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SEXUAL SIZE DIMORPHISM AND JUVENILE GROWTH RATE IN *LINYPHIA TRIANGULARIS* (LINYPHIIDAE, ARANEAE)

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ABSTRACT. On three separate occasions during the growth season four populations of the sheet web spider *Linyphia triangularis* were sampled, twice as immatures and once as adults. For the immature specimens, five linear size characteristics (length and width of the cephalothorax, length of tibia of the first leg, and length and height of the abdomen) were measured in the laboratory and compared with fresh weight. The best predictor of weight was abdomen length, closely followed by cephalothorax width. Cephalothorax width was used to compare the size of immatures with the adult size at time of maturity because the abdomen shrinks in the non-foraging adult males. Mean cephalothorax width was larger for males than for females in both immature and adult specimens. The difference increased from the earliest immature population samples to the adult samples. The relationship between cephalothorax width and abdomen length was linear and equal between the sexes over all immature samples. This means that there was no difference in the allocation of resources to body parts important to female fecundity (the abdomen) *vs.* body parts important to male fighting ability (the cephalothorax) between males and females. Selection for large male size thus seems to be greater than selection for large female size in this web-building spider, resulting in an overall faster growth rate in males. Males grow >10% larger than females despite the distinct protandry in this species.

Keywords: Sexual dimorphism, *Linyphia triangularis*, growth rate, spider

Web-building spiders have normally a sexual size dimorphism (SSD) with the female as the larger sex (Vollrath & Parker 1992; Head 1995; Foelix 1996; Coddington et al. 1997). This has been attributed to (1) the development of dwarf males, favored by a high selective adult mortality on males that relaxes sexual selection for large size (Vollrath & Parker 1992), and to (2) the development of giant females (Coddington et al. 1997) in response to fecundity selection for large females as suggested already by Darwin (Andersson 1994).

Both these views support the idea that natural selection favors larger size in female spiders because fecundity is positively correlated with female size in spiders, both intraspecifically (Rubenstein 1987; Suter 1990; Beck & Connor 1992; Higgins 1992) and interspecifically (Eberhard 1979; Marshall & Gittleman 1994; Simpson 1995). Females, which experience a constant and relatively low mortality risk throughout their lives, should grow large to maximize fecundity and reproductive success (Marshall & Gittleman 1994; Head 1995).

Males of web-building spiders run a similar mortality risk as females during juvenile stages, but after maturation they leave their protective web and move around in the vegetation searching for females. This behavior is probably associated with a high risk of mortality (Vollrath 1980), as moving around makes the male more vulnerable to predators and reduces energy reserves. Small size could give an advantage in avoiding visual predators (Gunnarsson 1998); and, because metabolism is lower for small spiders, more time can be used for reproductive activities (Reiss 1989; Blanckenhorn et al. 1995).

Linyphiid spiders exhibit all of the characters of other web-builders, except in regard to size dimorphism, where both sexes are of almost equal size (Vollrath & Parker 1992; Head 1995; Prenter et al. 1997). This probably depends on a more intense sexual selection for large male size through male-male competition over mating opportunities. Protandric mating systems seem to be the rule in linyphiid spiders (Toft 1989; Gunnarsson & Johnsson 1990; Watson 1990), probably because the first male has precedence in fertilization success (Austad 1982; Watson 1991). Males that wait too long for their final molt risk losing valuable mating opportunities because females reaching sexual maturity mate with the male present in their web. This means that the male growth period is shorter and, assuming an equal growth rate, adult males are expected to be smaller than adult females at maturity.

One linyphiid spider that lives on spruce branches and has a bi-annual life cycle, *Pityohyphantes phrygianus* (C.L. Koch 1836) has been shown to have a male-biased SSD (Gunnarsson 1988). Gunnarsson suggests that this depends on behavioral differences between sexes during winter when males, despite high risk of predation, forage more actively than females (Gunnarsson 1998).

