

Intriguing compensation by adult female spiders for food limitation experienced as juveniles

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We conducted a field experiment to test for food limitation in immature stages, and its consequences for mature females, in the territorial, cannibalistic spider *Lycosa tarentula* (L.). Randomly selected antepenultimate juveniles were provided supplemental prey until they matured, at which time supplemental feeding ceased. Immature stages of *L. tarentula* are food-limited. Supplemented juvenile spiders decreased foraging activity, disappeared at a lower rate and grew faster than the control spiders, which had been exposed only to ambient prey levels. Fed juvenile females were less hungry at maturity, as judged by an index of body condition, and showed higher mating success as adults, as judged by cohabitation rates with mature males. Foraging theory predicts that in order to compensate for residual effects of food limitation, adult female spiders that had experienced a shortage of prey as juveniles – the controls – would have to exhibit a greater increase in foraging activity upon maturing than the prey-supplemented group. Contrary to expectation, the control females did not increase their foraging activity, but the previously fed females did forage more actively as adults. Furthermore, the difference in mass gain during the mating period between the two groups was opposite from what the difference in change in foraging activity would predict. Control females, the spiders that had not changed their foraging activity, gained mass more rapidly than the previously fed females, with the result that the two groups were similar in mass by the end of the mating period. We hypothesize that an increased rate of sexual cannibalism may have been one mechanism by which control females compensated for the food limitation that they had experienced as immatures.

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Food shortages often limit growth, survivorship and fecundity (e.g. Boutin 1990, review of terrestrial vertebrates, and Wise 1993, review of spiders). Compensation for food shortages is usually achieved by increasing foraging activity (Stephens and Krebs 1986, Kramer 2001), maturing at a smaller size and/or earlier in the season (Roff 2001a, b), or emigrating to better habitat patches (Dingle and Holyoak 2001).

Spiders exhibit a diversity of compensatory responses to prey shortages, such as decreasing their metabolic

rate (Anderson 1970, 1974), maturing at a smaller size (Uetz 1992), increasing their foraging activity (Ford 1978, Carrel 1980, Olive 1982, Lubin and Henschel 1996, Kreiter and Wise, 2001) or emigrating to better habitat patches (Morse and Fritz 1982, Wagner and Wise 1997). Field experiments documenting food limitation in spiders usually have focused on either immature stages or mature females (reviewed by Wise 1993), but rarely has a single study detailed how food limitation among immature stages affects adult performance.

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One exception is that of Beck and Connor (1992), who demonstrated that although fixed adult size in female crab spiders *Misumenoides formosipes* (Thomisidae) varies with immature foraging rates, female fecundity depends more on foraging success as an adult than on size at maturity.

Food limitation among immature stages of spiders can affect adult female behavior and reproductive success by influencing two traits at maturity: fixed size and body condition. Immatures that experience greater food limitation mature at a smaller size as measured by a fixed dimension such as carapace width. The fixed size attained during the final molt sets a limit on fecundity, since fecundity and size at maturity are positively correlated in spiders (Petersen 1950, Enders 1976, Beck and Connor, 1992, Wise and Wagner 1992, Marshall and Gittleman 1994, Simpson, 1995, Arnqvist and Henriksson 1997). However, variation in size at maturity often explains only a moderate amount of the variation in fecundity (Wise and Wagner 1992, Johnson 2001), which suggests that ecological factors after maturity also play a role. Food-limited juveniles also are likely to reach adulthood with a poorer body condition, i.e. hungrier (Vollrath 1987), although variation in this trait has received less attention. Body condition can be measured by an index such as the quotient between abdomen width and carapace width, or as the residual of the regression of abdomen width on carapace width (Jakob et al. 1996, but see Kotiaho 1999, Marshall et al. 1999, García-Berthou 2001). The spider abdomen is flexible, expanding in size as more prey are ingested. Thus, the index of body condition reflects acquired energy as a proportion of the maximum energy that could be gained by a female of a particular fixed size, and thus it is directly related to future egg production. Energy demands of mature female spiders are likely to be greater than those of immatures because of the energy requirements of egg production, which leads to the prediction that mature females should exhibit a greater foraging activity than juveniles (Kreiter and Wise 1996, 2001). This prediction holds for the fishing spider *Dolomedes triton*, in which females switch to a higher foraging activity upon maturation (Kreiter and Wise 1996). A field experiment revealed that adult female fishing spiders are strongly food-limited: providing supplemental prey doubled fecundity and also caused foraging activity to resemble juvenile levels (Kreiter and Wise 2001).

