Senescence and food limitation in a slowly ageing spider

J. MOYA-LARAÑO*†

Unitat de Zoologia, Departament de Biologia Animal, Biologia Vegetal i Ecologia, Universitat Autònoma de Barcelona 08193-Bellaterra, Barcelona, Spain

Summary

1. Evidence for reproductive senescence in invertebrate natural populations is scant probably because most groups are short-lived or because they lack natural markers of age.

2. *Lycosa tarantula* (L.) (the Mediterranean Tarantula) (Araneae, Lycosidae) is a slowly ageing burrowing wolf spider, in which females can reproduce for two consecutive seasons. Females in their first reproductive season (1Y) can easily be distinguished from females in their second reproductive season (2Y) because the lack of pilosity in the latter.

3. The diet of 1Y and 2Y females was supplemented and their reproductive performance was compared with that of control, non-food supplemented females. The predictions were that senescent 2Y females would show a worse reproductive performance than 1Y females, and that they would not be able to improve their performance relative to 1Y after food supplementation.

4. The predictions were met. Older females gained less mass, laid smaller egg sacs, produced fewer spiderlings and, if food supplemented, invested a smaller fraction of their mass in egg sacs. Although 2Y females foraged less actively than younger females, 2Y did not improve their performance relative to 1Y following food supplementation. This pattern of changes provides evidence for reproductive senescence in a natural spider population.

Key-words: Burrowing wolf spider, *Lycosa tarantula*, reproductive performance, reproductive success, territorial predator

Functional Ecology (2002) **16**, 734–741

Introduction

The evolution of senescence, i.e. the decrease of reproductive performance or the increase in the probability of death with advancing age due to concomitant physiological changes (Finch 1990; Rose 1991), cannot be convincingly understood without comprehensive data from natural populations (Finch 1990; Kirkwood & Austad 2000). However, senescence is difficult to document in the wild for organisms that do not naturally have age markers (Rose 1991; Nisbet 2001). Within the latter organisms, only those that can be marked and followed for long periods of time can provide evidence for senescence (e.g. Bérubé, Festa-Bianchet & Jorgenson 1999).

According to Finch (1990) iteroparous organisms usually fit a pattern of gradual senescence with definite lifespans. Whereas there is extensive evidence for gradual senescence for wild vertebrate animals (Finch 1990; Promislow 1991; Mysterud *et al.* 2001; Nisbet 2001; Reznick *et al.* 2001), evidence is still scant for natural populations of invertebrates. This difference is likely to reflect the fact that most invertebrates are semelparous and die immediately after reproduction, fitting the 'rapid senescence and sudden death' category of Finch (1990), which makes the detection of senescence in the wild difficult.

Most female spiders in temperate zones live for only one season as adults (Gertsch 1979; Foelix 1996). Although some spiders (Mygalomorphs and Haplogynae Araneomorphs) can live for 10 or more years (Gertsch 1979; Finch 1990; Foelix 1996), either the fact that females moult every season or that they lack age markers makes keeping track of age in wild individuals difficult. Within the modern Araneomorph spiders (Entelegynae), the burrowing wolf spiders (Lycosidae) are among the few in which females can survive as adults for an entire year and produce a second egg sac during a second season, overlapping their reproduction with first year reproductive females (Humphreys 1976; McQueen 1978; Conley 1985; Framenau *et al.* 1996). Females of the Mediterranean

†Author to whom correspondence should be addressed. E-mail: jmoya2@uky.edu
*Present address: Department of Entomology, S-225 Ag Sci Bldg – North, University of Kentucky, Lexington, Kentucky 40546–0091, USA.

Tarantula *Lycosa tarantula* (L.) follow the latter pattern (Fernández-Montraveta & Ortega 1990; Parellada 1998; Moya-Laraño 1999), and mortality from senescence is likely because almost all 2Y females die during their second winter as adults (Parellada 1998). In this slowly ageing spider, first-year reproductive females can easily be distinguished from second-year females by the old condition of the cuticle due to the lack of associated hairs (Parellada 1998; Moya-Laraño 1999). Therefore, *L. tarantula* is an excellent model to document spider senescence in the wild because females have a natural age marker and females of both ages reproduce at the same time of the year.

Second egg sacs laid by spider females are usually smaller than first egg sacs (Marshall & Gittleman 1994). Although this may be an indication of reproductive senescence, a change in the environmental conditions at the end of the season could also explain the variation in the size of spider egg sacs. Therefore, conclusive proof of senescence can only be obtained in the field with an experiment in which both food availability and age are controlled for. The food of adult females was supplemented in the wild and the prediction was made that, under senescence, second year reproductive females would show a worse reproductive performance than first year reproductive females, and that they would be unable to improve their differences in performance by showing a relatively stronger response to food supplementation.

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. Further information can be found in Moya-Laraño *et al*. (1996), Lloret *et al*. (1999) and Moya-Laraño (1999). Like all wolf spiders, *L. tarantula* mothers carry the egg sac attached to their spinnerets. After hatching, the spiderlings cling to the dorsal surface of their mother's abdomen and remain inside the burrow with her until dispersing. Spiderlings hatch in September and disperse either that autumn or the following spring (Humphreys 1983; Parellada 1998). *Lycosa tarantula* spends its second winter as an immature instar, reaching adulthood in June or July, 21–22 months after hatching, when the mating season starts. Activity of adult females outside the burrow peaks at night (Ortega *et al*. 1992).