The species used in this study, *Linyphia triangularis* (Clerck 1757), is univoltine and inhabits low shrubs and bushes in many types of habitats in the southern part of Sweden. *Linyphia triangularis* overwinters as eggs, hatches in late March/early April, and grows to adult stage in about four months. Males molt to maturity about a week before females (Toft 1989; Stumpf 1990), and in southwestern Sweden the first adults are seen at the end of July. The adult males guard subadult females, fighting with other males over access to the female, and mate with the female immediately after maturation (Rovner 1968; Nielsen & Toft 1990), leaving mating plugs in the epigynum that impedes further copulation and/or reduce female receptivity (Stumpf 1990; Stumpf & Linsenmair 1995). These studies say nothing about a size dimorphism in either direction, but emphasize the fierce male fights that occur on the web of virgin females, presumably creating a strong sexual selection for large male size. This study was initiated to test whether sexual selection for large male size could overcome fecundity selection for large female size in a linyphiid spider with a continuous growth period. I used four separate populations to control for local variation in size or size dimorphism between populations.

METHODS

Four populations of *Linyphia triangularis* in southwestern Sweden were sampled to control for possible geographic or habitat variation. The NW site (Göteborg) and SW site (Halmstad) were within 5 km from the Swedish west coast, whereas the NE site (Skövde) and SE site (Värnamo) were inland sites. The SW site was a sparse pine forest, *Pinus sylvestris*, with mostly *Vaccinium myrtillus* as ground cover. The NW site was dominated by heather, *Calluna vulgaris*, with some junipers, *Juniperus communis*, as the only higher vegetation. The SE site is a pine forest, *Pinus sylvestris*, with mixed patches of *Vaccinium uliginosum* and *V. myrtillus* as ground cover. The NW site is on the edge of a mire, with scattered small (< 5 m) birches, *Betula* sp., and pines, *Pinus sylvestris*, as the only higher vegetation, and a ground cover of *Calluna vulgaris*, *Erica tetralix* and *Empetrum nigrum*. The shortest distance between two sites was about 100 km (SW-SE) and the longest distance was about 200 km (SW-NE).

The spiders were collected on three separate occasions from each site between 2 June–5 September 1996. The first sampling was planned to occur about four weeks before the expected maturation but, due to bad weather conditions, the sampling was delayed at two locations. The second sampling was done close to the expected maturation date, and the last sampling was made when the reproductive period was over. To ensure that all spiders had put up new webs, sampling was done only after at least 24 hours of relatively still, clear weather. On each occasion, at least 30 specimens were collected by ‘‘hand-to-jar’’ sampling at random co-ordinates in a selected area of about 10,000 m^2 with relative homogeneous vegetation. The spiders were brought to the laboratory and placed in darkness at 4 °C overnight before measuring.

On all non-adults I measured the length of the tibia on the first leg, the length (from clypeus to pedicel) and maximum width of the cephalothorax, and the length and height of the abdomen to the nearest 0.02 mm with an ocular eye piece on a Wild stereo-microscope. The fresh weight of the spiders was measured using a Sartorius electronic balance to the nearest 0.1 mg. To control the sex of each individual, the spiders were placed in 250 ml plastic jars and reared to maturity. Spiders that could not be unambiguously sexed before they died were excluded. In adults, most males had shrunken and severely distorted abdomens so only the cephalothoracic measurements were noted in these specimens. Statistical analyses were performed with StatView v.5.0 (SAS In-

Table 1.—Regression statistics of log^{10} weight against the different log^{10} linear measurements of body size in juvenile stages. Data from all sites are pooled.

Measurement (x)	Least squares regression on weight (y)	r^2
Cephalothorax length	$y = 0.095 + 2.833\ x$	0.861
Cephalothorax width	$y = 0.464 + 3.307\ x$	0.928
Tibia 1 length	$y = 0.080 + 1.963\ x$	0.714
Abdominal length	$y = -0.212 + 2.689\ x$	0.958
Abdominal height	$y = 0.349 + 1.939\ x$	0.738

stitute 1998) and SuperAnova v.1.11 for Macintosh (Abacus Concepts 1989).