These effects of prey shortages on spiders lead to the prediction that limitation experienced by juvenile spiders should affect their foraging behavior as adults. Thus, prey shortages during juvenile stages that lower an adult female's body condition should cause her to increase her foraging activity relatively more than adult females that acquired more resources as juveniles and matured with a better body condition.

Greenstone (1978) and Conley (1985) failed to find evidence in field studies that food limitation affects densities of wolf spiders (Araneae: Lycosidae). However, comparison of growth in field and laboratory conditions suggests that lycosids are food-limited in natural populations (Miyashita 1968, Anderson 1974, Breymeyer and Józwick 1975). Field experiments have uncovered direct evidence that food shortages affect foraging behavior, growth, rates of cannibalism and population densities of juvenile wolf spiders of the genus *Schizocosa* (Wagner and Wise 1996, 1997, Chen and Wise 1999).

The Mediterranean tarantula, *Lycosa tarentula* (L.), is a cannibalistic, territorial burrowing wolf spider (Fernández-Montraveta et al. 1991, Moya-Laraño et al. 1996, 2002). Adult females are food-limited (Moya-Laraño et al. 1998, Moya-Laraño 2002) and cannibalize both males and females (Moya-Laraño et al. 2002). Females with better body condition have improved fitness as measured by several parameters (Moya-Laraño 2002).

We conducted a field experiment in a natural, open population of *L. tarentula* to (1) test for food limitation in immature stages, and (2) determine the impact of juvenile food limitation upon adult female performance. We supplemented the prey of juvenile spiders and measured changes in foraging activity, survival, growth rate, and fixed size and body condition at maturity. In order to determine how food limitation during the immature stages affects the foraging performance, rate of mass gain, and mating success of adult females, food supplementation ceased as soon as the spider had matured.

Methods

Study site and species

The study was conducted in the "Parc Natural del Massís de Garraf", a protected area 30 km from Barcelona, Spain. The site is within the typical Mediterranean maquis, an association of low shrubs. This site is characterized by a strong summer drought (Lloret et al. 1999), which may potentially influence prey availability.

Upon maturing in late spring, male *L. tarentula* leave their burrows in search of females (Orta et al. 1993, Moya-Laraño et al. 1996). As in other burrowing wolf spiders (Miller and Miller 1986), males cohabit with females (Moya-Laraño 1999). Mating occurs inside the burrow only during daytime and the length of male-female cohabitation is correlated with female mating success (Moya-Laraño et al., in press). Further information about the natural history of this species (e.g. life cycle, phenology and fecundity) is available elsewhere (Fernández-Montraveta and Ortega 1990, Fernández-

Experimental design

During the antepenultimate and penultimate instars, designated as the juvenile period (JUV), we supplemented the natural prey intake of randomly selected immature *L. tarentula* and monitored, in both supplemental and control groups, foraging activity, survival, growth rate and cohabitation rates of sub-adult females and adult males. Because the sexes are not distinguishable in the field until the penultimate stage (Moya-Laraño 1999), documentation of foraging activity and disappearance rates during the juvenile stages includes both males and females. However, we also compared the foraging activity before and after maturation for the females that survived to adulthood. When a female molted to adulthood and became receptive to males, she entered the mating period (MAT). At this point we stopped food supplementation but continued observations. Thus we tested for food limitation among immature instars, and the effect of food limitation during the immature stages upon adult female performance. We predicted that females that had been food limited during juvenile stages would change to a significantly higher foraging activity upon maturity relative to non-food limited females, i.e. if juveniles were food limited, we expected a period \times treatment interaction to be significant and in the direction of CONTROL females increasing their foraging activity upon maturation relative to FED females. This prediction was based on the observation that adult females of another food-limited species of large non-web building spider forage greater distances than juveniles of the same size (Kreiter and Wise 2001). Adult female *L. tarentula* also appear to have higher energy demands than juveniles. With data from the present study and from data of other research conducted in the same field site during the same season (Moya-Laraño 2002), we estimated that the daily amount of mass gained per unit of body mass necessary for ante-penultimate females to reach the penultimate stage was $(0.009 \pm 0.003 \text{ mg day}^{-1} \text{ g}^{-1}, n = 38)$, which is only 37% of the estimated gain necessary for adult females to lay an egg sac $(0.024 \pm 0.001 \text{ mg day}^{-1} \text{ g}^{-1}, n = 24)$.

