Competing dwarf males: sexual selection in an orb-weaving spider

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Abstract

Hypotheses for the adaptive significance of extreme female-biased sexual size dimorphism (SSD) generally assume that in dimorphic species males rarely interfere with each other. Here we provide the first multivariate examination of sexual selection because of male–male competition over access to females in a species with 'dwarf' males, the orb-weaving spider *Argiope aurantia*. Male *A. aurantia* typically try to mate opportunistically during the female's final moult when she is defenceless. We show that, contrary to previous hypotheses, the local operational sex ratio (males per female on the web) is male-biased most of the season. Both interference and scramble competition occur during opportunistic mating, the former leading to significant selection for large male body size. Male condition and leg length had no effect on mating success independent of size. We discuss these findings in the context of the evolution of extreme female-biased SSD in this clade.

Introduction

Sexual size dimorphism (SSD), a difference in the mean body size of males and females, is a common phenomenon in the animal kingdom. Males are usually larger than females in homoiotherms, whereas females are typically the larger sex in poikilotherms (Andersson, 1994; Abouheif & Fairbairn, 1997; Fairbairn, 1997). The spiders (Araneae) are particularly interesting with regards to their pattern of SSD. In most species SSD is moderately female biased, but in certain genera of orb-weaving spiders (Orbiculariae) and crab spiders (Thomisidae) extreme SSD occurs: females are much larger than males and may weigh over a hundred times more than males (Head, 1995; Vollrath, 1998). A size difference between the sexes of comparable magnitude is otherwise found only in some marine and parasitic taxa and rotifers (Ghiselin, 1974; Andersson, 1994; Vollrath, 1998). Spiders are thus the only free-living terrestrial taxon where extreme SSD is common and the evolution and maintenance of extreme SSD in spiders has become a focus of

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current research. As yet, we are only beginning to disentangle the factors that are involved in this process (e.g. Vollrath & Parker, 1992; Coddington *et al.*, 1997; Prenter *et al.*, 1998, 1999; Schneider *et al.*, 2000; Moya-Laraño *et al.*, 2002).

Sexual size dimorphism is generally assumed to be adaptive (Fairbairn, 1990, 1997). Body size plays a central role in the life history of organisms and potentially affects fitness in many ways (Roff, 2002). Provided that body size is heritable, selection should lead to an optimal body size that maximizes fitness within given genetic, developmental and physiological constraints (Lande, 1980; Reeve & Fairbairn, 2001; Badyaev, 2002; Roff, 2002). The optimal body size often differs for males and females as a consequence of their different reproductive roles (Andersson, 1994; Fairbairn, 1997), and SSD can evolve in response to different net selection acting on males and females if the genetic correlation between the sexes is <1 (Lande, 1980; Reeve & Fairbairn, 2001). A number of sex-specific selection regimens have been proposed to explain the evolution and maintenance of extreme SSD in spiders (Darwin, 1871; Gerhardt, 1924; Ghiselin, 1974; Vollrath & Parker, 1992; Schneider *et al.*, 2000; Moya-Laraño *et al.*, 2002). There is good support for the hypothesis that fecundity selection favouring large size in females is an important factor

(Marshall & Gittleman, 1994; Head, 1995; Prenter *et al.*, 1999; Higgins, 2002; see also Reeve & Fairbairn, 1999), and females appear to have increased in size over evolutionary time in several orb-weaving spider lineages independently (Coddington *et al.*, 1997; Hormiga *et al.*, 2000). However, what keeps males small or why they have even decreased in size in some lineages is still not well understood (Prenter *et al.*, 1997, 1998; Walker & Rypstra, 2003; Foellmer & Fairbairn, 2004; but see Vollrath, 1998; Schneider *et al.*, 2000). In the absence of opposing selection, the genetic correlation between males and females would inevitably lead to a correlated increase in male size to some extent (Lande, 1980; Reeve & Fairbairn, 2001).

In orb-weavers, as in all web-building spiders, males leave their own web after their final moult and search for mates (Foelix, 1996). Male–male competition over access to females likely generates sexual selection for large body size in males of many spider species (reviewed in Elgar, 1998). Several studies have shown that large males usually win fights with smaller males and that large males can often obtain a favourable position on the web close to the female, even in some species of the highly dimorphic orb-weaver genus *Nephila* (Christenson & Goist, 1979; Vollrath, 1980; Miyashita, 1993; Elgar & Fahey, 1996; Elgar *et al.*, 2003; but see Elgar & Bathgate, 1996). The suggestion that interference competition might select for large male size in species with dwarf males is at odds with two major hypotheses about the evolution and maintenance of extreme SSD which assume that male–male interference competition is absent or weak and thus relatively unimportant in determining lifetime fitness (Ghiselin, 1974, pp. 192–197; Vollrath & Parker, 1992). Ghiselin's (1974) small-male hypothesis states that males may only rarely encounter each other in nature because of low population densities, and this likely applies to a crab spider (LeGrand & Morse, 2000). The differential mortality hypothesis (Vollrath & Parker, 1992) states that in sit-and-wait predators, such as orb-weavers, males rarely interfere with each other, because the operational sex ratio [OSR, the ratio of adult males to females that are ready to mate (Emlen & Oring, 1977; Kvarnemo & Ahnesjö, 1996)] is typically even or female-biased, which in turn would be the result of high male mortality during mate search.

However, little is known to date about how selection operates in spider populations. If the temporal distribution of receptive females is dispersed, for example if females reach sexual maturity asynchronously, the OSR might become highly male-biased (e.g. Grant *et al.*, 1995; Lindström & Seppä, 1996). Such an effect seems probable in many orb-weaving spiders. First, many species have been described as protandrous, that is males enter the pool of individuals ready to mate earlier than females (Foelix, 1996). Secondly, males tend to cohabit with penultimate females (females just one moult away from

sexual maturity) for days or even weeks and many males may accumulate on a given female's web during that period (McCook, 1890; Robinson & Robinson, 1980; Robinson, 1982; Howell & Ellender, 1984; Jackson, 1986; Hill & Christenson, 1988; Alayon Garcia & de Armas, 1990; Elgar *et al.*, 2003). An increasing OSR by definition increases competition among males, but the form of competition depends on the ability of males to defend females. At highly male-biased OSRs, resource defence might become uneconomical for males and the system might switch from interference to scramble competition, potentially changing patterns of selection on males (Grant *et al.*, 1995; Blanckenhorn *et al.*, 1998; Grant *et al.*, 2000; Grant & Foam, 2002; Mills & Reynolds, 2003; Weir & Grant, 2004).

