PARAMETERS AFFECTING FECUNDITY OF *LOXOSCELES INTERMEDIA* MELLO-LEITÃO 1934 (ARANEAE, SICARIIDAE)

Marta L. Fischer: Departamento de Biologia, Centro de Ciências Biológicas e da Saúde, Pontifícia Universidade Católica do Paraná. Núcleo de Estudos do Comportamento. Av. Silva Jardim, 1664/1101–CEP 80250–200–Curitiba, Paraná, Brazil. E-mail: nephilla@terra.com.br

João Vasconcellos-Neto: Departamento de Zoologia, Instituto de Biologia– Universidade Estadual de Campinas–UNICAMP–C.P. 6109–Campinas, São Paulo, Brazil. CEP 13083–970, Brazil.

ABSTRACT.   In this study, the process of egg sac construction and the factors that determine fecundity in the spider *Loxosceles intermedia* were analyzed by comparing lab-reared females that had mated only once ($n = 180$ ovipositions) and females with unknown reproductive histories ($n = 76$ ovipositions). Among females known to have mated only once ($n = 84$), the number of viable eggs correlated positively with the duration of mating and with the age of the female at the time of fertilization and decreased significantly with successive ovipositions. In females with unknown ($n = 36$) reproductive histories, up to three fertile egg sacs were obtained from the same female with a third oviposition being observed only once. Oviposition was more frequent among larger females than smaller females. Among the reproductive variables evaluated, there were correlations between the number of eggs and the weight of the female spiders. More fertile eggs were laid by females with unknown reproductive histories than by females that mated only once. The existence of more stable environmental conditions, abundant food, and multiple fertilizations are probable factors which favor greater fertility of *L. intermedia* in urban Curitiba, located in southern Brazil, and can partly explain the success of this species in occupying this ecological niche.

Keywords: Ovipositions, fertility, reproduction, mating success

Spider egg sacs protect developing eggs against abiotic (temperature, luminosity and relative humidity of the air) and biotic (predators and parasites) factors. Egg sac construction is a rigidly controlled and programmed behavior (Foelix 1996). Fecundity is often defined as the number of eggs or offspring an animal produces during each reproductive cycle (Begon et al. 1990). Various studies have examined fecundity in spiders (Cooke 1965; Levy 1970; Muniappan & Chada 1970) and, according to Downes (1985), the estimates of fecundity should include the number of emerged spiderlings and all of the individuals in different stages of development which belong to the same ovisac, including undeveloped eggs. Inter- and intraspecific variation in fecundity have been attributed to factors such as foraging success (Figueira & Vasconcellos-Neto 1993), temperature and humidity (Downes 1988), and photoperiod (Miyashita

1987). In addition, individual variation in reproduction have been attributed to factors such as size, age and physiological state of the female (Turnbull 1962; Eberhard 1979; Capocasale et al. 1984; Costa & Capocasale 1984; Fritz & Morse 1985), energy investment (Hoffmaster 1982), parental care (Enders 1976; Christenson & Wenzl 1980; Krafft 1982; Opell 1984; Nuessly & Goeden 1984; Downes 1984; Fink 1986; Ruttan 1991), spermatic depletion (Jackson 1978) and reproductive tactics (Killebrew & Ford 1985). Quantitative and qualitative fertility studies have been done in the laboratory for some Araneae species (Christenson et al. 1979; Downes 1985, 1987; Gonzales 1989; Willey & Adler 1989; Suter 1990; Wheeler et al. 1990). For this study, in which we examined a variety of factors that may influence reproductive success in *Loxosceles*, we defined fecundity as the total reproductive effort of the female (including multiple clutches).

The genus *Loxosceles* is cosmopolitan and is frequently associated with human settlements where the physical and environmental conditions favor an increase in the spider populations. Despite the medical importance of many species of this genus and their synanthropic habits, only a few studies have examined fecundity in *Loxosceles* species. These studies recorded only the number of eggs for *L. rufipes* (Lucas 1834) (Delgado 1966), *L. reclusa* Gertsch & Mulaik 1940 (Hite et al. 1966; Horner & Stewart 1967), *L. laeta* (Nicolet 1849) (Galiano 1967; Galiano & Hall 1973), *L. gaucho* Gertsch 1967 (Bücherl 1961; Rinaldi et al. 1997) and *L. hirsuta* Mello-Leitão 1931 (Fischer & Marques da Silva 2001). A comparative study of the number of eggs laid by *L. intermedia* and *L. laeta* was done by Andrade et al. (2000). Some of the studies (e.g., Bücherl 1961, Galiano 1967, Delgado 1966, Andrade et al. 2000) used spiders with unknown reproductive histories for characterization of fecundity of the respective species. The city of Curitiba (lat. 25°25′48″ S and long. 49°16′15″ W), capital of the Brazilian state of Paraná, has a large population of *Loxosceles* that is responsible for hundreds of bites each year, with the species being either: *L. intermedia* (90% of collections) or *L. laeta* (10% of collections) (Fischer 1994). The species *L. intermedia* has a restricted distribution to the south and southeast of Brazil. The wide distribution in the city and predominance of *L. intermedia* over *L. laeta* is related to many factors such as the more generalist habits of *L. intermedia*, as well as temperature and humidity favorable to *L. intermedia*. However, little is known of the factors which affect female fecundity in this species. In this study, we examined the reproductive potential and factors that affect the egg viability of *L. intermedia* females. These data will be useful for future experimental studies as well as management plans for the spiders to minimize spider bites. For the present study we compared the reproductive output of lab-reared females known to have mated once with virgin males (both males and females born and raised in laboratory, with known feeding history) with wild-caught adult females (number of mates, age and feeding history unknown).

