BEHAVIOURAL ECOLOGY

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Selection on male size, leg length and condition during mate search in a sexually highly dimorphic orb-weaving spider

Abstract Mate search plays a central role in hypotheses for the adaptive significance of extreme female-biased sexual size dimorphism (SSD) in animals. Spiders (Araneae) are the only free-living terrestrial taxon where extreme SSD is common. The "gravity hypothesis" states that small body size in males is favoured during mate search in species where males have to climb to reach females, because body length is inversely proportional to achievable speed on vertical structures. However, locomotive performance of males may also depend on relative leg length. Here we examine selection on male body size and leg length during mate search in the highly dimorphic orb-weaving spider *Argiope aurantia*, using a multivariate approach to distinguish selection targeted at different components of size. Further, we investigate the scaling relationships between male size and energy reserves, and the differential loss of reserves. Adult males do not feed while roving, and a size-dependent differential energy storage capacity may thus affect male performance during mate search. Contrary to predictions, large body size was favoured in one of two populations, and this was due to selection for longer legs. Male size was not under selection in the second population, but we detected direct selection for longer third legs. Males lost energy reserves during mate search, but this was independent of male size and storage capacity scaled isometrically with size. Thus, mate search is unlikely to lead to selection for small male size, but the hypothesis that relatively longer legs in male spiders reflect a search-adapted morphology is supported.

Keywords Body size · Energy reserves · Gravity hypothesis · Roving phase · Sexual size dimorphism

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Introduction

In most animal species, males and females differ conspicuously in morphological attributes, such as size or colour of body components. Ultimately, all manifestations of sexual dimorphism are probably rooted in the different reproductive roles of males and females and the resulting patterns of natural and sexual selection acting on the sexes (reviewed in Andersson 1994). The most prevalent form of sexual dimorphism in the animal kingdom is sexual size dimorphism (SSD) (Andersson 1994; Fairbairn 1997). Males are typically larger than females in mammals and birds, but in the vast majority of species (invertebrates and poikilothermic vertebrates), females are generally the larger sex (Abouheif and Fairbairn 1997; Fairbairn 1997). Accordingly, SSD in spiders is almost always female-biased, but spiders are unique in that it is the only free-living terrestrial taxon where extreme SSD is common (Ghiselin 1974; Andersson 1994; Vollrath 1998). In certain genera of orb-weaving spiders (Orbiculariae) females may weigh over a hundred times more than males (Head 1995; Vollrath 1998). A comparable magnitude in SSD is otherwise found only in some marine and parasitic taxa and rotifers (Ghiselin 1974; Andersson 1994; Vollrath 1998). Spiders thus offer a tangible system to study the evolution and maintenance of extreme SSD, yet SSD in spiders remains poorly understood (e.g. Coddington et al. 1997; Vollrath 1998; Walker and Rypstra 2003).

Generally, SSD can evolve if body size is heritable and if the genetic correlation between the sexes is less

than 1 (Lande 1980). SSD will then evolve as a result of different net selection pressures acting on the body sizes of males and females within given genetic and physiological constraints (e.g. Lande 1980; Reeve and Fairbairn 2001). Several hypotheses have been put forward about how natural and sexual selection might have contributed to the evolution and maintenance of extreme SSD in spiders (Darwin 1871; Gerhardt 1924; Ghiselin 1974; Vollrath and Parker 1992; Schneider et al. 2000; Moya-Laraño et al. 2002). Recent evidence suggests that within orb-weaving spiders females have increased in size over evolutionary time in several lineages independently (Coddington et al. 1997; Hormiga et al. 2000) and that selection for increased female fecundity is the major force driving this trend (Marshall and Gittleman 1994; Head 1995; Prenter et al. 1999; Higgins 2002). It is less clear, however, why males have stayed small or even have decreased in size in some cases (Prenter et al. 1997, 1998; Walker and Rypstra 2003; Foellmer and Fairbairn 2004; but see Vollrath 1998; Schneider et al. 2000). In orb-weaving spiders, males switch from a sedentary to a roving life-style after their maturation moult to search for females and no longer build catching webs (Foelix 1996). Therefore, one can distinguish three distinct episodes in a male orb-weaving spider's life during which male body size might be under selection: the juvenile phase, mate search (i.e. the "roving phase"), and mating. A new hypothesis focuses on the roving phase as an episode generating selection for small male size (Moya-Laraño et al. 2002). According to this "gravity hypothesis", smaller males might have an advantage over larger ones in species such as orb-weaving spiders, where males move through a three-dimensional habitat and have to climb to reach females. Smaller males are expected to be able to climb faster than larger males, because the average speed achievable on vertical structures is inversely proportional to body length (Moya-Laraño et al. 2002). Thus, smaller males might be better at finding females, which would give them an advantage in scramble competition, and might also be better at escaping predators. As predicted by the gravity hypothesis, SSD in spiders seems to increase with increasing height of female habitat (Moya-Laraño et al. 2002).