This study examines sexual selection on male body size and body size components because of male–male competition over access to females in the highly dimorphic orb-weaving spider *Argiope aurantia*. In *A. aurantia*, males mature on average about 1 week earlier than females (Foellmer, 2004). Males cohabit with penultimate females and wait for the female to undergo her final moult to reach sexual maturity. Anecdotal accounts suggest that at the time of a female's moult more than one male is often present on a given female's web (McCook, 1890; Robinson & Robinson, 1980; Howell & Ellender, 1984). Males try to mate with the female while she is moulting and fight vigorously over access to the female (Robinson & Robinson, 1980; Foellmer & Fairbairn, 2003). The female is completely defenceless during her moult and cannot resist a male's mating attempt and thus cannot exert any overt mate choice. This mating tactic is therefore referred to as 'opportunistic mating' (Robinson & Robinson, 1980; Foellmer & Fairbairn, 2003), and any pattern of precopulatory sexual selection on males in the context of opportunistic mating can unambiguously be ascribed to male–male competition. Males can also pursue an alternative mating tactic, if they encounter a mature, post-moult female during mate search. They usually approach and court a mature female directly and, if she is receptive, may mate with her (Robinson & Robinson, 1980; Foellmer & Fairbairn, 2003; Foellmer, 2004). In this situation, males do not face competing males but rather a cannibalistic female. Despite the fact that female attacks occur frequently, male body size is not under selection because of sexual cannibalism in this species (Foellmer & Fairbairn, 2004).

In *A. aurantia*, the sexes are not only dimorphic in size, but also in 'shape'. As is typical for spiders (Foelix, 1996), adult males have relatively longer legs than females (Foellmer, 2004). Therefore, to understand fully sexual dimorphism in spiders, it is important not only to examine selection on body size, but also to determine the adaptive significance of leg length independent of body size. Longer legs in male *A. aurantia* are favoured during mate search (Foellmer & Fairbairn, in press), but not during mating with cannibalistic females (Foellmer &

Fairbairn, 2004). Males use their legs extensively during fights and an advantage of relatively long legs during antagonistic encounters has been hypothesized (Prenter *et al.*, 1995; Bridge *et al.*, 2000), but no study has yet examined direct selection on leg length during combat in any spider. In this study, we determine mating success of male *A. aurantia* during opportunistic mating and estimate sexual selection on male body size and leg length using a multivariate approach to isolate selection targeted at the different components of size (Lande & Arnold, 1983; Brodie *et al.*, 1995; Fairbairn & Reeve, 2001). We examine whether the strength of sexual selection depends on the local OSR (see e.g. Jann *et al.*, 2000), i.e. number of males present on a female's web. Further, given that males may significantly deplete their energy reserves during mate search (Foellmer & Fairbairn, in press), we test whether male condition affects mating success. Finally, we put our results into the ecological context of the species by determining male dispersion with respect to available females and estimating the frequency of opportunistic mating in the field.

Methods

Data collection

We established a study site in an old field located on Île Perrot (45°22′N, 73°55′W), 31 km southwest of Montreal in Quebec, Canada in 2000. Our general approach was to collect penultimate female *A. aurantia* that were close to moult with any cohabiting males and to cage these temporarily in the field until the female moulted. This was necessary to estimate male mating success during opportunistic mating given that opportunistic mating occurs rarely at any given time and that males that do not achieve two insertions usually leave the female's web soon after her moult. A preliminary study showed that mating occurs in the cages at natural frequencies (Foellmer, 2004).

In a 1030 m^2 area we placed parallel transects 1.5 m apart and searched for penultimate and adult females along these transects two to three times per week during the mating season. We recorded female status (penultimate with catching web, penultimate close to moult, or adult) and number of cohabiting males. Females close to moult are recognized by the presence of a typical moulting web (with extensive barrier webs, but without visceral spirals). Mature females can be identified by the presence of the pronounced scape on the epigyne (the sclerotized genital plate on the ventral side of their abdomen). Penultimate females are similar to mature females in general appearance, but do not yet have a developed epigyne. We tagged web sites of penultimate females and inspected tagged sites for female status almost every day. Any penultimate female that we judged to be close to moult and that had one or more males cohabiting was collected with

the associated male(s). The females were immediately released into individual wood/fibreglass screen cages (30 × 30 × 24 cm) where they could build new moulting webs. We measured and marked all collected males and checked them for signs of pedipalp insertion on the same day of collection. In *A. aurantia*, the relatively large cap of the sperm transferring tube, the embolus (Levi, 1968; Foelix, 1996), breaks in 96% of insertions (Foellmer, 2004). This is easily detectable with a dissecting microscope and thus constitutes a good estimator of male insertion success. We thus use embolus breakage as an indicator of pedipalp insertion. Note that this means that we might have missed about 4% of palp insertions. Male *A. aurantia* use each palp only once, and invariably die during the second insertion (Foellmer & Fairbairn, 2003); they therefore can achieve a maximum of two insertions. Typically, males try to insert both palps into the same female (Foellmer & Fairbairn, 2003; Foellmer, 2004).

The morning following the day of capture, after the female had constructed a new web, we released all males into the cage with the female with whom they had been originally found. This was done in random order and into a corner where support structures of the female's web were not attached. We performed scan samples three times per day (10:00, 13:00, 16:00) and recorded female status (moulted or not) and the position of males. We distinguished the following three positions a male could assume: at the hub (very close to the female, often touching her with one or more legs), on the web (on the actual web plane between the frame and the hub), and elsewhere (in the barrier web, on other peripheral web structures such as support threads, or somewhere else in the cage). Note that females moult at the hub, hanging from a short moulting thread. The first scan was done at 16:00 hours on the day of release, giving males at least 6 h to assume new positions on the web (males typically find and enter a female's web rapidly after release into a cage). If individuals were interacting at the time of a scan, we observed and recorded any interactions (fights, mating) until these had ceased. After a female had moulted, any dead males were preserved and any other males were inspected for palp insertions, and then released where originally found. Therefore, these males had the opportunity to search again for other mates. Adult females were measured and also released where found.

