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Research article

Sexual differences in growth strategies of the wolf spider *Hygrolycosa rubrofasciata*

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Abstract. In invertebrates, the size at maturation is considered to be important for adult fitness. In the wolf spider *Hygrolycosa rubrofasciata*, however, it is only females that clearly benefit of larger size through augmented egg production, while male mating success is determined by display activity not related to size. Thus, we can expect conflicting growth patterns for the sexes. Additionally, populations differ greatly in adult size: individuals from dry habitats are smaller than those from wet habitats. To study the sexual differences in reaction norms of growth, we reared spiderlings from seven populations at two food levels under controlled laboratory conditions and compared size at sexual maturity. The shapes of reaction norms for adult size differed between the sexes. In females, the reaction norms were parallel, but individuals from dry habitats tended to grow larger at the given food levels. In males, there was a significant interaction between food level and population without any consistent differences between populations. Maturation time was a plastic character in both sexes with no genetic differences among populations. However, females on low food level matured later and significantly smaller in size than those on high food level. Males also matured later on low food level, but they were nearly of the same size as males that received more food. Female growth patterns reflected the strong selection for large size at maturity. However, the patterns for males were highly variable, which could be explained by the weak overall selection on male size, which means that any environmental factors can affect male growing patterns.

Key words: body mass, maturation, phenotypic plasticity, reaction norms

Introduction

In life history theory, age at maturity is generally determined by a balance between the advantages of short generation time and the advantages of large size (Stearns and Koella, 1986; Higgins and Rankin, 1996). When growth rate is slowed down by reducing the quality of food ectotherm animals tend to mature later and at smaller size (Gebhardt and Stearns, 1988; Berrigan and Charnov, 1994; Ebert, 1994). Males and females may have different strategies for optimising the maturation size and age. In red deer (*Cervus elaphus*), females mature about at age of 4 years irrespective of their size and males tend to reach certain size by delaying their maturation if necessary (Clutton-Brock *et al.*, 1982; Stearns and Koella, 1986). In the painted turtle (*Chrysemys picta*)

sexes also differ from each others in maturation time and size: females grow faster and mature later than males, and are thus larger and older than males at maturity (St Clair *et al*., 1994).

In the drumming wolf spider *Hygrolycosa rubrofasciata*, we expect females and males to have different growth and maturation strategies. In this species, female reproductive success is increased by larger body mass, which conforms to the general finding of positive correlation between female mass and fecundity (originally mentioned by Darwin, 1874, see also Honêk, 1993). Surprisingly, in *H. rubrofasciata* male body mass has not turned out to be connected to their mating success or drumming activity, the latter being the trait affecting their reproductive success by female choice (Kotiaho *et al*., 1996; Mappes *et al*., 1996; Kotiaho *et al*., 1998, 1999a).

Our former studies have revealed some significant phenotypic differences between adjacent populations, e.g. in drumming characters (Rivero *et al*., 2000) and especially in adult body mass. Typically, in moist habitats mature individuals of *H. rubrofasciata* are larger than on dry habitats. We used natural populations of the wolf spider *H. rubrofasciata* to study whether the two sexes differ from each others in growth and whether different populations are genetically differentiated. Dispersal in many spider species is much more limited than for example in many insects with wings. In *H. rubrofasciata*, there are no observations about dispersal through ballooning. Thus, we expect dispersal of this species to be very limited and therefore genetical differences might exist even between closely spaced populations.

In this experiment, we reared juvenile *H. rubrofasciata* from seven populations on two food levels and measured the reaction norms of male and female body mass and maturation time. We tested whether observed differences in adult body mass are caused by genetic variation among populations or if they are plastic responses to different environmental conditions. We particularly focused on the differences in growth between the sexes, since the body size has a different effect on fitness in females and males, and thus may be reflected on reaction norms of growth.

Materials and methods

The wolf spider *H. rubrofasciata* inhabits abandoned fields and bogs with deciduous trees. In this species, juvenile development typically lasts 3 years but may be completed in 2 years depending on growth conditions. Both females and males mature in the autumn of their third year. In bog habitats, which seems to be good growing environment for *H. rubrofasciata*, part of the males can mature in 2 years. In dry meadow habitats, instead, we have never observed 2 year maturation in males. Both sexes overwinter in adult stage, mate

in early May soon after snowmelt, and males die in the end of the mating season. In the highly seasonal environment of Finland, the reproduction of this species is very synchronous. Females carry eggsacs with them until the spiderlings hatch in late June. Females can survive for at least one more year and thus may reproduce several times.