Logistics of supplementing prey and handling spiders

From 23 April through 6 May 1996 we measured, marked and released back into their burrows 52 immature individuals, either antepenultimate or penultimate instars. The diet of 26 randomly selected spiders was supplemented 14 May–16 June by offering each spider

one live domestic cricket, *Achaeta domestica*, twice a week (FED treatment). Using forceps, we offered the cricket to each spider as it waited at the burrow mouth, this latter position being a form of sit-and-wait foraging behavior adopted by this species (Moya-Laraño 2002). The other spiders comprised the CONTROL treatment. Spiders in both treatments were disturbed at approximately the same rate, because females that were not artificially fed (CONTROL) were monitored for activity, while the FED females were fed and also monitored for activity (see below). We stopped providing supplemental prey to a spider in the FED treatment as soon as it had matured, i.e. at the end of the JUV period. On average each FED spider consumed 4.8 ± 1.3 (SE) crickets. Adult females in both FED and CONTROL treatments were followed throughout the mating period (MAT) to document survival, foraging behavior, growth, and rate of cohabitation with males.

It was usually necessary to extract *L. tarentula* from its burrow for marking and measuring. Details of these procedures can be found elsewhere (Moya-Laraño et al. 1996). Spiders were marked by applying a very small amount of green enamel paint to the legs; in ten years there has been no evidence that marking affects survival or performance of these spiders (Moya-Laraño 1999). Juvenile spiders were measured and marked again after each molt, including the final molt to sexual maturity.

Response variables

The following response variables were measured:

Foraging activity – Defined as the proportion of visits in which the spider was observed feeding on natural prey. Occasionally it was necessary to extract the spider from the burrow in order to determine if it was feeding. In most instances the spider had the prey in her fangs and it could be seen without extracting the spider from her burrow. If the spider was facing the bottom of the burrow, we extracted the spider and then looked for evidence of fresh prey inside the burrow. In other occasions the spider was feeding on a prey outside the burrow. The most frequent prey items in the diet of *L. tarentula* are small terrestrial isopods and small tenebrionids (Moya-Laraño et al. 2002), which were also the most frequent prey in the present study. Burrows were visited every other night (at least 24 hours after artificial food was provided during the JUV period) from 9 May through 12 July.

Rate of disappearance – A spider was considered to have disappeared if it was not in its burrow on two consecutive census dates.

Growth – Measured by three indices: daily rate of increase in mass, and final mass, for both JUV and MAT periods; and fixed size (carapace width) at the end of the JUV period. The sum of carapace and abdomen widths accurately predicts the mass of *L.*

tarentula (Moya-Laraño 1999; mass = 0.0007 (carapace width + abdomen width)^{2.63}, $R^2 = 0.99$, $n = 190$, $p < 0.001$; based on laboratory measurements of all burrowing instars). The JUV period lasted 48 ± 2 days. On the first census date when no male was observed near the burrow of any of the adult females, we considered that the mating season had ended, and all females were measured in order to estimate mass gain during the MAT period. The MAT period lasted 16 ± 2 days. The average rate of mass gain during a period was calculated as (final mass – initial mass)/elapsed days.

Body condition – Because the spider abdomen is flexible and expands as the spider stores nutrients, a good measure of body condition, i.e. a relative measure of the amount of energy reserves (the inverse of the hunger state), is any measure of abdomen size that is independent of fixed body size (Vollrath 1987, Jakob et al. 1996). For recently matured females, we used abdomen width controlled for fixed size at maturity as an index of body condition (Ward and Lubin 1993, Jakob et al. 1996; see the next section). For comparing the body condition of recently matured spiders with the body condition of the same females at the end of the mating period, we used abdomen width. This straightforward comparison is possible because the rate of mass change during the adult stage will affect only the expansion of the abdomen, but not the carapace width, which is fixed after the final molt to maturity. Body condition is a good indirect measurement of female reproductive success in *L. tarentula* because a higher body condition before laying an egg sac is correlated with a higher probability of survival; a shorter time to egg laying; and a larger egg sac, which tends to have more and heavier offspring (Moya-Laraño 2002). These parameters were not directly measured in the current study because we measured them in the above experiment, which included a significantly larger sample size and demonstrated the relationship between body condition and fitness.

