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Running performance as a function of body size, leg length, and angle of incline in male orb-web spiders, *Argiope aurantia*

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ABSTRACT

Background: The locomotor performance of various taxonomically distinct species depends on context-specific selection pressures. Superior locomotor performance presumably promotes male mate search success. Running performance on vertical structures is especially important in non-flying species, such as many spiders, because males navigate through high vegetation to find females. Yet recent empirical tests of the relationships of morphological traits, running performance, and angle of incline in spiders have been inconclusive.

Hypothesis: Achievable running speed of male orb-web spiders (*Argiope aurantia*; Araneidae) on vertical structures is moulded by natural selection on their morphology and locomotor performance. We predict that male body size and leg dimensions are positively related to running speed (in accordance with the recently proposed curvilinear gravity hypothesis) and that if past selection reflects adaptation to run on vertical surfaces, males run faster at steeper angles than on horizontal surfaces.

Methods: We conducted running performance trials in males of *A. aurantia*. The same males were used at five different incline angles: 0°, 22.5°, 45°, 67.5°, and 90°.

Results: Spider leg dimensions are strongly correlated with body size. Larger males ran faster at all incline angles. Independent of morphology, males tended to run faster at steeper inclines than on horizontal surfaces.

Keywords: body size evolution, morphology, orb-web spiders, running speed, sex-specific selection, sexual dimorphism.

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INTRODUCTION

In most animal species, mature males locate sexually receptive females and hence have to move more than females during this period of mate search (Andersson, 1994). This is particularly pronounced in web-building spiders, where females stay more or less sedentary throughout their life and adult males abandon their web-building habits to search for females (Vollrath and Parker, 1992; Moya-Laraño *et al.*, 2002). Hence, mate search has been hypothesized to generate selection limited to males that could result in different optimal adult body sizes in males and females in spiders and many other groups (Blanckenhorn, 2005). In this context, the following selection mechanisms have been invoked: small males have an agility advantage, especially when moving through a three-dimensional habitat or flying (Ghiselin, 1974); small males have an energetic advantage in species in which adult males have to feed to maintain stamina (Blanckenhorn *et al.*, 1995); large males have an energetic advantage in species in which adult males do not feed and thus live off their stored energy reserves (Foellmer and Fairbairn, 2005a); due to gravity small males have an advantage to reach females in species where males have to run up vertical structures, or bridge from plant to plant with own-made silk bridges to reach females (Moya-Laraño *et al.*, 2002; Corcobado *et al.*, 2010); and mate-searching males suffer from size-independent mortality, leading to a low probability of encountering females, and in turn to selection to mature early at a small size to minimize juvenile mortality (Vollrath and Parker, 1992). With the exception of the mechanisms based on energy use, these are not mutually exclusive and could operate in concert (Foellmer and Moya-Laraño, 2007). In addition, selection for a mate search-adapted phenotype can also be expected to operate on other traits besides overall size, such as favouring relatively longer legs in males to allow for wider strides and thus faster movement (Alexander, 2002; Foellmer and Fairbairn, 2005a; Moya-Laraño *et al.*, 2009), or locomotor performance traits such as high sprint speed capacity on the ecologically most relevant substrate (Calsbeek and Irschick, 2007) or in the most relevant context (Pruitt and Husak, 2010).

The most recent hypothesis explaining body size evolution based on mate search-related processes is the gravity hypothesis (Moya-Laraño *et al.*, 2002), and it has sparked considerable controversy (Foellmer and Fairbairn, 2005a; Brandt and Andrade, 2007a, 2007b; Foellmer and Moya-Laraño, 2007; Moya-Laraño *et al.*, 2007a, 2007b, 2009; Corcobado *et al.*, 2010; Prenter *et al.*, 2010a, 20109b). In its original conception, it stated that body mass is inversely proportional to achievable running speed on vertical structures, based on a simple biomechanical model (Moya-Laraño *et al.*, 2002), but this prediction has now been revised on the basis of a comprehensive comparative experimental study (Moya-Laraño *et al.*, 2009). The new curvilinear gravity hypothesis predicts a curvilinear relationship between body mass and running speed on vertical structures: below a threshold body mass of about 43 mg running speed should be positively related to body mass, and above the threshold running speed should be negatively related to body mass (Moya-Laraño *et al.*, 2009). This curvilinear relationship is hypothesized to be the result of the interplay of the scaling relationships of stride length, stride frequency, and power output with body size (Moya-Laraño *et al.*, 2009). However, empirical tests of running performance on vertical structures as a function of body mass or other body size indicators have yielded mixed results. Body mass was negatively related to running speed on vertical rods in the orb-weaver *Leucauge venusta* in an experiment that included both males and females to increase the available size range [sex was statistically controlled for (Moya-Laraño *et al.*, 2007b)]. This result supports the curvilinear gravity hypothesis, as most individuals in the study were heavier than 43 mg. Other experimental tests involving adult males of three

