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Evidence for Rensch's rule in an orb-web spider with moderate sexual size dimorphism

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ABSTRACT

Background: The sexes are often subject to different selection regimes. In some cases, these generate sexual size dimorphism. Rensch's rule postulates that male body size is more variable than female body size. The rule applies to many but not all animal groups. In spiders, sexual size dimorphism is extreme in cases of female gigantism and male dwarfism. These more widely studied species with extreme reversed sexual size dimorphism do not follow Rensch's rule.

Question: Do orb-web spiders with moderate sexual size dimorphism follow Rensch's rule?

Organism: The bridge spider, *Larinioides sclopetarius*, with moderate sexual size dimorphism and high developmental plasticity. We tested its sex specific variation in size and age at maturity.

Methods: We experimentally varied food supply during spider development. We measured leg length (as a measure for body size), body weight, and development time for 267 male and female spiders from 15 matrilines.

Results: Females reacted to decreasing food levels by prolonging developmental time and adding extra moults. Their body size was unaffected by the food supply. However, males that developed with a poor diet, despite adding extra moults and increasing their age of maturation, matured at smaller sizes than did well-fed males. Thus our results support Rensch's rule because male body size was affected by diet whereas female body size was not.

Keywords: bridge spider, genotype × environment interaction, *Larinioides sclopetarius*, life history, Rensch's rule, sexual size dimorphism.

INTRODUCTION

The body size of an organism is determined by the interaction of selective pressures that can act in opposing or congruent directions: fecundity, sexual, and viability selection (Blanckenhorn, 2005). Selection on viability favours accelerated development and small body sizes (Blanckenhorn, 2000, 2005) because a prolonged growth period results in a higher mortality risk due to predation, parasitism, and starvation before the onset of reproduction. Selection on fecundity acts only on females as the fitness advantage of more and/or larger eggs and offspring favours enhanced growth, since fecundity is often a direct function of body size. In general, males are more often a target of sexual selection than females (Roff, 1992; Stearns, 1992).

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Sexual selection and fecundity selection can oppose selection on viability if costly traits are favoured that increase mating and fertilization success (equilibrium model of Arak, 1988; Schluter *et al.*, 1991; Fairbairn, 1997; Blanckenhorn, 2000, 2005).

Life-history theory proposes a general and strong trade-off between size and age at maturity because everything else being equal, more time is needed to grow larger. The strengths of the various selection pressures and the balance between them naturally differ between the sexes, resulting in differences in size and age at maturity. A species is said to exhibit sexual size dimorphism if one sex is larger than the other (e.g. female spiders, insects, fishes, amphibians, reptiles; male birds, mammals) (Darwin, 1874; Arak, 1988; Le Boeuf and Reiter, 1988; Shine, 1988; Abouheif and Fairbairn, 1997; Fairbairn, 1997). When species are compared within given taxonomic groups, the degree of sexual size dimorphism often increases with body size in cases where males are larger and (less commonly) decreases with body size in cases where females are the larger sex, a pattern first described by Rensch (Rensch, 1959; Abouheif and Fairbairn, 1997).

Fairbairn and Preziosi (1994) developed a quantitative explanation of Rensch's rule by regression of the logarithm of female body size over the logarithm of male body size within a group of taxa or populations. Rensch's rule generally is supported if male body size shows higher variability than female body size (Fairbairn and Preziosi, 1994; Fairbairn, 2005; Blanckenhorn *et al.*, 2007).

Despite general support for the rule in most taxa, several studies (Abouheif and Fairbairn, 1997; Fairbairn, 1997; Foellmer and Moya-Laraño, 2007) did not find allometry patterns consistent with Rensch's rule in spiders. Extreme sexual size dimorphism is seen in species of spiders with giant females and dwarf males (for a review, see Foellmer & Moya-Laraño, 2007), and these have often been used as model organisms in which to examine the proximate causes for the evolution of sexual size dimorphism (Hormiga *et al.*, 2000; Blanckenhorn *et al.*, 2007; Foellmer and Moya-Laraño, 2007; Wilder and Rypstra, 2008; Moya-Laraño *et al.*, 2009). The allometry patterns that are inconsistent with Rensch's rule may result from large variation in female size and an unusually weak correlation of male and female body size (Fairbairn, 1997; Foellmer and Moya-Laraño, 2007; Kuntner and Coddington, 2009). It is not clear, however, whether these are exceptions to the rule or not. Hence, Rensch's rule may only be relevant to spider taxa with weak or even male-biased sexual size dimorphism. While Rensch's rule is formulated for interspecific comparisons, it is based on a general logic that can be tested within species, namely the different selective dynamics between the sexes. However, Fernández-Montraveta and Moya-Laraño (2007) presented the single study on *Lycosa tarantula*, which has moderate female-biased sexual size dimorphism. These authors found the existence of sex-specific canalization and resource allocation to maturation size, which is consistent with the logic behind Rensch's rule. Hence, more studies on spiders with moderate sexual size dimorphism are required to draw conclusions about the reasons behind the limited applicability of the rule to spiders.

The bridge spider *Larinioides sclopetarius* shows only weak sexual size dimorphism; males and females apparently have about the same body size. There are no confounding effects such as sexual cannibalism, monogamous males, or maternal care that may alter selection pressures on sexual size dimorphism. Thus, any life-history strategy of both sexes is likely to be governed by the three major selection pressures (sexual, fecundity, and viability selection) on growth patterns as well as variation in size, age, and weight at maturity. Based on Rensch's rule, female body size is expected to be canalized due to stabilizing selection (Fairbairn, 2005). However, bridge spiders show tremendous plasticity in all their developmental parameters (Kleinteich, 2010). This seems to be at odds with the expectation of a canalized female size at maturity.

