Eur. J. Entomol. **102**: 169–174, 2005
ISSN 1210-5759

Time of oviposition and reproductive success in *Argiope bruennichi* (Araneae: Araneidae)

Raymond LEBORGNE and Alain PASQUET

Expression et Evolution des Comportements, UFR STB, UHP Nancy I – B.P. 239, 54506 Vandoeuvre-les-Nancy Cedex, France;
e-mail: leborgne@scbiol.u-nancy.fr

Keywords. Time of oviposition, food intake, egg production, orb-web spiders, *Argiope bruennichi*, Araneidae

Abstract. Time of oviposition and investment in reproduction output are a crucial decision for animals which could affect their fitness. In this study, the factors determining the time of oviposition and the consequences it has for clutch size and juvenile survival were investigated in the orb-web spider *Argiope bruennichi*. Egg-sacs laid at different times in the field were collected and inspected for eggs, hatching success and presence of parasites. Relationships between spider body condition, clutch size and time of oviposition were established. The influence of supplementary food on the number of eggs in a clutch and on the time of oviposition was determined both in the field and laboratory. Early clutches were larger and the eggs in late clutches were not heavier than those in early clutches indicating that spiders invested more in eggs at the beginning of the reproductive period. Furthermore, eggs in late egg-sacs were less likely to hatch and more likely to be parasitized. Clutch size was linked to spider body condition but not the time of oviposition. In the field, additional food to females resulted in larger clutches but did not influence the time of oviposition. Laboratory experiments showed that the daily rate of prey consumption affected egg oviposition.

INTRODUCTION

Fitness in animals is often dependent on time of oviposition and reproductive output. Generally, females that choose the best time to lay their eggs ensure a better development of their offspring. For example, tits adjust the time of egg laying so that their chicks occur when prey availability is most abundant (Blondel et al., 1994). Thus animals that can adapt their oviposition time to environmental conditions or body condition could be at a selective advantage.

In arthropods, many factors influence time of oviposition. Body condition determined by the quantity of food ingested could influence the time of oviposition in two ways: females may complete their development and then that of their eggs. In some species, females may be fitted if they spend more time feeding and delay laying if environmental conditions are unfavourable for their offspring (Vancassel, 1984). Female spiders determine not only the number of eggs laid but also juvenile survival through the quantity of reserves in the eggs and the time of oviposition (Vollrath, 1987; Spiller, 1992; Tanaka, 1995). Body condition may influence reproductive success as the number of eggs laid depends on female size or weight (Briceno, 1987; Higgins, 1992; Tanaka, 1995) and there is often a relationship between the number of prey ingested and number of eggs produced (Spiller, 1992; Tanaka, 1995). In spiders intersexual conflict could also influence time of oviposition. In *Stegodyphus lineatus* females delay time of oviposition to avoid male infanticide (Schneider, 1999) and plasticity in oviposition time may have evolved as a result of this type of conflict (Elgar, 1992; Schneider & Lubin, 1998).

This last model is appropriate for species of spiders that exhibit maternal behaviour: i.e. females actively guard and defend their egg-sacs. In many spiders, however, males die before the females lay eggs and the females do not guard their egg-sac (Foelix, 1996). In such species, other factors are likely to determine the time of oviposition.

Our hypothesis is that in the annual spider (*Argiope bruennichi*) the time of oviposition should be viewed as a consequence of a trade-off between the need to obtain food for egg production and the best time for oviposition to ensure juvenile survival**.** To test this hypothesis, we first established that the time of oviposition has a direct effect on reproductive success and secondly that foraging effort affects not only egg production but also the time of oviposition.