Female cohabitation with males – Because cohabitation starts when females are subadults and lasts for several days into adulthood, we pooled cohabitation data from the JUV and MAT periods. All males that were within 20 cm of a female's burrow were considered to be cohabiting with her (Moya-Laraño et al., in press).

Statistical analyses

Treatment effects on immature spiders were analyzed by one-way ANOVA (*t*-tests), the non-parametric Wilcoxon–Mann–Whitney (W_x) test, or the log-likelihood ratio (*G*) test for comparing percentages. The body condition at maturity of CONTROL and FED females was compared by means of ANCOVA, using carapace width as the controlling variable and abdo-

men width as the dependent variable (García-Berthou 2001).

We utilized profile analysis (Ende 1993) to determine whether feeding treatment influenced how a response variable changed from the immature (JUV) to adult (MAT) periods for females that survived until the end of the experiment. This analysis is analogous to testing for the treatment \times time interaction in a repeated-measures ANOVA. The main advantage of profile analysis is that non-parametric statistics (i.e. Wilcoxon–Mann–Whitney test) can be used when ANOVA assumptions are not met. To test for significance in the rate of change (profile analysis), a new variable was obtained for every response variable under test, consisting of the difference of the value of the response variable between the MAT and the JUV periods for every individual spider (see Ende 1993 for more details).

Statistical tests of the effect of supplementing prey on responses of immatures (JUV period) are one-tailed because a priori hypotheses lead to predicting changes in one direction only. Effects on adult females, which are more complex, are tested with a two-tailed criterion. Data are presented as mean \pm SE.

Results

Food limitation in immature instars (JUV period)

Foraging activity – Providing supplemental prey during the JUV period reduced feeding activity on natural prey by 70% (Fig. 1a; $p(W_x) = 0.002$). None of the observed prey were conspecifics.

Rate of disappearance – The natural rate of disappearance of immature *L. tarentula* was ca 60%; supplementing prey intake halved this rate (Fig. 1b; $p(G_1) = 0.011$).

Date of maturation – Food limitation had no effect on the date of maturation. CONTROL and FED females both required 56 ± 3 days to reach maturation.

Growth – Providing prey to immature spiders increased their growth rate by ca 70% (Fig. 1c; ($p(t_{22}) = 0.009$)). Supplemented females were 25% heavier at maturity than females in the CONTROL group (Fig. 1d; $p(t_{22}) = 0.003$). Carapace width at maturity was marginally greater in the fed group (Fig. 2a; $p(t_{22}) = 0.072$).

Body condition at maturity – Body condition of females at maturity was significantly better in FED than in CONTROL spiders (Fig. 2b; ANCOVA controlling for carapace width, $p(F_{1,21}) = 0.001$).

Thus, prey-supplemented females reached adulthood with more reserves and probably at a slightly larger size, even though they had reduced their foraging activity on natural prey by 70% in response to receiving extra prey. The higher foraging activity of CONTROL spiders did not remove the effects of a relative scarcity of prey.