The integration of high developmental plasticity with an expected rigidity in life-history traits and weak or no sexual size dimorphism makes bridge spiders an interesting model organism in which to investigate patterns of life-history evolution. We performed feeding experiments to simulate three populations of bridge spiders with different food abundances to test for: (1) the impact of developmental plasticity on three life-history traits, namely size, weight, and age at maturity; (2) sex-related differences in these life-history traits; and (3) sex-specific responses to variable feeding conditions. We predict that Rensch's rule should apply to bridge spiders and we expect to find stabilizing selection on female size. Since the reproductive season is not synchronous, females may be expected to optimize body size rather than developmental time. Therefore, we hypothesize an increasing age at maturity in response to limited food. Low variation in female body size at the cost of longer development would reflect the balance between opposing selection for fecundity and viability. We expect a different solution to the trade-off between size and age at maturity for males. Male bridge spiders compete for access to females and body size predicts the likelihood of winning contests. We expect male body size to be under directional selection and vary more than body size of females. These differences between the sexes predict an interaction between sex and feeding regime. Our results will contribute to the discussion on the selective pressures influencing major life-history traits in arthropods.

METHODS

Study species

The bridge spider *Larinioides sclopetarius* (Clerck, 1757) (Araneae: Araneidae) is a nocturnal orb-web spider that is very abundant near water in urban habitats. Bridge spider colonies comprise individuals of all developmental stages. We collected spiders in HafenCity Hamburg, Germany (53°33′N, 09°59′E) close to the River Elbe. Individuals were collected from their webs on bridges and facades from May to October 2006 and in April 2007.

Rearing conditions

Field-collected bridge spiders (parent generation) were kept individually in plastic cups (females 400 ml, males 200 ml) and watered five times per week. Females were fed twice a week with 3–5 *Calliphora* sp.; males were fed with 5–10 *Drosophila melanogaster*. After maturation, females were transferred to Perspex frames ($36 \times 36 \times 6$ cm) where they built their orb-webs and were mated. After mating, females were returned to plastic cups and treated similarly to pre-mating conditions. Plastic cups inhabited by mated females were checked for the presence of egg sacs on 5 days each week. Egg sacs were weighed and then kept in Perspex boxes ($7 \times 14.5 \times 11.5$ cm) at temperatures of between 20 and 30°C. Egg sacs were watered five times per week until they hatched.

Feeding treatments

Ten days after hatching, 15 full-siblings were randomly separated in three different feeding treatments (high, low, and very low feeding conditions). Hatchlings for feeding experiments were derived from 24 females with 15 maternal lines and are either the F1 generation or the

F2 generation of the parent generation that was collected in the field. Spiderlings with high feeding conditions received *Drosophila melanogaster ad libitum*. In the low and very low feeding treatments, food was limited. All spiders were fed *Drosophila melanogaster* that were raised on a high nutrient diet with Carolina Biological Supply instant *Drosophila* medium Formula 4–24® and crushed dog food (Purina Matzinger Flocken-Vollkost Junior) according to Mayntz and Toft (2001). The first feeding was performed 15 days after hatching: spiders in the low feeding condition were fed three *D. melanogaster*, while spiders in the very low feeding condition received one *D. melanogaster* per week. With increasing age of spiders until maturation, we adjusted the number of fed *D. melanogaster* every 60 days by a factor of 1.5–2.0.

Spiderlings were fed twice a week, watered and checked 5 days per week for the presence of exuviae. Spiders were weighed after each moult (post-moult weight) using an electronic balance (METTLER TOLEDO XS105 DualRange) to an accuracy of 0.01 mg.

Of 360 spiderlings in the experiment, 267 reached adulthood. We recorded the size, weight, and age at maturity (i.e. development time) for each spider. Size at maturity was measured after natural death of the spiders by measuring the tibia–patella length of the first pair of legs to the nearest 0.01 mm using a LEICA MZ 16 stereomicroscope and LEICA IM500 imaging software (Version 4.0). Spiders grow through moults and rigid body parts such as the legs and the prosoma only change during moulting. Therefore, leg length (mostly tibia–patella length) or prosoma width or length are general measurements of body size in spiders. Body mass, however, increases within moults and the highly flexible opisthosoma allows large short-term changes of body mass, for example before or after oviposition. Body mass is therefore not a reliable measurement of size in spiders.

Statistical analysis

We used the REML (restricted maximum likelihood) method for fitting mixed-model analyses of variance (ANOVAs) to estimate the effects of feeding treatment and sex on the size, age, and weight at maturity. Feeding treatment and sex were fixed factors and family was the random factor. All residuals were normally distributed, except for age at maturity (see Table 1). Furthermore, the regression analyses were used to test the effects of development time on size and weight at maturity within treatments and sexes with and without family as random factor. Exclusion of the family effects in all calculated models did not alter the results. To test all differences among the least square means in the model, we

Table 1. Results of ANOVA for the effects of feeding level (treatment) and sex on size, weight, and age at maturity of spiderlings ($n = 267$)

		Size at maturity		Weight at maturity		Age at maturity*	
Variable	d.f.	*F*	*P*	*F*	*P*	*F*	*P*
Treatment	2	10.22	**<0.0001**	61.71	**<0.0001**	1035.92	**<0.0001**
Sex	1	50.00	**<0.0001**	293.08	**<0.0001**	59.38	**<0.0001**
Sex × treatment	2	10.65	**<0.0001**	2.75	0.0656	11.41	**<0.0001**

* Residuals of age at maturity were not normally distributed. Re-analysis with a GLMM and Poisson distribution and a loglink function revealed the same results as the ANOVA. For simplicity, we kept the ANOVA.

used Tukey's HSD test. The statistical analyses were performed using JMP® 7.0.2 (SAS Institute Inc.) for Microsoft® Windows. For models that are fitted with the REML method, JMP® does not calculate *F*-ratios or *P*-values for the random factor family.