We measured the following traits of males: prosoma width (at the broadest point), opisthosoma length and width (at the broadest point), and the combined patella–tibia length of each of the eight legs. We used the average patella–tibia length of each leg pair for later analysis. If one leg of a pair was missing, the length of the remaining leg was used. For females we measured prosoma width. All measurements were taken from the dorsal aspect under a dissecting microscope with individuals held gently between two lids of Petri dishes balanced with

cotton. Repeatability of all measurements was >0.89 ($n = 10$, $k = 3$ repeated measures). Prosoma width and patella–tibia length are fixed traits, i.e. they do not change after the final moult. Opisthosoma dimensions do change with the nutritional status of the individual. Adult males rarely feed; the opisthosoma of males therefore shrinks during the adult life as the stored reserves in the opisthosoma are used up (Foelix, 1996). Opisthosoma dimensions can therefore be used to estimate male condition.

Our analyses are based on 45 females and 111 males captured between 28 July and 29 August 2000. We caged a mean number of 2.5 males per female, ranging from 1–7 (Fig. 1). Males were caged for a mean duration of 1.9 days (range 1–4).

Data analysis

We performed a principal components analysis (PCA) with Varimax rotation on all variables to obtain a variable representing overall male size. Varimax rotation optimizes factor solutions by making large factor loadings larger and small factor loadings smaller, so that variables are ideally correlated with only one of the extracted factors (SPSS Inc., 1997). PCA extracted two components. The first component (PC1) of the rotated solution explained most of the variance (64%) and was highly correlated with fixed morphological traits (range of factor loadings = 0.91–0.94), but not with opisthosoma length and width (factor loadings = 0.13 and 0.39). The second component (PC2) explained 26% of the variance and was highly correlated with opisthosoma dimensions (factor loadings = 0.81 and 0.93), but not with fixed traits (range of factor loadings = 0.22–0.26). Thus, PC1 can be interpreted as an estimator of overall fixed male size, and PC2 as an estimator of male condition.
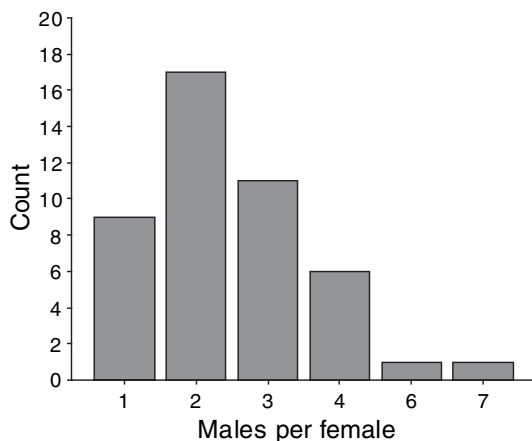

Fig. 1 Frequency distribution of the number of males per female for females caged in the experiment. Females: $n = 45$; males: $n = 111$.

The individuals in our experiment were temporarily confined in cages. However, because we caged males according to their natural association pattern and released any males that did not achieve both insertions, we consider each male as an independent data point in the analyses ($n = 111$). We estimated selection on male body size and body size components using standard selection gradient analysis (Lande & Arnold, 1983; Fairbairn & Reeve, 2001). Prior to analysis we standardized variables to z-scores with a mean of zero and a standard deviation of one: $z_i = (x_i - \bar{x})/s_x$. Our fitness measure, insertion success, was converted to relative fitness by dividing individual absolute fitness by the mean absolute fitness: $w'_i = w_i/\bar{w}$. We estimated net selection (direct selection and indirect selection through selection on phenotypically correlated characters combined) on a given trait using univariate regression models. The linear model ($w'_i = c + \beta_{uni} z_i$) estimates directional selection, whereas the quadratic model ($w'_i = c + \beta_1' z_i + \beta_2 z_i^2$) estimates the univariate nonlinear selection gradient ($\gamma_i = 2 \beta_2$) and thus the curvature of the fitness function (indicating either stabilizing or disruptive selection). Note that the univariate linear selection gradient is equivalent to the selection intensity (standardized selection differential). We estimated direct linear selection on body size components using a multivariate regression model ($w'_i = c + \Sigma\beta_{multi,j} z_{ij}$) containing all fixed male morphological traits, but not PC1. The multivariate model thus estimates selection directly targeted at a given trait holding the other traits in the model constant. We did not attempt to estimate multivariate nonlinear gradients to preserve power. When testing the effect of additional variables, such as male condition, we first evaluated the full model including interaction terms. If more than one interaction term was present in the model, we first tested globally for any kind of interaction using a multiple partial F-test. If this was found to be significant, we tested individual interaction terms (Kleinbaum *et al.*, 1998, p. 191). If no significant interaction was detected, models were simplified by removing the interaction terms to test for main effects (Kleinbaum *et al.*, 1998, pp. 186–193). Because the residuals from the regression analyses were not normally distributed, we used the randomization software RT (Manly, 1992) for significance testing by randomizing the dependent variable 9999 times. To visualize the pattern of selection we calculated cubic spline estimates of the univariate fitness surfaces for all fixed morphological traits (Schluter, 1988).

We used Morisita's index of dispersion (Krebs, 1999) to examine the distribution of males on webs of females. The Morisita index is calculated as $I_\delta = n[(\Sigma x^2 - \Sigma x)/((\Sigma x)^2 - \Sigma x)]$, where x equals the number of males per web. An index value of 1 indicates a random distribution, a value >1 indicates an overdispersed distribution and a value <1 an underdispersed distribution.