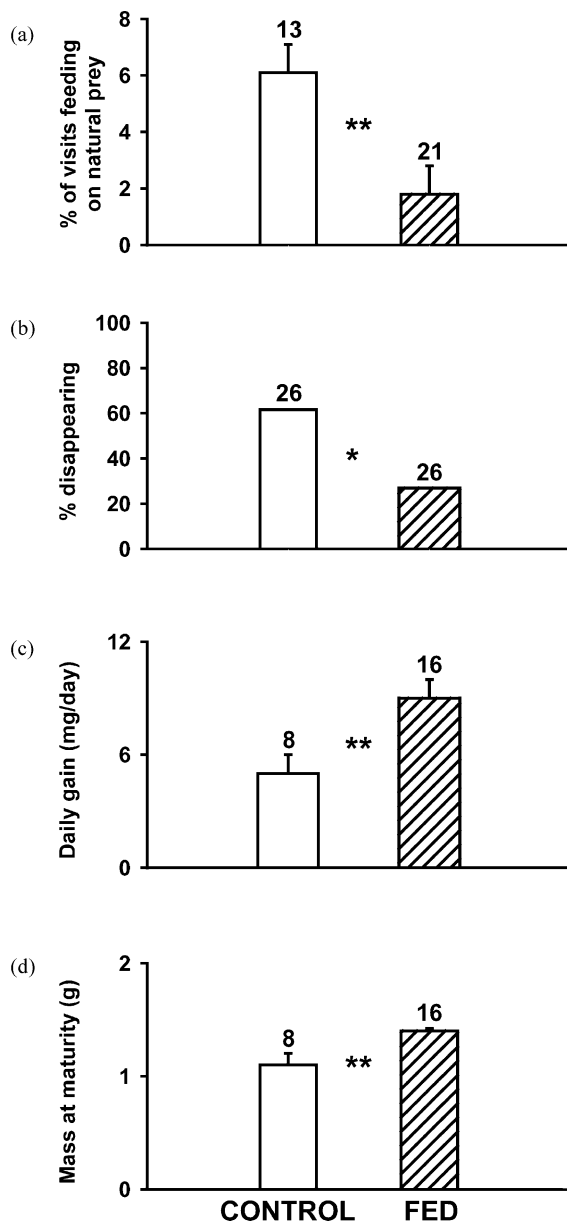


Fig. 1. Effects of food supplementation during the juvenile period (ante-penultimate and penultimate instars) of *Lycosa tarentula* during the field experiment. Because the sexes of antepenultimate instars cannot be distinguished, data on foraging activity and disappearance rate include both males and females. a) Foraging activity. b) Rate of disappearance from the burrow. c) Growth-daily gain in mass of females during the juvenile period. d) Mass at maturity of females. Sample sizes are indicated above each bar. Error bars are SE. * $p < 0.05$; ** $p < 0.01$.

Effect of immature food limitation on adult females during the MAT period

Foraging activity – CONTROL adults, which had experienced the greater food limitation as immatures, did not increase their foraging activity from JUV to MAT

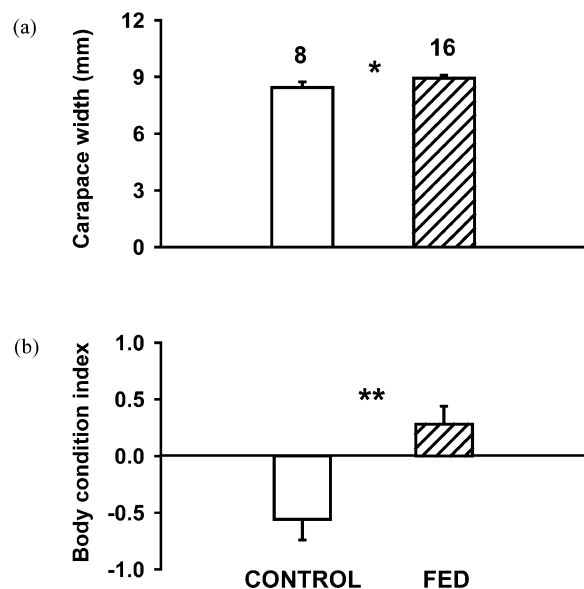


Fig. 2. Effects of juvenile food supplementation on fixed and plastic traits of adult female *L. tarentula* during the field experiment. a) Carapace width (fixed trait). b) Body condition (plastic trait). The residuals of the regression of abdomen width on carapace are used as an Index of Body Condition for illustrative purposes; the hypothesis was tested by ANCOVA (see text). The effect of food supplementation had a stronger impact upon female body condition than upon female carapace width. Error bars are SE. * $p < 0.1$; ** $p = 0.001$.

more than did FED spiders. In fact, CONTROL females did not switch to a higher foraging activity at all, but FED spiders did so (Fig. 3a; profile analysis, $p(W_x) = 0.037$). Because the error bars for the MAT period overlap substantially (possibly due to fewer visits to the burrows during this period), activity during the MAT period does not differ significantly between CONTROL and FED treatments. However, this similarity does not invalidate the profile analysis, which compares the rates of change, with the standard errors being a combination of the JUV and MAT standard errors. In fact, the standard errors of the difference do not overlap (results not shown).

Growth – During the MAT period, the daily mass gain of CONTROL females was $3 \times$ that of FED females, a complete reversal of the difference between treatments in growth during the JUV period (Fig. 3b; profile analysis, $p(t_{22}) = 0.001$). The increased feeding rate of CONTROL females during the MAT period completely compensated for the effects of food limitation that they experienced as immatures, because CONTROL and FED mass and body conditions had converged by the end of the mating period (Fig. 3c, d; profile analysis, $p(t_{22}) = 0.012$, $p(t_{22}) = 0.005$; final values, $p(t_{22}) = 0.235$, $p(t_{22}) = 0.978$, for mass and body condition, respectively).