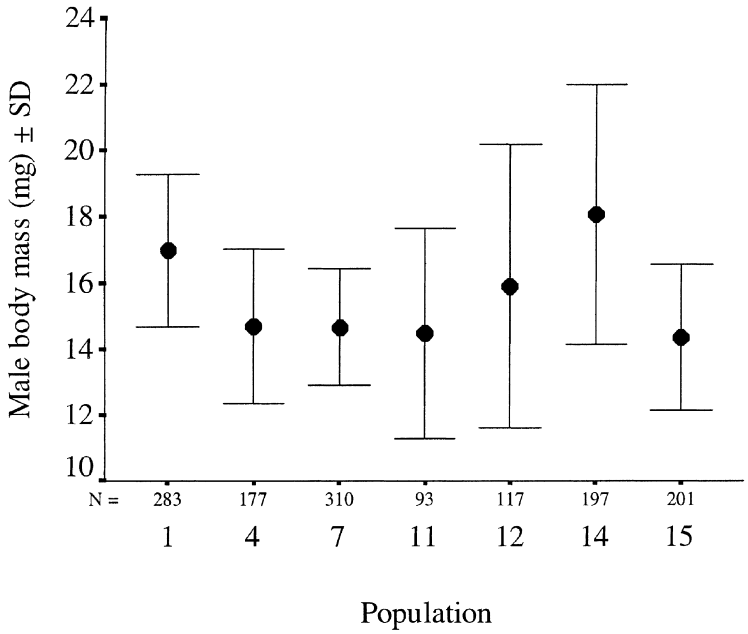
Males court females by drumming, i.e. hitting their abdomen on dry leaves. Females use these drumming signals in mate choice. To confirm the relationship of male body mass to drumming activity, *H. rubrofasciata* males were collected from two populations in Sipoo, southern Finland in two successive years 1995 and 1996. In the laboratory, males were weighed to the nearest 0.1 mg and their drumming activity was recorded. Methods for data collecting and the measurement of drumming activity are described in Rivero *et al.* (2000). The effect of mature female body mass on their fecundity was obtained from mature females collected from six populations from Sipoo soon after snowmelt in spring 1997. In the laboratory, females were weighed to the nearest 0.1 mg, fed *ad lib.* with fruit flies *Drosophila melanogaster* during the whole experiment and mated with males collected from the same populations. When spiderlings had hatched, the number of live offspring from their first successful eggsac was recorded.

To study the growth differences between the sexes and among the populations we used spiderlings from seven populations in Sipoo, southern Finland, located at least 1 km from each others, except populations 14 and 15 which are situated practically next to each other. However, since there was a difference in male body masses between sites 14 and 15 (Fig. 1a), they were included in this experiment as separate populations. All study populations were large in size (estimated population size several thousand individuals) and they represented different habitat types (Table 1).

About hundred spiderlings were collected from each of the seven populations in Sipoo at the beginning of September 1997. All the collected spiderlings had hatched the same summer, i.e. they all were about 2 months old. Field collected juveniles differed in body mass between populations (Kruskal–Wallis non-parametric test: $\chi^2 = 245.4$, $\mathrm{df} = 6$, $p < 0.001$), but these differences are not related to adult body masses, since the correlation between these variables is not positive (Fig. 1b). In laboratory, juvenile spiders were weighed to nearest 0.01 mg and placed individually in labelled plastic containers. Spiderlings were systematically divided into two treatments (low and high food level) assuring that the initial mean masses of groups were similar.

In the lab each spiderling was reared in cylindrical, 60 mm high and 40 mm diameter sized transparent plastic containers. The bottom of the container was cast from a mixture of 90% plaster and 10% active carbon, and in the cap there were small holes to ensure adequate airflow. Inside the container there was a piece of *Sphagnum* sp. moss. The temperature of the rearing room was kept

a)



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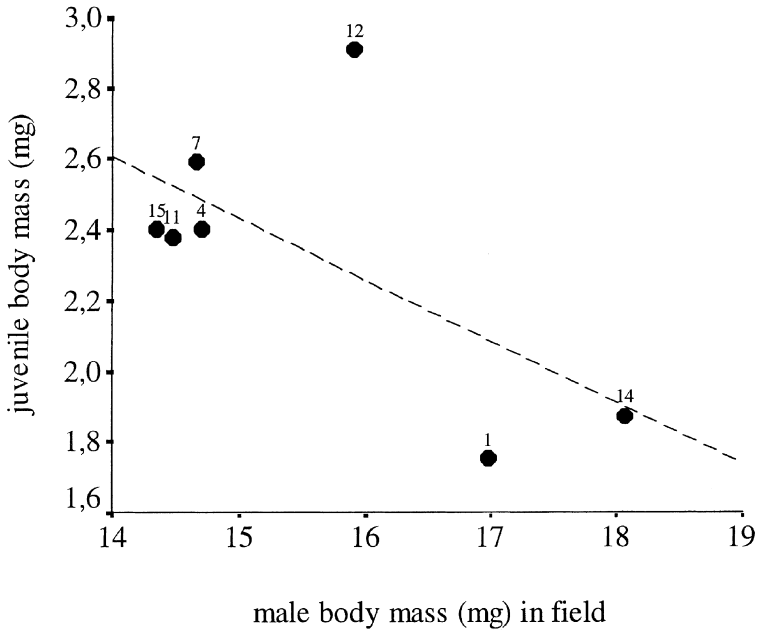


Figure 1. (a) Differences between populations in adult male body masses (collected from study populations in spring 1997). (b) Correlation between adult male body masses and juvenile body masses (Spearman's rho: $R = -0.43$, $p = 0.337$). Each dot represents one population.