highly dimorphic web-building spider species and one little dimorphic jumping spider did not find any predictive power of body size, leg length or mass [*Latrodectus hesperus* (Brandt and Andrade, 2007a); *Argiope keyserlingi*, *Nephila plumipes*, and *Jacksonoides queenslandica* (Prenter *et al.*, 2010a, 2010b)]. Instead, larger size conferred an advantage on horizontal surfaces in the ground-dwelling *L. hesperus* (Brandt and Andrade, 2007a) and *J. queenslandica* (Prenter *et al.*, 2010a). Field studies that have examined the relationship between male body size and mate search success have also yielded varied results: larger males were favoured in a population of *Argiope aurantia*, a species with males well below the 43 mg threshold (Foellmer and Fairbairn, 2005a); smaller or intermediate-sized males were favoured in *Nephila clavipes* (Vollrath, 1980; Linn, 2001), for which the male size range includes the threshold (these results support the predictions of the curvilinear gravity hypothesis); and no relationship between male size and mate search success was found in *Latrodectus hasselti*, *N. plumipes*, and a second population of *A. aurantia*, hence not supporting the curvilinear gravity hypothesis (Andrade, 2003; Foellmer and Fairbairn, 2005a; Kasumovic *et al.*, 2007).

The study of performance traits, their importance independent of and in interaction with morphology, has gained considerable interest in recent years (Vanhooydonck *et al.*, 2007; Irschick and Le Galliard, 2008; Irschick *et al.*, 2008). For example, the funnel web spider *Agelenopsis aperta* exhibits inter-population variation in context-dependent running speed (Pruitt and Husak, 2010). Selection has probably maximized running speed capacity in the most relevant ecological context in each population (e.g. predator escape or territory defence). In the Anolis lizard *Anolis sagrei*, interaction effects of locomotor performance, morphology, and habitat use were reported by Calsbeek and Irschick (2007). The sprint speed advantage of long limbs manifested itself only on broad surfaces, and these were indeed favoured by the lizards in nature. These examples demonstrate that performance traits can be shaped by natural and sexual selection independently of external morphology (for example, by selection on metabolic rates) or in interaction with morphological traits, and that performance should be higher in contexts or habitats in which individuals have evolved.

Here we first test the hypothesis that body mass and external morphology affect achievable running speed in males of the highly dimorphic orb-web spider *Argiope aurantia* [adult body mass female/male ratio ≈ 50; adult body length female/male ratio ≈ 3.5 (M.W. Foellmer, unpublished data; Levi, 1968)], which is one of a few species with extreme sexual size dimorphism for which a considerable amount of information about patterns of selection on male body size and leg length exists (Foellmer and Fairbairn, 2004, 2005a, 2005b; Foellmer, 2008; Inkpen and Foellmer, 2010). The results of this study can thus be placed in the broader context of body size evolution of this species. Importantly, we test for a relationship between locomotor performance and male mass as well as morphology at five different angles: 0°, 22.5°, 45°, 67.5°, and 90°. Clearly, in nature individuals do not simply run on horizontal or vertical structures but move through a complex vegetation network that likely includes all possible angles between 0° and 90° (Hannunen, 2002). Thus, for example, a positive relationship between size and speed at 0° but not at 90° provides only limited insight if we do not know how the relationship changes over different angles. In addition, previous studies used different substrates for the horizontal and vertical running trials, hence potentially confounding the angle effect (e.g. Brandt and Andrade, 2007a; Prenter *et al.*, 2010a). We avoid this by using the same substrate for all angles. A field study showed that overall large size was favoured during mate search in one population of *A. aurantia* (see above), which was due to selection for longer legs, while in a second population only direct selection on the third leg pair was detected, with no

overall size effect (Foellmer and Fairbairn, 2005a). Hence, the current study allows elucidation of the underlying mechanism of the detected selection pattern in the field.

We then test the hypothesis that locomotor performance (running speed) is affected by factors other than external morphology by evaluating the consistency (i.e. repeatability) of male running performance across contexts (i.e. the five angles of incline) with and without statistically removing the effect of morphology. A significant repeatability across contexts with the effect of morphology removed would point to traits other than external morphology, such as metabolic rates, being important for running performance, which can be a form of performance capacity on which selection could act directly (Irschick *et al.*, 2008).