EXPERIMENTAL DESIGN

At the end of the mating period of 1996, 74 first-year reproductive females (1Y) and 16 second-year reproductive females (2Y) were measured, marked and released back into their burrows (Moya-Laraño *et al*. 1996; Moya-Laraño 1999). Half of each age group was randomly assigned to a food-supplementation treatment (FED) and half to a control (CONTROL) group, creating a 2×2 factorial design (Food × Age). Because the time from the mating period until egg-laying was expected to be short, food supplementation was intensive. One cricket was offered nightly to each spider in the FED treatment on four consecutive nights from 14 to 17 July, at which time each female was measured again in order to evaluate the differential gain in mass.

LOGISTICS OF MEASURING RESPONSE VARIABLES

The carapace and abdomen width of each spider were measured (Moya-Laraño 1999; Moya-Laraño *et al*. 2002). While carapace width is a fixed trait in adult female araneomorph spiders, their abdomen expands as they acquire nutrition for the eggs (Foelix 1996). Abdomen width is therefore a good index of the hunger status of a female spider (Ward & Lubin 1993; Jakob, Marshall & Uetz 1996; Moya-Laraño *et al*. 2002). Including carapace width and abdomen width, or alternatively carapace width and total mass, in a multivariate statistical analysis, provides a measurement of both fixed size at maturity and relative body condition or hunger status (i.e. controlling for fixed size) (Moya-Laraño *et al*. 2002). The width of the abdomen was measured before and after food supplementation and immediately after the female laid the egg sac.

RESPONSE VARIABLES

Rate of disappearance

A spider was considered to have disappeared from the study population, either because it had died or had abandoned its burrow and emigrated from the study plot, if it was not in its burrow on two consecutive census dates. Burrow relocation within the plot was not considered as a possibility because no spider was ever found within the study area after having disappeared from the burrow. Therefore, mortality and emigration are the most reasonable causes of disappearance.

Rate of mass gain

The rate of mass gain before and after artificial feeding was calculated using estimates of mass based upon the sum of carapace and abdomen width, which reliably predicts the mass of *L. tarantula*: mass = 0·0007 (carapace width + abdomen width)$^{2·63}$; R^2 = 0·99, N = 190, P < 0·001 (Moya-Laraño 1999).

Reproductive performance

Five aspects of reproductive performance for the season were measured. (1) *Time to lay the egg sac* – measured

in days. Because this variable is a 'time-to-event' type of variable, and these normally have a log-normal distribution, and would therefore violate the assumption of normality, it was log-transformed for statistical analysis (Moya-Laraño & Wise 2000). (2) *Egg sac volume* – because the egg sac is an irregular ovoid, the r^3 term in the equation for the volume of a sphere was estimated as $[(0.5)^3 (D1)(D2)(D3)]$, where D1, D2, D3 are the diameters corresponding to the three orthogonal axes that cross the central point of the egg sac. (3) *Number of spiderlings* – when the spiderlings hatched in September, the female was coaxed outside her burrow and the spiderlings removed from her abdomen by gently sucking them off with a pooter. After counting the spiderlings, female and spiderlings were then carefully returned to the burrow with the help of a funnel. (4) *Spiderling mass* – a subsample of 10 spiderlings per female was taken to the laboratory and weighed to the nearest 0·0001 g to obtain an estimate of mean mass invested per spiderling by each female. (5) *Maternal investment* – measured as the difference between the female mass before laying the egg sac and the female mass immediately after the deposition of the egg sac. The mass of the female before laying the egg sac was estimated using the formula:

$$W_{BES} = W_{AFS} + \Delta W_{control}\Delta t, \qquad \text{eqn 1}$$

where W_{AFS} is the mass of the female immediately after food supplementation, $\Delta W_{control}$ is the daily change of mass within the control treatment and Δt is the number of days elapsed until the deposition of the egg sac. Because there was a significant age effect on the rate of mass gain (see Table 2a and Fig. 1a), $\Delta W_{control}$ for 1Y females was different ($+20.9$ mg day^{-1}) from that for 2Y females (-9.5 mg day^{-1}). The estimated maternal investment allowed a test of whether the mass invested in the egg sac relative to the mass available for reproduction differed among groups.

Foraging activity

Every second night all burrows were examined and the surrounding area was searched; this routine continued from 19 July until egg sacs were laid (17 ± 1 SE days) and each spider was visited 9 ± 0.3 SE times. Wolf spiders are easily found at night because their eyes reflect the light of a headlamp (Wallace 1937). Activity of females with egg sacs was not monitored, as *L. tarantula* lays only one egg sac per season (Orta *et al.* 1993). Thus, activities when carrying an egg sac are unlikely to reflect energy demands for reproduction in the immediate future.