RESULTS

Size at maturity

Table 1 shows the relationship between size at maturity, feeding treatments, and sex. Size at maturity in bridge spiders was significantly influenced by feeding treatment and sex. Bridge spiders under increased feeding conditions were larger than those in other treatments, regardless of their sex. Feeding treatment influenced size at maturity differently in the two sexes as reflected by the significant interaction between sex and treatment. Males attained a larger maximum size with increasing feeding level and reached a higher maximum tibia–patella length. Female size at maturity on average was not influenced by the feeding treatments (Fig. 1).

The distribution of size classes (i.e. separation of size ranges in 11 classes) differed between females and males (Fig. 2). Females that were reared in the high treatment occupied the narrowest range of size classes (size at maturity ranged from 4.5 to 6.0 mm). In the low and very low feeding conditions, the number of occupied classes increased; in the very low feeding treatment, the range of size classes was widest (size at maturity ranged from 3.5 to 6.25 mm). In male bridge spiders, the occupation of size classes was shifted towards classes for larger sizes with increasing feeding level. The lowest classes were occupied by individuals that were reared under limited feeding conditions (size at maturity ranged from 4.25 to 6.5 mm); the highest classes were only occupied by spiders that had unlimited food (size at maturity ranged from 5.0 to 7.0 mm).

Weight at maturity

Weight at maturity depended significantly on feeding treatment and sex (Table 1). There was no significant interaction of sex and treatment for weight at maturity. Spiders that were reared under high feeding conditions were about 25% heavier than spiders that grew under low or very low feeding conditions. Regardless of feeding level, females were about 40% heavier than males. Average weight at maturity (±standard error) was 60 mg (±1.42) for females and 38 mg (±0.84) for males.

Age at maturity

The effect of feeding treatment and sex on age at maturity is shown in Table 1. Feeding treatment and sex had a significant effect on age at maturity. Spiders that were reared under high feeding conditions reached maturity at a younger age than spiders under limited food. On average, spiders in the high feeding condition needed 71 days (±2.33) until maturation; under very low feeding conditions, the period from hatching to maturation was extended by a factor of 3.7 (i.e. 269 ± 4.62 days). The effect of food level on age at maturity differed between the sexes (Fig. 1). Males matured on average 26 days earlier than females, although under high feeding conditions, males and females matured at the same age.

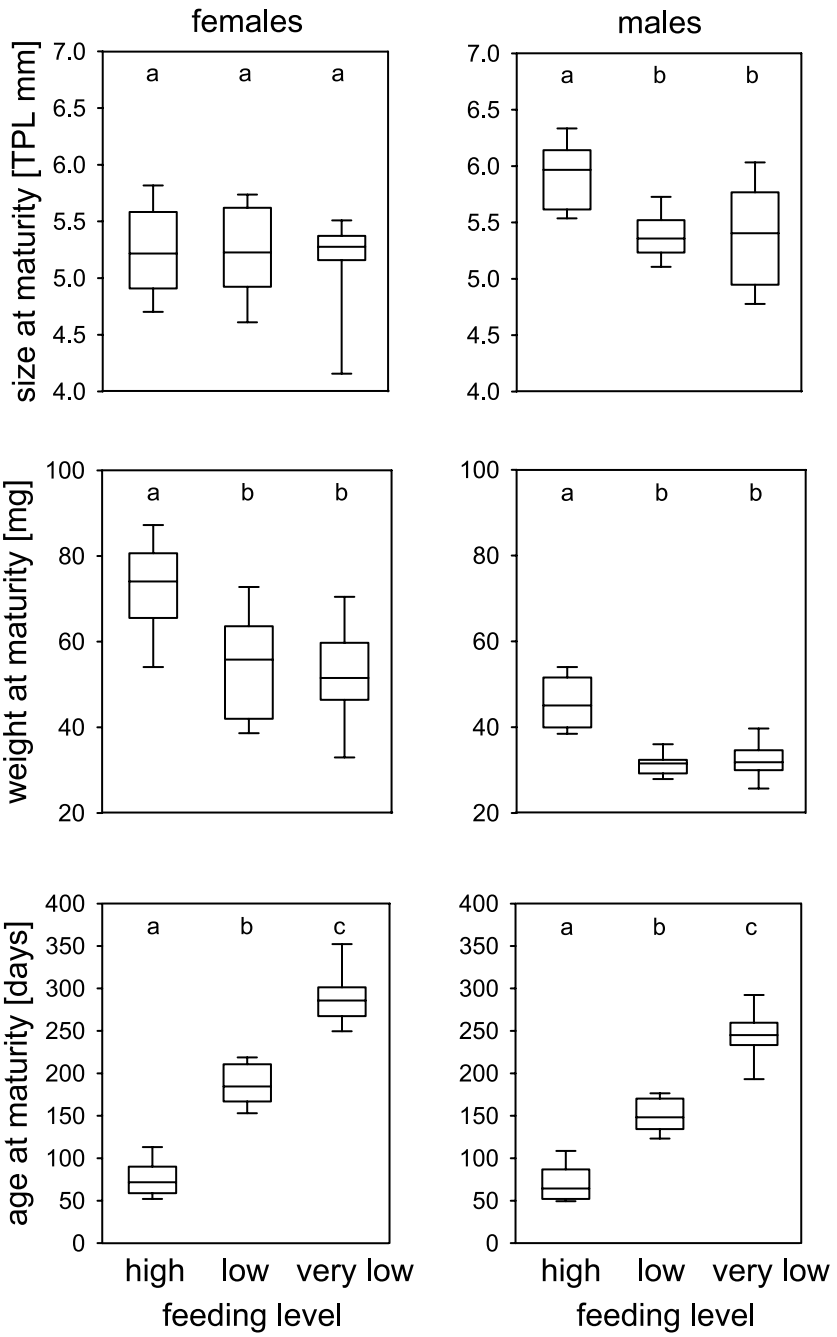


Fig. 1. Box plots for comparison of various life-history traits at different levels of food in female (left) and male (right) bridge spiders. Box plots that are not connected by the same letter are significantly different. Feeding condition influenced all life-history traits examined in this study similarly for the two sexes. Only size at maturity (tibia–patella length = TPL) of females is independent of food availability. All values for siblings within the same treatment and sex were averaged.