Results

Only two males had one palp already used when collected. Here we present the results of analyses involving only palp insertions achieved during our experiment; however, inclusion of the two palp insertions achieved prior to collecting did not change any of the results. In our experiment, forty-two males (37.8%) did not achieve any insertion, 22 (19.8%) achieved one insertion and 47 males (42.4%) achieved two insertions. Females received on average 2.6 (SD = 1.2, range = 0–6) insertions, while mating with a mean of 1.6 (SD = 0.8, range = 0–4) males.

Direct observations of male–male interactions

While males were waiting for females to moult, we observed three fights between males, that is in three out of a total of 329 scan samples performed (= 0.9%), excluding mating events. By extension, given that males were on average caged for 1.9 days (= 2736 min), this means that per cage, males spent an estimated total of 2736 min × 0.9% ≈25 min fighting during cohabitation. We observed opportunistic mating involving seven females, and in all cases males were interacting antagonistically. In four cases males were fighting frantically to insert a pedipalp, and we saw two males being attacked during their first insertion. In the three other cases we started our observation after one male had already achieved two insertions and was dead, stuck in the female. In all seven cases, other males tried to pull out dead males and succeeded in three instances (see also Foellmer & Fairbairn, 2003).

Selection on male morphology

The univariate linear selection gradients for general male size (PC1), prosoma width (PROWI), and the average patella–tibia length of each of the four leg pairs (PATI1–4) were all positive and significant, whereas none of the univariate nonlinear gradients was significant (Table 1). Thus there was no evidence of stabilizing or disruptive selection. Further, the multivariate linear gradients were not significant, indicating that none of the traits was directly targeted by selection independently of the other traits included in the multivariate model (Table 1). Taken together, this suggests that males were under directional selection for overall large body size during opportunistic mating, leading to significant net selection for a broader prosoma and longer legs (Fig. 2).

As the number of males per female varied considerably, the selective environment (i.e. the local OSR) was not equal for all males. Therefore, competition over access to the female can be expected to vary accordingly and to affect the intensity of selection on male body size and male mating success in general. We tested this by including the number of males per female in the analysis together with general male size (PC1). Both the number of males per female and male body size were significant predictors of male mating success, but the intensity of selection on male size was not significantly affected by the number of competing males (interaction: $\beta = 0.009$, SE = 0.054, $n = 111$, ns; main effects after dropping the interaction term: males per female, $\beta = -0.135$, SE = 0.050, $n = 111$, $P = 0.0076$; PC1, $\beta = 0.259$, SE = 0.077, $n = 111$, $P < 0.001$). A second model with males per female grouped into two categories (two or fewer males per female and more than two males per female) confirmed this result (not shown). Hence, our data suggest that mean male mating success decreases as the number of males present on a female's web, and thus the local OSR, increases (Fig. 3a). Further, males are under strong selection for large body size when they have to compete with other males, irrespective of the number of males present on the web. Although the overall ANOVA indicated no significant effect of number of competing males on selection intensity, visual inspection of selection intensities estimated for overall male size (PC1) for different levels of the local OSR separately (i.e. for cases with one, two, three, and more than three males present per female) reveals a tendency for the intensity of selection to increase with increasing number of males per female, and this effect might level off at higher values for the OSR (Fig. 3b). Note, however, that none of the selection intensities for the different OSR categories was

Table 1 Selection gradients with standard errors and *P*-values for the five fixed morphological traits and PC1 (general body size).

Trait	β_{uni}	SE	P	γ_{uni}	SE	P	β_{multi}	SE	P
PC1 (size)	**0.303**	0.077	0.0004	0.005	0.054	0.9677			
PROWI	**0.283**	0.078	0.0003	0.071	0.058	0.5535	0.214	0.189	0.2652
PATI1	**0.256**	0.079	0.0016	0.100	0.060	0.4162	−0.344	0.327	0.2963
PATI2	**0.278**	0.078	0.0008	0.116	0.058	0.3371	0.272	0.274	0.3349
PATI3	**0.269**	0.078	0.0005	0.088	0.055	0.4054	0.004	0.223	0.9860
PATI4	**0.272**	0.078	0.0011	0.088	0.057	0.4658	0.153	0.293	0.5978

Relative fitness is based on insertion success. Coefficients that are significant after correction for multiple significance tests are in bold.
β_{uni}, univariate linear gradients; γ_{uni}, univariate nonlinear gradients; β_{multi}, multivariate linear gradients; PROWI, prosoma width; PATI1 to PATI4, the average patella–tibia lengths of the four leg pairs. All analyses: $n = 111$.
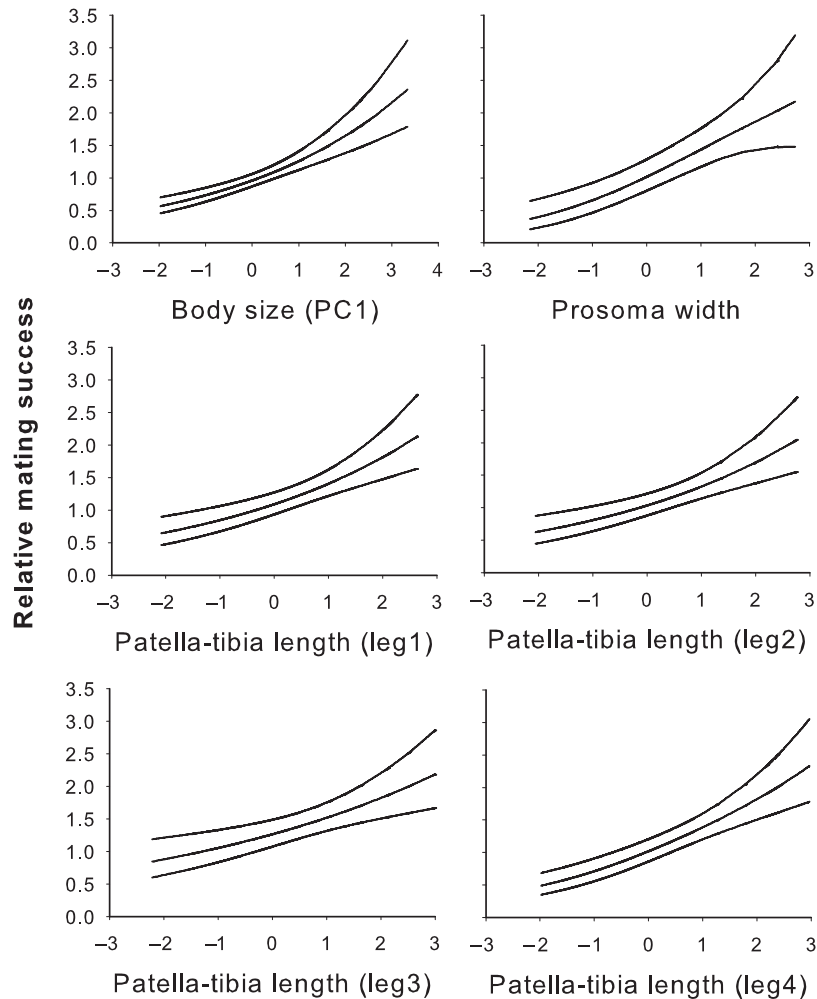
Fig. 2 Univariate fitness surfaces (cubic spline estimates) for overall male body size (PC1) and male body size components with standard errors (based on bootstrapping).