Table 1. Description of the seven study populations. Soil samples were collected on 8th July 1997. Soil moisture, pH and thickness of soil litter were determined from 10 soil samples from each study area. Examples of most common plant species of each habitat are also given

Population	Habitat type	Soil moisture (%)	pH (l)	Soil litter thickness (cm)	Typical vegetation
1	Ditched bog	64	4.51	4.5	*Betula pubescens*, *Eriophorum vaginatum*, *Juncus filiformis*, *Sphagnum angustifolium*
4	Dry abandoned field	18	6.15	1.7	*Anthriscus sylvestris*, *Agrostis capillaris*, *Trifolium medium*, *Taraxacum* sp.
7	Moist meadow	54	4.64	3.5	*Deschampsia cespitosa*, *Peucedanum palustre*, *Epilobium angustifolium*, *Juncus filiformis*
11	Dry meadow	29	5.81	2.0	*A. sylvestris*, *A. capillaris*, *T. medium*, *Elymus repens*
12	Moist meadow	44	4.80	4.6	*Peucedanum palustre*, *Lysimachia vulgaris*, *Calamagrostis purpurea*, *Filipendula ulmaria*
14	Moist Meadow	50	4.48	2.8	*E. angustifolium*, *L. vulgaris*, *Rubus idaeus*, *Deschampsia cespitosa*
15	Moist meadow	54	4.58	3.2	*D. cespitosa*, *Viola palustris*, *E. angustifolium*, *P. palustre*

between 20–22 °C and ordinary fluorescent lights together with wide-spectrum light bulbs illuminated the room.

High food level juveniles got three times more food than low food level juveniles. This difference between food levels was proportional rather than absolute, since we do not have any exact data from spiderlings' feeding rates in natural conditions. The feeding regimes were as follows: the first 12 weeks the low food level spiderlings got two fruit flies (*D. melanogaster*)/week and the high level individuals got six fruit flies/week. The next 2 weeks spiderlings were fed with three and nine fruit flies, respectively. After 14 weeks growing season the spiderlings spent a 4 weeks winter-period at temperature of 3 °C. Before the cold period all juveniles independent of the food level got three fruitflies. After overwintering the experiment continued with same conditions as they were before (temperature 20–22 °C and three or nine fruitflies/individual/week). The fruitflies were vitamin-enriched with shaking them in vitamin powder (2:0 calcium, no phosphorus powdered supplement with vitamins, carnivorous reptile formula. T-rex, Ocean Nutrition Corporation, San Diego, CA, USA). For the

fifth week after wintering the fruitflies were replaced for 1 week with springtails (Collembola: *Folsomia fimetaria*). Spiderlings were given springtails instead of fruitflies; six springtails for low and 18 for high group. After this week rearing was continued with fruitflies until the spiderlings maturated.

The mortality of juveniles was relatively high during the experiment, probably due to the narrow diet, despite the vitamin enrichment of fruitflies. Thus, high mortality and reduced growth of spiderlings may be due to that fruitflies *D. melanogaster* are not food of best quality for spiders (Toft and Wise, 1999a, b), and Collembola *F. fimetaria* has appeared to be toxic reducing growth and reproduction of spiders (Marcussen *et al.*, 1999). The adult size of spiderlings was also smaller compared to field collected adults. Still, there was a clear difference between the two food levels.

Spiderlings were raised in laboratory until they reached maturity, i.e. they appeared with fully developed sexual characters. In females this is when the sclerotized plate in epigynum is fully thickened and hard (Foelix, 1996), and in males when they had changed dark in coloration and had fully developed pedipalps. Spiders were then weighed to the nearest 0.1 mg and this body mass measurement was considered as the size at maturation. In *H. rubrofasciata* the body mass of matured individuals has high repeatability (99.4%) and thus it is a good measure of body size (Kotiaho *et al.*, 1996). The age at maturation was counted in days from the beginning of the laboratory rearing to the maturation. The 4 week wintering period was considered as a 1 week growing period to correct for the reduction in growth during this time.

Results

Size and reproductive success

Drumming activity is a highly variable sexual signal by males, and corroborating earlier studies body mass was not correlated with drumming activity (Fig. 2). Neither were there any correlations between these variables in males from this population in another year (Stormossa, 1996: $r = 0.06$, $p = 0.382$, $n = 207$) or in another population (Stenberg, 1996: $r = 0.14$, $p = 0.151$, $n = 104$). Data for comparing female size and fecundity was collected in 1997 from six populations. The correlation coefficient (weighted mean r) was attained by using the Schmidt–Hunter method to combine the six estimates, each from one population (Hedges and Olkin, 1985). In females, the body mass was positively correlated with the number of offspring she is able to produce ($r = 0.57$, $p < 0.001$, $n = 58$) (Fig. 3). Females small in size had greater variability in number of offspring than did larger females which, however, produced invariably more offspring.