METHODS

Adult males were collected from their own webs on which they moulted to maturity in an old field near Peterborough, Ontario, Canada on 16 and 17 July 2007. Hence none of these males had engaged in mate search yet, during which they may have experienced selection on the traits under consideration. They were kept in small plastic vials (26×67 mm) for 2–4 days before the experimental trials. The trials lasted 3 days. All males were photographed with a Nikon CoolPix 4500 (for later measurement) and weighed with a Mettler Toledo AB135 analytical balance prior to the running trials. For the photographs, males were transferred into a Petri dish with a scale bar and cotton for cushioning. A series of photographs was taken of each male for measurement with SigmaScan©. We measured cephalothorax (prosoma) width, abdomen width and length, the patella–tibia length of all eight legs, and the femur width of the first leg pair. All widths were taken at the broadest point of a given trait. Patella–tibia lengths and femur widths were calculated as averages for each leg pair. Repeatability for all measured traits was >0.92 (for all traits: $n = 10$, $k = 3$).

For the running trials, we constructed wooden frames that allowed fixing cylindrical dowelling of 8 mm diameter at five different angles: 0°, 22.5°, 45°, 67.5°, and 90°. We chose 8 mm rods because this was the diameter closest to the natural diameter of goldenrod, *Solidago* spp. (Heard and Cox, 2009), the dominant plants in successional habitats in which *A. aurantia* are commonly found. The horizontally fixed rod was 10 cm above ground so that males were free to choose running upright or upside down. This arrangement ensured that the angle effects were not confounded by differences in running surface and probably reflects a more realistic scenario than providing them with a sandpaper track (e.g. Prenter *et al.*, 2010a), because male *A. aurantia* are frequently seen running through the vegetation but never run on the ground and are never caught in pitfall traps (own observations; Jennings and Graham, 2007). Increments of 10 cm were marked along the rod and males could run a maximum distance of 100 cm. All trials were conducted during the day in the same room the males were kept in and at ambient room temperature (mean ± S.D. = 23.8 ± 1.4°C). All races were recorded using a digital video camera (SONY DCR-HC52). Males were used in random order for each of the five angles (total sample size: $n = 47$), but we set a minimum rest time of 10 min for each male between races (Riechert and Johns, 2003). Males were released at the bottom of the rod (or at one end for horizontal trials) and carefully touched with a brush to stimulate running along the rod if necessary. We 'chased' males with the brush, but avoided any pushing. We tried each male at every angle, and an additional two times at a randomly chosen angle to calculate the repeatability for running speed. However, for some males we could not perform successful running trials at all angles; therefore, samples sizes for the various analyses differ slightly. Repeatabilities for speed were as follows: $R = 0.68$ ($n = 7$,

$k = 3$) for 0°, $R = 0.70$ ($n = 8$, $k = 3$) for 22.5°, $R = 0.41$ ($n = 8$, $k = 3$) for 45°, $R = 0.58$ ($n = 10$, $k = 3$) for 67.5°, and $R = 0.74$ ($n = 8$, $k = 3$) for 90°.

For statistical analysis, all morphological traits and running speeds were log-transformed. Before log-transformation, body weight was cube-root transformed to bring the variable to the linear scale. We performed a principal component analysis (PCA) with Varimax rotation to reduce the number of predictor variables. The PCA extracted two components explaining 90% of the total variance (PC1: 81.8%, PC2: 8.2%). All morphological traits were highly correlated with PC1 (range of factor loadings: 0.85–0.94), but not with PC2 (range of factor loadings: 0.15–0.29), whereas body mass was highly correlated with PC2 but not with PC1 (factor loadings: 0.97 vs. 0.25). Therefore, PC1 can be interpreted as an estimator of overall body size, which includes the 'fixed' traits that do not change after the maturation moult (cephalothorax width and all leg traits), as well as the abdomen dimensions that change with, for example, the nutritional state of the individual (Foellmer and Fairbairn, 2005a). On the other hand, PC2 reflects residual body mass, or mass load independently of body size, and is thus a likely indicator of body condition (Moya-Laraño *et al.*, 2008).