statistically significant (OSR = 1: $P > 0.4$; for all other groups: $0.1 > P > 0.05$). In the case of single males per female, selection for large male size would not be expected, but in the other cases nonsignificance was probably due to low power because of reduced sample sizes. When we increased power by grouping all cases with more than two males per female together ($n = 69$), selection on size was significant ($\beta = 0.331$, SE = 0.116, $P < 0.01$). Therefore, larger sample sizes would be required to confirm the subtle effects the local OSR might have on the selection intensity as suggested here.

The number of males per female was uncorrelated with collection date (Spearman's rank correlation coefficient $R_s = 0.192$, $n = 45$, ns). Although male size (PC1) increased over the breeding season (Pearson's correlation coefficient $R_p = 0.277$, $n = 111$, $P < 0.01$), the intensity of selection on male body size did not change over the season, as indicated by the non-significant interaction

term for collection date × PC1 from the multiple regression of male fitness on collection date and PC1 (interaction: $\beta = 0.004$, SE = 0.011, $n = 111$, ns; main effects after removing the interaction term: collection date, $\beta = -0.001$, SE = 0.011, $n = 111$, ns; PC1, $\beta = 0.305$, SE = 0.081, $n = 111$, $P \leq 0.001$). Hence we could not detect any seasonal variation in the intensity of selection on male body size during opportunistic mating.

Effect of male condition

To test whether male condition had an effect on male mating success, we performed a multiple regression analysis with condition (PC2), male body size (PC1), and number of males per female as predictors of relative fitness, as any effect of male condition might vary with varying male size and/or competitor number. Male condition had no effect on male mating success (multiple
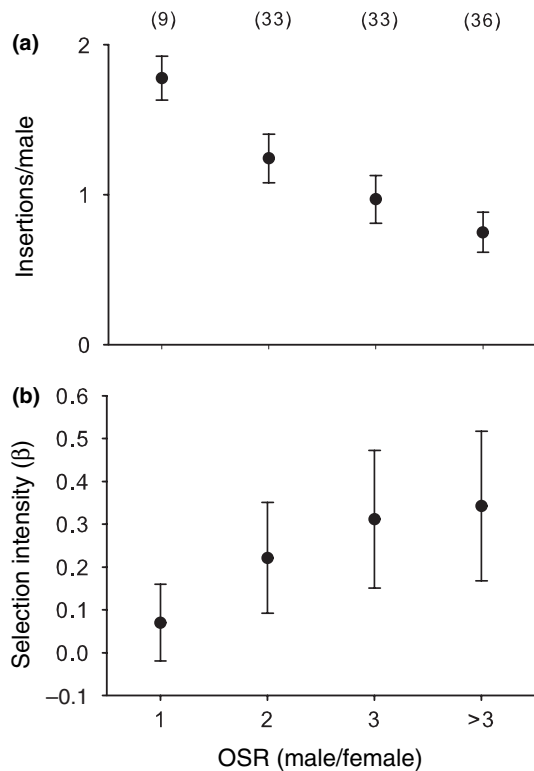
Fig. 3 Mean number of insertions per male (a) and the intensity of selection on overall male body size (b) as a function of the operational sex ratio (OSR). Error bars represent standard errors. Selection intensities are the regression coefficients from the univariate regression of relative fitness on male body size (PC1) performed for the different OSR categories separately. The numbers in parentheses on top of the upper panel indicate the sample sizes for each category. See text for further details.
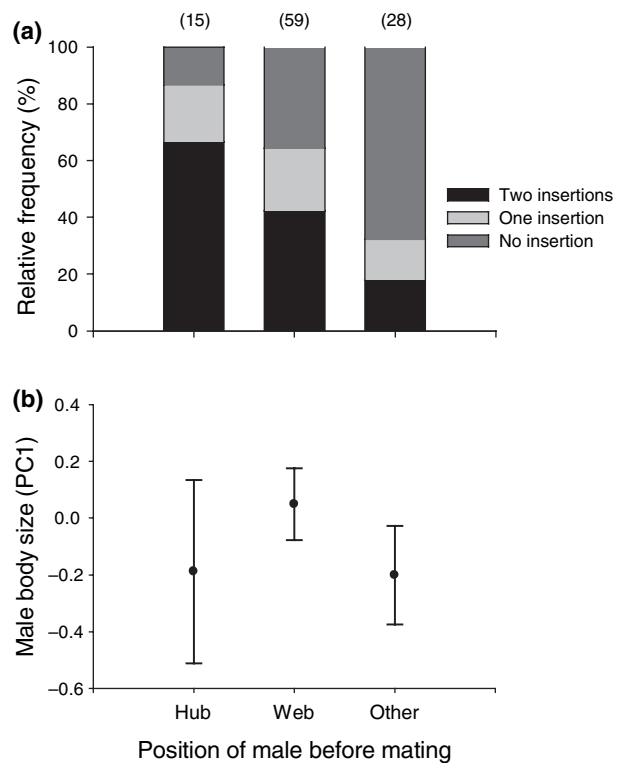
Fig. 4 Relative frequency of insertion success (a) and mean overall size with standard errors (b) for males at different positions at the last scan before opportunistic mating. The category 'Other' includes males that were in the barrier web, on other peripheral web structures, or somewhere else in the cage. Only cases with two or more males are included ($n = 102$). The numbers in parentheses on top of the bars indicate the sample sizes for each group of males.

