Laboratory observations on the development and reproduction of *Erigone atra* Blackwall, 1833 (Araneae, Linyphiidae)

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Summary

Juvenile development, food intake and reproduction of *Erigone atra* were studied in the laboratory at different temperatures and feeding regimes. Relatively high temperatures (20°C) result in short generation times (*c.* 40 days) and a large number of offspring (*c.* 200 eggs in 20 days). Below 10°C there is almost no reproduction or growth. The food intake and reproduction are closely related to food supply, indicating that this species possesses important characteristics of relevance to biological control.

Introduction

Erigone atra Blackwall is one of the commonest spiders of open habitats, and in many cases one of the first pioneers on regularly disturbed land. Linked to this abundance is its ability to disperse widely by means of aeronautic behaviour (the most frequently caught aeronaut in our region, cf. Duffey, 1956). This ability cannot, of course, be the only explanation for the species' abundance, and most probably other characteristics such as a large number of offspring and fast development also play important roles. Although the developmental rate and reproduction is relatively easy to study under laboratory conditions, such investigations have not yet been done for many species of spiders. Schaefer (1976) reared spiders at different temperatures and in so doing greatly enlarged our understanding of the life cycle of spiders. Comparable investigations were carried out by Aitchison (1984), Baert (1980), Buche (1966), Kajak (1978), Kessler (1971), Nentwig (1983), Turnbull (1962), Van Praet & Kindt (1979) and Van Wingerden (1977).

It proved to be very difficult to understand the life cycle pattern of a population of *E. atra* in an intensively grazed pasture (near Ghent, Belgium) by means of occurrence in quadrat and pitfall samples. We needed additional observations about the conditions that are required for rapid development. We therefore assessed under laboratory conditions the influence of two factors (temperature and food supply), proven to be of great importance for regulation of the life cycle of many spider species (cf. Schaefer, 1976; Kajak, 1978).

Methods

On 27 November 1985, we captured adult females and males from the pasture and brought them to the laboratory where they were kept at 20°C. Because earlier (on 29 October) we had collected females that produced only unfertilised eggs, we now kept the females together with males for about three days. The females were then placed individually in petri-dishes (3.5 cm diameter) with a bottom of *c.* 0.3 cm depth of plaster of Paris (this was moistened regularly to maintain a relative humidity close to 100%). All further experiments were done with this same type of vessel. The females were fed with *Drosophila melanogaster* and they all laid one or more cocoons. The eggs were kept in constant darkness at 20°C. When the spiderlings emerged they were separated and used for the following experiments.

a. Juvenile development and mortality at different temperatures

The day the spiderlings emerged, they were placed in different temperatures. Juvenile development was observed in a total of 35 individuals divided into the following constant-temperature regimes: 5, 10, 15 and 20°C. During the first and second juvenile instars the spiders were fed with an excess of collembolans (fam. Isotomidae). Every day at least 15 springtails (of similar size as the juvenile spider) were added. The third and fourth instars received *Drosophila melanogaster*. Every day four flies were added (which was also an excess food quantity). Observations on moulting and mortality were made daily. These experiments (in contrast to b and c) were done in constant darkness. This was the only way for us to achieve constancy of the lower temperatures, owing to the limitations of our laboratory conditions. Because we found (see results) that photoperiod is not important (if at all) in determining juvenile develop-

	Initial number of individuals	I	II	III	IV
5°C	9	86 ± 5(8)*	>150		
10°C	11	22.5 ± 0.3(11)	42 ± 3(11)	109 ± 9(7)	145,157,167(3)
15°C	8	9.8 ± 0.8(8)	19 ± 2(8)	33 ± 8(7)	47 ± 9(7)
20°C	7	4.9 ± 0.6(7)	8.7 ± 0.4(7)	14 ± 1(7)	20 ± 2(7)
20°C (LD 16:8)	139	5.2 ± 0.1(129)	9.2 ± 0.1(128)	13.0 ± 0.1(126)	18.2 ± 0.1(125)

Table 1: Cumulative duration of the four juvenile instars at different temperatures (mean number of days ± 95% C.I.). In brackets: number of surviving individuals. *mean for the five individuals that had the first moult, 3 other individuals were still alive, but had not moulted after 150 days, when we stopped the experiment.

ment, we assume that the results for the relationship between juvenile developmental rate and temperature are meaningful.