MATERIAL AND METHODS

Argiope bruennichi (Scopoli)

In Lorraine (France), *A. bruennichi* juveniles appear in spring and adult females occur from August to October. Females construct an egg-sac near their web, which is spun above the ground and attached to grass. They stay on the egg-sac for a few days and the eggs start developing immediately. Females die in October and juveniles hibernate in the egg-sac during winter. The eggs may be parasitized, mainly by the Hymenopteran *Tromatobia ornata* (Rollard, 1987). This parasite has a similar development to that of *A. bruennichi*: adults appear in autumn and the females lay their eggs inside spiders' egg-sacs where they develop and from which the adult wasps disperse the following spring (Rollard, 1987).

Production under natural conditions

The study area was fallow land 15 km west of Nancy (France). Two 100 m^2 areas were delimited and surveyed for egg-sacs twice a week, so that the date of oviposition could be determined to within three or four days. Each egg-sac was marked with a dot of paint and its position marked by a flag. The studies run for two consecutive years. In the first year all the egg-sacs were collected in December. In the second year, some of them were collected in December and others in March in order to determine the rate of egg development during winter. All egg-sacs were preserved in 70% alcohol. When these egg sacs were opened in the laboratory either only eggs, or eggs with juveniles, or only juveniles were found. Presence of parasites was noted. Total production was estimated by counting the number of eggs and juveniles in an egg-sac.

Oviposition occurred from September to October with a peak in the middle of September. During the two years of the study, a total number of 112 egg-sacs were collected. In both years, more than half were collected before September 15. After this date, the number of egg-sacs collected per day decreased. According to these observations, the oviposition period could be divided into two subperiods: egg-sacs laid before September 15, called "early egg-sacs" and after this date, called "late egg-sacs". We compared egg number and egg development in these two subperiods.

To establish the relationship between the number of eggs in an egg-sac and egg size, a supplementary set of egg-sacs were collected. They were removed along with the female if present and examined in the laboratory on the same day. As the eggs are in a compact ball wrapped in silk, it was very difficult to extract and measure them. Therefore, it was assumed that egg size was correlated with egg weight and balls of eggs extracted from the egg-sacs were weighed, dried in a drying oven (24 h at 50°C) and then reweighed. Then the eggs were separated and counted. Relationships between mean egg weight per egg-sac, egg number, and time of oviposition were determined. Females were weighed on a Sartorius balance (Basic BA 110S to 0.1 mg) and measured under a binocular microscope using a micrometer. The following features were measured: length and width of the prosoma, and length of tibia plus patella of the first leg (P1).

As these measurements do not give a good indication of a spider's state, residuals of the total weight of spiders before oviposition were regressed against each of these measurements (length of P1, width and length of the prosoma). As it was not possible to measure the weight of spiders just before oviposition, the sum of a spider's weight just after ovipovition plus that of its egg-sac was used.

Influence of food intake on the number of eggs and time of oviposition

Field experiment

This experiment was conducted in 2 plots (200 m^2 each) different from those where the egg-sacs were collected, but situated in the same biotope. Spiders were chosen at random: half of them were not manipulated and the other half received supplementary natural food (grasshoppers, weight: $\bar{x} \pm SE = 259 \pm 16$ mg, n = 102; Pasquet & Leborgne, 1990, 1998). The spiders were surveyed daily and those without web or those observed eating prey were not fed. Thirty spiders received from 1 to 8 supplementary prey items over a three weeks period.

Length and width of the abdomen of all spiders were measured at the beginning and end of the experiment using an electronic-digital calliper. These measurements were used to estimate their weight. To obtain the relationship between abdomen length and width, and weight, thirty spiders were measured, brought back to the laboratory and weighed (regression of weight on length, $R^2 = 0.79$, n = 30, $p < 0.001$, and weight on width, $R^2 = 0.81$, n = 30, $p < 0.001$).

Each female laid its egg-sac close to its web (mean distance between the web and egg-sac, $\bar{x} \pm SE = 0.42 \pm 0.11$ m, n = 13). Each egg-sac was marked with a dot of paint and its position with a flag. In December, egg-sacs were collected and brought back to the laboratory where their contents were determined.