We included in the statistical analyses the speed for the longest continuously run distance for a given trial. Because distances run varied from 10 to 90 cm, we tested first whether distance run and speed were correlated. Our general approach for analysis was to run a repeated-measures General Linear Model (rmGLM) with PC1 and PC2 as predictors and speed as the response, and subsequently multiple regressions for each angle separately with PC1 and PC2 as predictors and speed as the response. The interaction terms ($PC1 \times PC2$) were never significant in the regression models and were thus omitted to simplify the models (Kleinbaum *et al.*, 1998). We conducted these analyses in SPSS v.17. In addition, we performed a stepwise regression analysis for each angle to identify the traits most relevant for running performance. The full model contained the log-transformed variables prosoma width, average patella–tibia lengths for legs 1–4, average femur 1 width, abdomen width, and abdomen length, as well as the first cube-root then log-transformed variable body mass. We used the backward stepwise procedure in R ['step' algorithm (R Development Core Team, 2010)] with the Akaike Information Criterion (AIC) as the basis for model selection. We then used the R package 'AICcmodavg' to calculate AICc weights for each model during the stepwise process and to estimate the evidence ratio (ratio of AICc weights) for the best final model when compared with the second best model. The second-order AIC (i.e. AICc) is more accurate when sample sizes are not very large. Because AIC and AICc are only informative when compared with other models, evidence ratios (for best models relative to the second best models) rather than AICc values or AICc weights are provided. The *P*-values for the final models were obtained using Type-III tests (R package 'art').

We also tested whether individual performance was consistent across contexts (angles) by calculating the repeatability of speed across the five angles. We used the ANOVA method within the package 'rptR' of R, which performs significance tests and estimates confidence intervals for repeatability (R) by means of permutation and bootstrap, respectively (Nakagawa and Schielzeth, 2010). We estimated repeatability both without removing the effect of morphology and then on the residuals of a model of speed against morphology (PCs above). This allowed us to determine whether morphology had a substantial effect on the consistency of individual performance and whether there was significant repeatability across contexts that could be explained by traits other than external morphology.

Table 1. Descriptive statistics for the untransformed trait values and running speeds

Trait	Unit	mean	s.d.
Prosoma width	mm	2.04	0.23
Abdomen width	mm	1.70	0.23
Abdomen length	mm	3.44	0.48
Patella–tibia length 1	mm	4.62	0.60
Patella–tibia length 2	mm	4.38	0.56
Patella–tibia length 3	mm	2.09	0.27
Patella–tibia length 4	mm	3.66	0.49
Femur width 1	mm	0.53	0.06
Weight	mg	18.74	6.43
Speed 0°	$cm \cdot s^{-1}$	6.70	2.24
Speed 22.5°	$cm \cdot s^{-1}$	7.04	2.31
Speed 45°	$cm \cdot s^{-1}$	7.19	2.07
Speed 67.5°	$cm \cdot s^{-1}$	7.69	2.67
Speed 90°	$cm \cdot s^{-1}$	7.45	2.89

Note: Patella–tibia lengths are the averages for the respective leg pairs, while femur width 1 is the average for the first leg pair ($n = 47$).

RESULTS

The descriptive statistics for the untransformed trait values and running speeds are given in Table 1. Running speeds were not correlated with distance run for the angles 0° to 67.5° (range of r values = 0.11–0.24, $n = 44$ for 0°, otherwise $n = 43$, all $P > 0.1$), but speed was positively correlated with distance run for 90° ($r = 0.33$, $n = 42$, $P = 0.032$). The repeated-measures GLM revealed a significant angle effect on speed, but no significant interaction of angle with PC1 or PC2 (Table 2, Fig. 1). The linear contrast for angle was significant ($F = 6.503$, d.f. = 1, $P = 0.016$), whereas all higher-order contrasts were not (quadratic: $F = 0.101$, d.f. = 1, $P = 0.753$; cubic: $F = 0.026$, d.f. = 1, $P = 0.873$; order 4: $F = 1.500$, d.f. = 1, $P = 0.230$). Hence, running speed increased with increasing angle (Fig. 1), and pairwise comparisons showed that running speed at 0° was significantly lower than running speeds at angles of 67.5° and 90° ($P < 0.05$; all other pairwise comparisons, $P > 0.1$).

PC1 was positively associated with running speed at all angles, whereas PC2 was never significant (Table 3, Fig. 2). Hence, larger males achieved higher speeds at all angles, but residual body mass had no effect. Selection of the best regression models indicated that for angles 0°, 22.5°, and 90°, long first legs are most important for achieving high running speed, whereas for angles 45° and 67.5°, thick first legs appeared most relevant. However, models that included PTL1 (long first legs) were better supported by AICc evidence ratios than models including FW1 (thick first legs) (Table 4). Note that for 90° the model with the lowest AIC included PTL1 and AL as significant predictors, and that AL had a negative slope, indicating that spiders with longer abdomens climbed more slowly.