b. Juvenile development and mortality at different feeding regimes

Two feeding regimes were used. One group of 48 spiders received food only on Monday, Wednesday and Friday: each time collembolans were added until 3 individuals were present (some may have been left from previous feeding). The second group of 139 spiders had an excess of collembolans during the whole juvenile stage. The experiments were done at 20°C and a light-dark cycle of LD 16:8. Observations on moulting and mortality were also carried out daily.

c. Reproduction, food intake and mortality of adults at different feeding regimes

During the whole juvenile stage all spiders were fed with an excess of collembolans. After the matural moult we divided the female spiders (55 individuals) into 5 groups which received different feeding rates:

1 fly every 3 days
1 fly every day
3 flies every day
6 flies every day
9 flies every day

Uneaten flies as well as prey remains were removed daily. Fresh prey were added in accordance with the feeding regimes given above. For the first three days after the last moult almost all females were kept
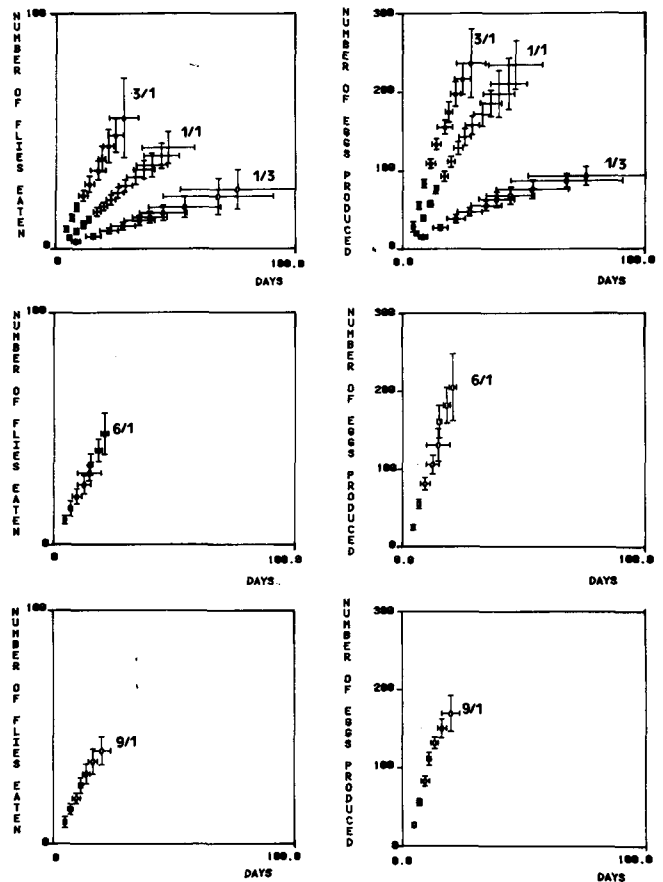

Fig. 1: Cumulative duration in days of the four juvenile instars at 2 feeding regimes (representative individual observations are shown; o = surplus of collembolans; * = 3 collembolans fed, 3 times a week). For males 48 high feeding regime and 17 low feeding regime individuals survived to maturity. For females these numbers were 77 and 15 respectively.