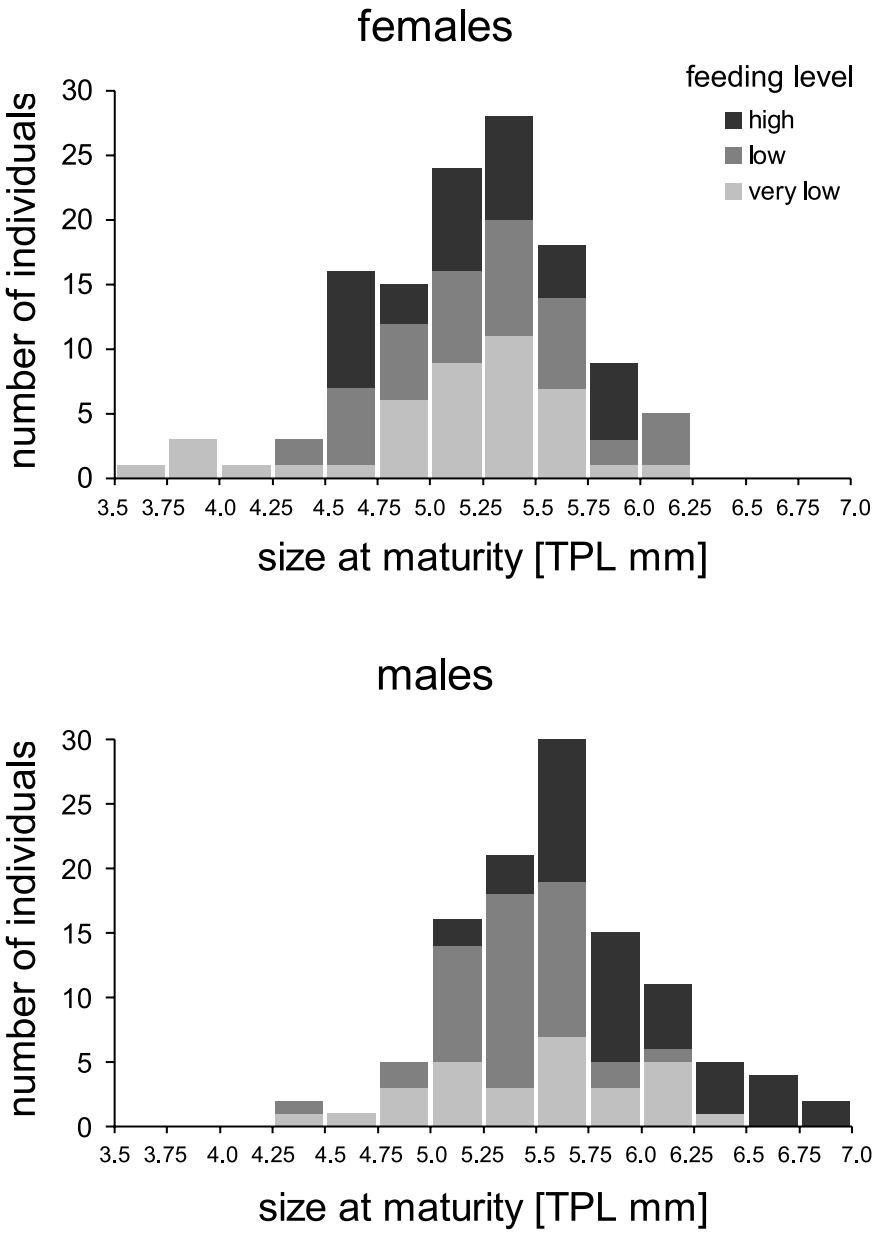


Fig. 2. Distribution of sizes at maturity (tibia–patella length = TPL) in female and male bridge spiders under various feeding conditions (high, low, and very low). Females under very low feeding conditions occupy all size classes observed; under high feeding conditions, females occupy a narrower range of size classes. Males under varying feeding conditions do not differ in the number of size classes occupied. Small size classes are only occupied by poorly fed males; only males in the high feeding condition attain the largest size classes.

The impact of development time on size and weight at maturity

Size at maturity significantly depended on development time, except for females under high and males under low feeding conditions (Fig. 3, Table 2). For females in the low and females and males in the very low feeding condition, size was positively correlated with development time. Males in the high feeding treatment showed a negative correlation (Fig. 3).

Development time had a significant impact on weight at maturity, except in the case of female spiders in the high feeding condition (Fig. 4, Table 2). For females and males in the low and very low feeding conditions, weight at maturity increased with a prolonged development time; males in the high feeding condition showed a decrease in weight at maturity (Fig. 3).

Family × treatment interactions

In each family there were three possible strategies in reaction to feeding treatment: first, the life-history trait (size, weight, or age at maturity) decreased with decreasing food (solid line); second, the life-history trait increased with decreasing food (dashed line); and third, the life-history trait decreased and increased between feeding conditions (dotted line) (Fig. 4).

All three strategies were observed for size at maturity in females. In four families, females increased their size with decreasing food, five families exhibited the inverse trend, and the other families did both. Males from five families decreased their size with decreasing food; one family showed an increase in size with decreasing food. None of the families showed an increase in weight with reduced feeding condition: either the weight decreased or there was no clear trend for increasing food. This was true for females and males.

In all families, the effect of feeding condition on age at maturity was similar: they showed an increase in age at maturity with decreasing food, independent of sex. The number of moults generally increased under limited food in both sexes. Some families showed an alternating response to different feeding conditions.