Laboratory experiment

Thirty females were put individually into wooden frames (50×50×10 cm) enclosed by two window panes and maintained in the laboratory. The spiders were thought to be ready to feed when they built a web in the cages and were then fed grasshoppers ($\bar{x} \pm SE = 124 \pm 2$ mg, n = 234). After prey consumption, the prey remains rejected by the spiders were weighed. The difference in the fresh weight of the prey and the remains was used as the measure of the quantity of food ingested. The experiment lasted until the spiders laid at least one egg-sac. Egg-sac content was determined as previously.

RESULTS

Time of oviposition and reproductive success

Number of eggs and/or juveniles

Number of eggs (and/or juveniles) per egg-sac differed significantly between the two years (Two way ANOVA $F_{2,112} = 8.9$, $p < 0.01$, first year $\bar{x} \pm SE = 201 \pm 14$, n = 44, second year $\bar{x} \pm SE = 146 \pm 9$, n = 68). Early egg-sacs contained more eggs than the later ones ($F_{2,112} = 10.3$, $p < 0.01$, early egg-sac $\bar{x} \pm SE = 190 \pm 10$, n = 61, late egg-sac $\bar{x} \pm SE = 141 \pm 12$, n = 51) in both years (interaction between year and egg-sacs $F_{2,112} = 0.3$, ns).

Relationships between number of eggs and egg weight

The above results showed that spiders produce more eggs at the beginning of a season, but in terms of fitness this could be offset if the spiders invest more reserves in the late produced eggs. To determine if this is the case, thirty-three egg-sacs were collected just after oviposition. The mean dry mass per egg for each egg-sac was deter-

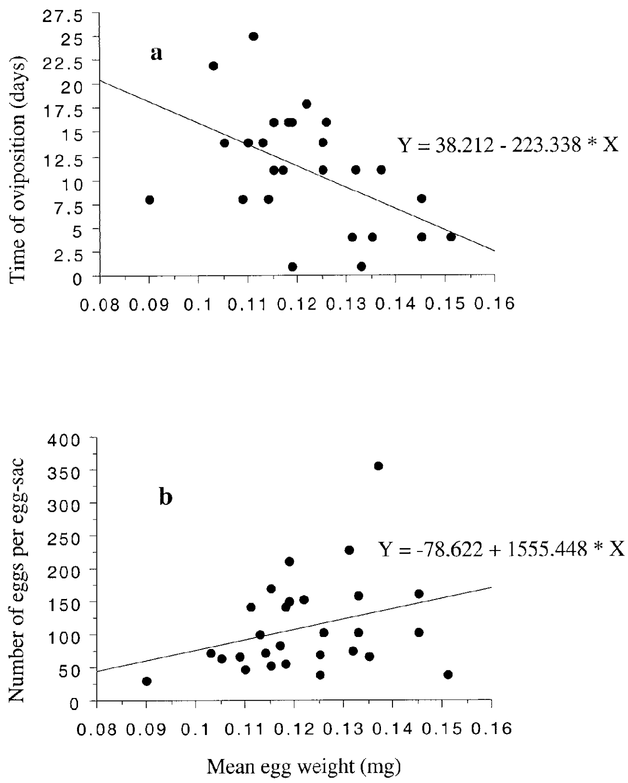

Fig. 1. Dependence of (a) the time of oviposition and (b) the number of eggs per egg-sac on mean egg weight (mg).