RESULTS

I considered weight as the measure best reflecting the general size of the animals. However, the contrasting adult lifestyles of males and females make the use of adult weight difficult to accurately assess the actual size at maturity. In order to establish the linear measurement that provided the best estimate of general size in *L. triangularis*, I made a logarithmic regression of five linear measurements against the weight of immature spiders. The adults were not used for this test as the adult male specimens were more-or-less starved and had severely shrunken abdomens. The correlation was high for all the measures in juveniles (Table 1), but the best predictor of weight in the juvenile specimens was abdomen length, closely followed by cephalothorax width. I chose cephalothorax width as indicator of general size instead of weight or other size measurements including the abdomen because this study focuses on the comparison between SSD in juveniles and adults. The deterioration of the males' abdomen during their non-feeding, mate-searching adult life inhibits the use of weight or abdomen length for this purpose.

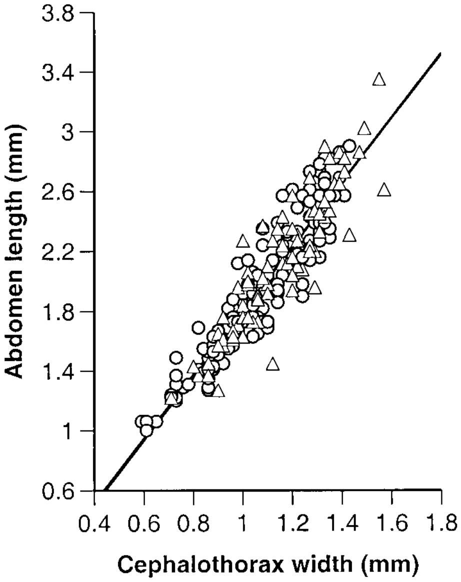

Figure 1.—The relationship between cephalothorax width and abdomen length in immature *Linyphia triangularis*. ○ = females, △ = males. Regressions are: female abdomen length = −0.37 + 2.18 × cephalothorax width, r^2 = 0.84; male abdomen length = −0.36 + 2.16 × cephalothorax width, r^2 = 0.80.

In order to examine if there was any difference between males and females in allocation of resources to different body parts, i.e., if the relative size of the cephalothorax *vs.* the abdomen changed during growth, I performed a one factorial ANCOVA on abdomen length with sex as factor and cephalothorax width as covariate. Males and females had very similar expected abdomen length for any given cephalothorax width and the only significant factor in the analysis is the covariate, cephalothorax width ($F = 934, 3$; $P < 0.0001$). Neither the interaction term, sex∗cephalothorax width ($F = 0, 029$; $P = 0, 86$), nor the singular factor, sex ($F = 0, 007$; $P = 0, 93$), had any effect on abdomen length. The regression lines describing the relationship between maximum cephalothorax width and abdomen length are virtually the same for males and females (Fig. 1). This means that there is no difference between males and females in the relative growth rate of different body parts in juvenile stages.

Males were, on average, larger than females in maximum cephalothorax width in all samples except in the second sample at site SE. In the first sampling at the four sites, males were on average 9–14% larger than females.