Table 2. Results of the regression analysis for the effect of age at maturity on size and weight at maturity, and the effect of weight at maturity on size at maturity by feeding level (treatment) and sex of spiderlings ($n = 267$)

				Females		Males	
x	*y*	Feeding level	d.f.	*F*	*P*	*F*	*P*
Age at maturity	Size at maturity	High	1	0.81	0.3752	10.43	**0.0028**
		Low	1	14.38	**0.0005**	0.21	0.6522
		Very low	1	35.83	**<0.0001**	15.31	**0.0008**
Age at maturity	Weight at maturity	High	1	0.46	0.4995	11.68	**0.0020**
		Low	1	61.20	**<0.0001**	39.64	**<0.0001**
		Very low	1	43.04	**<0.0001**	20.49	**<0.0001**

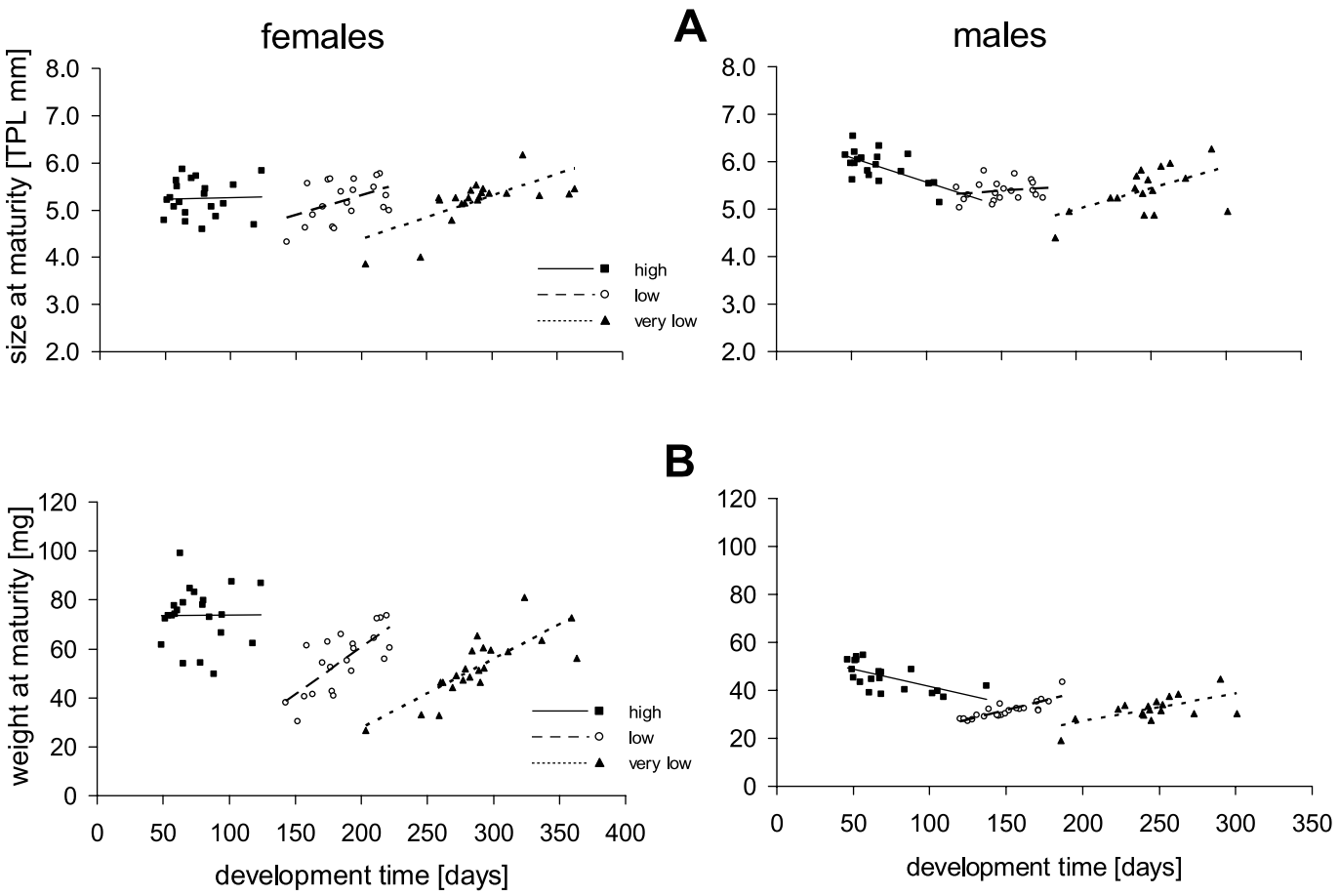
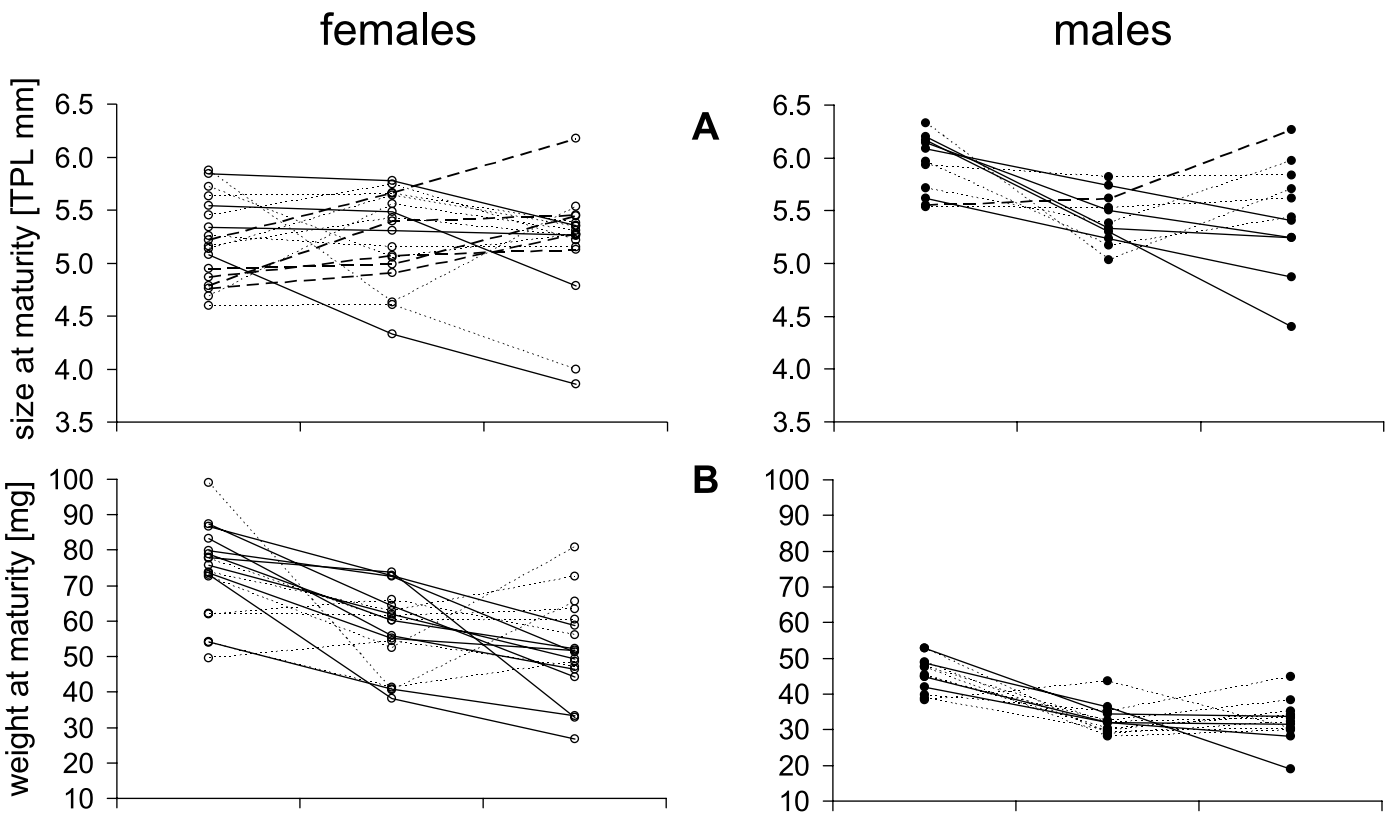