Finally, individuals ran consistently across angles (speed: $R = 0.650$, CI = [0.505, 0.796], $P = 0.001$), even beyond morphological differences (residual speed: $R = 0.446$, CI = [0.268, 0.624], $P = 0.001$). Therefore, spiders that ran fast at 0° were also fast at all other angles, and

Table 2. Results of the repeated-measures GLM, with running speed at the five different angles as the response variable and PC1 and PC2 as predictors

Source	Type III sum of squares	d.f.	Mean square	F	P
Angle	0.380	4	0.095	2.505	0.046
Angle × PC1	0.047	4	0.012	0.310	0.871
Angle × PC2	0.063	4	0.016	0.412	0.799
Angle × PC1 × PC2	0.041	4	0.010	0.263	0.901
Error(angle)	4.356	112	0.039		

Note: The repeated-measures GLM assumption of sphericity was not violated (Mauchly's $W = 0.772$, $\chi^2 = 6.83$, d.f. = 9, $P = 0.656$).

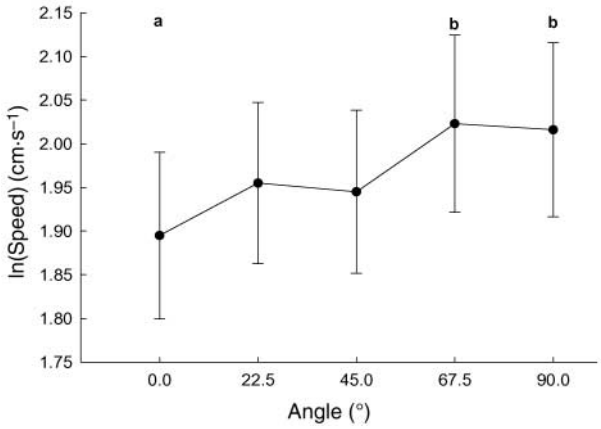

Fig. 1. Marginal means within 95% confidence intervals for running speed at the five angles from the repeated-measures GLM, with speed as the response variable and PC1 and PC2 as predictors (see Table 2). Different letters at the top of the figure indicate groups that differ significantly from each other ($P < 0.05$).

this was consistent despite the fact that morphology had an effect on running performance and that running performance increased with angle.

DISCUSSION

Male body size was a significant predictor of running speed in the present study: larger males ran faster at all angles. Of all the possible body size components that explain running performance, leg traits (length and diameter) appear to be the most relevant. We found no 'morphology × angle' interaction, indicating that steepness does not affect the relationship between morphology and performance. Importantly, we found that independently of morphology, males tend to run faster on steeper surfaces. Furthermore, even beyond the effects of morphology males that ran faster on horizontal dowels also ran faster at all other angles. Only at an inclination of 90° was abdomen length, a non-muscular body part involved in locomotion, a significant predictor in the final model revealed by stepwise

Table 3. Results of multiple regression analyses conducted for each angle separately

Angle	Trait	*b*	S.E.	*t*	*P*
0°	(Constant)	1.84	0.04	43.20	<0.001
	PC1	0.18	0.04	4.39	<0.001
	PC2	0.04	0.04	0.88	0.383
22.5°	(Constant)	1.91	0.04	47.97	<0.001
	PC1	0.17	0.04	4.34	<0.001
	PC2	0.05	0.04	1.13	0.265
45°	(Constant)	1.93	0.04	54.33	<0.001
	PC1	0.13	0.03	3.76	0.001
	PC2	0.03	0.04	0.67	0.507
67.5°	(Constant)	1.99	0.04	48.31	<0.001
	PC1	0.16	0.04	3.89	<0.001
	PC2	0.08	0.05	1.84	0.073
90°	(Constant)	1.95	0.05	40.82	<0.001
	PC1	0.17	0.05	3.61	0.001
	PC2	0.07	0.05	1.37	0.179

Note: Interaction terms were never significant and are omitted here. PC1 is interpreted as overall structural size; PC2 represents only residual body mass (see text).

Table 4. Results of the stepwise regression analyses

Angle	Model	Significance of slopes	AICc evidence ratio
0°	ln[Speed] = −0.9 − 1.0 ln[AL] + 2.6 ln[PTL1]	ln[AL]: $P = 0.117$, ln[PTL1]: $P < 0.001$	3.3
22.5°	ln[Speed] = −0.3 + 1.4 ln[PTL1]	ln[PTL1]: $P < 0.001$	3.0
45°	ln[Speed] = 2.7 + 1.2 ln[FW1]	ln[FW1]: $P < 0.001$	1.3
67.5°	ln[Speed] = 2.9 + 1.4 ln[FW1]	ln[FW1]: $P < 0.001$	1.3
90°	ln[Speed] = −0.8 − 1.6 ln[AL] + 3.1 ln[PTL1]	ln[AL]: $P = 0.023$, ln[PTL1]: $P < 0.001$	2.6