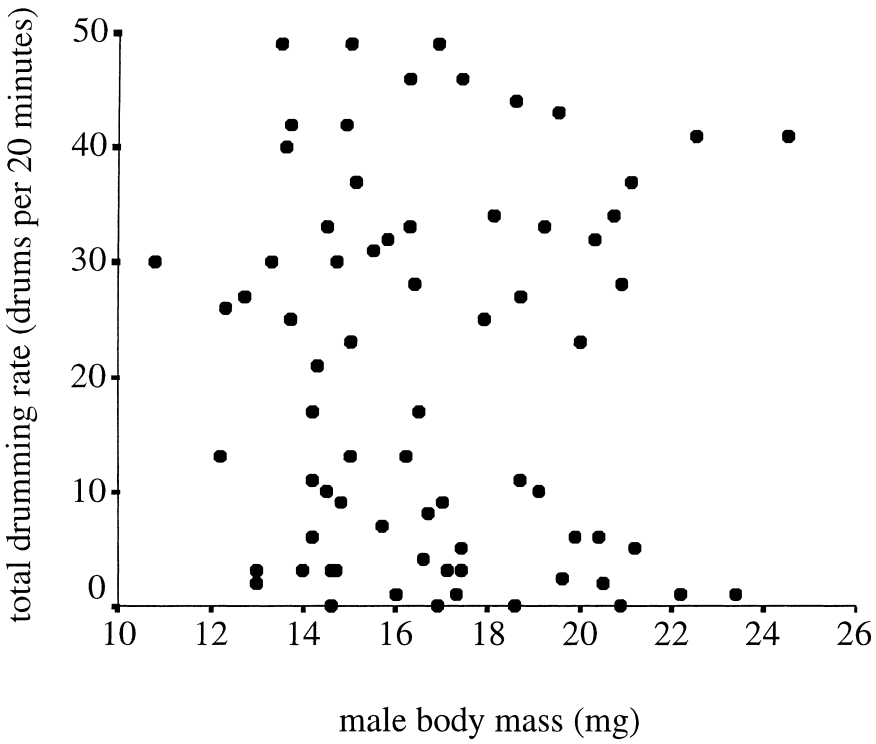


Figure 2. Male drumming rate against body mass in population Stromossa (1 in Table 1) in 1995 ($r = -0.04$, $p = 0.718$, $n = 71$).

General tests for differences in adult body mass

There was no 3-way interaction in adult body mass between population, food level and sex (3-way ANOVA, see Table 2). However, there were significant 2-way interactions between population and food level and between sex and food level, but no 2-way interaction between population and sex. In this model, food levels and sexes differed from each others, but populations did not. Because of the clear difference in adult body mass between the two sexes and the different importance of the body mass to individual fitness in females and males, the data was further analysed separately for females and males.

Females

In females, there was no interaction in adult body mass between population and food level (2-way ANOVA: $F_{6,139} = 0.17$, $p = 0.984$) (Fig. 4a). However, populations differed significantly from each others in adult body mass ($F_{6,139} = 4.22$, $p = 0.001$) and spiders grew larger on high food level

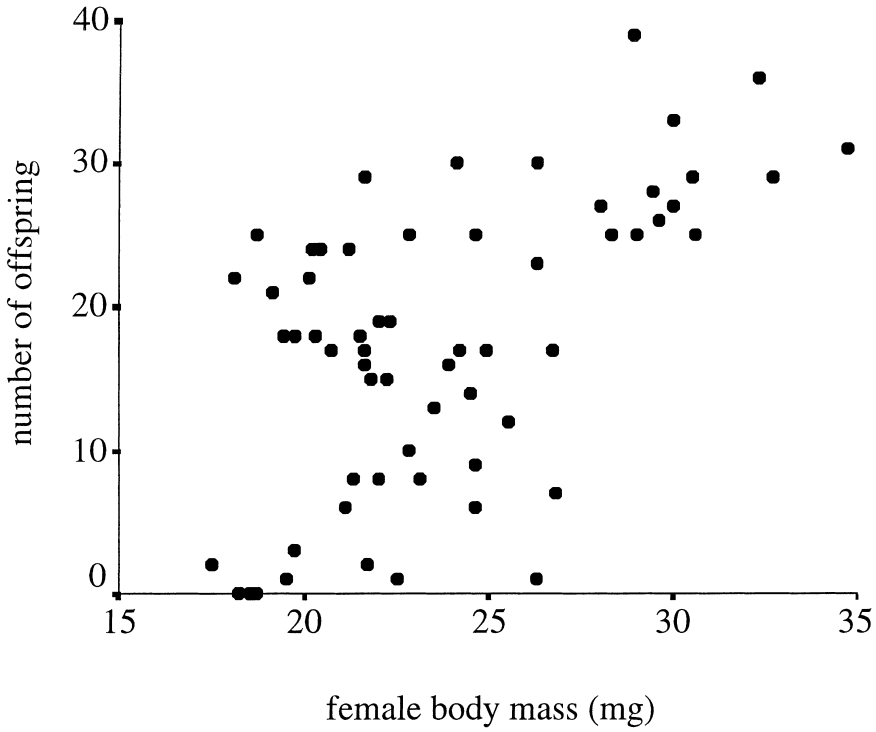


Figure 3. The correlation between female body mass and the number of live offspring.