A small male advantage in scramble competition has so far been demonstrated mostly in aerial species (some insects and birds), where small males are favoured either because they are more agile, or because they have an energetic advantage (reviewed in Blanckenhorn 2000). Generally, in species where mature males have to feed to maintain stamina, small males should have an energetic advantage because their lower metabolic requirements enable them to spend more of their time and energy searching for females and mating (Reiss 1989; Blanckenhorn et al. 1995; Blanckenhorn 2000). However, in species where adult males do not or only rarely feed, such as in orb-weaving spiders, large males might actually be at an energetic advantage, because of their lower mass-specific metabolic rate (Calder 1984; West et al.

2000). Large males may also be able to store disproportionately more reserves than small males if this capacity scales allometrically with size (Calder 1984), and these effects might trade-off with the gravity-advantage of small males. Indeed, it has been suggested that intermediate sized males might have a higher probability of successfully travelling to a female's web in the orb-weaver *Nephila clavipes* (Vollrath 1980; Christenson 1990).

In this study we investigate selection on male body size during mate search in the sexually highly dimorphic orb-weaving spider *Argiope aurantia*. We use a multivariate approach to isolate selection targeted at different components of size (Lande and Arnold 1983; Brodie et al. 1995). This is particularly important because adult (but not juvenile) male spiders generally have relatively longer legs than females (Foelix 1996; Foellmer 2004). Thus, to fully understand sexual dimorphism in spiders it is important to determine the adaptive significance of leg length independent of body size. Longer legs in male spiders have been hypothesized to confer an advantage during mate search and also during antagonistic interactions among males and during mating with cannibalistic females (Elgar et al. 1990; Prenter et al. 1995; LeGrand and Morse 2000; Bridge et al. 2000), but no study has yet examined the independent effects of selection on leg length and body size other than in the context of sexual cannibalism (Foellmer and Fairbairn 2004). Therefore, we examine direct and net selection on both body size and leg length during mate search in *A. aurantia*.

In this paper we present the results of a cross-sectional study comparing males that were found and measured before and after a phase of mate search. We examine whether male body size and/or leg length is under selection during the roving phase in *A. aurantia*. Previous hypotheses predict that smaller males and/or males with relatively longer legs should be favoured during mate search, i.e. they should be more likely to be found with females. Further, we investigate the relationship between male size, storage capacity of energy reserves, and loss of condition (energy reserves) during mate search. This will help to clarify whether large males might be at an energetic advantage in orb-weavers.

Materials and methods

Study species

Argiope aurantia is a large orb-weaving spider common in successional habitats (old fields) throughout eastern North America (Levi 1968). Sexual size dimorphism is pronounced; females are about 3–4 times longer than males (Levi 1968). Males mature on average about 1 week earlier than females and leave the web on which they moulted to adulthood to search for females. Males pursue two alternative mating tactics, depending on the type of female they encounter (Robinson and Robinson

1980; Foellmer and Fairbairn 2003). If a male encounters a penultimate female (a female just one moult from adulthood), he typically cohabits with her on peripheral web structures and waits for her to moult. During cohabitation, males may occasionally scavenge prey items present in the female's web. Males try to mate with the female while she is moulting and thus completely defenceless (opportunistic mating). On the other hand, if a male encounters a mature female, he courts her on her web and, if the female is receptive, may mate with her. However, males show a strong preference for penultimate females (see Foellmer and Fairbairn 2003), and throughout the mating season are mostly associated with penultimate females that are close to moult (Foellmer 2004). Males that do not achieve copulation in either situation rove off again and search for another female.

Data collection

We sampled two populations in Quebec, Canada. One population was located on Île Perrot (45°22′N, 73°55′W), 31 km southwest of Montreal (sampled in 2000, called sample 1 hereafter), the other was near Phillipsburg (45°04′N, 73°03′W), 65 km southeast of Montreal (sampled in 2002, referred to as sample 2). Both sites were old fields with invading shrubs and abundant goldenrod (*Solidago* sp.). To examine whether male morphology is under selection during the roving phase, we compared adult males collected on their own moulting webs (i.e. before they engaged in mate search) with males collected from webs of females that were potential mates. Since male *A. aurantia* frequently cohabit with penultimate females, but only rarely with mature females (see above), most males were collected from penultimate females close to moult. We did not collect males that were cohabiting with penultimate females that were not close to moult, because these females might still relocate, before males have an opportunity to mate with them. Thus, mate search cannot be considered at least potentially completed in these cases. 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. Adult males are easily distinguishable from juveniles by their developed pedipalps, a dark brown colour and elongated legs.