Fig. 3. Regression plots for the impact of development time on size (A) and weight (B) at maturity in female (left) and male (right) bridge spiders. Solid squares and solid line represent the high feeding condition, open circles and dashed line the low feeding condition, and solid triangles and dotted line the very low feeding condition. Development time influences weight and size at maturity depending on feeding treatment and sex. All values for siblings within the same treatment and sex were averaged.


females
males
A
B
size at maturity [TPL mm]
weight at maturity [mg]
6.5
6.0
5.5
5.0
4.5
4.0
3.5
100
90
80
70
60
50
40
30
20
10

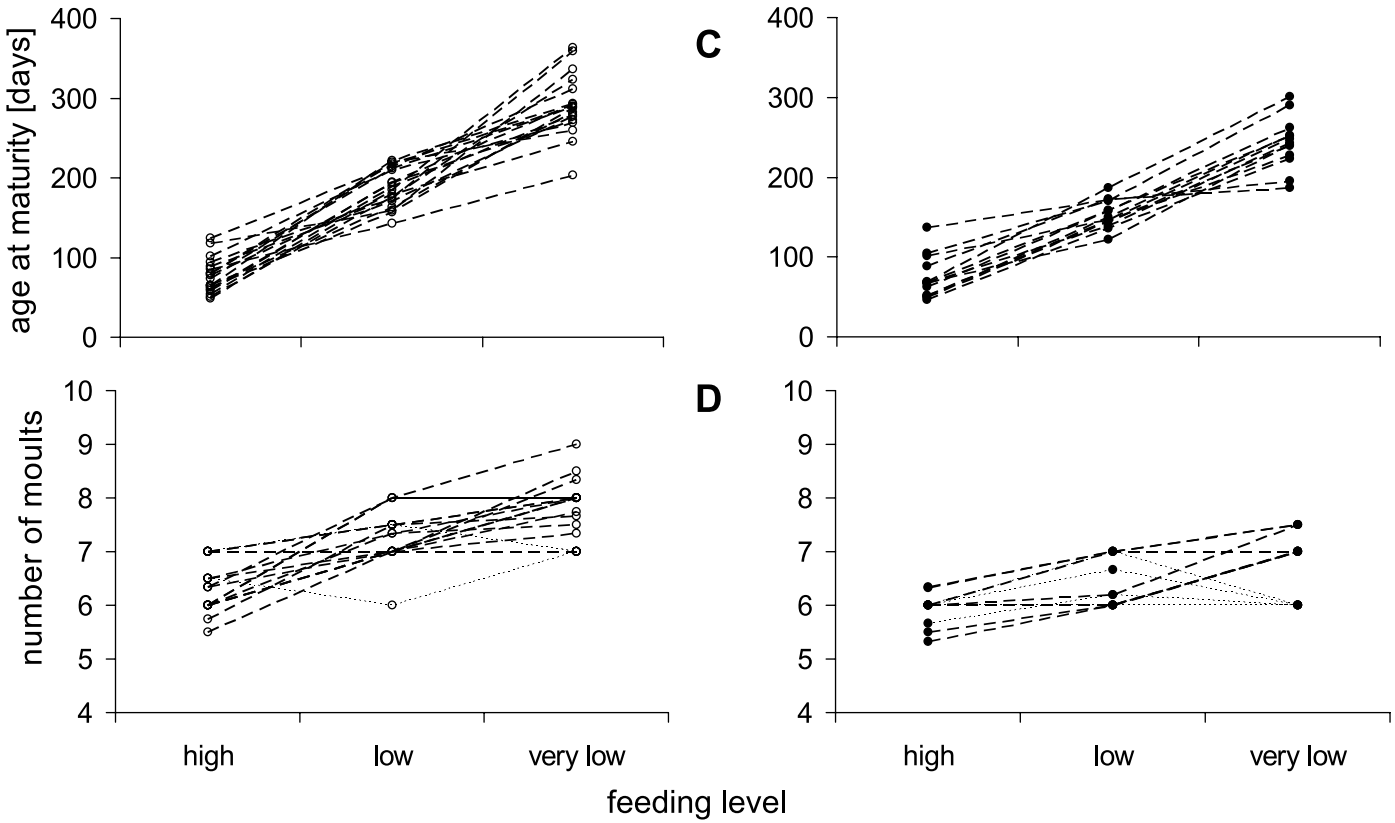


Fig. 4. Genotype × environment interactions for size at maturity (A), weight at maturity (B), age at maturity (C), and the number of moults (D). There are three possible reaction norms for individuals within families (i.e. genotypes) in response to different feeding treatments (i.e. environment): first, the life-history trait (size, weight, or age at maturity) decreases with decreasing food (solid line); second, the life-history trait increases with decreasing food (dashed line); and third, the life-history trait decreases and increases between feeding conditions (dotted line). Only genotypes that were represented by at least one individual within each treatment were considered.

DISCUSSION

Our study confirmed a considerable impact of feeding treatments on major life-history traits such as size, weight, and age at maturity of *Larinioides sclopetarius* in both sexes. Effects were generally similar on the sexes, except for size at maturity in females, which was unaffected by juvenile food availability. In accordance with our predictions, we provide support for the hypothesis that female size is less variable than male size. Trade-offs between development time (age at maturity) and size as well as weight at maturity were apparent in the food-restricted treatments and females showed a stronger relation (steeper slopes, Fig. 3) between size and weight at maturity with development time than males.

Impact of food availability on life-history traits

Bridge spiders that were raised under unlimited food availability grew larger and heavier and reached maturity at a younger age than individuals under limited food treatments. Similar results were reported for *Zygiella x-notata* (Araneidae) (Mayntz *et al.*, 2003) and *Pholcus phalangioides* (Pholcidae) (Uhl *et al.*, 2004). However, this pattern is not generally applicable to spiders: in *Lycosa tarantula* (Lycosidae), spiders that were reared with limited food were younger at maturity than individuals in a high feeding treatment (Fernández-Montraveta and Moya-Laraño, 2007). We suggest that there are two different strategies in response to limited prey abundances: optimizing size at the expense of development time (*L. sclopetarius*, *Z. x-notata*, *P. phalangioides*) or optimizing development time at the expense of size (*L. tarantula*). Thus, there might be differences in the relative selection strength for body size measured as leg length and timing of maturation that may be related to seasonality. If seasonality influences developmental strategies, we would expect that selection constrains development time at the expense of size in spiders with a short reproductive seasonal time frame. Indeed, *Z. x-notata*, *P. phalangioides*, and *L. sclopetarius* are spider species that occur in urban habitats (Uhl, 1998; Mayntz *et al.*, 2003) in which seasonality and timing of reproduction might be less important for reproductive success than size at maturity. Seasonality is much more pronounced for *L. tarantula*, with a mating season restricted to early summer (Moya-Laraño, 2002).