partial F-test for an interaction: $F_{4,103} = 1.377$, ns; main effects after excluding the interaction terms: males per female, $\beta = -0.134$, SE $= 0.051$, $n = 111$, $P < 0.01$; PC1, $\beta = 0.259$, SE $= 0.077$, $n = 111$, $P \leq 0.001$; PC2, $\beta = -0.0170$, SE $= 0.076$, $n = 111$, ns), which suggests that energy reserves did not limit male competitive success.

Effect of the male's position on the web

With respect to achieving insertions, males that assume a position close to the female shortly before or during her moult can be expected to have an advantage over males that are farther away, for example in the barrier web. We tested this using only cases with more than one male per female ($n = 102$). Males that were closer to the female at the last scan prior to mating achieved more insertions than males that were farther away (Fig. 4a; $\chi_4^2 = 15.0$, $P < 0.01$). However, overall male size (PC1) did not differ for males that were at the hub,

on the web, or elsewhere at the last scan (Fig. 4b; $F_{2,100} = 0.75$, ns). Consequently, both male position prior to mating and male body size were significant predictors of male mating success independently of each other (multiple partial F-test for an interaction: $F_{4,94} = 1.302$, ns; main effects after excluding the interaction terms: males per female, $\beta = -0.061$, SE $= 0.055$, $n = 102$, ns; PC1, $\beta = 0.258$, SE $= 0.077$, $n = 102$, $P \leq 0.01$; position prior to mating, $\beta = -0.457$, SE $= 0.122$, $n = 102$, $P \leq 0.001$). The larger the male and the closer the male was to the female prior to her moult, the higher the male's mating success.

If a male's position prior the female's moult is so important, it might be advantageous for a male to keep the most favourable position over time. However, the number of pedipalp insertions was not associated with the relative frequency with which males were recorded at the hub during the caging period (two insertions: mean $= 13.9\%$, one insertion: mean $= 14.6\%$, no insertion: mean $= 10.5\%$, Kruskal Wallis $\chi_2^2 = 2.43$, ns), and many males were actually never seen at the hub (median

for all three insertion groups = 0%). This suggests that males are not able to defend a hub position, which is in line with the finding that males found at the hub prior to mating were not larger than other males. Note also that more than one male may be present at the hub with the female; it is thus not a position that one male can occupy exclusively.

Lost legs

Thirty-one males (27.9%) lost at least one leg during opportunistic mating [McNemar's test (Zar, 1996) for paired sample nominal scale data: $P < 0.001$]. Males that lost at least one leg were smaller than those that did not (PC1: mean = −0.38, SE = 0.12 vs. mean = 0.15, SE =0.12, $t_{89.8} = 3.17$, $P < 0.01$; equal variances not assumed). Twenty-five males (22.5%) were initially missing at least one leg, but this did not affect male mating success or the intensity of selection on male size (general linear model with relative fitness as the response: missing leg × PC1 interaction, $F_{1,107} = 1.335$, ns; main effects after excluding the interaction term:

missing leg, $F_{1,108} = 0.180$, $P > 0.6$; PC1, $F_{1,108} = 13.726$, $P < 0.001$). Therefore, male competitive ability was not adversely affected by initially missing legs, but smaller males were more likely to lose a leg during interactions on the web.

Female size

If the size of available females changes over the season, then this could affect male fitness, because of the presumed higher fecundity of larger females. However, the size of females in our experiment was not correlated with maturation date ($R_p = -0.139$, $n = 45$, ns).

Dispersion of males and the relative frequency of opportunistic mating

To evaluate the impact on lifetime reproductive success of selection for large male body size during opportunistic mating, we have to determine the relative occurrence of opportunistic mating in the field. If opportunistic matings are rare in nature, this selection may have little
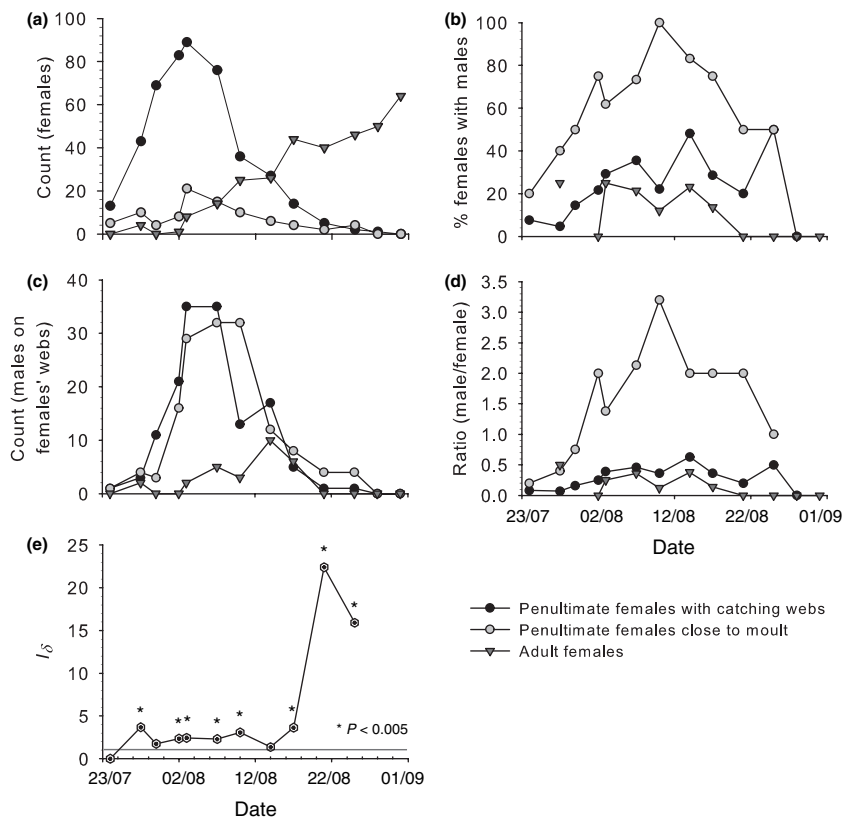