We thoroughly searched the vegetation on each side of a given path using water sprayers to increase the visibility of web structures (Tolbert 1976). Sampling regimes differed slightly between samples. For sample 1, the collection of adult males was done over a period of 1 month (23 July –24 August 2000) as part of a larger field study using a 1,030 m^2 area through which parallel

transects were placed 1.5 m apart. We searched for males on their moulting webs along ten randomly chosen 20 m long transects on about every second day. The whole study area was searched almost daily for penultimate females and associated males. Collected males were measured and marked on the same day of collection. If a male was found twice, only the first sighting was counted. Because we searched more frequently and a larger area for males on females' webs than for males on moulting webs, our analyses are based on 111 males collected on females' webs and 52 males found on moulting webs. For sample 2, we haphazardly established paths within an approximately 1,000 m^2 area. We then searched for males along these paths on 3 days per week from 30 July to 15 August 2002. We collected 51 males on moulting webs and 58 males on females' webs, and measured all males the day following collection. Males were not returned to the site.

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. 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 (see above). Therefore, the opisthosoma of males shrinks during the adult life as the stored reserves in the opisthosoma are used up (Foelix 1996), and opisthosoma dimensions can be used to estimate male condition.

Data analysis

Our general approach was to estimate selection on males using logistic regression (Kleinbaum et al. 1998) with web type as the response variable. We set the response to 0, if the male was found on his own moulting web and to 1, if the male was found on a female's web. Because we did not follow individuals from web to web, we cannot estimate selection gradients sensu Lande and Arnold (1983). However, our data allows us to estimate selection on male morphology qualitatively by comparing different males found before and after they had engaged in mate search. We employed regression models in an analogous fashion to selection gradient analysis. Univariate models are used to estimate net selection on a trait, while multivariate models estimate direct selection on a given trait, independent of the other traits in the model (Lande and Arnold 1983; Fairbairn and Reeve 2001). Linear coefficients estimate directional selection. Nonlinear coefficients estimate the curvature of the

fitness function and thus indicate stabilizing or disruptive selection.

Variables were log-transformed prior to analysis to normalize distributions. We performed a principal components analysis (PCA) with Varimax rotation on all variables measured for each sample separately 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 1997). For each sample, PCA extracted two components. The first component (PC1) of the rotated solution explained most of the variance (63% for sample 1, 66% for sample 2) and was highly correlated with the fixed morphological traits (range of PC1 factor loadings for fixed traits 0.88–0.97, for opisthosoma dimensions 0.15–0.35). The second component (PC2) explained 27% (sample 1) and 28% (sample 2) of the variance and was highly correlated with opisthosoma length and width (range of PC2 factor loadings for fixed traits 0.20–0.28, for opisthosoma dimensions 0.86–0.95). Thus, PC1 can be interpreted as an estimator of overall fixed male size, and PC2 as an estimator of male condition.

We analysed male fitness as a function of the general size of males using PC1 as the independent variable in univariate regressions. We also estimated direct selection on fixed body size components in multivariate regression models and net selection using univariate regression. We did not attempt to estimate nonlinear components for the multivariate model to preserve power. For regression analyses, prosoma width and patella-tibia lengths were standardized to a mean of zero and a standard deviation of one to facilitate comparisons. Note that because we cannot estimate selection gradients, we report the untransformed logistic regression coefficients. In analyses of covariance (ANCOVA), we first tested for an interaction between variables. 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).

Results

Selection on male morphology

In sample 2, all fixed morphological traits of males that were caught on females' webs were on average larger than those of males that were caught on their own moulting web (Fig. 1). In sample 1 no such trend is observed. Accordingly, logistic regression suggests significant selection for overall larger males during the roving phase in sample 2, but not in sample 1 (Table 1). The quadratic terms for PC1 are not significant for either sample, indicating that overall male size was not under stabilizing, disruptive or asymptotic selection. Examination of direct selection on male body components using multiple logistic regression revealed the following pattern (see Table 1). In sample 1, we detected significant direct selection for longer patella-tibia of the third leg pair. There appeared to be also a tendency for selection to favour males with a narrower prosoma, but this was not significant after correcting for multiple comparisons. Note that because we have performed 19 significance tests within each sample, our α-level for a Type-I error rate of 5% is 0.0027. However, correcting for multiple tests has not become standard in selection analyses (e.g. Blanckenhorn et al. 2003). Therefore, we also indicate results that are significant at the 0.05 level. In sample 2, none of the traits in the model were significant independently of each other. Interestingly, the sign of the coefficient for prosoma width is also negative, but just not significant. Tolerances in both analyses were