Fig. 2: Cumulative food intake (number of flies eaten) and reproduction (number of eggs laid) versus the total number of days after matural moult for different feeding rates. The mean values (± 95% C.I.) at the times of successive cocoon deposition are given. Feeding regimes: 1/3 = 1 fly every 3 days; 1/1 = 1 fly every day; 3/1 = 3 flies every day; 6/1 = 6 flies every day; 9/1 = 9 flies every day.
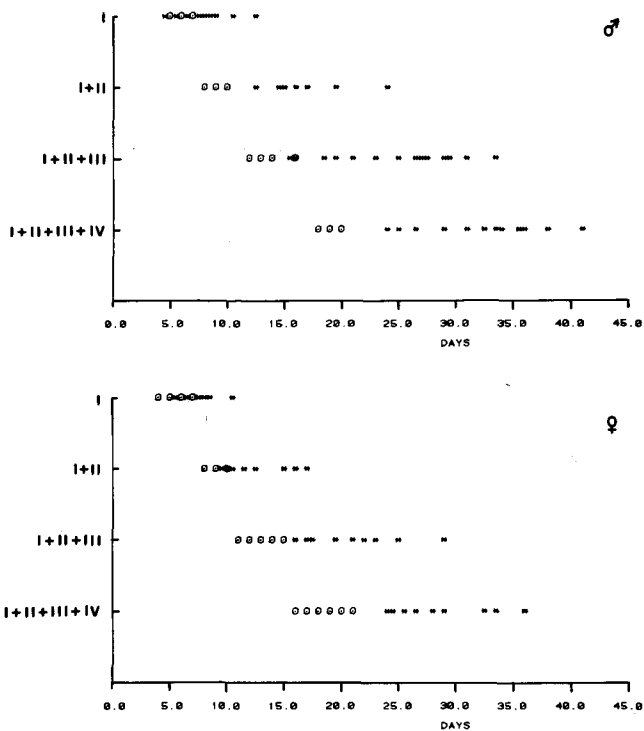
together with a male. Observations on food intake (number of flies eaten), reproduction (cocoon and number of eggs per cocoon) and mortality were done daily until all females died. The experiments were carried out at 20°C and a light-dark cycle of LD 16:8. Because many flies were found dead without being eaten (only the integument of consumed prey remains), we tried to discover if these were killed by the spider (wasteful killing) or not. To do this, the three highest feeding rate experiments were carried out for twelve days, but without spiders in the petri-dishes; dead flies were counted daily.

Results

a. Juvenile development and mortality at different temperatures

The mean cumulative durations of the four juvenile instars at different temperatures are shown in Table 1. Development is very fast at high temperatures. At 20°C the spiders become adult in 20 days. This period lengthens clearly with decreasing temperature. At 10°C it lasts some 150 days. At 5°C most spiders only moult once during 150 days and 3 spiders even fail to do that. Juvenile mortality also rises drastically at lower temperatures. _E. atra_ thus seems to be adapted to

having a fast development during summer and probably does not grow during winter.

As well as rearing *E. atra* in constant darkness, we also reared it in a photoperiod of LD 16:8 (see b and c). These results (for 139 individuals) are also included in Table 1 and are very similar to those obtained in constant darkness. In both photoperiods the spider shows a fast development. Van Praet & Kindt (1979) found that the development time within the cocoon is also short at high temperatures (c. 15 days at 20°C). Thus *E. atra* is potentially able to go through more than 1 generation during the warm season of the year at our latitude.

b. Juvenile development and mortality at different feeding regimes

To assess the effect of prey abundance on juvenile development two feeding rates were used. The results for the two feeding regimes are contrasted in Fig. 1. For both sexes, low food supply causes a pronounced increase in the duration of all juvenile instars. The variation in the individual values also increases, implying a large individual variation in the ability of the spiderlings to catch prey at low availability. When receiving an excess of food the whole juvenile stage for males and females respectively lasts 18.7 ± 0.2 and 17.9 ± 0.2 days (mean $\pm$ 95% C.I.). Student's t-test shows this to be a significant difference ($p < 0.01$). At the low feeding rate, these periods increase respectively to 31.9 ± 2.6 and 28.9 ± 2.2 days (mean $\pm$ 95% C.I.), but they do not differ significantly ($0.05 < p < 0.10$). The males of *E. atra* are somewhat larger than the females, so it seems reasonable that they take a little longer to become adult.

At the highest feeding regime mortality was very low. We started with 139 individuals of which 10, 1, 2 and 1 died during the successive instars; thus only 10% died. For the low feeding rate we followed 48 individuals. Twelve, 1, 3 and none died during the successive instars (i.e. a juvenile mortality of 33%).

c. Reproduction, food intake and mortality of adults at different feeding regimes

For each feeding regime we determined for each successive deposited cocoon the mean cumulative number of days since the matural moult, the mean cumulative number of flies consumed and the mean cumulative number of eggs produced by the mother. These results are shown in Fig. 2. In Table 2 we have presented the reproductive life span (i.e. the total
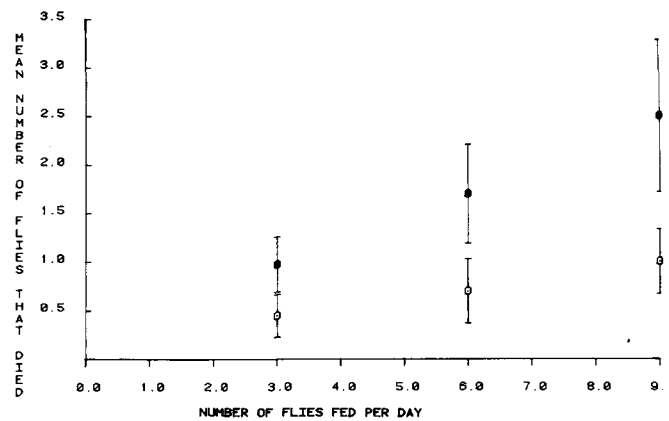