Spider foraging activity was categorized by the following behaviours:

1. *Inside* – the spider could not be seen after looking into the burrow, but was extracted when a fine wire was inserted.

2. *Mouth* – the spider was waiting at the burrow's mouth, just inside the lip of the turret, looking outwards.
3. *Top* – the spider was resting on top of the burrow's turret.
4. *Back* – the spider was at the burrow's mouth, but was looking inside the burrow, i.e. with its spinnerets facing the observer.
5. *Outside* – the spider was located on the ground outside the burrow.
6. *Feeding* – the spider was found with a natural prey item between her fangs.

The first five activity categories are mutually exclusive, but a spider may exhibit category 6 (*Feeding*) when showing any of the other behaviours. Category 6 reflects only the frequency of feeding on natural prey, because behavioural observations started 2 days after prey supplementation had finished. For analysis, the ratio of the number of counts of each category for each spider to the number of visits in which the spider was located was used.

Rather than analyse each activity measure separately, principal components analysis (PCA) was used to create a single variable that reflected foraging activity. In constructing this variable the behavioural frequencies (behaviours from 1 to 5) for animals in all treatments were included. The behaviour *Outside* was strongly and positively correlated with PC1 (factor loading = 0·74), and *Mouth* was strongly and negatively correlated with PC1 (factor loading = −0·90). The remaining behavioural categories showed an intermediate correlation with PC1. This clear separation of related categories makes PC1 a good index of foraging activity. A spider with a negative factor score tended to spend relatively more time at the burrow's mouth (sit-and-wait foraging behaviour), whereas a spider with a positive factor score tended to spend relatively more time outside the burrow (active hunting behaviour). In addition, the positive correlation ($r = 0.3731$; $N = 90$; $P < 0.001$) between PC1 scores and the behaviour *Feeding* supports the conclusion that the PC1 scores are good indicators of foraging activity. Spiders that are more often outside the burrow also feed more frequently, indicating that they are going out more frequently in order to increase the chances of finding and catching prey (i.e. active foraging).

STATISTICAL ANALYSES

Because the experimental design was unbalanced and the effect of other continuous variables on the continuous response variables was of interest, results were analysed by means of multiple least squares regression, including the main effects as dummy (binary) variables (Hardy 1993) (i.e. Food: FED = 1, CONTROL = 2; Age: 1Y = 1, 2Y = 2). This is because, for instance, the effects of size and body condition may be uncovered
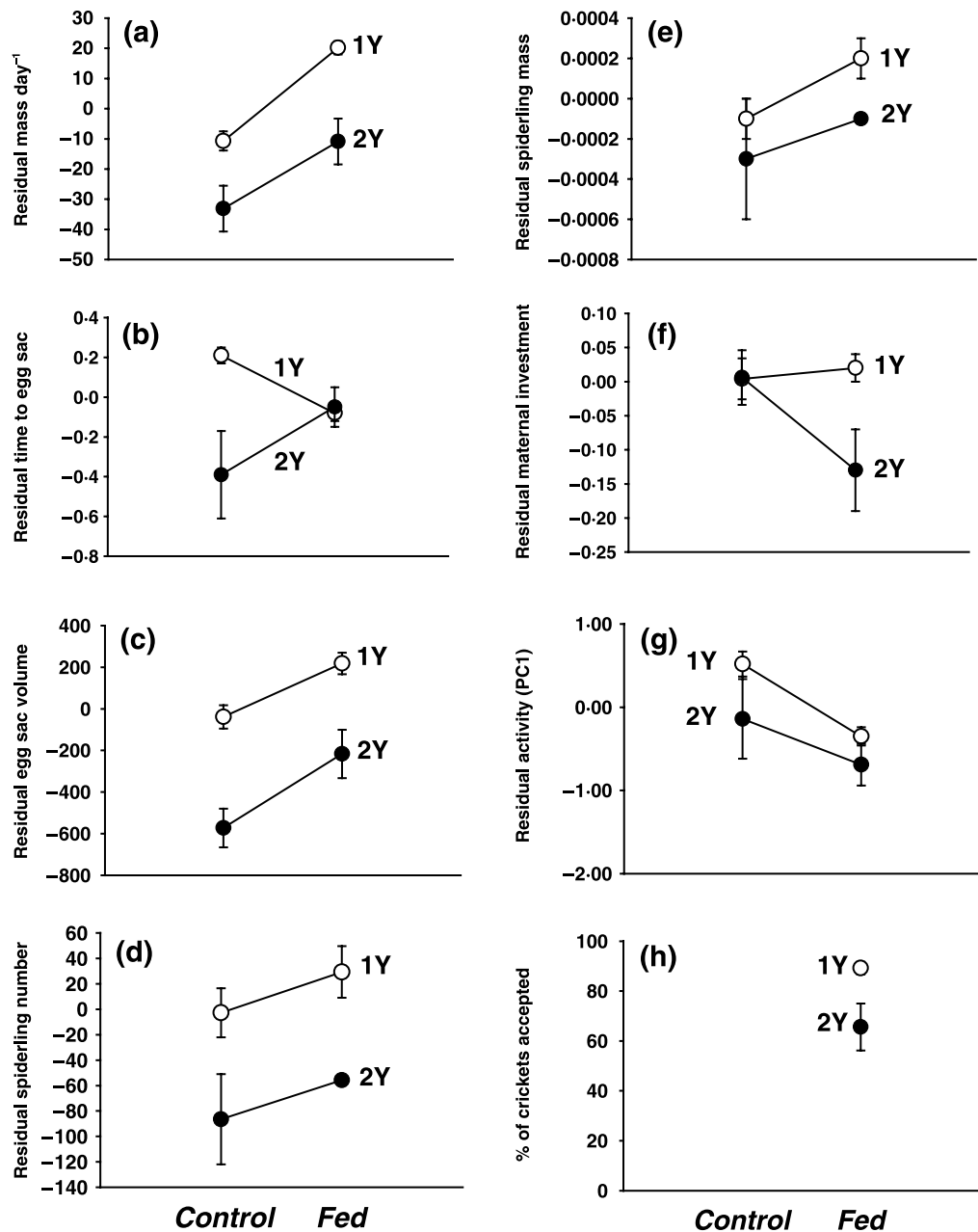
Fig. 1. Residuals of response variables after controlling for the effect of continuous variables. Statistical analyses and the continuous variables included for the calculation of residuals can be found in Table 2: (a) daily change in mass; (b) time to lay the egg sac; (c) egg sac volume; (d) spiderling number; (e) spiderling mass; (f) maternal investment; (g) foraging activity; (h) percentage of accepted crickets. Details about the calculation of variables are in the text.