Fig. 1a–e Means (±SE) of the fixed morphological traits for male orb-weaving spiders that were caught on moulting webs before mate search (*before*), and on females' webs after mate search (*after*). Fixed traits are **a** prosoma width and **b–e** the average patella-tibia lengths of the four leg pairs. Sample 1: $n = 52$ (*before*), $n = 111$ (*after*). Sample 2: $n = 51$ (*before*), $n = 58$ (*after*)
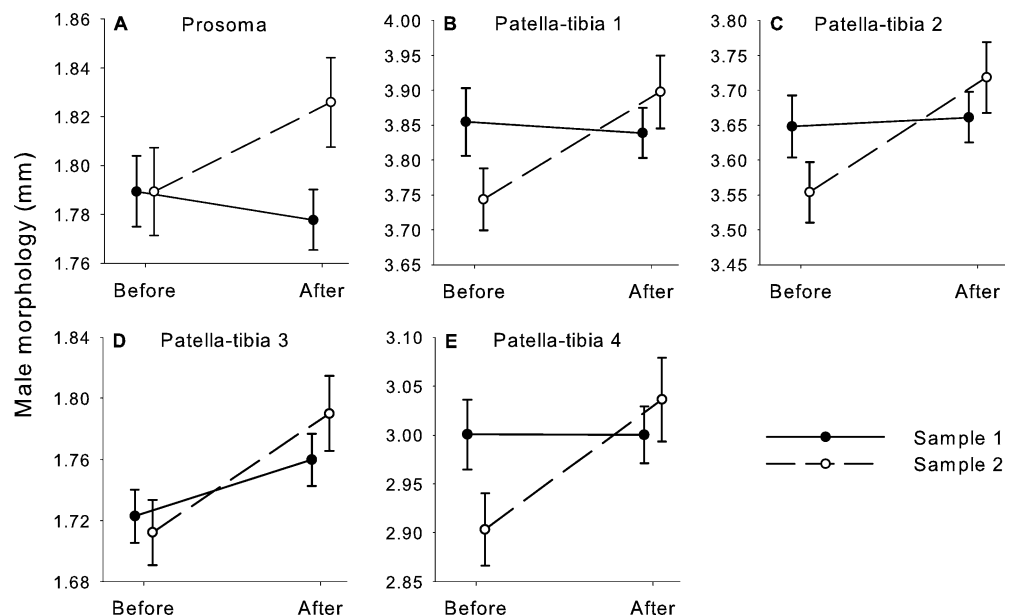
all > 0.02, suggesting that multicollinearity was not a problem in our multiple regression models, because tolerances > 0.001 are generally acceptable (see Fairbairn and Preziosi 1996). None of the fixed body components was under net selection in sample 1 (Table 1). For sample 2 our analyses suggest that the patella-tibia for all legs was under directional net selection, and that

longer legs were favoured. Nevertheless, if we apply the strict criterion $\alpha = 0.0027$, then none of the coefficients are significant. In this case, however, the coefficients for all legs are consistently significant at the 0.05 level and the differences between means are obvious (see Fig. 1). Thus we do consider this result relevant. Taken together, these results suggest that in sample 2 there was selection for generally larger size in males, but that this was due to selection for longer legs, with direct selection on prosoma width tending to be negative.

We tested whether the size of males caught on moulting webs and of males caught on females' webs changed over the season to determine whether a seasonal effect could be a possible confounding factor in our analyses (Fig. 2a). In sample 1, general male size (PC1) is not a function of maturation date ($y = -0.07 - 0.01x$; $df = 1,48$; $F = 0.29$; $P = 0.593$), but the size of males on females' webs increased over the season ($y = -0.67 + 0.04x$; $df = 1,109$; $F = 7.59$; $P = 0.007$). In sample 2, maturation date was negatively correlated with PC1 ($y = 0.13 - 0.09x$; $df = 1,49$; $F = 7.15$; $P = 0.010$), whereas the size of males on females' webs did not change significantly as the season progressed ($y = 0.50 - 0.01x$; $df = 1,52$, $F = 0.13$; $P = 0.720$). This could mean that the result suggesting selection for larger males during mate search is confounded by maturation date. Instead of larger males, males that mature earlier might be selected for, and the size effect would then just be due to the correlation between size and maturation date. To control for seasonal effects we modelled general male size (PC1) as a function of web type (fixed factor)

Table 1 Results for logistic regression analyses of the probability of finding a male on a web of a female as a function of fixed male morphological traits and PC1 (general body size). Values given are the univariate linear (b_{ul}), univariate nonlinear (b_{un}) and multivariate linear (b_{ml}) coefficients with standard errors and P-values for each sample (*S1*: sample 1; *S2*: sample 2). Univariate linear coefficients are estimated without nonlinear terms in the model. Coefficients that are significant after correction for multiple comparisons are in bold. *PROW*: prosoma width, *PATI1 – PATI4*: average patella-tibia length of the respective leg pair

Trait	b_{ul}	SE	P	b_{un}	SE	P	b_{ml}	SE	P
S1									
PC1	0.28	0.18	0.124	0.23	0.17	0.169			
PROWI	−0.11	0.17	0.511	0.29	0.16	0.067	−0.84	0.40	0.035
PATI1	−0.05	0.17	0.764	0.09	0.13	0.492	−0.75	0.72	0.293
PATI2	0.02	0.17	0.899	0.19	0.14	0.186	0.65	0.69	0.345
PATI3	0.21	0.18	0.221	0.30	0.17	0.084	**1.40**	0.45	0.002
PATI4	−0.02	0.17	0.923	0.20	0.14	0.177	−0.48	0.63	0.444
S2									
PC1	**0.71**	0.23	0.002	0.03	0.19	0.866			
PROWI	0.27	0.19	0.159	0.00	0.15	0.982	−0.94	0.51	0.068
PATI1	0.43	0.20	0.036	0.18	0.17	0.299	−0.64	1.43	0.652
PATI2	0.48	0.21	0.022	0.18	0.18	0.326	0.76	1.56	0.628
PATI3	0.46	0.21	0.025	0.15	0.19	0.429	0.48	0.67	0.472
PATI4	0.46	0.21	0.028	0.13	0.17	0.437	0.81	0.97	0.407