Cohabitation with males – Supplemented females had a higher rate of cohabitation with males – all 15

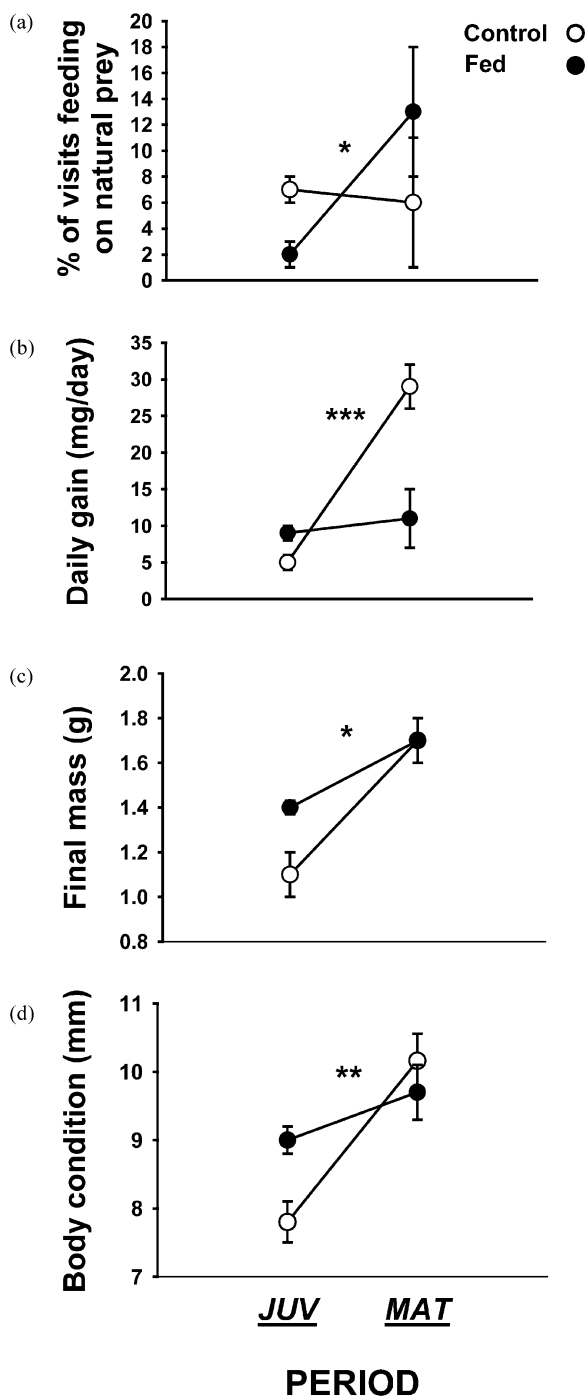


Fig. 3. Change in relationship of control and food-supplemented *L. tarentula* females from the juvenile (JUV) to mating (MAT) periods during the field experiment. a) Foraging activity. b) Daily gain in mass. c) Mass at the end of each period. d) Body condition (abdomen width in mm) at the end of each period. Statistical significance of the difference between CONTROL and FED in rate of change from juvenile to mating periods as revealed by Profile Analysis (details in text). Error bars are SE. * $p < 0.05$; ** $p < 0.005$; *** $p = 0.001$.

females in the FED group were observed with at least one suitor, whereas only 3 of 7 females in the CONTROL treatment were observed cohabiting with a male ($p(G_1) = 0.002$).

Discussion

Immature *L. tarentula* clearly are food-limited. Increasing prey availability above ambient levels decreased their rate of disappearance from the study population and increased the growth rate of immature females. Disappearance from the population probably was the result of mortality, because no marked spider was recaptured. FED spiders likely had a lower mortality rate because they foraged from the burrow less often, as shown by their lower rate of foraging activity on natural prey. Juvenile food limitation affected females entering the adult stage by decreasing their total mass and body condition at maturation.