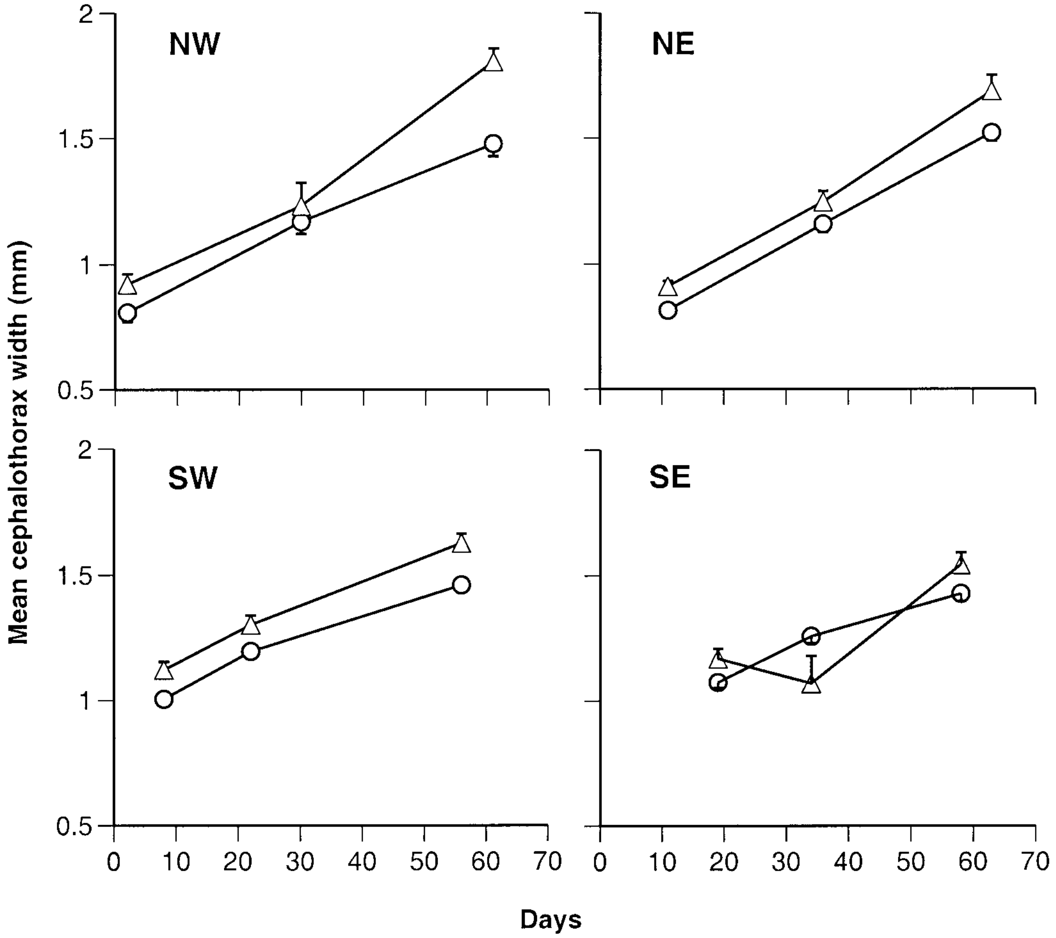

Figure 2.—Development of mean cephalothorax width ± S.E.M. in four populations of *Linyphia triangularis* in SW Sweden. The first sampling yielded only immatures. In the second sampling adults found in the populations were excluded and in the third sampling only adults were found. NW, NE, SW, SE = population labels after relative geographic position. Day 1 = July 1. ○ = females, △ = males.

Mean male cephalothorax width ranged from 0.91 mm in the NE site to 1.17 mm in the SE site, while female mean cephalothorax width ranged from 0.81 mm in the NW site to 1.07 mm in the SE site (Fig. 2). Male abdomen length was on average 12–17% larger than female abdomen length in the four sites.

In the second sampling, made just before the expected molt to maturity, the mean cephalothorax width of males was on average 5–9% larger than that of females in three sites. In the fourth site (SE), few subadult males were found (*n* = 2); and they were much smaller than the subadult females. Male cephalothorax width at this occasion ranged from 1.07 mm in the SE site to 1.30 mm in the SW site, while female cephalothorax width ranged from 1.16 mm in the NE site to 1.26 mm in the SE site (Fig. 2). The abdomen length varied in a similar way, the males being 7–13% larger than females at three sites, but 28% smaller at the SE site.

The third sampling was made about three weeks after the normal time for maturation. The average cephalothorax width of adults was larger for males than for females in all areas (8–22%). The absolute difference of the average maximum cephalothorax between males and females width was larger in all populations compared to the initial collection. Male adult mean cephalothorax width ranged from 1.54 mm in population SE to 1.81 mm

Table 2.—ANCOVA on cephalothorax width with site and sex as factors and date of sampling as a covariate.