Fig. 3: Mean number ($\pm$ 95% C.I.) of flies that died within 24 hours, but were not consumed, at different feeding rates (open circles = control experiment).

duration between the matural moult and the deposition of the last cocoon), the total food intake and the total numbers of eggs and cocoons produced per feeding regime. For the 3 lowest feeding regimes the females of *E. atra* show a distinct increase in food consumption as well as in total reproductive production with an increased food availability. The change in the reproduction is caused partly by a higher number of cocoons deposited, but mainly by more eggs per cocoon. The diameters of a number of individual eggs from females at each feeding regime were measured, but no significant differences were found between them. Up to a feeding rate of one fly per day almost all offered prey items are eaten. For the three highest feeding regimes no significant differences were observed in the food intake or in the reproduction, so we may conclude that at 3 flies fed a day the maximum consumption is already attained.

Unfertilised females also produce cocoons, but less frequently and they also eat less. We also followed a few males under the same conditions for about 40 days and at a feeding regime of 6 flies a day. These males also have a low consumption of only about 1 fly every 4 days.

For the females we also observed another phenomenon: in Fig. 3 we see that the number of flies found dead but unconsumed after 1 day, is significantly larger in the petri dishes with spiders than in the control experiment (this could only be studied at higher feeding regimes because at the lower ones almost all flies were eaten in the experiment). Moreover we see that mortality increases with increased prey density. A

Feeding regime	Number of individuals	Reproductive life span (days)	Total number of flies eaten	Total number of eggs laid	Number of cocoons produced	Number of eggs per cocoon
1 fly every 3 days	12	50.5 ± 18.5	16.9 ± 6.1	72.6 ± 20.3	7.1 ± 2.2	10.2 ± 0.7
1 fly every day	12	36.0 ± 10.1	33.2 ± 9.1	171.8 ± 51.2	10.4 ± 3.3	16.4 ± 0.7
3 flies every day	12	28.8 ± 6.1	51.9 ± 12.9	223.2 ± 41.3	9.6 ± 1.7	23.3 ± 1.3
6 flies every day	9	23.8 ± 8.0	47.1 ± 17.4	186.9 ± 64.1	7.8 ± 3.0	23.9 ± 1.4
9 flies every day	10	21.1 ± 6.0	42.2 ± 13.7	168.0 ± 44.5	7.0 ± 2.2	24.1 ± 1.4

Table 2: Mean values ($\pm$ 95% C.I.) of the reproductive life span (i.e. total duration between matural moult and deposition of last cocoon), total food intake and total numbers of eggs and cocoons produced for different feeding regimes.

logical explanation seems to be that the spider kills more prey than can be consumed ("wasteful killing").

Another interesting observation is that at the low feeding rates the individual prey items are much more completely eaten (a smaller part of the prey is left); this can be seen as an adaptation to increase reproduction as much as possible at low food supplies. We would thus expect that the spiders lay more eggs per quantity of flies eaten when the feeding regime becomes lower. For each feeding regime we calculated the number of flies that were eaten per egg produced (see Table 3). There is a positive correlation between the consumption per egg produced and the food supply (Spearman rank, $0.01 < p < 0.05$). The relatively high value at the lowest feeding regime may be due to the need for a larger fraction of the food consumption for metabolism without reproduction. In Fig. 4 the mean number of flies eaten per day is plotted against the mean number of eggs laid per day (mean of the reproduction during the whole reproductive life span, i.e. from the time the female becomes adult until the last cocoon is laid) for all specimens of all feeding regimes used. By linear regression we determined that reproduction stops at a feeding regime of about 1 fly fed every 12 days (mean value). This would thus be the amount of food needed for metabolism without reproduction. If we now use only the food that is needed for reproduction in our calculation, smaller values of the number of flies eaten per egg produced are obtained (see Table 3). By calculation of the Spearman rank correlation coefficient we now find a highly significant positive correlation between number of flies needed per egg produced and food availability ($p < 0.001$); this confirms our expectation.