In the laboratory, non-burrowing juvenile wolf spiders forage more widely when fewer prey are present (Wagner and Wise 1997). Other field experiments have uncovered evidence that immature spiders are food-limited (reviewed by Wise 1993), and a recent field experiment revealed that juveniles of a genus of non-burrowing wolf spider are strongly food-limited (Chen and Wise 1999). However, strong food limitation during the juvenile stage does not necessarily mean that a shortage of prey limits population density from generation to generation, because effects of food limitation may disappear during the adult stage. For example, Beck and Connor (1992) found in a crab spider that variation in foraging success of adult females tended to dampen, although not necessarily compensate for completely, the effects of food limitation shown by juveniles. In general, food limitation of juveniles need not translate into effects on female growth and fecundity. For example, a superabundance of prey for adults would weaken the effects of food limitation among juveniles, particularly if food limitation of the younger instars affects body condition, and not fixed size, at maturity. Even effects on survival might disappear due to decreased rates of density-dependent mortality and reduced competition at lower densities of adults. Rarely, though, have studies examined whether or not changes in foraging behavior, prey abundance, intensity of competition or density-dependent mortality rates of adults compensate for the effects of food limitation of juveniles (Wise 1993).

In our study, CONTROL females that survived to adulthood compensated for the effects of food limitation experienced as juveniles, because during the mating period they dramatically increased their mass gain, eventually achieving the same mass as the previously fed females. Compensation, however, was only partial.

Food-limited females had lower cohabitation success with males, which probably reflected lower mating success (Moya-Laraño et al., in press); and there is direct field experimental evidence that females are still food-limited after the mating period and that they have to attain a mass of ca 2.4 g before laying the egg sac (Moya-Laraño 2002). Furthermore, compensation by surviving females may not have compensated, at the level of population limitation, for lower survival rates of food-limited juveniles. Nevertheless, at the level of individual females the degree of compensation was striking.

Surprisingly, compensation during the MAT period did not result from a higher foraging rate for conventional prey than that displayed by FED females. This result suggests that compensation for juvenile food limitation did not result from a superabundance of prey for adult females or from reduced competition. A more feasible explanation is that the degree of food limitation experienced by CONTROL females during antepenultimate and penultimate stages was sufficiently severe to make sexual cannibalism a preferable foraging strategy as an adult. Although sexual cannibalism by female *L. tarentula* has been shown in the field (Moya-Laraño et al. 2002, Moya-Laraño et al., submitted), sexual cannibalism has not been shown, on the basis of direct evidence, to provide a substantial source of energy for this species, or for any spider, in an open, natural population. Therefore, the unexpected compensation for juvenile food limitation observed in our study is particularly intriguing. A plausible alternative explanation for why FED females switched to a higher foraging rate relative to CONTROL females is that crickets did not provide juvenile females with all the necessary nutrients. There is evidence that food quality affects fitness in wolf spiders (Uetz et al. 1992, Toft and Wise 1999, Mayntz and Toft 2001); therefore, the latter hypothesis will have to be tested with further research. However, the size and diversity of natural prey for *L. tarentula* appear to be small compared to the size and potential quality of conspecifics (Moya-Laraño et al. 2002).

However, four lines of evidence support the hypothesis that courting males were a significant source of alternative prey for female Mediterranean tarantulas that were food-limited as juveniles:

(1) CONTROL females were less likely than FED females to be found cohabiting with a male. This difference is consistent with higher rates of sexual cannibalism among CONTROL females, because hungrier females are more likely to kill and consume approaching males (Liske and Davis 1987, Birkhead et al. 1988, Kynaston et al. 1994, Andrade 1998, Schneider and Elgar 2001). An alternative explanation is that males were choosing larger and/or less hungry females

(Thornhill 1976, Lawrence 1992). There exists evidence that males prefer larger or better-fed females in mantids (Lawrence 1992, Maxwell 1998, 1999) and in a spider (Prenter et al. 1994), but there is counter-evidence in another spider (Riechert and Singer 1995). Sexual cannibalism and male choice are not mutually exclusive hypotheses to explain the pattern of male-female cohabitation that we observed. It is reasonable that males in a sexually cannibalistic species would prefer to court better-fed females, because the chance of surviving the encounter and visiting other females is higher (Lawrence 1992). In fact, additional data on *L. tarentula* suggest that males prefer to mate with females in better condition and, somewhat paradoxically, with smaller females, probably to minimize cannibalistic attacks (Moya-Laraño et al., in press). Thus, both higher rates of sexual cannibalism from CONTROL females and male choice for less cannibalistic females can explain the observed pattern. However, additional evidence supports the hypothesis that hungry females were feeding on males.