only after controlling for the effects of Food and Age. The significance of the interaction term (Food × Age) was tested using hierarchical regression, in which the coefficients of determination between regression models with and without the interaction term were compared (Jaccard, Turrisi & Wan 1990). Binary response variables were tested with multiple logistic regression. The interaction term (Food × Age) was tested for significance by comparing the fit of models with and without the interaction term (Hardy & Field 1998).

Because of their potential influence on the response variables, spider size (carapace width) and initial mass (i.e. before food supplementation started) were

included in most of the multivariate analyses as controlling variables. Since the latter variable is included along with carapace width, it is used as an index of initial spider body condition. When testing for differences in spiderling number, spiderling mass was included as a covariate and vice versa. This is because there was a strong negative correlation between spiderling mass and spiderling number, probably reflecting the classic trade-off between egg size and number, which may result when females maximize their fitness differently in different environmental situations (Fox & Czesak 2000; Messina & Fox 2001). To test for differences in relative maternal investment (i.e. total

invested mass relative to the total available for reproduction) among groups, the mass of the female before laying the egg sac (W_{BES}), as well as her carapace width, were included as covariates within a regression model predicting maternal investment. Including W_{BES} in the model as a covariate as well as for calculating maternal investment (the dependent variables) will not affect parameter estimation nor the *P*-values for the other variables (Smith 1999; Moya-Laraño, Halaj & Wise 2002). Indeed if only the mass of the female after laying the egg sac is used as the dependent variable in the regression analysis, the parameter estimates are identical but with opposite sign and the *P*-values are exactly the same (results not shown). Controlling for W_{BES} was necessary because the prediction was made that senescent 2Y females would invest less of their available mass (i.e. W_{BES}) relative to 1Y females.

Results

RATE OF DISAPPEARANCE

Nineteen spiders disappeared from their burrow before laying an egg sac. Neither Food nor Age affected the disappearance rate. However, the better the initial condition of the spider, the lower the probability that she would disappear from her burrow [logistic regression: $P(\chi_4^2) = 0.001$] (Table 1a).

Between the time that egg sacs were produced and spiderlings began to emerge, *c*. 50% of the *L. tarantula* burrows in the study plot were dug out by Red Foxes (*Vulpes vulpes*), a common predator of the Mediterranean Tarantula (Moya-Laraño 1999; Moya-Laraño *et al*. 2002). Neither Food nor Age affected the probability of female disappearance before spiderlings emerged from the egg sac [logistic regression: $P(\chi_4^2) = 0.826$] (Table 1b).

RATE OF MASS GAIN

Both Food and Age affected the rate of mass gain (Tables 2a and 3, Fig. 1a). After food supplementation ceased, FED spiders gained mass at a higher rate than CONTROL spiders and 1Y females gained mass at a higher rate than 2Y females. In fact, 2Y spiders, rather than gaining mass, lost 9·5 mg per day. Larger spiders gained mass at a faster rate, whereas spiders in better initial condition gained mass at a slower rate (Table 2a).