Females of *E. atra* seem to produce cocoons during the whole of their adult life. When they receive enough food they die less than 10 days after they have made their last egg sac. In our experiment, the eggs were not fertilised from about the fifth cocoon onwards. The reproductive life span (time between matural moult and deposition of the last cocoon) is strongly dependent on the food supply (see Fig. 5). With the Spearman rank correlation coefficient a negative correlation between reproductive life span and feeding rate was determined ($p < 0.01$, $n = 55$). Figure 5 also shows that the mean value of the total reproduction reaches an optimum at a feeding regime of 3 flies a day. Indeed a positive correlation is found between total reproduction and feeding regime for the 3 lowest feeding regimes (Spearman rank, $p < 0.01$, $n = 36$) and

Fig. 4:   Mean number ($\pm$ 95% C.I.) of eggs produced per day at different feeding rates.

a negative correlation for the three highest feeding regimes ($0.01 < p < 0.05$, $n = 31$). The total number of cocoons shows less variation (see Table 2).

For the study of the population dynamics of a species it is important to know whether the reproduction is dependent on the age of the individual animal. A decrease in reproduction can be due to a decrease in the number of eggs per cocoon and/or an increase in the number of days between the deposition of two cocoons. To determine the importance of both aspects we calculated the Spearman rank correlation coefficient between (a) the number of eggs per cocoon and the rank of the cocoon, and (b) the number of days between the deposition of two cocoons and the rank of the last of the two. In these calculations we used the individual values from the second deposited cocoon onwards for each feeding regime separately. For the relation between the number of eggs per cocoon and the rank of the cocoon the 95% confidence limits of the linear regression coefficient b were also calculated (see Sokal & Rohlf, 1981). The results of these calculations are shown in Table 4. The number of eggs per cocoon decreases significantly with rising age for all feeding regimes. This decrease seems to become more distinct when the feeding regime gets higher (the absolute value of the regression coefficient becomes larger). The number of days between the deposition of two cocoons increases a little as the spider gets older but not always significantly, especially not under conditions of food shortage. We thus can conclude that reproduction decreases according to the age of the spider and that this is mainly due to a decrease in the number of eggs per cocoon and to a lesser extent to an increase in the number of days between the production of two cocoons. The number of flies eaten between two cocoons however does not seem to decrease with rising age (Table 4). We may thus conclude that the conversion of food into eggs is less efficient for older animals (metabolism becomes less efficient).

Discussion

Spiders are a very heterogeneous group with regard to their life cycle pattern (cf. Schaefer, 1976, 1987; Toft, 1975; Tretzel, 1954). Similar patterns, however,

Feeding regime	Number of flies	
	A	B
1 fly every 3 days	0.23 ± 0.04	0.18 ± 0.03
1 fly every day	0.20 ± 0.03	0.19 ± 0.03
3 flies every day	0.23 ± 0.02	0.22 ± 0.02
6 flies every day	0.26 ± 0.04	0.23 ± 0.03
9 flies every day	0.25 ± 0.03	0.24 ± 0.03