Table 2. Effects of population, food level and sex on adult body masses in *H. rubrofasciata*

Source	df	Type III MS	*F*	*P*
Population	6	7.30	1.77	0.106
Sex	1	154.74	37.55	< 0.001
Food	1	145.33	35.26	< 0.001
Population × sex	6	6.46	1.57	0.158
Population × food	6	8.85	2.15	0.049
Sex × food	1	23.98	5.82	0.017
Population × sex × food	6	5.12	1.24	0.285
Error	233	4.12	–	–

($F_{1,139} = 43.68$, $p < 0.001$). In this model, the initial body mass of each juvenile was included as covariate since it was statistically significant ($F_{1,139} = 15.61$, $p < 0.001$), and correlated positively with the female adult body mass.

In order to examine whether the environment of each population influences the norms of reaction, we ran a PCA for correlated environmental variables presented in Table 1 (moisture, pH, and litter thickness of the habitat). The

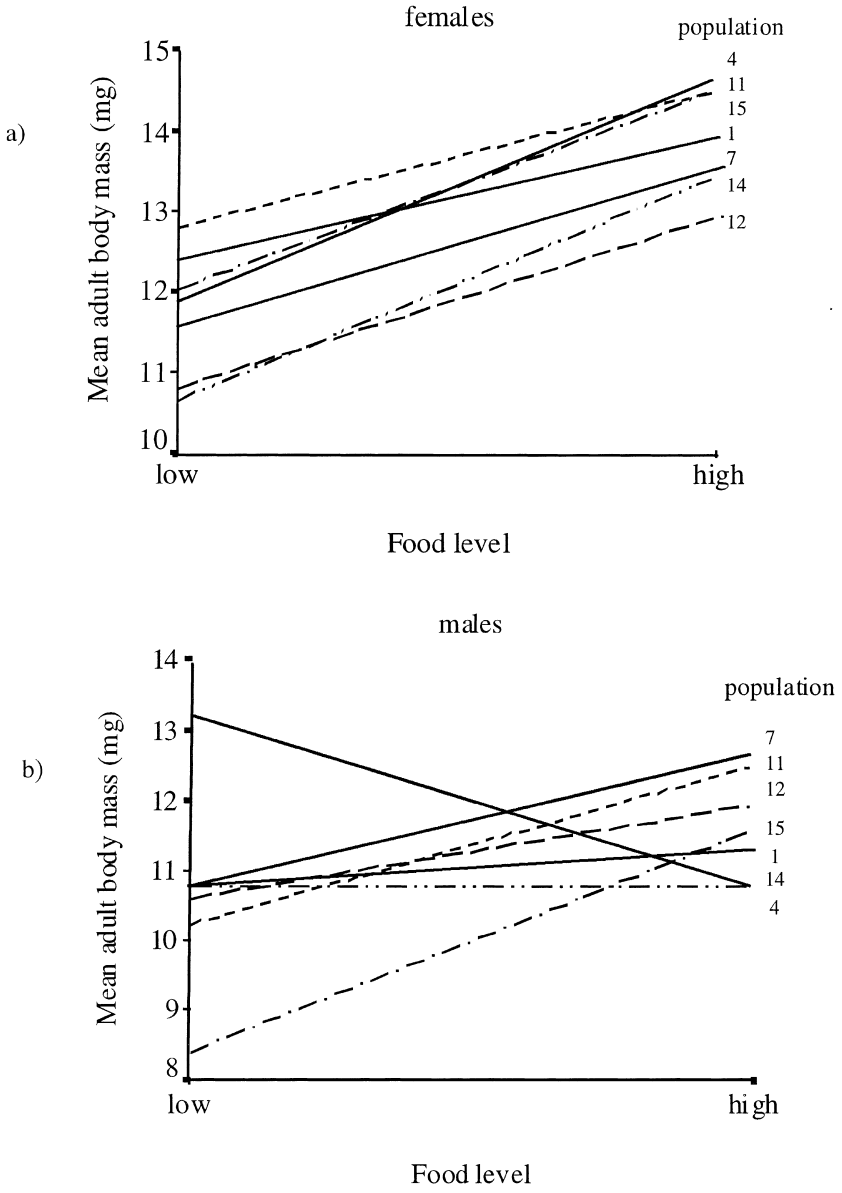


Figure 4. Reaction norms of adult body masses (mg) in two food levels. Each line represents one population. (a) Females and (b) males.

first principal component explained up to 88.9% of the variation and the higher values on this axis indicate habitat which is moist, with low pH and thick soil litter layer, i.e. bogs. The first main component obtained from PCA was used as the environmental factor in following regression analysis. The

mean adult female body mass in each population (in low and high food level) was explained by the amount of food, but not quite significantly by the environmental factor (linear regression: $R^2 = 0.80$, $F_{2,11} = 22.45$, $p < 0.001$; number of flies per week: $\beta = 0.86$, $t = 6.42$, $p < 0.001$; environment: $\beta = -0.26$, $t = -1.91$, $p = 0.083$). There was a tendency of female *H. rubrofasciata* originating from meadow-type (dry, higher pH and less soil litter) to grow better in laboratory conditions, even though females from bog habitats are naturally larger in size as reflected by the negative slope.