REPRODUCTIVE PERFORMANCE

Time to lay the egg sac and egg sac volume

The effect of food supplementation on the time to lay the egg sac was complex, but there was a clear effect of age (Tables 2b and 3, Fig. 1b). Although both Food and Age were significant, interpretation is subjected to the fact that including the interaction term improved

Table 1. Logistic regressions on the probability of disappearance from the burrow

	Beta	*t*	df	*P*
(a) Disappearance before egg sac				
Food	0·861	1·4	85	0·1575
Age	0·415	0·5	85	0·6043
Carapace width (mm)	0·604	1·2	85	0·2380
Initial mass (g)	−4·042	−3·2	85	0·0017
(b) Disappearance before hatching				
Food	−0·285	−0·6	85	0·5380
Age	0·484	0·8	85	0·4550
Carapace width (mm)	−0·087	−0·2	85	0·8357
Initial mass (g)	−0·309	−0·4	85	0·6691

the model significantly (Table 2b). Running two separate models, one for each age class, showed that food supplementation had an effect by shortening the time of egg laying in FED spiders relative to CONTROL spiders for 1Y females [$P(t_{50}) < 0.001$] but not for 2Y females [$P(t_8) = 0.418$]. This effect persisted even when the volume of the egg sac was controlled for. Both spider size (positively) and initial condition (negatively) significantly contributed to the time to lay the egg sac.

Both food supplementation and age had an effect on the volume of the egg sac (Tables 2c and 3, Fig. 1c). FED spiders laid larger egg sacs than CONTROL spiders and 1Y spiders laid larger egg sacs than 2Y spiders. Both spider size and initial condition contributed positively to the size of the egg sac.

Spiderling number and mass

The number of spiderlings was not affected by the feeding treatment but was affected by age. FED spiders produced the same number of spiderlings as CONTROL spiders, whereas 2Y females produced significantly fewer spiderlings than 1Y females (Tables 2d and 3, Fig. 1d). The fact that the interaction term was not significant needs to be considered with caution because there was only one fed 2Y female. There was a strong negative partial correlation between spiderling number and mass.

After controlling for spiderling number, an effect of feeding treatment became apparent (Tables 2e and 3, Fig. 1e). FED females invested in heavier offspring than CONTROL females. As above, the fact that the interaction term was not significant needs to be considered with caution because there was only one fed 2Y female. Also, spiders that had a better initial condition invested in heavier spiderlings (Table 2e).

Maternal investment

Supplementing spiders with food had no effect on relative maternal investment. While age was significant, the interaction between Food and Age was also marginally significant (Tables 2f and 3, Fig. 1f). Both FED

Table 2. Hierarchical multiple regression analyses testing for the effect of Food and Age, and controlling variables, on several female responses

	r_{parc}	t	R^2	F	df	P
(a) Mass gained per day (mg)						
Food	−0·678	−8·5			85	<0·0001
Age	−0·553	−6·1			85	<0·0001
Carapace width (mm)	0·241	2·3			85	0·0247
Initial mass (g)	−0·361	−3·6			85	<0·0006
Full model			0·632	36·5	4,85	<0·0001
Food × Age				0·6	1,84	0·4507
(b) Time to lay the egg sac (days)						
Food	0·186	1·5			62	0·1422
Age	−0·395	−3·4			62	0·0013
Carapace width (mm)	0·285	2·3			62	0·0224
Initial mass (g)	−0·523	−4·8			62	<0·0001
Egg sac volume (mm³)	0·185	1·5			62	0·1432
Full model			0·496	12·2	5,62	<0·0001
Food × Age				14·5	1,61	0·0003
(c) Egg sac volume (mm³)						
Food	−0·486	−4·5			66	<0·0001
Age	−0·597	−6·0			66	<0·0001
Carapace width (mm)	0·279	2·4			66	0·0215
Initial mass (g)	0·331	2·8			66	0·0059
Full model			0·5833	23·1	4,66	<0·0001
Food × Age				0·3	1,65	0·5872
(d) Spiderling number						
Food	−0·336	−1·7			23	0·1011
Age	−0·478	−2·6			23	0·0157
Carapace width (mm)	−0·079	−0·4			23	0·7071
Initial mass (g)	0·361	1·9			23	0·0758
Spiderling mass (mg)	−0·716	−4·9			23	<0·0001
Full model			0·607	7·1	5,23	0·0004
Food × Age				0·0	1,22	1·0000
(e) Spiderling mass (mg)						
Food	−0·414	−2·2			23	0·0397
Age	−0·307	−1·5			23	0·1352
Carapace width (mm)	0·138	−0·7			23	0·5099
Initial mass (g)	0·517	2·9			23	0·0081
Spiderling number	−0·716	−4·9			23	<0·0001
Full model			0·616	7·4	5,23	0·0003
Food × Age				0·0	1,22	1·0000
(f) Maternal investment (g)						
Food	−0·155	−1·2			62	0·2213
Age	−0·387	−3·3			62	0·0016
Carapace width (mm)	−0·403	−3·5			62	0·0010
Mass before laying (g)	0·775	9·7			62	<0·0001
Full model			0·912	161·4	4,62	<0·0001
Food × Age				3·1	1,61	0·0810
(g) Foraging activity (PC1)						
Food	0·432	4·4			85	<0·0001
Age	−0·211	−2·0			85	0·0498
Carapace width (mm)	0·151	1·4			85	0·1629
Initial mass (g)	−0·310	−3·0			85	0·0035
Full model			0·275	8·1	4,85	<0·0001
Food × Age				0·4	1,84	0·5371
(h) Percentage of crickets eaten						
Age	−0·486	−3·6			41	0·0010
Carapace width (mm)	−0·119	−0·8			41	0·4472
Initial mass (g)	−0·067	−0·4			41	0·6697
Full model			0·251	7·0	2,42	0·020

and CONTROL 1Y females invested relatively the same proportion of their body mass in their egg sac, whereas 2Y females that were supplied with food showed a lower maternal investment relative to CONTROL females.