Fig. 2a–d a, c General body size (*PC1*) and **b, d** condition (*PC2*) as a function of observation date for male orb-weaving spiders caught on their moulting web before mate search [before (*black circle*)] and on a female's web after mate search [after (*open circle*)] for two sample sets. The *arrow* indicates an outlier in terms of its influence on the regression equation as identified by regression diagnostics (see text); the regression line shown here is based on the model containing the outlier
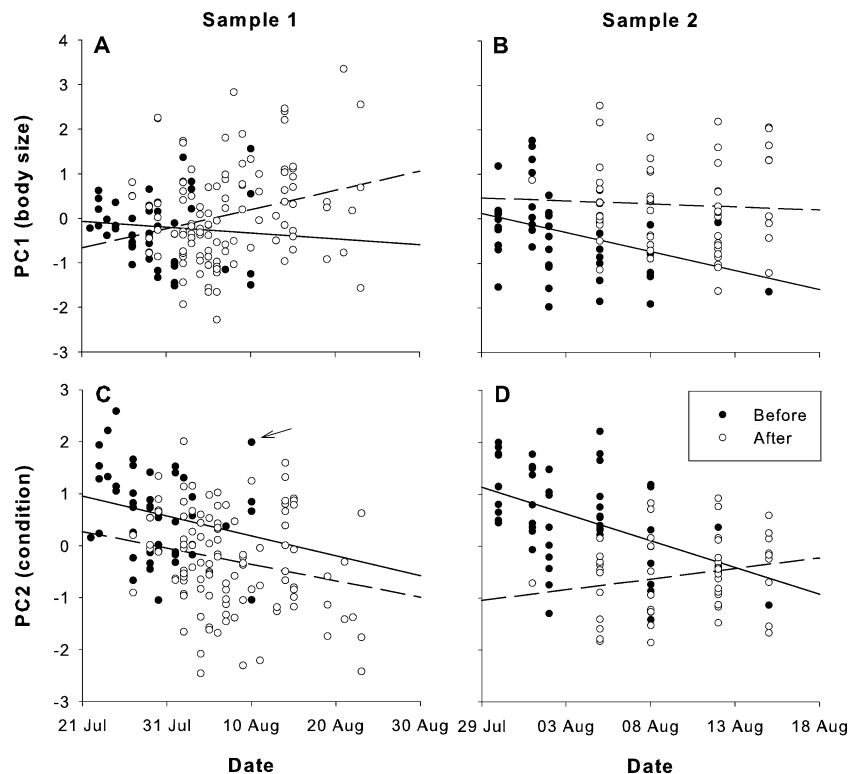
Table 2 Results of general linear models of general male size (*PC1*) and condition (*PC2*) as a function of web type and observation day for each sample. Where not reported, interaction terms were not significant (see text for details)

Source	SS	*df*	*F*	*P*
PC1				
Sample 1				
Model	7.95	2	4.13	0.018
Web type	0.01	1	0.01	0.942
Observation day	5.56	1	5.78	0.017
Error	152.05	158		
Sample 2				
Model	13.90	2	7.87	< 0.001
Web type	13.24	1	14.98	< 0.001
Observation day	3.26	1	3.69	0.058
Error	90.10	102		
PC2				
Sample 1				
Model	33.98	2	21.30	< 0.001
Web type	8.74	1	10.96	0.001
Observation day	5.99	1	7.51	0.007
Error	126.02	158		
Sample 2				
Model	43.41	3	24.13	< 0.001
Web type	17.67	1	29.46	< 0.001
Observation day	1.34	1	2.24	0.137
Web type×observation day	7.24	1	12.07	< 0.001
Error	60.59	101		

and observation day (covariate) (Table 2). The interaction term web type×observation day was not significant in either case (sample 1: $F = 2.96$, $df = 1$, $P = 0.087$; sample 2: $F = 2.09$, $df = 1$, $P = 0.151$). When these were dropped from the models, observation day was a significant predictor of male size in sample 1 (Table 2). In sample 2, the effect of web type was highly significant, while observation day was marginally significant (see Fig. 2a). Thus, inclusion of sampling date does not change our conclusions concerning selection on male size in sample 2. Further, the majority of males matured during the first half of the season (see Fig. 2a), and potential mates were abundant during the second half and males were accordingly associated with them. Given this, it is difficult to see why late maturing males would not be able to reach a female other than for the fact that they were smaller.