Fig. 5 Seasonal change in the frequencies of penultimate and adult females and adult males and their association patterns at the study site. (a) Absolute frequency of penultimate females with catching webs, penultimate females close to moult, and adult females. (b) Relative frequency of the three types of females that were found with cohabiting males. (c) Absolute frequency of adult males cohabiting with each of the three types of females. (d) cohabiting male to female ratio for the three types of females. (e) Morisita's index of dispersion for males per female for all three types of females combined; the grey line at $I_d = 1$ denotes a random distribution.

evolutionary significance. Our transect searches revealed the following pattern. Penultimate females that are close to their final moult were never frequent in the study population relative to younger penultimate females (e.g. still with catching webs) and mature females. From the males' perspective, therefore, penultimate females close to moult were both spatially and temporally rare and dispersed (Fig. 5a). Yet, about half of all males that were cohabiting with females were associated with penultimates close to moult, and most penultimate females close to moult were found with cohabiting males during most of the mating season (Fig. 5b,c). Further, the male to female ratio was much higher for penultimate females close to moult than for other penultimate or adult females and equalled at least two most of the time, although females with no males were included in this calculation (Fig. 5d). Consequently, the dispersion of males cohabiting with females (all three types of females considered) was significantly clumped over almost the entire mating season, as is indicated by values of Morisita's index of dispersion that are significantly >1 (Fig. 5e). If we weight the percentage of penultimate females close to moult that are associated with males (Fig. 5b) by the actual number of these females in the field at a given time (Fig. 5a) and multiply this by the proportion of opportunistically mated females in the experiment (0.95), we obtain that on average 62% of females were mated opportunistically at our site. Taken together, this suggests that males show a strong preference for penultimate females close to moult and that opportunistic mating occurs frequently in *A. aurantia*.

Discussion

Our results clearly demonstrate precopulatory sexual selection on body size in male *A. aurantia* due to male-male competition over access to newly-moulted adult females. When males compete for these 'opportunistic' matings, larger males are more successful. All measured fixed morphological traits, prosoma width and average patella–tibia length of each of the four leg pairs, were under significant net selection, favouring an increase in trait dimensions. We did not find any evidence for stabilizing or disruptive selection. Further, none of the traits was directly targeted by selection independent of the others, indicating that selection favours overall large body size. The absence of evidence for selection favouring longer legs when body size is held constant (i.e. in the multivariate model) does not support the hypothesis that relatively longer legs in males are favoured during male contests (Prenter *et al.*, 1995; Bridge *et al.*, 2000).

During competition for opportunistic matings, males may gain advantage through both scramble and interference competition. Males interact aggressively while cohabiting with a female, and once the female has commenced moulting they fight fiercely over access to the female and often attack any male that has inserted a pedipalp (see also Robinson & Robinson, 1980; Foellmer & Fairbairn, 2003). Almost 30% of males lost at least one leg and the probability of leg loss was higher for smaller males. Legs that were lost were probably autotomized in self-defence during escalated contests (Foelix, 1996; Punzo, 1997). This indicates that interference competition is important during opportunistic mating and that large males have an advantage during combat. However, we also found that the proximity of a male to the female on the web prior to the female's moult predicted male mating success independently of body size. Males do not defend the hub position, unlike in other orb-weavers (e.g. Christenson & Goist, 1979; Elgar & Fahey, 1996), and therefore, success in maintaining position near the hub, and hence in obtaining matings, appears to be due to scramble competition rather than direct contest. Thus, both interference and scramble competition probably operate during opportunistic mating in *A. aurantia*, and interference competition results in selection for large body size in males.

Males congregated on webs of penultimate females close to moult. Most males (92%) faced at least one competitor, but the number of males per female, i.e. the local OSR, had no significant overall effect on the intensity of sexual selection on male body size. Nevertheless, mean male mating success did decrease with increasing local OSR, probably because dead males stuck in females function as mating plugs (Foellmer & Fairbairn, 2003), and the comparison of selection intensities at different levels of the OSR suggests that selection intensity may increase as the OSR increases from one to three. When three or more males are present with the female, 'sneaking' an insertion, for example while other males are fighting, can be expected to become a viable option (Grant *et al.*, 1995; Kvarnemo *et al.*, 1995). Such a strategy could result in relaxation of selection favouring large males when the OSR is strongly male-biased (see Grant *et al.*, 1995; Mills & Reynolds, 2003). Although selection on body size in males was significant even when only cases with three or more males per female were considered, indicating that interference competition was still important at higher levels of the OSR, the increase in selection intensity with OSR does appear to level off at this level of competition. Thus, the possibility that the intensity of selection levels off at high OSRs because of sneaking by smaller males remains open for further investigation.

Male condition did not influence male mating success. During mate search, adult male *A. aurantia* do not actively forage and hence lose condition (i.e. energy reserves) (Foellmer & Fairbairn, in press). Our results suggest that males arriving on a female's web nevertheless have sufficient reserves of energy to successfully compete over access to the female. Note that in our experiment males were unlikely to be able to feed,

because no prey item was in any of the webs that females constructed in the cages. In *A. aurantia*, male condition is negatively correlated with maturation date, perhaps because males trade off energy reserves with achieved adult size (Foellmer & Fairbairn, in press). Males start to mature about a week earlier than females and all males have become adult by the middle of the mating season (Foellmer & Fairbairn, in press). Thus, later-maturing males probably do not have to survive as long before finding females and so do not need as much energy in reserve and may therefore invest relatively more in achieved body size (Roff, 2002). Our finding that male body size but not condition affected mating success supports this argument.