FORAGING ACTIVITY

Both Food and Age affected female foraging activity (Tables 2g and 3, Fig. 1g). FED females showed lower activity than CONTROL females and 1Y females showed more activity than 2Y females. Spiders with better initial body conditions showed lower foraging activity (Table 2g).

Within the FED spiders, 1Y females accepted significantly more crickets than did 2Y females (Table 2h, Fig. 1h). The initial condition had no effect on how many crickets were accepted by spiders in the FED group. The fact that the initial body condition was controlled for indicates that 2Y females accepted fewer crickets independently of the spider hunger status.

Discussion

Both food limitation and age affected several biological parameters of *L. tarantula* females. Food-supplemented females gained more mass, laid their egg sacs earlier if they were in their first reproductive season, laid larger egg sacs, produced heavier offspring and showed lower foraging activity than control females, indicating food limitation in adult females (Wise 1993; Lubin & Henschel 1996; Kreiter & Wise 2001). A previous experiment suggested that adult *L. tarantula* females can decrease the effect of food limitation suffered as antepenultimate and penultimate instars by feeding on males during the mating season (J. Moya-Laraño, J. M. Orta-Ocaña, J. A. Barrientos, C. Bach & D. H. Wise unpublished data). The present study shows that when males are no longer around in the population, females still suffer food limitation.

Older females lost mass, laid smaller egg sacs, produced fewer spiderlings, tended to invest relatively less of their available mass for reproduction in their egg sacs if they were food supplemented, foraged less actively and, within the FED group, accepted fewer crickets than the females that were on their first reproductive season. Contrary to the pattern in younger females, food supplementation did not affect the time at which older females laid their egg sacs. The reduced performance of older females, as well as their inability to improve their performance by showing a stronger response to food supplementation, is evidence of senescence (Williams 1957; Partridge & Barton 1996; Kirkwood & Austad 2000). The small sample size of older females could have affected the results due to the lack of statistical power, especially after the fox predation. Thus the lack of statistically significant results, especially in the interaction terms, must be treated with caution. Nevertheless, the analyses resulted in

Table 3. Means, standard errors and sample sizes (parentheses) for the different response variables in the experiment

	1Y		2Y	
	FED	CONTROL	FED	CONTROL
Mass gained per day (mg)	55 ± 3 (37)	21 ± 3 (37)	20 ± 6 (8)	−9·5 ± 6 (8)
Time to lay the egg sac (days)	17 ± 1 (31)	19 ± 1 (27)	13 ± 1 (6)	10 ± 3 (7)
Egg sac volume (mm^3)	1502 ± 66 (31)	1260 ± 61 (27)	954 ± 136 (6)	744 ± 63 (7)
Spiderling number	274 ± 33 (12)	261 ± 22 (13)	154 ± 0 (1)	142 ± 28 (3)
Spiderling mass (mg)	2·6 ± 0·5 (12)	2·5 ± 0·6 (13)	2·7 ± 0 (1)	2·8 ± 1 (3)
Maternal investment (mg)	1243 ± 38 (29)	992 ± 42 (26)	370 ± 42 (6)	232 ± 104 (6)
Foraging activity (PC1)	−0·30 ± 0·12 (37)	0·52 ± 0·15 (37)	− 0·69 ± 0·32 (8)	−0·35 ± 0·52 (8)

several statistically significant age differences, probably reflecting a large magnitude of the senescence effect (i.e. large difference between 1Y and 2Y females). Although senescence for a spider has been shown previously in the laboratory (Austad 1989), the same study failed to find evidence for senescence in natural conditions. Second egg sacs (clutches) laid by female spiders are usually smaller (Marshall & Gittleman 1994), which suggests that senescence is widespread in spiders. In the wild, however, smaller second egg sacs can also be explained by changes in the environment as the season progresses. Because spiders that differed in one year of age were compared within the same environment, senescence is the most likely explanation for the pattern found in this study. One may argue that differences in the seasonal environment in which the spiders of different age grew can also explain the differences. However, if older females would have grown up in a poorer environment, we would have observed 2Y females trying to reach the reproductive status of 1Y by foraging more actively, accepting more crickets and investing a proportionately larger amount of mass in their egg sacs. Since the pattern was the opposite, senescence is a better explanation for the poorer performance of older females.

Although to understand the evolution of ageing, finding evidence for reproductive senescence is as relevant as finding an increase in the death rate due to senescence (Kirkwood & Austad 2000), documentation of reproductive senescence in the wild is still scant. In fact, only a few studies on long-lived iteroparous invertebrates in natural populations show either a positive correlation between the death rate and age, or a negative correlation between reproductive output or performance and age (Rotifera: Edmondson 1945; Bivalvia: Macdonald & Bayne 1993; Cephalopoda: Cortez, Castro & Guerra 1995). However, changes in reproductive output with age may reflect changes in food availability that are not necessarily related to age. The present experiment ruled the latter possibility out because food availability was experimentally manipulated. Thus, the results reported here demonstrate the existence of reproductive senescence in an invertebrate natural population.