Source	*df*	Sum of squares	Mean square	*F*-value	*P*-value
Site	3	1.142	0.381	20.586	≤0.0001
Sex	1	0.94	0.094	5.060	0.025
Date of sampling	1	12.262	12.262	663	≤0.0001
Site × Sex	3	0.009	0.003	0.154	0.93
Site × Date	3	0.504	0.168	9.085	≤0.0001
Sex × Date	1	0.053	0.053	2.865	0.091
Site × Sex × Date	3	0.042	0.014	0.751	0.52
Residual	323	5.971	0.018		

in the NW population, while female adult mean cephalothorax width ranged from 1.43 mm in the SE population to 1.52 mm in the NE population. All population means of female cephalothorax width were lower than those of male cephalothorax width (Fig. 2).

These results were tested for differences in cephalothorax width with a full interaction, two factor ANCOVA with collection day as a covariate, to control for the time differences between dates of collection, and with sex and site as singular factors (Table 2). There was one significant interaction term in the ANCOVA between site and date of collection. The date of collection, as well as the site of origin, also was highly significant as singular factors; but as the interaction term between these two factors was also significant, these factors cannot be considered independently (Sokal & Rohlf 1995). However, the singular factor sex was not involved in any significant interaction terms and had a significant effect on cephalothorax width ($P = 0.0252$). That shows that males on average have a larger cephalothorax width than females across all sites and times examined.

DISCUSSION

The results in this study show that sexual size dimorphism in *L. triangularis* is generally male-biased in all stages and populations surveyed (Fig. 2). Males are larger than females both as juveniles (first sampling, mostly pre-subadult stages) and as adults despite their earlier maturation. The size difference, measured as cephalothorax width, increases from the juvenile stages sampled in early July to the adult stages sampled in August. This suggests that males reach a greater weight and overall size at maturity than females do. If so, males have a higher juvenile growth rate than females, as a solution to two apparently opposing selection pressures on male size in this species. First, males need to mature earlier than females. Female *L. triangularis* mate with the male present immediately after molting to maturity (Toft 1989) and first male to mate with the female sires most of the offspring (Stumpf 1995). This gives males a shorter period of time for growth. Second, because of intense male fights for access to unmated females, males also need to become as large as possible to be able to defend or take over subadult females from other males.

The decrease of the SSD in the second sampling (compared to the first) in some of the populations is probably due to the low numbers of subadult males found in the sample, and that these males were probably smaller than the rest of the cohort. This could depend on (1) reproductive success that is increasing with size but decreasing as time of maturity is delayed and (2) the decision to molt to maturity that will be a compromise between optimal size and age. The result of this would be that larger males mature earlier than small males (Stearns 1992) and that a late sample would then necessarily underestimate the average size of subadults.

Sex-related variation in growth rate was previously described by Wiklund et al. (1991) for the butterfly *Pieris napi* L. 1758 in southern Sweden. This butterfly is partially bivoltine with discreet generations and must diapause as pupae during winter. Males are generally larger than females; but the difference varies depending on the season, as does the mechanism by which the size dimorphism is achieved. Overwintering pupae produce a first generation of adults in the spring. The eggs laid by these adults can either develop directly, producing a second generation of adults the same year, or they can develop slower into diapausing pupae. Wiklund et al. (1991) shows that the growth rate of the time-stressed larvae that develop directly to second generation adults are higher than for those that develop to diapausing pupae. In the directly developing larvae, males achieve a greater size than females through a higher growth rate. In the diapausing individuals males grow larger than females because they have a longer development time. The authors suggest that growth rate must be considered as a life history trait in its own right amenable to evolutionary change and not as a parameter controlled passively by temperature and food availability in the environment.

The male-biased SSD described in this study is unusual among web-building spiders, and has not been described in other members of the family. Earlier works of SSD in spiders have often used only the total body length as measure of general size, and this may in part explain the difference from the pattern found here. Male-biased SSD in cephalothorax size has previously been described in a study on the orbweaver *Metellina segmentata* (Clerck 1757) by Prenter et al. (1995). They suggested that the size dimorphism found in the adults of this species depends on sex-specific allocation of resources. This hypothesis states that, because eggs are more costly to produce than sperm, the females make a larger investment in reproductive tissues (i.e., the abdomen). Males can therefore transfer more of their energy to other body parts that assist them in finding and guarding females (such as longer walking legs and a larger, more powerful cephalothorax). However, the large reproductive costs for females are the eggs and the yolk associated with the eggs. Even though oocytes are to some extent present at sexual maturity, the largest part of the egg, the yolk, is not added to the oocytes until after copulation (Seitz 1971). Therefore, the costs of reproductive structures that develop before maturity are likely to be similar in males and females and should not have an effect on overall size dimorphism at maturity.