Table 3:   Mean number ($\pm$ 95% C.I.) of flies eaten per egg produced for different feeding regimes (A: total food intake is used in the calculation; B: only food needed for reproduction is used).
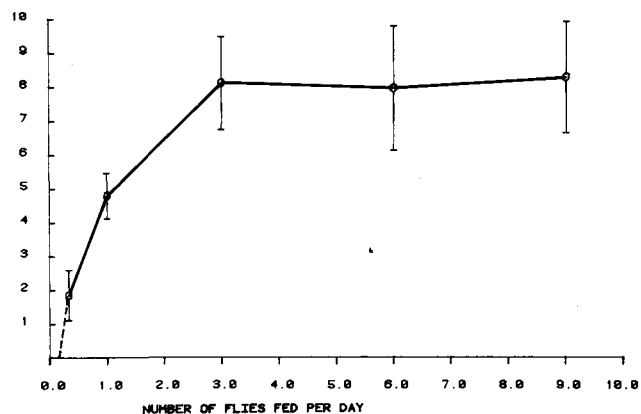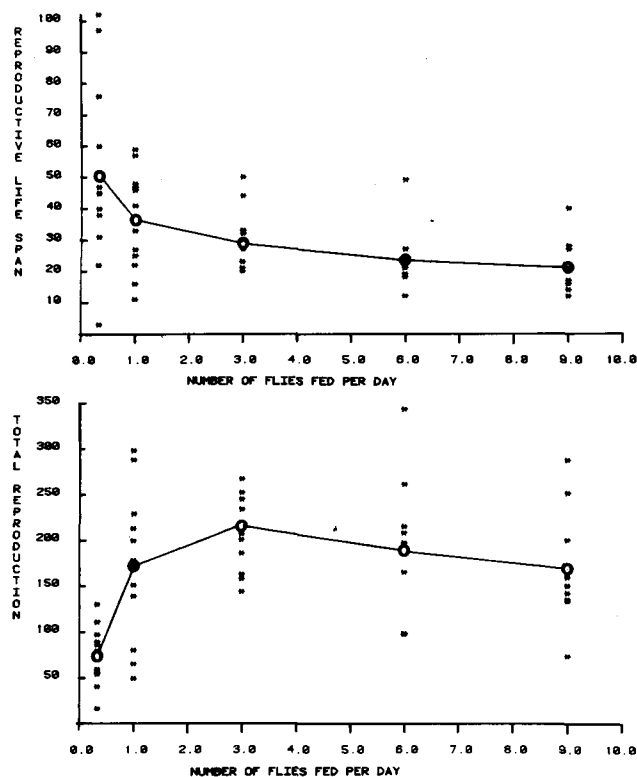
Fig. 5: Reproductive life span (in days) (upper) and total reproduction (number of eggs) (lower) at different feeding rates. Representative individual observations (*) and mean values (o) are shown.

are often found for species living in the same or comparable habitats. This is true for *E. atra* and *Oedothorax fuscus* (Blackwall) (cf. De Keer & Maelfait, in press). The influence of temperature on juvenile development is similar for both species. Around and below 10°C, *E. atra* develops somewhat slower, but the difference between the two species is very small in comparison with the difference both species show to spiders with a different phenological pattern. Buche (1966) reared *Macrargus rufus* (Wider) and *Centromerus sylvaticus* (Blackwall) at different temperatures. In nature these spiders reproduce during the cold season and only have one generation a year. Buche (loc.cit.) found that the juvenile phase takes more than two months for *C. sylvaticus* and seven months for *M. rufus* at 15°C. Schaefer (1976) also found much longer developmental periods for species such as *Floronia bucculenta* (Clerck), *Linyphia triangularis* (Clerck), *Centromerita bicolor* (Blackwall) and others, all of which have only one generation a year.

At the lowest feeding regime the juvenile mortality is relatively low in comparison with that of *O. fuscus* under the same conditions (c.f. De Keer & Maelfait, 1987). For the latter species we found a mortality of more than 90% and the only juvenile that survived took more than 50 days to become adult. *E. atra* seems to be better at coping with low prey availabilities. This can be an important advantage for survival in habitats where prey may be scarce, for example in pioneer situations or recently disturbed habitats where *E. atra* is often found in large numbers.

Concerning the large reproduction at high temperatures, *E. atra* and *O. fuscus* again resemble each other very closely. Under optimal conditions the reproduction of *O. fuscus* (3.6-7.2 eggs a day at 20°C) is somewhat smaller than we observed for *E. atra* (4.4-11.8 eggs a day at 20°C) but this difference is not very pronounced. On the other hand the amount of food eaten to produce a certain number of eggs is significantly lower for *E. atra* (0.38-0.90 flies eaten per egg produced for *O. fuscus*; mean value for *E. atra*: 0.23 flies), which shows that *E. atra* is extremely efficient at converting food to eggs. This is again an obvious advantage for surviving in places with low prey availability, e.g. dry summer situations in open habitats, when the prey populations have retreated beneath the soil surface (cf. Van Wingerden, 1977).