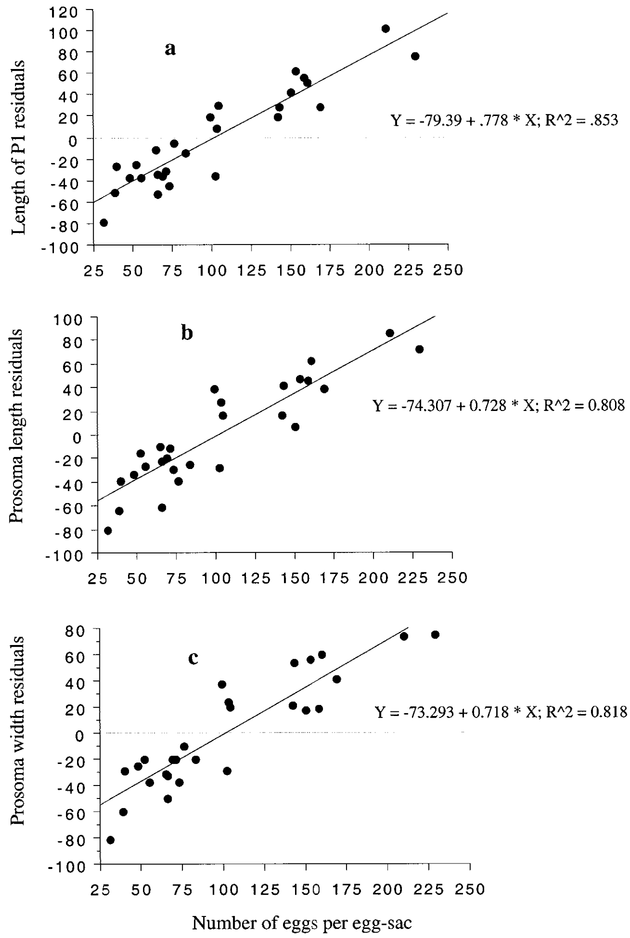

Fig. 2. Dependence of the residuals of the body characteristics (against spider body weight) of the spiders after laying on the number of eggs per egg-sac (a: length of the P1, b: length of the prosoma and c: width of the prosoma).

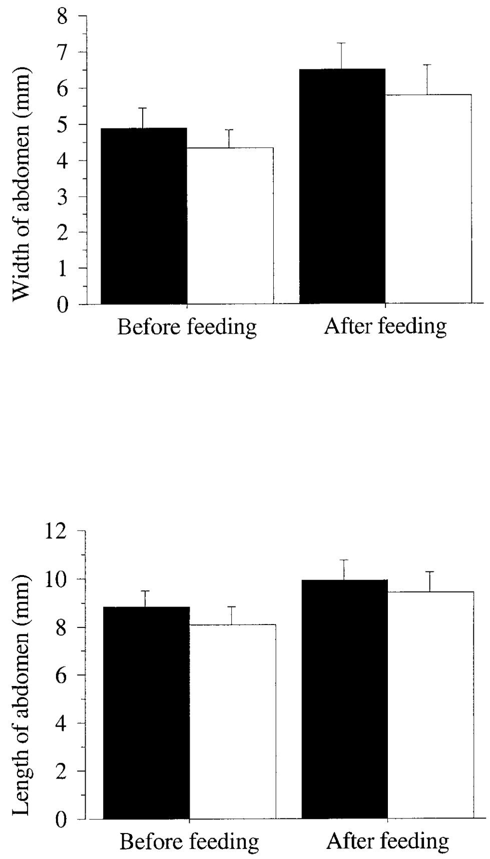

Fig. 3. Characteristics of fed (black) and non-fed (white) spiders in the field experiment.

mined by dividing the total mass of dry eggs by the number of eggs. This decreased with time (Fig. 1a, $R^2 = 0.182$, $F = 6.90$, $n = 33$, $p = 0.01$). Moreover, there was a tendency for the mean dry egg mass to increase with the number of eggs per egg-sac (Fig. 1b, $R^2 = 0.091$, $F = 3.09$, $n = 33$, $p = 0.09$). This suggests that early egg-sacs contained more and larger eggs than late egg-sacs. Thus, the reproductive effort was greatest at the beginning of the season.

Table 1. Number of early and late egg-sacs collected in December and March that contained eggs, juveniles or juveniles and eggs. Early and late egg-sacs are defined according to the time of oviposition, before or after mid September (see Methods).