Variances in maturation time were highly different between the two food levels, and in general, variation in maturation time was greater in juveniles grown on low food level (Fig. 5a). Therefore, the data were analysed using non-parametric two-way ANOVA (Zar, 1996) for ranked data. Maturation times used were mean population maturation times calculated separately for food levels. The test variable H was calculated as SS_{source}/MS_{total}, and it asymptotically follows the χ^2 distribution with df_{source}. There was no interaction between food level and population in maturation time ($H = 1.70$, $df = 6$, $p > 0.950$). Populations did not differ in maturation time ($H = 2.85$, $df = 6$, $p > 0.750$), but on high food level, spiders matured significantly earlier than on low food level ($H = 75.72$, $df = 1$, $p < 0.001$).

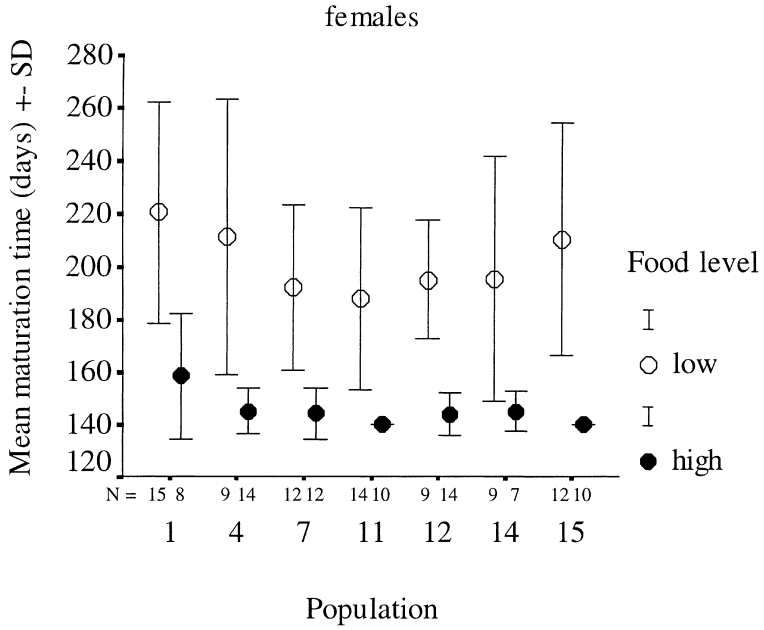
Males

There was a significant interaction between population and food level in determining final body masses of matured male spiders ($F_{6,93} = 2.45$, $p = 0.030$) (Fig. 4b). Spiders grown on high food level grew larger than spiders grown on low food level ($F_{1,93} = 5.05$, $p = 0.027$) but there was no significant main effect of populations ($F_{6,93} = 1.33$, $p = 0.250$). The initial body mass of each juvenile was included as covariate in the first model, but since it was not significant, it was left out of the final model (covariate: $F_{1,92} = 2.05$, $p = 0.155$).

The mean adult body mass of males in each population (in low and high food level) was explained neither by the amount of food, nor by the environmental factor (obtained from PCA in the same way as in females) (linear regression: $R^2 = 0.25$, $F_{2,11} = 1.79$, $p = 0.212$; number of flies per week: $\beta = 0.42$, $t = 1.59$, $p = 0.139$; environment: $\beta = -0.27$, $t = -1.02$, $p = 0.330$).

The maturation time was longer in males grown on a low food level than on males grown on a high food level (Fig. 5b) and also the variances in maturation time were greater in males grown on scarce food regime than in good food conditions. Because the variances were strongly heteroskedastic, the non-parametric two-way ANOVA was applied to ranked data. There was no interaction between populations and food levels in maturation time ($H = 4.89$, $df = 6$, $p > 0.500$). There were no differences among populations ($H = 1.99$,

a)



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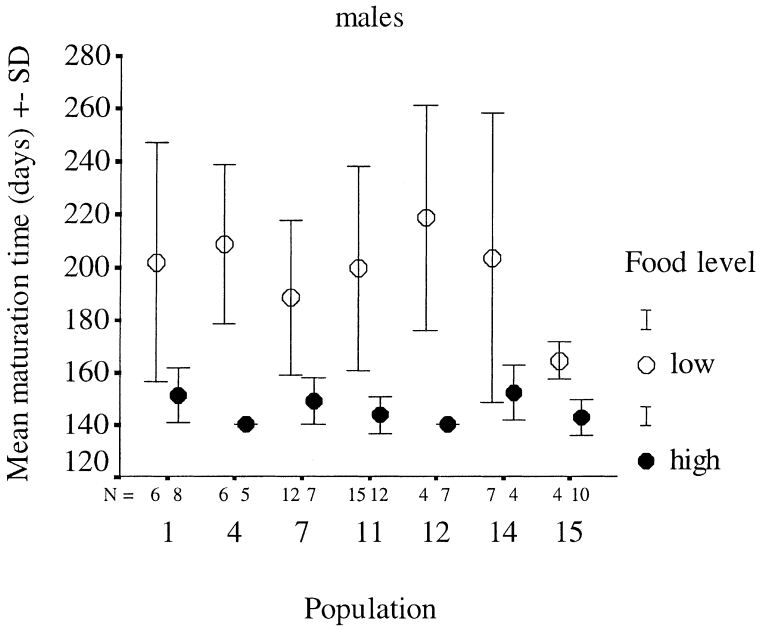

Figure 5. Mean maturation times (+SD) in low food level (white dots) and high food level (solid dots). (a) Females and (b) males.

df = 6, $p > 0.900$), but spiderlings matured earlier on high food level than on the low food level ($H = 50.06$, df = 1, $p < 0.001$).