Note: The full models included all measured traits (see text for details). AL = abdomen length, PTL1 = average patella–tibia length of the first leg pair, FW1 = average femur width of the first leg pair.

analysis. Males with a relatively longer abdomen ran slower at 90° than males with shorter abdomens. This indicates that mass load may have a negative effect on climbing. However, residual mass (PC2) was never significant, suggesting that the particular shape (relatively long abdomen) could have been important here. For instance, longer abdomens may mean heavier loads at the tip of the body, thus switching the centre of gravity backwards and making gravity a stronger constraint for climbing. Nevertheless, because PC2 reflects

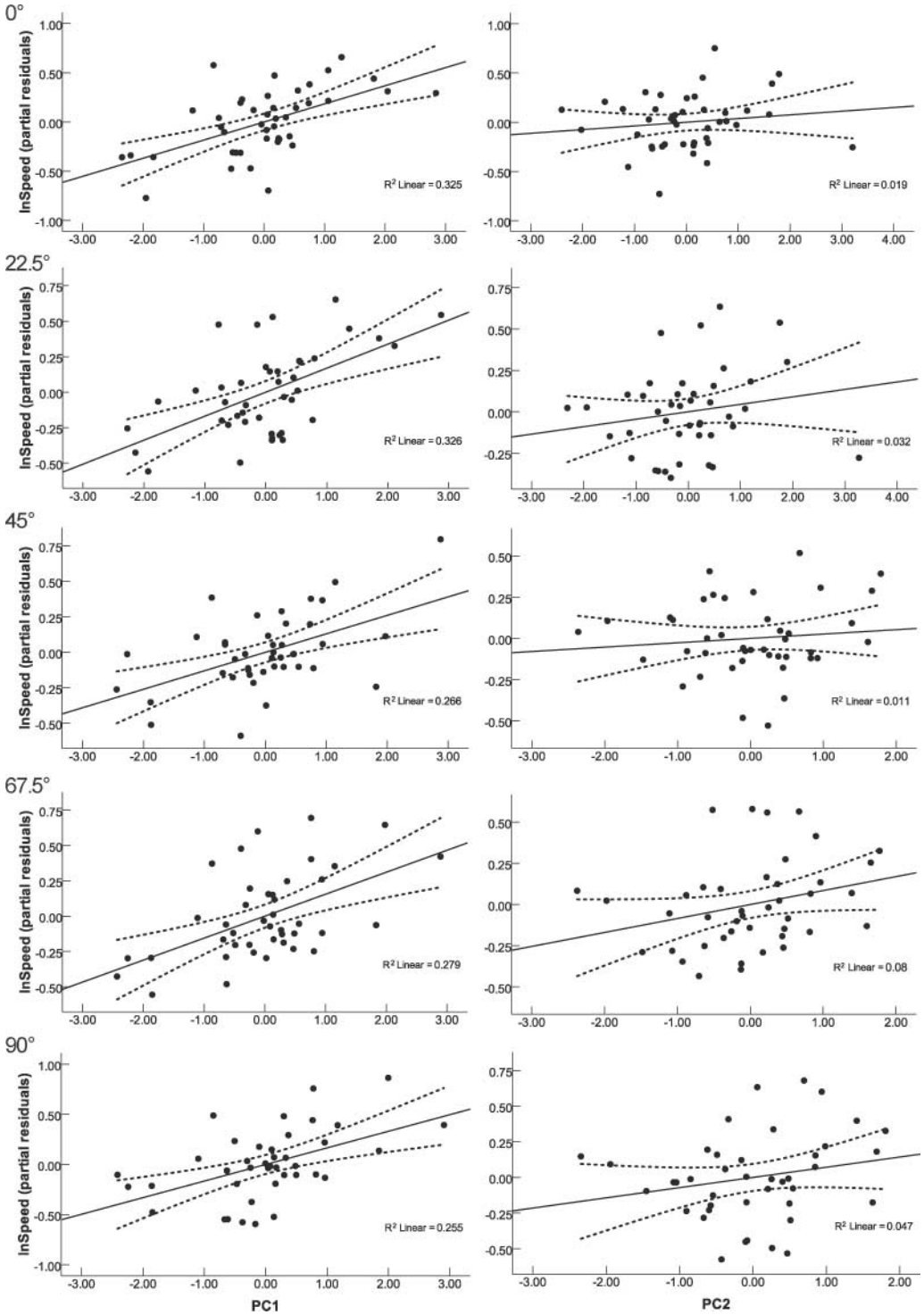

Fig. 2. Partial regression plots for running speed as a function of PC1 and PC2 for each angle. Linear fit lines with 95% confidence bands are shown. See Table 3 for the complete models.

residual mass and thus condition as well, negative effects of mass and any positive effects of condition may have cancelled each other out.