Sex-specific differences in bridge spiders

Weight and size

Females of *L. sclopetarius* are heavier than males, although the weight gain over instars shows no significant difference between males and females (Kleinteich, 2010). The combination of a similar weight gain per instar with a longer development time and more instars for females inevitably results in females becoming the heavier sex at maturity. However, the pattern is different if the rigid body parts such as legs are considered. Male *L. sclopetarius* weigh less but mature with longer leg length than females despite their shorter development time (Kleinteich, 2010). Hence, we find a moderate male-biased sexual size dimorphism in bridge spiders of about 10%.

Males invest more in leg length and shorten developmental time through minimizing the number of instars required at maturation. Females invest in weight gain and in size but grow more slowly. These differences follow the general pattern of females' maximizing fecundity

and males maximizing body size (leg length and prosoma size). Spider species differ in the components and strength of sexual selection but large male body size is generally favoured under contest competition and under female choice. Although male–male and female–male interactions were not the focus of this paper, male–male competition in bridge spiders is repeatedly observed in the field and during mating in the laboratory. It is often observed that several males court a single female (personal observation). Thus, sexual selection, either by contest competition or female choice, might be a mechanism responsible for increased male leg length.

Besides sexual selection, male size is believed to be also a target of natural selection (Blanckenhorn, 2000, 2005; Huber, 2005). The effect of natural selection on the leg length of male spiders was previously demonstrated for *Argyoneta aquatica* (Cybaeidae). An increased leg length was proposed to increase the mobility of males under water (Schütz and Taborsky, 2003). However, underwater locomotion is considerably different from terrestrial locomotion: on land, usually the smaller males are more mobile (Foelix, 1996). Whether natural selection favours elongated leg length in male *L. sclopetarius* remains speculative.

Development time

In *L. sclopetarius*, males were protandrous with a shorter development time than females. Protandry is frequently observed in spiders (LeGrand and Morse, 2000; Maklakov *et al.*, 2004; Uhl *et al.*, 2004). In seasonal species, protandry was hypothesized to be advantageous if: (1) females are more abundant early in the season (Andersson, 1994), (2) mating occurs immediately after female moulting (Robinson and Robinson, 1980; Miyashita and Hayashi, 1996; Foellmer and Fairbairn, 2003), (3) mate-guarding takes place (Fromhage and Schneider, 2005; Kuntner *et al.*, 2009), or (4) first male priority occurs (Drengsgaard and Toft, 1999). However, bridge spiders are non-seasonal (Schmitt and Nioduschewski, 2007), and selective pressures for protandry are less obvious. In bridge spiders, receptive females are present throughout the year, due to overlapping generations. Thus, protandry likewise has no or little relevance for competition for females. We assume a connection between a shorter development time and the reduced weight at maturity of males (40% of female weight). Males are suggested to be lighter (and thus faster in development) because they have to allocate fewer resources for sperm production than females do in ova production (Darwin, 1874; Andersson, 1994).