Maturation time vs. adult body mass

When mean maturation time in each population was plotted against adult body mass the individuals grown on high and low food level formed clearly distinct groups (Fig. 6). Females grown on high food level matured earlier and grew larger in size than did females grown on low food level. Males that received more food also matured earlier than males with less food, but the final body mass was less clearly affected by the food level. Among males, the variation was higher on low food level both in maturation time and in adult body mass than it was on high food level. To study whether this variation was different between the sexes, we calculated the difference in maturation time (maturation time in high food level – maturation time in low food level) and the difference in adult body mass (mean adult body mass in high food level – mean adult body mass in low food level) and tested these between the sexes. Females and males did not differ in maturation time (Paired samples *t*-test: $t = -0.50$, df = 6, $p = 0.637$). There was a tendency for a difference of adult body mass between females and males (Paired samples *t*-test: $t = 2.10$, df = 6, $p = 0.081$), since the mean difference was over two-fold in females (2.27 mg) compared to males (0.96 mg).

Discussion

Both sexes appeared to have genetic differences among populations, but the shapes of reaction norms for adult body mass were different in females and males. Females from all populations grew larger in size on high food level while males had more variation in response to food conditions. Although, maternal effects and the very early growth conditions could have partly affected the final body masses of spiders, it is unlikely that differences between populations in adult body masses are entirely due to differences in non-genetic factors. Juvenile body masses did not correlate positively with field collected adult male body masses (Fig. 1b), and mean population juvenile body masses in the beginning of experiment were uncorrelated with the final mean population body masses either in males (non-parametric Spearman correlations: low food level: $r_s = 0.00$, $n = 7$, $p = 1.000$; high food level: $r_s = 0.45$, $n = 7$, $p = 0.310$) or in females (non-parametric Spearman correlations, low food level: $r_s = -0.22$, $n = 7$, $p = 0.641$; high food level $r_s = -0.31$, $n = 7$, $p = 0.504$). From a previous study (Parri, 1999) the resemblance between offspring and sire in body mass is high ($h^2 = 0.67$), and thus it is feasible to