Our results are largely congruent with the findings of a field study that documented significant net selection for relatively longer legs in male *A. aurantia* and as a consequence also for large body size in one population, whereas in another population significant direct selection for longer third legs was detected (Foellmer and Fairbairn, 2005a). The third leg pair is the shortest (see Table 1), and it is conceivable that it can constrain locomotor performance. In the present study, the length of the first leg pair clearly appeared most important for achieving a high running speed. Thus our data provide a functional explanation why long legs and by extension large size tend to be selected for in this species, consistent with the hypothesis of Foellmer and Fairbairn (2005a). Whether bridging contributes to selection on morphology in this context remains to be determined. The threshold above which bridging should be constrained is at a body mass of about 100 mg (Corcobado *et al.*, 2010), well above the body mass range of male *A. aurantia*, but selection might of course operate on morphology during bridging.

The fact that, independently of morphology, males ran faster at steeper slopes, is intriguing and suggests that the verticality of the habitat in which this species lives has selected for better vertical versus horizontal performances. For example, in the blue-spotted salamander *Ambystoma texanum*, anti-predator performance is positively associated with the presence of fish predators as well as the historical duration and consistency of selection imposed by predators (Eastman *et al.*, 2009). [For additional examples, see Introduction.] Since *Argiope aurantia* males are well below the threshold weight beyond which gravity constrains mobility and beyond which there is a negative relationship between body mass and climbing [i.e. 43 mg (Moya-Laraño *et al.*, 2009)], selection for vertical mobility, particularly to the extent that it is independent of morphology and body size, seems little constrained. To gather additional support for this latter hypothesis, it would be interesting to test ground-dwelling species on vertical surfaces. The prediction would be that these species would perform better on the ground than on vertical surfaces. Interestingly, in *L. hesperus*, which lives closer to the ground than *A. aurantia*, males run 1.4 times faster on the ground than they climb [re-analysis of data from Table 1 in Brandt and Andrade (2007): mean climbing speed = 7.2 $cm \cdot s^{-1}$ (95% CIs: 6.6–7.8), mean running speed on the ground = 10.1 $cm \cdot s^{-1}$ (95% CIs: 8.8–11.4)], providing support for the above prediction.

The relatively high repeatability found across contexts (angles) has important evolutionary implications. First, repeatability in performance can be an indication that performance has a quantitative genetic basis (Roff, 1997) and thus that it can be shaped by natural selection (but see Naya, 2010). But note that repeatability sets the upper limit to heritability, but does not in itself demonstrate a quantitative genetic basis for observed variation. Second, it means that selection in one context (e.g. running on vertical surfaces) will very likely result in animals performing better in another context (e.g. horizontal surfaces), suggesting that performance traits other than morphology are also genetically correlated. Since performance is better on vertical surfaces (see above), it is likely that the observed better performance of larger animals on horizontal surfaces is a by-product of selection for performance on vertical surfaces. Indeed, walking on the ground is unlikely to be a mechanism used by these males. To our knowledge, they are never caught in pitfall traps (own observations; Jennings and Graham, 2007), and horizontal locomotion is probably restricted to branches or twigs, as modelled in our experiment. Furthermore, if vegetation is dense enough, small orb-weaving spiders should rather use bridging (i.e. running upside-down on

own-made silk bridges) to move from plant to plant (Corcobado *et al.*, 2010; Rodríguez-Gironés *et al.*, 2010). Prenter *et al.* (2010b) similarly found that running speed was repeatable across 0° and 90° angles for males of two species of orb-web spiders (*Nephila plumipes* and *Argiope keyserlingi*), but not for males of the jumping spider *Jacksonoides queenslandica*. This points to the possibility that running and 'climbing' are functionally not much different in these orb-weaver males, including *A. aurantia*, and this may be because they fall below the 43 mg 'gravity threshold' (Moya-Laraño *et al.*, 2009). Note in this context that Prenter *et al.* (2010b) used different substrates for the different angles, unlike in the present study. Males running at 0° incline ran on a flat surface, while males running at 90° ran up a dowel.