Effects on male condition

Adult males are expected to lose condition over time, because they rarely feed. We tested whether males lose condition during mate search while controlling for observation date by modelling condition (PC2) as a function of web type (fixed factor) and observation day (covariate) (Table 2, Fig. 2b). In sample 1 the interaction term web type × observation day was not significant ($F = 0.05$, $df = 1$, $P = 0.821$). When the interaction term was dropped from the model, both web type and observation day were strong predictors of male condition. In sample 2 the interaction term was significant,

and also the web type effect. Thus, males did lose condition during mate search in both samples. Males may also mature with less stored reserves for their size, i.e. in poorer condition, towards the end of the season, because the amount of reserves becomes less important. Thus, males might trade-off the amount of stored reserves with the achieved size at the maturation moult as the season progresses. To examine the temporal effects on male condition, we regressed condition (PC2) on observation day for males caught on their moulting web and males caught on a female's web separately, because loss of condition in these two groups reflects different phenomena. The condition (PC2) of males on their moulting webs is negatively correlated with maturation date in sample 2 ($y = 1.14 - 0.10x$; $df = 1,49$; $F = 10.24$; $P = 0.002$), but this is not significant in sample 1 ($y = 0.95 - 0.04x$; $df = 1,48$; $F = 2.52$; $P = 0.119$). However, regression diagnostics identified an outlier in terms of the influence on the regression line (see Fig. 2b; Cook's $d×(n-k-1) = 0.46×48 = 22.08 >$ the critical value of 16.39, Kleinbaum et al. 1998, p 731). If this data point is excluded from the analysis, then the regression equation becomes $y = 1.09 - 0.06x$ ($df = 1,47$; $F = 6.00$; $P = 0.018$), and we would see the same trend as in sample 2. Thus, there is a general trend for males moulting later in the season to be in poorer condition. In sample 1, males that were caught on females' webs were also in poorer condition as the season progressed ($y = 0.27 - 0.03x$; $df = 1,109$; $F = 5.06$; $P = 0.027$). In sample 2, no such trend was observed ($y = -1.04 + 0.04x$; $df = 1,52$; $F = 2.40$; $P = 0.128$). The discrepancy between samples could be due to the extended sampling period in sample 1. Because we searched for males on females webs for longer in 2000, we might have been more likely to find males in poor condition at the end of the season. Indeed, restricting the comparison to the same time period in the two samples (Julian dates 30 July –15 August) renders the relationship nonsignificant ($y = 0.08 - 0.02x$; $df = 1,89$; $F = 0.62$; $P = 0.432$).

To test whether males store or lose energy reserves disproportionately with size, we need to examine the scaling relationship between the amount of stored reserves and body size. For this purpose, size-corrected condition indices, such as a principal component or residuals, are not useful. Instead, we used as an estimate of the amount stored reserves the opisthosoma area calculated as the ellipse defined by opisthosoma width and length [opisthosoma area = (width/2)×(length/2)×π], which allowed us to express stored reserves as a function of a suitable size measurement (prosoma width). In our analyses we used square-root transformed opisthosoma area to bring it to the same biological scale as prosoma width. We first regressed opisthosoma area on prosoma width for males caught on their moulting web. The 95% confidence interval of the slope of the regression of log-transformed variables included the slope of 1, which is the expectation of isometry (sample 1: $b = 0.89$; 95% CI = 0.58–1.37; sample 2: $b = 0.87$; 95% CI = 0.40–1.33).

Table 3 Results of a general linear model of log(opisthosoma area$^{0.5}$) as a function of web type and log(prosoma width) for both samples. Interaction terms were not significant (see text for details)

Source	SS	df	F	P
Sample 1				
Model	0.14	2	44.83	< 0.001
Web type	0.05	1	30.14	< 0.001
Log (prosoma width)	0.09	1	54.85	< 0.001
Error	0.25	159		
Sample 2				
Model	0.19	2	47.98	< 0.001
Web type	0.11	1	56.95	< 0.001
Log (prosoma width)	0.10	1	50.78	< 0.001
Error	0.20	104		

Therefore, larger males are not able to store reserves disproportionately compared to smaller males. We then tested whether males lose stored reserves disproportionately with size by including all males in the analysis. If loss of energy reserves is a function of male size, the slope of opisthosoma area regressed on prosoma width should differ between males caught on moulting webs and males caught on females' webs. In a general linear model with log(opisthosoma area$^{0.5}$) as the response, web type as a fixed factor, and log(prosoma width) as the covariate, the interaction term was not significant in either case, indicating that the slopes did not differ (sample 1: $F = 1.06$, $df = 1$, $P = 0.305$; sample 2: $F = 0.43$, $df = 1$, $P = 0.512$). The effect of both web type and prosoma width were highly significant in both samples (Table 3, Fig. 3). This confirms that males lose condition as they search for females and shows that loss of condition does not depend on male size.

Discussion

Contrary to the prediction of the gravity hypothesis, we did not detect selection for small male size during the roving phase in *A. aurantia*. Overall larger males were actually more likely to reach a female's web in one of our two sampled populations, and this appeared to be the result of selection for longer legs. We did not find any evidence for stabilizing or disruptive selection on male body size or leg length.