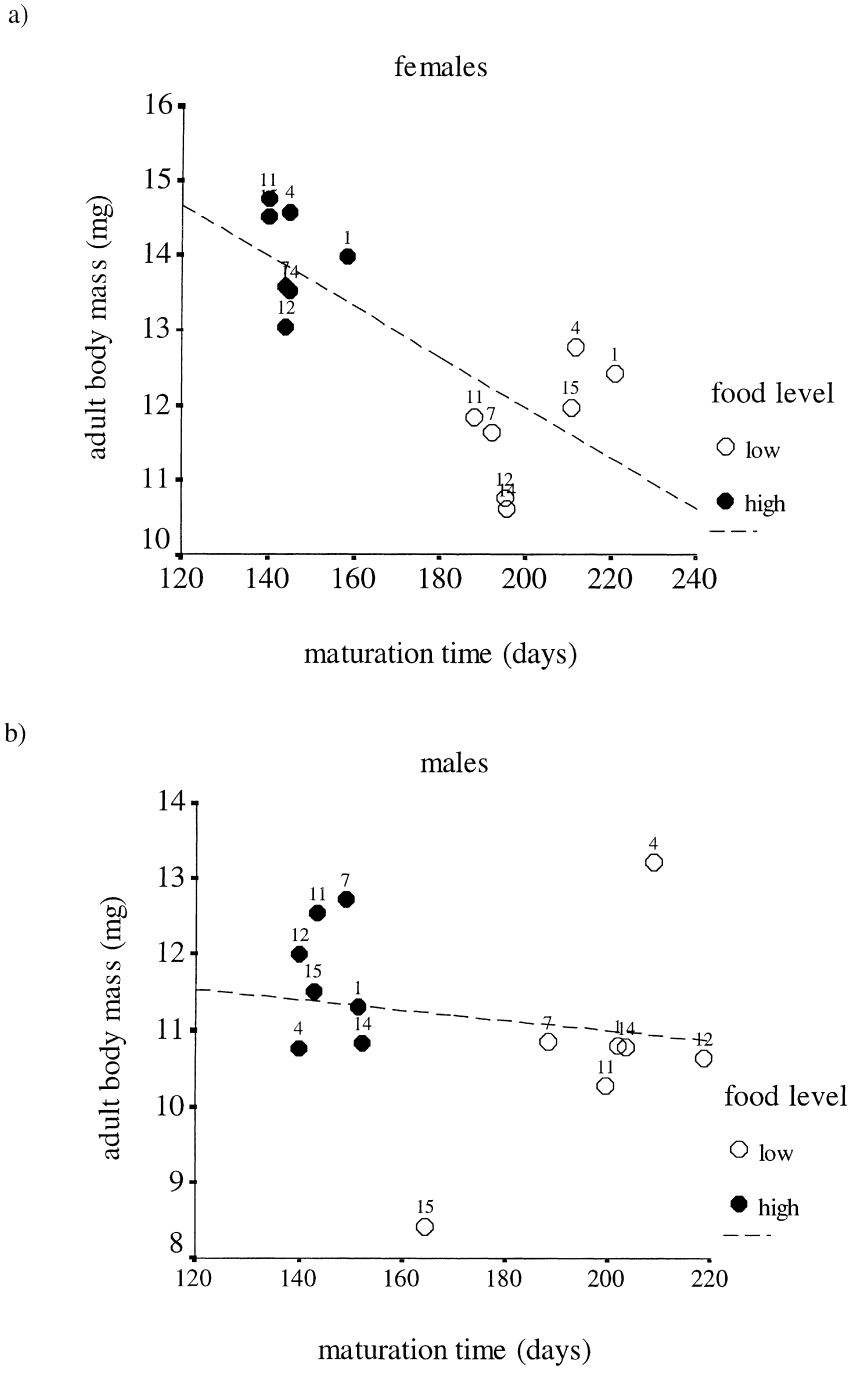

Figure 6. Mean maturation times of each populations on high and low food levels plotted against mean adult masses. (a) Females and (b) males.

conclude that differences in adult body mass among populations have a major genetic component.

The reaction norms for final body mass were parallel in females, but there were significant differences among populations. The lack of interaction between population and food level indicates that females may have a strong selection pressure to grow as large as possible. This conclusion is concordant with observations that the body size is directly correlated with the fecundity of female arthropods (Roff, 1992; Honêk, 1993; Savalli and Fox, 1998), as is the case in *H. rubrofasciata* (Fig. 3).

Compared to females, male spiderlings seem to be less prone to grow as large as possible. Variability in male size may still be high, since maturation in nature can take place only after the second or third summer of growth. Male spiders from some populations matured at a certain size independently of the given amount of food, which may indicate that they attempted to reach certain minimum or optimal size before maturation. This result may well arise from the lack of any strong relationship between size and mating success in males. In such a situation, even factors weakly related to survival or mating success may cause the apparently erratic male growth patterns in different populations. In this and previous studies, no correlation between male sexual activity (drumming rate) and body mass has appeared (Kotiaho *et al.*, 1996; Mappes *et al.*, 1996, Kotiaho *et al.*, 1998, 1999a, see also Fig. 2) and large males have not achieved any more matings than smaller ones (Kotiaho *et al.*, 1996). Furthermore, male body size has not been found to affect their overwintering survival (Kotiaho *et al.*, 1999b). However, larger males survived better than smaller ones in laboratory conditions when they were manipulated to increase their drumming activity (Mappes *et al.*, 1996) and larger males performed slightly better in male–male competition (Kotiaho *et al.*, 1997). In contrast, energetic costs of drumming are huge, particularly in large males (Kotiaho *et al.*, 1998). While size of males may have some fitness effects, these effects are contradictory and weak as compared to the strong positive effects of large size in females.

In *H. rubrofasciata* populations were genetically differentiated within distances of only a few kilometres. These differences between populations are likely to be adaptations to some local environmental conditions, since females from naturally poorer habitats had a tendency to grow better in constant laboratory conditions. Males from populations four and 11 (dry habitats, see Table 1) are naturally small in size (Fig. 1a) and females from these populations were the largest when grown on high food level in laboratory. There may be a shortage of food in these dry habitats and thus females might be forced to use the available food efficiently. Males from these two dry habitats were not the largest ones when grown on high food level. Since the male body mass is not as strongly correlated to any fitness

measures it is not so easy to predict what the optimal growth strategy would be.

The maturation time of both female and male spiders was longer on low food level than on the high food level. On low food level, there were some individuals that matured relatively early, but also some individuals that were unable to do so and thus had to delay their maturation. There were no genotype-environment interactions or differences among populations, suggesting that the maturation time in *H. rubrofasciata* is plastic, and not genetically differentiated trait among populations.

Females maintained on low food level were smaller in size and matured later than females grown on high food level. However, while male spiders grown on low food level also matured later than males on high food level, they were only slightly smaller than male spiders grown on high food level. Stearns and Koella (1986) suggest that most organisms should mature neither at a fixed size nor at a fixed age, but along an age-size trajectory. In general, age at maturity is determined by a balance between the advantages of short generation time and those of large size. Different kind of environmental stress can lead to different outcome: ectotherms tend to mature later at smaller size when their growth rates are lowered by reducing food quality but they tend to mature later at larger size when growth rate is lowered by reduction in temperature (Berrigan and Charnov, 1994). Results from our experiment are consistent with these results in respect to females, but the pattern for males is less clear.

In conclusion, the differences in adult body mass between closely located populations seem to have a genetic component the tendency being that investment in growth is higher in poor environments where natural sizes of spiders are the smallest. Female growth patterns reflected the strong selection for large size at maturity which increases female fecundity. In males the growth patterns were highly variable and males did not have any clear tendency to grow as much as possible. The size of male is only weakly, if at all, correlated with fitness related traits and somewhat erratic variation in growth patterns may be explicable to the weak overall selection on male size allowing any unknown local factors to play a role.

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