There are currently three main hypotheses that explain the evolution of senescence (reviewed in Finch 1990; Rose 1991; Kirkwood & Austad 2000; Partridge 2001; Tatar 2001): the 'mutation accumulation' hypothesis (Medawar 1952), the 'antagonistic pleitropy' hypothesis (Williams 1957) and the 'disposable soma' hypothesis (Kirkwood 1977). All three hypotheses share the common prediction that selection should favour rapid senescence when the rate of extrinsic mortality is high. In light of the latter prediction, one would not expect to find slow ageing in the present *L. tarantula* population because the high mortality rate (>50%) due to predation from foxes would have selected for rapid senescence and sudden death. However, fox predation may not be as high in natural systems, because evidence suggests that foxes are attracted to the spiders due to the human presence near the burrows (Moya-Laraño 1999). In fact, slow ageing could have evolved in burrowing wolf spiders due to the protection that the burrow provides against predation (Shook 1978; Kirkwood & Austad 2000).

In conclusion, this study provides evidence that food limitation and age significantly affect reproductive performance and foraging behaviour of adult Mediterranean Tarantula females. Therefore, *L. tarantula* can be added to the list of slowly ageing organisms showing senescence in the wild.

Acknowledgements

References

Austad, S.N. (1989) Life extension by dietary restriction in the bowl and doily spider, *Frontinella piramitela*. *Experimental Gerontology* **24**, 83–92.

Bérubé, C.H., Festa-Bianchet, M. & Jorgenson, J.T. (1999) Individual differences, longevity, and reproductive senescence in bighorn ewes. *Ecology* **80**, 2555–2565.

Conley, M.R. (1985) Predation versus resource limitation in survival of adult burrowing wolf spiders (Araneae: Lycosidae). *Oecologia* **67**, 71–75.

Cortez, T., Castro, B.G. & Guerra, A. (1995) Feeding dynamics of *Octopus mimus* (Mollusca, Cephalopoda) in Northern Chile waters. *Marine Ecology* **123**, 497–503.

Edmondson, W.T. (1945) Ecological studies of sessile Rotatoria. II. Dynamics of populations and social structures. *Ecological Monographs* **15**, 141–172.

Fernández-Montraveta, C. & Ortega, J. (1990) Some aspects of the reproductive behavior of *Lycosa tarantula fasciiventris* (Araneae, Lycosidae). *Journal of Arachnology* **18**, 257–262.

Finch, C.E. (1990) *Longevity, Senescence and the Genome*. University of Chicago Press, Chicago, IL.

Foelix, R.F. (1996) *Biology of Spiders*. Oxford University Press, Oxford.

Fox, C.W. & Czesak, M.E. (2000) Evolutionary ecology of progeny size in arthropods. *Annual Review of Entomology* **45**, 341–369.

Framenau, V., Dieterich, M., Reich, M. & Plachter, H. (1996) Life cycle, habitat selection and home ranges of *Arctosa cinerea* (Fabricius,1777) (Araneae, Lycosidae) in a braided section of the Upper Isar (Germany, Bavaria). *Revue Suisse de Zoologie*, 223–234.

Gertsch, W.J. (1979) *American Spiders*. Van Nostrand Reinhold, London.

Hardy, I.C.W. & Field, S.A. (1998) Logistic analysis of animal contests. *Animal Behaviour* **56**, 787–792.

Hardy, M.A. (1993) *Regression Analysis with Dummy Variables*. Sage Publications, Newbury Park, CA.

Humphreys, W.F. (1976) The population dynamics of an Australian wolf spider, *Geolycosa godeffroyi* (L. Koch 1865) (Araneae: Lycosidae). *Journal of Animal Ecology* **45**, 59–80.

Humphreys, W.F. (1983) Temporally diphasic dispersal in siblings of a wolf spider: a game of Russian roulette? *Bulletin of the British Arachnological Society* **6**, 124–126.

Jaccard, J., Turrisi, R. & Wan, C.K. (1990) *Interaction Effects in Multiple Regression*. Sage Publications, London.

Jakob, E.M., Marshall, S.D. & Uetz, G.W. (1996) Estimating fitness: a comparison of body condition indices. *Oikos* **77**, 61–67.

Kirkwood, T.B.L. (1977) The science of ageing. *Nature* **270**, 301–304.

Kirkwood, T.B.L. & Austad, S.N. (2000) Why do we age? *Nature* **408**, 233–238.

Kreiter, N.A. & Wise, D.H. (2001) Prey availability limits fecundity and influences the movement pattern of female fishing spiders. *Oecologia* **127**, 417–424.

Lloret, F., Casanovas, C. & Penuelas, J. (1999) Seedling survival of Mediterranean shrubland species in relation to root: shoot ratio, seed size and water and nitrogen use. *Functional Ecology* **13**, 210–216.