Blanckenhorn *et al.* (2007) hypothesized that differences in growth rate (i.e. size increase), rather than development time, are generally responsible for sexual size dimorphism. Our results on bridge spiders confirm Blanckenhorn and colleagues' (2007) hypothesis. Furthermore, Blanckenhorn *et al.* (2007) showed that sexual size dimorphism in spiders was more strongly related to differences in development time than in other arthropods. However, in *L. sclopetarius*, the size differences (in terms of leg length) between males and females are independent of differences in development time. In contrast, although males develop faster, they have longer legs; in other words, the shorter development time is overcompensated by a higher size increase per moult. The hyperallometric leg growth relative to females is likely true for prosoma size as well (which was not measured in our study). Females take longer to develop and are 40% heavier than males. The Araneae species considered in the study of Blanckenhorn *et al.* (2007) all had a female-biased sexual size dimorphism. However, in some arthropod species with male-biased sexual size dimorphism, males show a tendency to grow faster than females (Blanckenhorn *et al.*, 2007). This is analogous to our results and could be a more general trend for arthropods with male-biased sexual size dimorphism.

Sex-specific differences in response to food availability

Female size at maturity is independent of food availability but the range of sizes (in terms of leg length) varied with different prey abundances. In the high feeding treatment, more females reached the average (presumably 'optimal') size than under low or very low feeding conditions; the range variation in size at maturity is lower for females with unlimited food. By increasing the development time, females under limited feeding conditions potentially reach the same size on average as females with unlimited food. These results show that high developmental plasticity does not necessarily force life-history traits to be variable.

In contrast to females, male size at maturity did depend on the feeding treatment: a rich diet increased male leg length. Based on the assumption that body size in males and females is under different selective pressures (Blanckenhorn, 2000, 2005), we suggest for *L. sclopetarius* that natural selection acts to stabilize female body size (leg length), while sexual selection acts directional to increase male body size (leg length). The comparatively higher variance of male size over female size in bridge spiders is consistent with Rensch's rule (Rensch, 1950; Fairbairn, 2005). This is interesting, because Rensch's rule was regularly found not to apply to spiders (Foellmer and Moya-Laraño, 2007), except for *Lycosa tarantula*, which shows a moderate female-biased sexual size dimorphism (Fernández-Montraveta and Moya-Laraño, 2007). Our results present the first evidence for the patterns behind Rensch's rule in a spider species with male-biased sexual size dimorphism.

Trade-offs and genotype × environment interactions

The well-established life-history trade-offs between age and size at maturity, and between age and weight at maturity do not apply to female and male *L. sclopetarius* under unlimited feeding conditions. A decrease in age at maturity is predicted to result in decreasing size and weight at maturity (Roff and Fairbairn, 2007). Under unlimited food, however, in female bridge spiders, there is no relationship between development time and either size or weight at maturity; in males, size and weight at maturity decrease with increasing age at maturity (Fig. 3).

The discrepancy between these expectations and our results could be due to the following reasons: (1) a direct genetic impact on life-history traits, and (2) genotype × environment interactions.

In this study, we did not investigate genetic effects: if we separate the data into genetic lineages, the number of replicates is too low for robust statistical analyses on genetic effects. However, a preliminary statistical analysis that included only genetic lineages that were represented by at least three females and three males in each feeding treatment suggested a potential relationship between female, but not male, parentage and size or weight.

Genotype × environment interactions describe variable responses to alternating environmental conditions by different genotypes (Falconer, 1952; Via and Lande, 1985). In natural populations, there seems to be an abundant genetic variation for plastic responses, which makes the evolution of plasticity possible (Pigliucci *et al.*, 2006). There are two opposite patterns of reaction based on two proposed genotypes in *L. sclopetarius* (Fig. 4): (1) decrease of size and weight under limited feeding conditions (genotype I), and (2) increase of size and weight under limited feeding conditions (genotype II). Relative to individuals with genotype I, individuals with genotype II increase their number of moults substantially in favour of larger sizes and greater weights if exposed to decreased prey abundances.

CONCLUSION

Our feeding experiment distinguished influences of prey abundance on major life-history traits (size, weight, and age at maturity) in the bridge spider *L. sclopetarius*. High prey abundance resulted in larger and heavier spiders that reached maturity at a younger age, than spiders under limited food availability. Males and females show similar responses in their life-history traits to variable prey availabilities, except in the case of size, where female spiders are canalized. We argue that the size at maturity of female spiders is under stabilizing selection and showed on average no response to different feeding conditions. In contrast, males showed more variability in their size, a pattern consistent with Rensch's rule. The comparison of males and females in our study exposed a weak male-biased sexual size dimorphism in bridge spiders, although males are the lighter sex with shorter development time. Thus, this makes bridge spiders the first documented case of male-biased sexual size dimorphism in combination with Rensch's rule in spiders. Future analysis of whether Rensch's rule is applicable to spiders should therefore not focus exclusively on species with extreme cases of female-biased sexual size dimorphism, but should also include spiders with weak or male-biased sexual size dimorphism.

In addition to sex-related responses to variable environments, we also found genotype × environment interactions in *L. sclopetarius*. Based on genotype × environment interactions, we propose the presence of different life-history strategies that are optimized for different environments. The high phenotypic plasticity may allow bridge spiders to be an extremely successful species in heterogeneous environments. However, the adaptive significance of genotype × environment interactions remains to be justified by future studies. Furthermore, the mechanism that underlies genotype × environment interactions needs to be resolved. The integration of experimental life-history research with molecular biology to explain different responses to variable environments will potentially reveal new insights in the evolution of life histories.

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