(2) CONTROL adult females did not switch to a higher foraging activity compared to spiders in the previously fed group, yet gained mass $3 \times$ as fast, strongly suggesting that CONTROL spiders were capturing high-quality prey that came to them.

(3) Male *L. tarentula* could be such high-quality prey. Males weigh ca 1 g (0.99 ± 0.04 g; $n = 42$) and their carapace width is $> 90\%$ that of females. Using an approximate assimilation efficiency of 30% for wolf spiders (Hagstrum 1970, Humphreys 1977, Workman 1978), one can calculate that the observed gain of mass by each CONTROL spider during the mating season could have been achieved by consuming 1.7 ± 0.24 males, compared to a consumption equivalent of 0.6 ± 0.23 males in the FED group. Thus, cannibalism of a single male by each CONTROL female could account for the differences in mass gain between CONTROL and FED groups.

(4) The hypothesis of sexual cannibalism is further supported by evidence from a population of *L. tarentula* in southern Spain (Almería). First, in the Almería population intra-cohort cannibalism (of which 80% of the prey items are males) contributes up to 50% of the biomass intake by adult females (Moya-Laraño et al. 2002). Secondly, *L. tarentula* females that were observed feeding on a male in natural conditions in Almería had better body-condition indices and survived at a higher rate (Moya-Laraño et al., in press).

Despite the prevalence of cannibalism among generalist arthropod predators (Polis 1981, Elgar and Crespi 1992), there is scant evidence from studies of natural populations that sexual cannibalism enhances female reproductive success (reviewed by Johns and Maxwell 1997). Hurd et al. (1994) present indirect field evidence

suggesting that mated females of the Chinese mantid *Tenodera aridifolia sinensis* will continue to attract males in order to reduce food limitation. A field experiment with the fishing spider *Dolomedes triton* (Spence et al. 1996) uncovered no evidence that sexual cannibalism benefits the female, but possible compensatory effects of cannibalism cannot be ruled out. The investigators released marked adult females onto ponds after they had mated in enclosures. Before being released, some females had been allowed to feed upon their mates and some had not. At the end of the study, spiders from both groups had the same fecundity. If males were still present in the population, females that had not cannibalized their mates in the enclosures (i.e. the more food-limited females) could have cannibalized males in the ponds, and as a consequence compensated for the effects of food limitation in the enclosures. The authors do not indicate whether or not males were present on the pond when the females were released. Andrade (1996) found no evidence that sexual cannibalism benefits females of the red back spider *Latrodectus hasselti*; however, because sexual dimorphism is very pronounced in this species, the absence of a clear reproductive benefit to females of cannibalizing males is probably due to the small size of the latter.

Three laboratory studies have found that females significantly increase a fitness component by feeding on males (mantids – Birkhead et al. 1988, spiders – Elgar and Nash 1988, Johnson 2001). Other laboratory studies have failed to uncover any advantage to females from sexual cannibalism (Arnqvist and Henriksson 1997, Fahey and Elgar 1997, Maxwell 2000). However, if females adjust their aggressive behavior towards males according to food availability under natural conditions, laboratory studies attempting to uncover advantages of sexual cannibalism as a compensating mechanism in nature are difficult to interpret.

Our experiment provides considerable indirect evidence that sexual cannibalism compensated for the effects of food limitation experienced by juveniles. However, if male *L. tarentula* are such high-quality prey, why is there no evidence that females in the FED group also cannibalized males? Some may have, but most apparently did not, probably because of the risk for females of either remaining unmated, or having only some of their eggs fertilized, if they kill males before the sperm necessary to fertilize all of the eggs has been transferred (Elgar 1992). We can hypothesize that mating success was lower in CONTROL females, because we know that the duration of cohabitation is strongly correlated with the probability of mating (Moya-Laraño et al., in press). Thus, although female mass at the end of the mating period were similar in the two groups, eventual reproductive success of the CONTROL females may have been lower because of a possibly lower mating success. Additional research is needed to determine the extent to which compensation may not have been complete.

In summary: our experiment has shown that in a natural population of the Mediterranean tarantula, food limitation of juvenile stages affects their foraging behavior, survival and growth rate as juveniles, female body condition at maturation, and female mating success. Furthermore, the experiment revealed changes in female behavior that were correlated with compensation for the effects of food limitation as measured by mass at the end of the mating period. Although the actual mechanisms of compensation remain unclear and merit additional investigation, sexual cannibalism appears to have played a major role.

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