We did not detect any seasonal effects influencing male mating success or the intensity of selection on male body size (see e.g. Blanckenhorn *et al.*, 1999; Jann *et al.*, 2000). The transect counts showed that penultimate females close to moult were spatially and temporally rare and dispersed, and the ratio of males per penultimate female close to moult was strongly male-biased throughout most of the mating season. In contrast, the sex ratio was female-biased for penultimate females not close to moult and, importantly, for mature females during the entire season. This suggests that interference competition on the web is irrelevant when males approach mature, post-moult females (see Foellmer & Fairbairn, 2004), and also that many adult females are probably unavailable as mates at any given time, as has been suggested previously (Foellmer, 2004). Finally, earlier maturing males did not have the advantage of mating with larger and presumably more fecund females, as might be the case in other species (Miyashita, 1993).

Our study thus demonstrates the importance of recognizing the OSR at a local level (Lawrence, 1986; Grant *et al.*, 1995; Jann *et al.*, 2000). Even as the overall sex ratio becomes female-biased because of male mortality during mating and mate search, the local OSR remains male-biased until the end of the mating season, leading to significant sexual selection for larger males because of interference competition. Most females are mated opportunistically in *A. aurantia*, and interference competition is therefore an important factor determining male lifetime fitness in this species. Males may also compete indirectly via success in locating females and order of arrival on the web, i.e. scramble competition 'on the ground' (vs. on the web) (e.g. Schwagmeyer & Woontner, 1986; LeGrand & Morse, 2000). Males have days to reach a given penultimate female and accumulate on webs of these females accordingly. Given that no male can assume a favourable position on the web and defend it, reaching a penultimate female's web first is unlikely to be important. During mate search, longer legs tend to be favoured as males with longer legs are probably faster runners, leading to selection for overall large body size in males (Foellmer & Fairbairn, in press). Therefore, the mechanisms proposed by Ghiselin (1974)

and Vollrath & Parker (1992) based on the assumption that sexual selection due to interference competition is relaxed because of low population densities or a high male mortality during mate search, are unlikely to be relevant for the maintenance of extreme SSD in *A. aurantia*. The fact that males are able to congregate on webs of penultimate females close to moult even at the end of the season argues further against high travel mortality. Indeed, the proposed stage-dependent mortality difference between males and females (Vollrath & Parker, 1992) has not been found in a burrowing wolf spider (Walker & Rypstra, 2003; but see Andrade, 2003), and the prediction of the differential mortality hypothesis that SSD should be related to life-history differences (sit-and-wait vs. actively hunting foragers) in spiders was not supported (Prenter *et al.*, 1997, 1998).

Male–male interference competition has also been suggested to favour large male size in species of the genus *Nephila* (Christenson & Goist, 1979; Vollrath, 1980; Miyashita, 1993). Given that male cohabitation with females is a common phenomenon and that large males have been shown to win in contests in several orb-weavers (e.g. Robinson & Robinson, 1980; Alayon Garcia & de Armas, 1990; Elgar *et al.*, 2003), sexual selection for large size in males because of interference competition among males probably operates as well in other highly dimorphic orb-weavers. At least in one crab spider species, however, population densities seems to be low enough to render male contests unimportant (LeGrand & Morse, 2000). Recently, small male *Nephila edulis* have been shown to employ a more efficient mating tactic in the absence of direct competitors (Schneider *et al.*, 2000). Male size is very variable in this orb-weaver species; small males can approach the female directly, whereas larger males insert their palps through a whole they cut into the web. As a result, smaller males achieve longer copulations and hence higher fertilization success than larger ones (Schneider *et al.*, 2000). However, although this example does provide the first evidence of a small male mating advantage in a spider and shows possible limits to achieving an ever larger size in males, the overall significance of this is uncertain, given that larger males often prevent smaller ones from mating in *N. edulis* (Elgar *et al.*, 2003).

There is also little support to date for other hypotheses about a small male advantage in spiders. A growing number of studies have shown now that sexual cannibalism (e.g. Darwin, 1871; Elgar & Fahey, 1996) is unlikely to be relevant in selecting for or maintaining small size in males (e.g. Schneider *et al.*, 2000; Foellmer & Fairbairn, 2004). In a first direct evaluation of the gravity hypothesis (Moya-Laraño *et al.*, 2002), Foellmer and Fairbairn (in press) found that contrary to predictions, not small males, but males with longer legs tended to be favoured during mate search in *A. aurantia*, leading to selection for overall larger males. Consequently, in

A. aurantia, there is probably overall selection for large body size in males during the adult stage (Foellmer & Fairbairn, 2004; Foellmer & Fairbairn, in press). Taken together, we still have only a very incomplete picture of the factors that drive body size evolution in males of species with extreme female-biased SSD (Prenter *et al.*, 1998; Blanckenhorn, 2000; Foellmer, 2004; Foellmer & Fairbairn, 2004; Foellmer & Fairbairn, in press). The evidence suggest little co-evolution between the sexes in highly dimorphic lineages (Abouheif & Fairbairn, 1997; Fairbairn, 1997), and more studies investigating selective processes and genetic architecture in spiders are certainly needed. Obviously, body size is determined through selection operating throughout the life-history of animals, and selection on adult individuals is only one aspect of this. In *A. aurantia*, selection for large size during adulthood is probably counterbalanced by viability selection favouring reduced growth during the juvenile stages – compared with females, at least. Unfortunately, it will be almost impossible to measure selection on juvenile spiders as small individuals that moult regularly are extremely difficult to sample repeatedly in the wild. Therefore, accurate estimates of selection through the juvenile stages are likely to remain elusive.

In summary, we have shown that in *A. aurantia* there is strong selection for large size in males because of male–male competition over access to females, contradicting current hypotheses for the adaptive significance of extreme SSD in spiders which assume little or no selection on male body size because of interference competition (Ghiselin, 1974; Vollrath & Parker, 1992). We did not detect an advantage of having relatively longer legs in the context of male contests, as had previously been proposed (e.g. Bridge *et al.*, 2000). The factors driving body size evolution in males of species with extreme female-biased SSD remain poorly understood and warrant further investigation.

Acknowledgments

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