Also, if there was a difference in resource allocation prior to maturity between females and males of *L. triangularis*, one would expect a significant interaction term in the ANCOVA on abdomen length and the slope of the correlation between cephalothorax width and abdomen length (Fig. 2) would be steeper for females than for males. Instead, the slopes between size measurements are virtually identical for males and females. The ANCOVA reveals no difference between males and females in growth of different body parts. This suggests that size dimorphism in *L. triangularis* depends on an overall higher growth rate in males, as opposed to a sex-related allocation of resources between body parts.

In *Pityohyphantes phrygianus*, Gunnarsson (1988) showed that subadult males were significantly larger than subadult females in both cephalothorax width and abdomen height both before and after winter. A re-analysis of the data shows that the relationship between the two measurements varies considerably between years and time of season, but the changes are similar for males and females within each sample. This suggests that overall growth rate is higher for males in this species as well and that allocation of resources does not differ between sexes. *Pityohyphantes phrygianus* is biannual and overwinters twice before maturing in the second spring. In spite of the female-biased primary sex ratio (Gunnarsson & Andersson 1992), it seems to be strong selection on large male size. Males grow larger probably because they forage more actively during winter than females. But foraging actively increases risk of predation, and the result is a more female-biased sex ratio after winter (Gunnarsson 1998).

For *L. triangularis*, which is a species with a continuous growth period from egg to adult, such an explanation is not possible. Nevertheless, an increased growth rate during juvenile stages would also benefit the female fecundity, unless there is some cost invoked by a high growth rate. Costs could be developmental, for example, if a too-large mass increment between molts would make molting difficult, resulting in loss of one or more limbs—or death. Costs could also arise from a risk-prone feeding behavior, such as responding indiscriminately to any vibration in the web as if it were prey. This would increase the chance that prey falling onto the web is caught, but it also increases the risk to become prey to a larger predator. All of these costs should result in a differential mortality of males, affecting the sex ratio of the adult population, and possibly also increase the variance of male sizes compared to female size variance. From the data in this study, it is not possible to conclude if there are sexual differences in mortality resulting in a skewed sex ratio in the adult population. Toft (1989) noted that there is an even sex ratio in *L. triangularis* just before maturity and concluded that the operational adult sex ratio therefore is male-biased. This suggests that such costs are negligible.

Another explanation for this male-biased size dimorphism in both juvenile and adult populations could be that males get a headstart in life. This could occur either because male eggs hatch earlier than female eggs or because male eggs are larger than female eggs. Some egg sacs produced by females in the laboratory were allowed to hatch, but there was no apparent differentiation in hatching date within egg sacs. Other egg sacs were opened and the diameter of the eggs within each egg sac was measured. There was no deviation from an expected normal distribution of egg size within these egg sacs (unpubl. data). No study on spiders that I am aware of has reported a differential investment in male and female eggs nor a differential hatching time between eggs. Differential investment might also be very unlikely as the fertilization occurs together with oviposition when the yolk of the egg already has been supplied (Foelix 1996). In conclusion, this work shows that males are larger than females at maturity in *L. triangularis* and that this depends on differences in behavior or physiology that affect the growth rate during juvenile stages. This result suggests that, because of competition for mating opportunities, selection for large size in males is stronger than is selection for large size in females. Since there is no evidence on costs of rapid growth in males, this could mean that there is intraspecific competition that affects males and females asymmetrically. It is also possible that female lifetime reproductive success does not increase monotonically with size, hence the optimal body size for a female is lower than the maximum attainable size.

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