (SA) spider was missing both legs ($Y=1/(1+(\exp(1.13-10.08X)))$) and when the size-disadvantaged (SD) spider was missing both legs ($Y=1/(1+(\exp(-0.55-10.08X)))$) (Table 1). Points above indicate wins by size-advantaged spiders; points below indicate wins by size-disadvantaged spiders.

appendages can reduce a jumping spider's ability to win intrasexual conflicts.

Mechanisms by which injury reduces an animal's ability to win conflicts remain to be studied, but some possibilities can be suggested. Animals are expected to assess each other during conflicts as a means of economically determining relative status (Enquist & Leimar 1983). Spiders might assess the injury state of rivals so that the intact spider takes into account its rival's disadvantage by persisting longer, or acting more aggressively, than it would were the rival intact. Because *T. planiceps* males have long, dark, robust forelegs, and because salticid eyes have extraordinary acuity and motion sensitivity (Forster 1982; Blest et al. 1990; Harland et al. 1999), *T. planiceps* should be able to perceive the waving and posturing of a rival's forelegs.

Assessment of rivals is not the only potential mechanism by which larger and less injured rivals gain victory. Instead, each rival may persist in a manner consistent with its own ability alone such that inferior rivals usually reach their limits first (Mesterton-Gibbons et al. 1996; Whitehouse 1997; Taylor et al. 2001; Taylor & Elwood, in press). Rather than assessing rivals, injured spiders might assess the ability they have lost as a consequence of their own injury state and compensate for the loss by becoming less persistent, or acting less aggressively (more cautiously), when in conflict with intact (or less injured) rivals or with rivals they cannot accurately assess. For example, injured spiders might have a greater tendency to retreat while still at a distance because they estimate themselves as having a physical disadvantage during embracing. Injured spiders that are also large may persist

regardless of their injury because there is a greater chance that they will have a size advantage that exceeds the injury disadvantage. It is also possible that spiders in these intrasexual conflicts use both assessment of rival injury state and size and persistence based on their own injury state and size. How animals in conflicts integrate different sources of information about their own and their rival's ability is a cognitive question that appears to warrant further investigation.

Although we have been able to estimate size-equivalent loss of conflict-winning ability associated with foreleg autotomy in *T. planiceps* males, we are currently unable to translate this into an estimate of fitness costs. In many species of jumping spiders, males readily enter into conflicts (usually interpreted as 'contests') even when they could easily avoid each other by simply walking away (Jackson & Cooper 1991). In most cases, there is no obvious resource at stake. Hence we cannot ascertain the trade-offs faced by males during these conflicts other than to say that there are surely some costs to conflicts (energy, predator exposure, time) that require some balancing benefits to winners if we seek an adaptive explanation for these activities. The nature and extent of these benefits remain elusive.

Loss of ability in intrasexual conflicts is only one of many potential costs associated with autotomy in *T. planiceps* and other jumping spiders. For example, we might expect that males missing forelegs would also be disadvantaged when foraging, climbing, defending themselves against enemies and courting prospective mates. Autotomy may allow spiders to escape enemies, but their reprieve is incomplete. The negative effects of autotomy on fitness must be at least equalled by the risks of death or more extreme injury before autotomy is an economically justified choice. Spiders should also accept some costs (e.g. lost foraging opportunities) to avoid situations where they are confronted with choosing between death and autotomy.

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