	First year		Second year			
	Collected in December		Collected in December		Collected in March	
	Early	Late	Early	Late	Early	Late
Juveniles	15	3	15	8	18	6
Eggs	0	18	1	11	0	5
Juveniles + Eggs	8	0	4	0	0	0
Total	23	21	20	19	18	11

Development of the eggs

During the two years, 112 egg-sacs were collected of which only 12 contained juveniles and eggs (Table 1). These 12 egg-sacs were all early egg-sacs and contained between 60% and 98% of juveniles and were not included in the analysis comparing egg-sacs with juveniles or eggs only.

In the first year, 100% of the early egg-sacs contained juveniles compared to only 14% of the late egg-sacs (Table 1, Fisher's exact test, $p < 0.0001$). In the second year, results were similar whatever the date of collection (Table 1, Fisher's exact test, December 95% vs 42%, $p = 0.0004$; March 100% vs 54%, $p = 0.004$). Combining the results for both years, 98% of the early egg-sacs contained juveniles compared to only 33% of the late egg-sacs. For the late egg-sacs, there was no difference in the proportion with juveniles of those collected in December and in March (42% vs 54%, Table 1, Fisher's exact test, $p = 0.70$). Thus, time of oviposition determined egg development, which ceased during winter.

Parasitism

Percentage of parasitism (number of egg-sacs parazited/total number of egg-sacs collected) differed in the two years (21% vs 43%, Fisher's exact test, p =

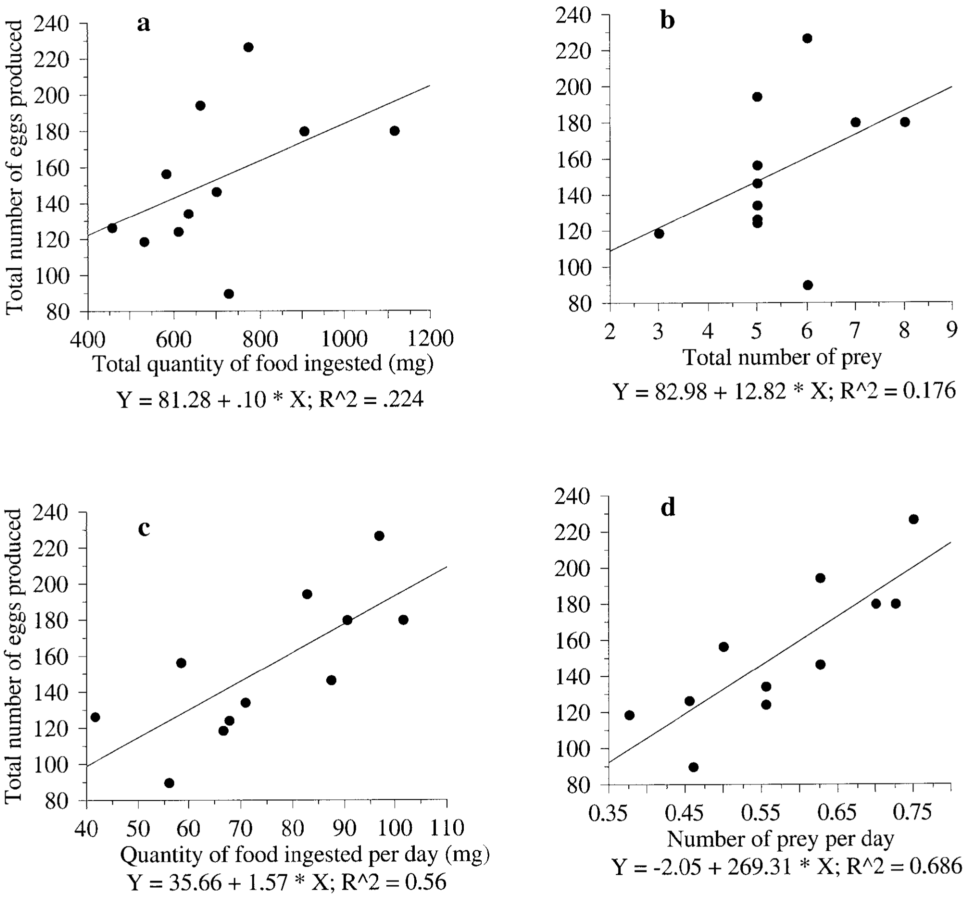

Fig. 4. Relationships between the number of eggs in the first egg-sac and quantity of food ingested in terms of: a: total quantity of food ingested, b: total number of prey eaten, c: mean quantity of food ingested per day, d: mean number of prey per day.