Female *A. aurantia* build their webs about 80 cm above the ground between tall herbs or bushes (Enders 1974). While this in itself is likely to represent a substantial climb for a 5 mm long male, a male will often have to travel a long distance (several metres) through the vegetation to find a mate (Foellmer, personal observation, see also LeGrand and Morse 2000). Therefore, gravity is potentially an important factor in this species. There are several explanations why we might not have found a small male advantage in *A. aurantia*. According to the gravity hypothesis small males would be favoured because they are able to climb faster and are thus better at finding females and/or at escaping predators. To what extent scramble competition might operate in *A. aurantia* is unknown. Males typically cohabit with a penultimate female for days while waiting for her to undergo the maturation moult during which they try to mate with her (opportunistic mating: Robinson and Robinson 1980; Foellmer and Fairbairn 2003). By the time a female moults, in most cases more than one male has arrived on the web (McCook 1890; Foellmer 2004), so perhaps larger (i.e. slower) males often have enough time to reach a female. The majority of females are mated opportunistically in the field and males cannot defend a favourable position on the web during opportunistic mating so that the order of arrival on the web has probably no effect on male mating success (Foellmer 2004). Thus, reaching a penultimate female's web first is unlikely to be important. Nevertheless, some males mate with mature, post-moult females. Since females typically mate with only one or two males (Foellmer 2004), being first likely becomes relevant in this situation. Males are certainly expected to be vulnerable to predation during mate search (Vollrath and Parker 1992; Foelix 1996; Andrade 2003). *A. aurantia* is diurnal and males travel during the day (Foellmer, personal observation); they are therefore at risk of being caught by visually hunting predators such as jumping spiders (Wise 1993). Larger males have longer legs and are thus likely to be better runners at least on horizontal structures, because they are capable of longer

Fig. 3 Opisthosoma area$^{0.5}$ as a function of prosoma width for male orb-weaving spiders caught on moulting webs before mate search [before (*black circle*)] and caught on females' webs after mate search [after (*open circle*)] for two sample sets, **a** and **b**. Log$_{10}$ axis scales are used for both variables
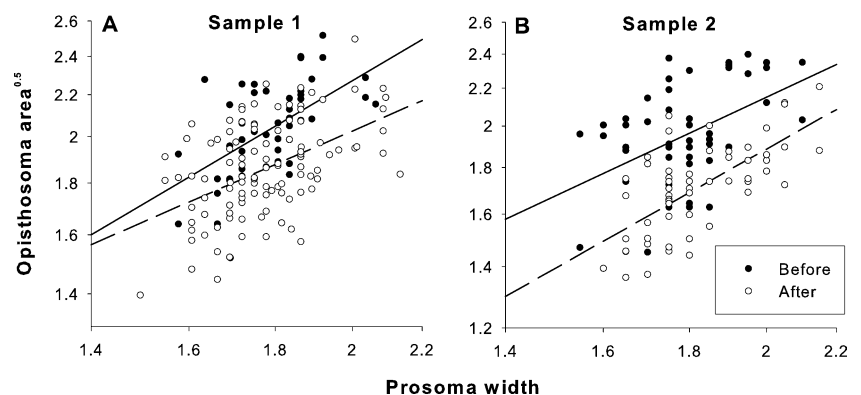
strides (Foelix 1996). In wolf spiders, larger individuals achieve a higher speed in one species, but not in another (Amaya et al. 2001). However, wolf spiders are adapted to move in a more two-dimensional habitat; their legs are all of similar length and equipped with adhesive hairs (Foelix 1996). This makes comparisons between wandering spiders and orb-weaver males difficult. Nevertheless, it might be that it is the ratio of vertical to horizontal structures a male has to travel on that determines which body features have a selective advantage during mate search and that gravity might become important only in species where females live high up in trees.

In our first sample, we detected a tendency for selection directly targeting prosoma width, favouring males with a narrower prosoma. We also found significant direct selection for longer legs of the third pair, based on multivariate analysis. However, this did not translate into significant net selection for either trait, probably due to the phenotypic correlation between these and the other traits that were not targeted by selection (Lande and Arnold 1983). The third leg pair is the shortest of all leg pairs and is probably constraining the locomotive performance of a male on substrate other than silk threads (Foelix 1996). Shorter third legs likely confer an advantage in the context of web construction and prey handling on the web, and this probably balances selection for longer third legs during mate search. Selection favouring a narrower prosoma seems surprising as it is believed that the same conditions that favour longer legs in males also favour a broader prosoma, because it accommodates much of the leg musculature (Prenter et al. 1995; Foelix 1996). However, we detected a similar tendency also in sample 2, and it is conceivable that narrower males might have an advantage when moving through the vegetation.