Lubin, Y. & Henschel, J. (1996) The influence of food supply on foraging behaviour in a desert spider. *Oecologia* **105**, 64–73.

Macdonald, B.A. & Bayne, B.L. (1993) Food availability and resource allocation in senescent *Placopecten magellanicus*: evidence from field populations. *Functional Ecology* **7**, 40–46.

Marshall, S.D. & Gittleman, J.L. (1994) Clutch size in spiders: is more better? *Functional Ecology* **8**, 118–124.

McQueen, D.J. (1978) Field studies of growth, reproduction, and mortality in the burrowing wolf spider *Geolycosa domifex* (Hancock). *Canadian Journal of Zoology* **56**, 2037–2049.

Medawar, P.B. (1952) *An Unresolved Problem of Biology*. Lewis, London.

Messina, F.J. & Fox, C.W. (2001) Egg size and number. *Evolutionary Ecology. Concepts and Case Studies* (eds C. W. Fox, D.A. Roff & D.J. Fairbairn), pp. 113–127. Oxford University Press, Oxford.

Moya-Laraño, J. (1999) *Limitación por el alimento, territorialidad y canibalismo en la tarántula mediterránea*, Lycosa tarentula *(L.) (Araneae, Lycosidae)*. PhD Thesis, Autonomous University of Barcelona, Barcelona.

Moya-Laraño, J. & Wise, D.H. (2000) Survival regression analysis: a powerful tool for evaluating fighting and assessment. *Animal Behaviour* **60**, 307–313.

Moya-Laraño, J., Orta-Ocaña, J.M., Barrientos, J.A. & Cases, A. (1996) Dynamics of a population of burrowing wolf spiders. Is there any competition? *Revue Suisse de Zoologie*, 491–499.

Moya-Laraño, J., Halaj, J. & Wise, D.H. (2002) Climbing to reach females: Romeo should be small. *Evolution* **56**, 420–425.

Moya-Laraño, J., Orta-Ocaña, J.M., Barrientos, J.A., Bach, C. & Wise, D.H. (2002) Territoriality in a cannibalistic burrowing wolf spider. *Ecology* **83**, 356–361.

Mysterud, A., Yoccoz, N.G., Stenseth, N.C. & Langvatn, R. (2001) Effects of age, sex and density on body weight of Norwegian red deer: evidence of density-dependent senescence. *Proceedings of the Royal Society of London B* **268**, 911–919.

Nisbet, I.C.T. (2001) Detecting and measuring senescence in wild birds: experience with long-lived seabirds. *Experimental Gerontology* **36**, 833–843.

Orta, J.M., Moya, J. & Barrientos, J.A. (1993) Datos fenológicos de una población de Lycosa tarantula fasciiventris L. Dufour, 1835, en el Noroeste de la Península Ibérica (Araneae, Lycosidae). *Bolletino Della Accademia Gioenia Di Science Naturali* **26**, 15–26.

Ortega, J., Ruiz, M. & Fernández-Montraveta, C. (1992) Daily patterns of locomotor activity in a lycosid spider. *Journal of Interdisciplinary Cycle Research* **23**, 295–301.

Parellada, X. (1998) Identificació i dades biològiques de tres espècies de taràntules (Araneae: Lycosidae) al Garraf. *Trobada d'Estudiosos Del Garraf* **II**, 15–25.

Partridge, L. (2001) Evolutionary theories of ageing applied to long-lived organisms. *Experimental Gerontology* **36**, 641–650.

Partridge, L. & Barton, N.H. (1996) On measuring the rate of ageing. *Proceedings of the Royal Society of London B* **263**, 1365–1371.

Promislow, D.E. (1991) Senescence in natural populations of mammals: a comparative study. *Evolution* **45**, 1869–1887.

Reznik, D., Buckwalter, G., Groff, J. & Elder, D. (2001) The evolution of senescence in natural populations of guppies (*Poecilia reticulata*): a comparative approach. *Experimental Gerontology* **36**, 791–812.

Rose, M.R. (1991) *Evolutionary Biology of Aging*. Oxford University Press, Oxford.

Shook, S.S. (1978) Ecology of the wolf spider, *Lycosa carolinensis* Walckenaer (Araneae, Lycosidae) in a desert community. *Journal of Arachnology* **6**, 53–64.

Smith, R.J. (1999) Statistics of sexual size dimorphism. *Journal of Human Evolution* **36**, 423–459.

Tatar, M. (2001) Senescence. *Evolutionary Ecology. Concepts and Case Studies* (eds C.W. Fox, D.A. Roff & D.J. Fairbairn), pp. 128–141. Oxford University Press, Oxford.

Wallace, H.K. (1937) The use of the headlight in collecting nocturnal spiders. *Entomological News* **48**, 107–111.

Ward, D. & Lubin, Y.D. (1993) Habitat selection and the life history of a desert spider, *Stegodyphus lineatus* (Eresidae). *Journal of Animal Ecology* **62**, 353–363.

Williams, G.C. (1957) Pleitropy, natural selection and the evolution of senescence. *Evolution* **11**, 398–411.

Wise, D.H. (1993) *Spiders in Ecological Webs*. Cambridge University Press, Cambridge.