0.008). In the first year parasitism was higher for late than for early egg-sacs (32% vs 8%, Fisher's exact test, $p = 0.047$), but there was no difference in the second year (41% vs 44%, Fisher's exact test, $p = 1$).

In conclusion, the time of oviposition was directly linked to production and egg development. Females that reproduced early laid more and larger eggs, which were more likely to start developing immediately.

Food intake and egg production

Relationships between body condition and production

Production (number of eggs) was not directly correlated with spider size (number of eggs vs length of P1(a): $R^2 = 0.090$, $F = 0.21$, $n = 27$, $p = 0.65$, vs prosoma length: $R^2 = 0.030$, $F = 0.78$, $n = 27$, $p = 0.38$, vs prosoma width: $R^2 = 0.034$, $F = 0.88$, $n = 27$, $p = 0.36$), but highly correlated with body condition (see methods) whatever the size characteristic of spiders was used (Fig. 2, number of eggs vs length of P1 residuals (a): $R^2 = 0.853$, $F = 145.2$, $n = 27$, $p < 0.0001$, vs prosoma length residuals (b): $R^2 = 0.808$, $F = 102.1$, $n = 27$, $p < 0.0001$, vs prosoma width residuals (c): $R^2 = 0.818$, $F = 112.5$, $n = 27$, $p < 0.0001$).

In a natural population, the time of oviposition was not correlated with spider body condition (time of oviposition vs length of P1 residuals: $R^2 = 0.009$, $F = 0.22$, $n = 27$, $p = 0.64$, vs prosoma length residuals: $R^2 = 0.013$, $F = 0.32$, $n = 27$, $p = 0.57$, vs prosoma width residuals: $R^2 = 0.026$, $F = 0.57$, $n = 27$, $p = 0.42$).

Field experiment

The field experiment tested the influence of food intake on production and time of oviposition. While it was not possible to weigh the spiders in this experiment, abdomen size (measured in the field) was used (see methods). Prior to feeding spiders, there was no difference in abdomen: size of the spiders in the two areas (length of abdomen: t-test, $t = 0.40$, $df = 33$, $p = 0.69$, width: t-test $t = 0.81$, $df = 33$, $p = 0.42$) so the data were pooled for the analysis. Before feeding, abdomen size of the spiders of the fed group did not differ from those of the non-fed group (Fig. 3; t-test, length: $t = 1.3$, $df = 33$, $p = 0.20$, width: $t = 1.5$, $df = 33$, $p = 0.14$). After feeding, the abdomen of all the spiders increased in size to the same extent in both groups (Fig. 3; t-test, length: $t = 1.6$, $df = 33$, $p = 0.12$, width: $t = 1$, $df = 33$, $p = 0.33$). Although feeding did not affect the spider abdomen size of all the spiders, fed spiders did produce more eggs per egg-sac (result for the first egg-sac of each spider; fed spiders $\bar{x} \pm SE = 189 \pm 14$, $n = 14$, non fed spiders $\bar{x} \pm SE = 125 \pm 27$, $n = 11$, t-test, $t = 1.97$, $df = 23$, $p = 0.032$).

There was no difference between fed and non fed spiders in the delay between the start of feeding and time of oviposition (fed spiders, $\bar{x} \pm SE = 6.8 \pm 0.8$ days, $n = 13$, non-fed spiders, $\bar{x}$ ±SE = 8.3 ± 1.5 days, n = 7, t-test, t = 0.93, df = 18, p = 0.36).