Not all spiders show a positive correlation between number of eggs produced and food supply. Turnbull (1962) and Kessler (1971) showed respectively that *Linyphia triangularis*, and *Pardosa lugubris* (Walck.) and *P. palustris* (Linn.), produce a constant number of eggs, even under conditions of food shortages. In *L. triangularis*, for example, when food becomes more abundant the weight of an individual egg increases owing to an enlargement of the amount of yolk. A larger yolk percentage increases the probability of survival of the eggs during the winter. This is in agreement with the findings of Anderson (1978) who showed that the energy values for eggs of spiders which overwinter in the egg phase are larger than those of spiders which do not do so. The energy content of the eggs of *E. atra* has not been measured, but we may expect that it does not change since there is a close relation between food intake and number of eggs produced. As already mentioned, there is also no

Feeding regime	(a) S.r. corr. coefficient r_s	(a) Regression coefficient b	(b) S.r.corr. coefficient r_s	(c) S.r.corr. coefficient r_s
1 fly every 3 days	−0.6433 ($p < 0.01$) ($n = 90$)	−0.53 ±0.18	−0.0394 ($p > 0.10$) ($n = 78$)	−0.06761 ($p > 0.10$) ($n = 78$)
1 fly every day	−0.6677 ($p < 0.01$) ($n = 124$)	−0.54 ±0.12	0.2219 ($0.05 > p > 0.01$) ($n = 112$)	0.1725 ($0.10 > p > 0.05$) ($n = 112$)
3 flies every day	−0.5404 ($p < 0.01$) ($n = 115$)	−1.00 ±0.35	0.4413 ($p < 0.01$) ($n = 103$)	0.1060 ($p > 0.10$) ($n = 103$)
6 flies every day	−0.5486 ($p < 0.01$) ($n = 70$)	−0.86 ±0.37	0.3460 ($p < 0.01$) ($n = 61$)	0.1773 ($p > 0.10$) ($n = 61$)
9 flies every day	−0.6939 ($p < 0.01$) ($n = 70$)	−1.4461 ±1.22	0.4063 ($p < 0.01$) ($n = 60$)	0.2274 ($0.10 > p > 0.05$) ($n = 60$)

Table 4: Spearman rank correlation coefficient r_s between (a) number of eggs per cocoon and the rank of the cocoon, (b) the duration (in days) of the period between the deposition of two cocoons and the rank of the last of the two, and (c) the number of flies eaten between the deposition of two cocoons and the rank of the last of the two. For (a) the linear regression coefficient b was also calculated. These calculations were done separately for each feeding regime.

increase in individual size of the eggs with increasing food consumption.

From fieldwork in an intensively grazed pasture we obtained an idea of the real life cycle of *E. atra*. In spring (March-April), females which had overwintered as adults, produced eggs. These eggs gave rise to new adults (first generation) in early summer. Copulation took place during summer, and in July-August many cocoons could again be observed. Most descendants of these eggs became adult in September and October (second generation). A part of the female population is already fertilised before winter, but egg production takes place after it. So we observe two generations a year. Copulation, egg ripening and deposition, embryonal development and juvenile development all take place during the warm season. Indeed, as shown above, high temperatures are needed for fast juvenile development and also for embryonal development (cf. Van Praet & Kindt, 1979). Losses of individuals due to mass dispersal can easily be counterbalanced by the large reproduction and short development times. *E. atra* is also able to develop and reproduce at low feeding rates; therefore, as already noted earlier, it is well adapted to be an early coloniser of new habitats, where prey may be scarce, and also adapted to life in disturbed open places such as pastures and other agro-ecosystems, where a large part of the population is frequently destroyed or driven away by agricultural management and severe winter conditions.

Riechert & Lockley (1984) noticed that most spiders do not satisfy the classical predator-prey model, because this model is based on a high prey specificity of the predator. Most spiders are generalist predators. This also implies, however, that they are not dependent on the density of a given prey; they are present as a community with a more or less constant population size. Therefore and because they take prey in proportion to its availability, spiders are able to suppress the increase of their prey populations before specialists show sufficient numbers to have a distinct influence (cf. Kajak, 1965; Mansour *et al.*, 1983). For *E. atra* reproduction, food intake and also the efficiency of prey consumption are strongly correlated with the food availability. *E. atra* may thus have a density-dependent influence on its prey populations by increasing its predation rate and number of descendants when the number of prey increases. The species thus shows an immediate functional response, while the observed increase in egg production could be a starting point for a numerical response. In this way it may be able (within given limits) to control the size of its prey populations. This could be strengthened if "wasteful killing" also occurs under field conditions. The species thus possesses many characteristics of relevance to biological control.

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