Our study is the first to investigate selection on leg length during mate search independently of body size in any spider. Previous work on highly dimorphic spider species suggested stabilizing selection on male body size during mate search in *Nephila clavipes*, based on the finding that males grouped in intermediate size classes were more likely to be caught again after interweb travel than males in extreme size classes (Vollrath 1980; Christenson 1990). Andrade (2003) has shown that males suffer from a high mortality during mate search in the redback spider *Latrodectus hasselti*, but that mortality was statistically independent of male size. However, there was a nonsignificant trend for larger males to be more likely to survive, and, as pointed out by Andrade (2003), the power of the statistical test was relatively low. Redback spiders build their webs near the ground, so it is perhaps not surprising that a small male advantage due to the gravitational force was not detected in this species. In the less dimorphic wolf spider *Hygrolycosa rubofasciata*, mortality during mate search appears to be independent of body size, but increases with increasing mate-searching activity (Kotiaho et al. 1998a, 1999). Clearly, more studies on highly dimorphic

species are needed to evaluate to what extent males suffer from size-selective mortality during mate search.

We found that in *A. aurantia*, stored energy reserves estimated as opisthosoma area scaled isometrically with prosoma width at maturation. Therefore, larger males were not able to store disproportionately more reserves than smaller ones. Males lost condition (i.e. energy reserves) during mate search, and the rate of condition loss seemed to be independent of male size. This is somewhat surprising, as larger males can be expected to lose condition at a lower rate per unit mass, because the mass-specific metabolic rate scales generally as body mass$^{-1/4}$ (West et al. 2000). Perhaps our sample sizes were not large enough to detect such an effect or the occasional food intake by males is sufficient to overcome any effects due to differences in mass-specific metabolic rate. However, although the universal scaling relationships between metabolic rate and body mass have been confirmed in a variety of spiders (e.g. Anderson 1970; Greenstone and Bennet 1980; Watson and Lighton 1994), it has been suggested that the relationship between body mass and mass-specific metabolic rate can even be positive in males of a wolf spider (Kotiaho et al. 1998b). An investigation of sex-specific metabolic rates in *A. aurantia* might be interesting, since to our knowledge this has so far been done for only two spider species (Watson and Lighton 1994; Kotiaho 1998). In any case, based on our data male *A. aurantia* of a particular size seem unlikely to have an advantage during mate search or mating due to their energy storage capacity, but more direct tests of this hypothesis might shed further light on the issue.

We detected a trend for earlier maturing males to be in better condition. Our condition index reflects the amount of stored energy reserves a male has available for his adult life span and thus probably reflects an allocation decision with respect to overall achieved size versus stored reserves for future use (Roff 2002). Males that begin their adult life with fewer reserves after moulting need not necessarily be of poorer quality in terms of their immediate performance, e.g. during combat – as long as they have sufficient energy. However, they are expected to have lower endurance, i.e. they cannot search for suitable females or wait for females to moult as long as males in better condition. Therefore, the negative relationship between male condition and maturation date suggests that males may trade off achieved adult size with the amount of stored reserves. Males start to mature about a week earlier than females and as the season progresses energy reserves might become less important, because females start to mature and potential mates are thus more readily available. This is reflected by the fact that during the first two and half weeks that males were associated with females, the condition of these males did not appear to change and only later in the season were males in poorer condition. Thus early maturing males in high condition probably lost more condition, because they had to wait on average longer for penultimate females to moult. We do not know to

what extent males die of starvation before they get to mate, but it is known that adult male orb-weavers generally senesce rapidly and die within weeks (e.g. Andrade 2003). Nevertheless, male *A. aurantia* die during insertion of their second pedipalp and therefore will most often mate with only one female (Foellmer and Fairbairn 2003), so perhaps only energy needed to achieve a single mating is important.

In conclusion, we detected selection for large body size during mate search in male *A. aurantia* in one out of two sampled populations, while male body size seemed to be neutral in the other. Thus we did not find support for the gravity hypothesis. During mating with cannibalistic females, male size appears to be neutral in *A. aurantia* (Foellmer and Fairbairn 2004), and during opportunistic mating large males are favoured (Foellmer 2004). Therefore, in this species there is probably overall selection for large male size during the adult stage and this is probably counterbalanced by viability selection favouring reduced growth during the juvenile stages. Males lose condition during mate search, but males of a particular size are unlikely to be at an energetic advantage given that energy reserves scale isometrically with size at maturation and loss of condition is not a function of size. We detected net selection for longer legs in one population, but not for a broader prosoma. This suggests that relatively longer legs in males are the result of selection during the roving phase, supporting an existing hypothesis that relatively longer legs in male spiders reflect a search adapted-morphology (Prenter et al. 1995; Foelix 1996; LeGrand and Morse 2000). Finally, it should be pointed out that selection often varies in space and time (e.g. Blanckenhorn et al. 1999; Ferguson and Fairbairn 2000; Jann et al. 2000). Experiments that directly investigate how body size and leg length determine a male's ability to move through different types of vegetation would further improve our understanding of the significance of the roving phase for body size evolution in male orb-weaving spiders.

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