Laboratory experiment

Of the thirty spiders brought back to the laboratory, twenty-nine captured and ingested prey; eight laid one egg-sac and three laid two egg-sacs. At the beginning of the experiment, there was no difference in weight between spiders that produced an egg-sac ($\bar{x}$ ± SE = 75 ± 8 mg, n = 11) and those that did not ($\bar{x}$ ± SE = 96 ± 11 mg, n = 18, t-test = 1.3, df = 27, p = 0.20). Spiders that produced at least one egg-sac ate more prey ($\bar{x}$ ± SE = 12 ± 1, n = 11, and $\bar{x}$ ± SE = 6 ± 1, n = 18, t-test, t = 4.8, df = 27, p < 0.001) and ingested more food ($\bar{x}$ ± SE = 1485 ± 165 mg, n = 11, and $\bar{x}$ ± SE = 705 ± 67 mg, n = 18, t-test, t = 4.3, df = 27, P < 0.002) than those that did not produce an egg-sac. There was no relationship between the number of eggs in the first egg-sac and the total number of prey eaten (Fig. 4a, F = 1.92, R^2 = 0.17, n = 11, p = 0.20) or the quantity of food ingested (Fig. 4b, F = 2.60, R^2 = 0.22, n = 11, p = 0.14), but a highly positive correlation with the rate of prey capture (mean number of prey per day) (Fig. 4c, F = 19.70, R^2 = 0.69, n = 11, p = 0.001) and the mean daily food intake (Fig. 4d, F = 11.47, R^2 = 0.56, n = 11, p = 0.008).

DISCUSSION

Our results confirm the suggestion of Vollrath (1987) that relationships exist between foraging decisions, development and fitness. In conclusion, body condition and food intake in *A. bruennichi* influence egg production but not the time of oviposition.

Many different factors influence the time of oviposition: level of resources for juveniles, body condition of the female, conflict between the sexes, mating strategy, egg parasitism… As in most species of spiders, *A. bruennichi* starts ovipositing after the males have disappeared. So in this case, time of oviposition could not be a response to conflict between the sexes (Schneider, 1999). In spiders it is known that body condition influences the number or the size of the eggs (Briceno, 1987; Spiller, 1992; Spence et al., 1996). This was confirmed for *A. bruennichi* in which an increased consumption of food resulted in a greater number of eggs being produced. The results presented here are also the first clear evidence that body condition does not influence the oviposition time.

The supplying of prey to *A. bruennichi* indicated that the time of oviposition is not determined by the last meal. The time to oviposition is possibly the time required by females to develop their ovaries and not a response to an abundance of prey.

Our data shows that the spiders do not modify their investment in eggs depending on the time of oviposition. Thus *A. bruennichi* appears to be unable to compensate by producing fewer but higher quality eggs late in the season. However, as egg composition was not determined, it is unknown whether spiders can vary the reserves they put in the eggs, but the dry mass of the eggs was higher for the early than for the late clutches. Thus, even if the opportunity to change egg composition exists the early breeding spiders invest more in eggs than the late breeders.

In this species, eggs start developing immediately after laying, and after about two weeks hatch produce mobile, coloured first instars spiders (Rollard, 1987). These young spiders stay in the egg-sac until they disperse the following spring: all the juveniles leave the egg-sacs at the same time which does not depend on the time of oviposition.

Two hypotheses could be proposed to account for early oviposition

First, the cost of parasitism: the incidence of parasitism varied from year to year but it was important (up to 44% of the egg-sacs were parasitized), the more so for late laid egg-sacs. In France, the life cycle of the main parasite of *A. bruennichi* egg-sacs (*Tromatobia ornata*) is very similar to that of the spider. Adult females of *T. ornata* lay their eggs in autumn and their juveniles emerge the following spring (Rollard, 1987). The coincidence in the time of oviposition of both the host and the parasite means the spider is likely to be parasitized if the parasite is present. But as only egg-sacs with eggs were parasitized by *T. ornata* (Rollard, 1987), females of *A. bruennichi* that lay their eggs early have an advantage as their eggs may complete their development before the parasite attacks.