Our study and earlier results for *A. aurantia* indicate that mate search is an important period in the life of males, leading to selection on morphology and performance. Our results are also consistent with the curvilinear gravity hypothesis (Moya-Laraño *et al.*, 2009), which states that up to a body mass threshold of 43 mg – note that the entire body size range for male *A. aurantia* is below this threshold (Table 1) – larger males run faster on vertical structures. However, the picture is different for other species. In five of eight species for which running trials at horizontal and vertical angles have been conducted, or for which there is at least data for mate search success in relation to body size, no relationship between a given size estimator and speed or mate search success has been reported [although in no case the opposite pattern of that predicted by the curvilinear gravity hypothesis has been documented – see Introduction (Brandt and Andrade, 2007a; Kasumovic *et al.*, 2007; Prenter *et al.*, 2010a)]. Brandt and Andrade (2007) found no relationship between body mass and climbing performance in males of the widow *Latrodectus hesperus*. Instead, they found a positive relationship between body size and running performance on flat surfaces. However, in the congener *L. hasselti*, no effect of body size on mate search access was found, although this might have been due to limited power (Andrade, 2003). Importantly, *Latrodectus* spp. live relatively close to the ground and often live in arid habitats with sparse vegetation (Levi, 1959). Selection on climbing performance is probably not important in these systems, and other factors, such as high travel mortality favouring early maturation at a small size (Vollrath and Parker, 1992; Andrade, 2003; Kasumovic and Andrade, 2006), may be operating and contributing to the evolution and maintenance of extreme sexual size dimorphism in this genus. Prenter *et al.* (2010a) tested climbing performance for three species at different substrate diameters, in addition to running performance on flat surfaces. For the little dimorphic jumping spider *Jacksonoides queenslandica*, they found that, similar to *L. hesperus*, body size was positively correlated with running speed on flat surfaces but not with climbing speed. For the two highly dimorphic orb-web spider species *Argiope keyserlingi* and *Nephila plumipes*, they found no relationship between body size, relative leg length or body mass and running or climbing performance (Prenter *et al.*, 2010a). Achieving a high speed on vertical structures as an escape mechanism might not be as important for *J. queenslandica*, since jumping spiders can escape effectively by jumping from one piece of vegetation to the next (Foelix, 1996). However, the results for the two orb-weavers are interesting. *Nephila plumipes* females build their webs high up in the vegetation, so this species should be a prime candidate for vertical movement to be important. However, in this species individuals are often found in aggregations and juvenile males build their webs typically in close proximity to females; penultimate males are often found cohabiting with females, attaching their webs to a female's web (Elgar *et al.*, 2003; Kasumovic *et al.*, 2007). Thus, mature males probably travel small distances to reach females, which would explain why they might not be under strong selection to achieve high speeds on vertical substrates. In line with this argument, Kasumovic *et al.* (2007) did not find any

morphological correlates with mate search success in *N. plumipes*. The result for *Argiope keyserlingi* is difficult to interpret at this time and more data are needed on this species.

In all of the species discussed in the previous paragraph, as well as in *Argiope aurantia*, male mass ranges are below the 43 mg threshold of the curvilinear gravity hypothesis. This means that for species that live in high habitats, gravity might still have been important for initial evolution of extreme sexual size dimorphism (see above; Moya-Laraño *et al.*, 2009), but other factors must clearly contribute to the maintenance of currently observed levels of sexual size dimorphism. Our results, as well as those of previous studies (Foellmer and Fairbairn, 2004, 2005a, 2005b; Foellmer, 2008; Inkpen and Foellmer, 2010), indicate that, in *A. aurantia*, adult males experience selection for large body size in the mate search and mating context, the latter being a result of male–male interference competition as operational and effective sex ratios are typically male biased. The factors that are currently contributing to the maintenance of extreme sexual size dimorphism in *A. aurantia* are still not fully understood. Recent results indicate that males pursue a foraging strategy that maximizes survival during the juvenile stage, at the cost of slower growth and matuation at a relatively small size, possibly to offset a high adult mortality during mate search (Inkpen and Foellmer, 2010). Females, on the other hand, exhibit a more aggressive foraging strategy, grow faster than males and go through more instars, to reach a large size, probably to maximize fecundity (Inkpen and Foellmer, 2010).

CONCLUSIONS

Consistent with the curvilinear gravity hypothesis, we found that in a species in which all males are smaller than the threshold of 43 mg, larger males climb faster. Running speeds were highly repeatable, even across contexts (angles). The finding that males ran faster at steep angles than on horizontal structures suggests that in species living on tall vegetation, selection for running performance on steep structures has been stronger than for running performance on flat surfaces. Faster speeds of larger animals seem to be attained by (positively) correlated leg traits. This means, however, that we do not understand yet which factors drive the maintenance of current levels of sexual size dimorphism in species with males that fall below the 43 mg threshold of the curvilinear gravity hypothesis, including *A. aurantia* (Foellmer and Fairbairn, 2004, 2005a, 2005b; Foellmer, 2008; Inkpen and Foellmer, 2010). Therefore, more work at the population level, including surveying natural selection in the wild, is urgently needed.

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