Secondly, a period of cold temperature just after egg laying could delay egg development (see late egg-sac). In this case the time of oviposition is very important and there is a clear benefit of laying before the onset of cold conditions.

Our results show that the time of oviposition is essential for egg development; but nevertheless some spiders laid their eggs late in the season. This may be because *A. bruennichi* is more common in the south and west of Europe where the climatic conditions are more favourable (in particular the winters are not so cold) than in the east of France. This species is now considered to be an invasive species and to have recently spread (during the last decades) into the northern and eastern parts of France (Nancy) and as a consequence is now exposed to new factors of selection.

ACKNOWLEDGEMENTS. This work was funded by a grant from the French Ministry of Research and from the CNRS (URA CNRS, n°1293). We thank Y. Lubin (Mitrani Center for Desert ecology, Sede Boker Campus, Israel) and anonymous referees for their helpful comments on an earlier draft of this manuscript.

REFERENCES

BLONDEL J., DIAS P., LAMBRECHTS M., MAISTRE M., PERRET P. & CARTAN-SON M. 1994: Les oiseaux dans leur habitat. *La Recherche* **25**: 528–536.

BRICENO R.D. 1987: How spiders determine clutch size? *Rev. Biol. Trop*. **35**: 25–29.

ELGAR M.A. 1992: Sexual cannibalism in spiders and other invertebrates. In Elgar M.A. & Crespi B.J. (eds):

Cannibalism: Ecology and Evolution among Diverse Taxa. Oxford University Press, Oxford, pp. 128–155.

FOELIX R.F. 1996: *Biology of Spiders. 2nd ed.*Oxford University Press, Oxford, 384 pp.

HIGGINS L.E. 1992: Developmental plasticity and fecundity in the orb-weaving spider Nephila clavipes. *J. Arachnol.* **20**: 94–106.

PASQUET A. & LEBORGNE R. 1990: Prey capture and prey selection from insects intercepted by trap in four orb-weaving spider species. *Acta Oecol.* **11**: 513–523.

PASQUET A. & LEBORGNE R. 1998: Behavioral tactics for prey capture and prey ingestion in two sympatric spiders. *Netherl. J. Zool.* **48**: 39–52.

ROLLARD C. 1987: *La biocénose associée aux Araneides en landes armoricaines. Etude des relations Insectes-Araignées.* PhD. Thesis, University of Rennes, France.

SCHNEIDER J.M. 1999: Delayed oviposition: a female strategy to counter infanticide by males? *Behav. Ecol.* **10**: 567–571.

SCHNEIDER J.M. & LUBIN Y. 1998: Intersexual conflict in spiders. *Oikos* **83**: 496–506.

SPENCE J.R., ZIMMERMANN M. & WOJCICKI J.P. 1996: Effect of food limitation and sexual cannibalism on reproductive output of the nursery web spider Dolomedes triton (Araneae, Pisauridae). *Oikos* **75**: 373–382.

SPILLER D.A. 1992: Numerical response to prey abundance by Zygiella x-notata. (Araneae, Araneidae). *J. Arachnol.* **20**: 179–188.

TANAKA K. 1995: Variation in offspring size within a population of the web-building spider Agelena limbata. *Res. Popul. Ecol.* **37**: 197–202.

VANCASSEL M. 1984: Plasticity and adaptative radiation of dermapteran parental behaviour: results and perspectives. *Adv. Stud. Behav.* **14**: 51–80.

VOLLRATH F. 1987: Growth, foraging and reproductive success. In Nentwig W. (ed.): *Ecophysiology of Spiders.* Springer, Berlin, pp. 357–370.

Received October 11, 2004; revised and accepted December 8, 2004