METHODS

Egg sac construction.—Details of egg sac construction were observed in ten females chosen randomly, based on direct *ad libitum* observations.

Fecundity of females reared in the lab and mated once.—The fecundity of 84 females born, raised and mated once in the laboratory was evaluated. And, because we had detailed information about mating and maturation of these spiders, we looked at correlations of fecundity with duration of mating and age of the females. The spiders used in this study were kept in the laboratory from November 1994–December 1999. The spiders were maintained at ambient temperature 21.4 ± 2.3 °C, $n = 19$; range = 16.2–24.7 °C, air humidity 73.9 ± 11.4%, $n = 19$; range = 57.8–95.7 with lighting from 12:12 L:D cycle. The air temperature and relative humidity were monitored daily using a thermohydrograph. Young spiders were kept in 120 ml plastic containers (diameter of base 4.8 cm). All spiders were fed up to the 4th instar a standardized diet consisting of two larval and adult *Drosophila melanogaster* twice a week. After the 4th instar, the spiderlings were fed two *Tenebrio molitor* larvae twice a week and were placed in plastic containers (750 ml), lined with paper and kept in a laboratory in the Department of Zoology at Federal University of Paraná.

Once mature, the virgin females were each mated once with virgin males that had also been raised in laboratory. The mating of all the couples ($n = 84$) was induced during January–April 1996. The virgin females copulated with a single male and the duration of mating was the time that the embolous were inserted in the receptacles of the female, in a single encounter, typically 1289 ± 822 sec, $n = 84$; range = 73–3733 sec (Fischer & Vasconcellos-Neto 2000). Once the females had been mated and egg sacs constructed, the egg sacs were maintained with the female, at the site of oviposition, until spiderlings had emerged from the egg sacs. The relationships between the total number of eggs, the number of spiderlings, and the number of unhatched eggs versus the duration of mating and age of the female were examined.

Fecundity of wild-caught females with unknown reproductive histories.—Sixty four females were collected from residences in Curitiba and maintained in the laboratory until egg sacs were deposited. For this portion of the study we were most interested in cor-

relation in body size with fecundity. Mature spiders were collected from March–June 1994 and were maintained in individual containers. Temperature ranged from 18 °C to 29 °C and air humidity ranged from 63–88% humidity (details in Tables 4 & 5) from June 1994–November 1995. Temperature and humidity were measured for each individual. The egg sacs were laid between September 1994–March 1995. Thirty six of the 64 females constructed egg sacs. When the spiderlings emerged, they were weighed and fixed in 70% alcohol. In order to evaluate the influence of the weight of the female on her fecundity, the adult female was weighed to the nearest 0.1 mg an analytical electronic balance immediately after oviposition. In addition we measured cephalothorax area (length $\times$ width in mm) and the femur length of right leg I using a stereoscopic microscope with an ocular micrometer.

The number of hatched eggs was considered as an index of egg viability. Besides this index we also measured number of egg sacs, the total number of eggs, unhatched eggs, spiderlings, and the duration of incubation. We investigated correlations of these variables with female cephalothorax area (mm^2), female weight after oviposition, spiderling weight, average of natural temperature and relative humidity during the incubation period, and the time between consecutive ovipositions.

Statistical analysis.—The chi-squared test was used to assess differences between the number of females that laid eggs and those which did not, relative to their size. For this, the females were divided into two groups, i.e. those with a cephalothorax area less than or greater than 15 mm^2. Matrix correlations and multiple linear regression were used to examine the relationships between the parameters and the fecundity variables in females with unknown reproductive histories. Student's t test was used to compare the fecundity parameters between consecutive ovipositions when the variances were homogeneous and the Kruskal-Wallis (H) test was used when variances were not homogenous. The Mann-Whitney (U) test was used to compare the fecundity parameters between females with only one fertilization and those with unknown reproductive histories.

Male and female voucher specimens are deposited in Arachnological collection Dra. Vera Regina von Eicksted in the section of poisonous arthropods of the Imunologic Production and Research Center (SESA-PR), Piraquara, Paraná, Brazil.

RESULTS

Egg sac construction.—Egg sac construction began with the substrate being covered with thin silk threads. The female spider moved in circles with the abdomen directed towards the center of the web in order to join the radiating points. The female subsequently positioned herself vertically to begin egg laying. Approximately 30 min later, as soon as the egg mass became granular and the outline of each egg was visible, the spider started to construct the cover. The abdomen was placed over the eggs and threads were woven attaching the apex of the egg mass to the substrate. The abdomen was moved left to right and up and down, with the body being turned clockwise and counter-clockwise. Construction of the cover required about 4 h ($n = 10$). The first silk was similar to that of the substrate, with thicker threads being added through movements of the abdomen, legs and pedipalps. After finishing the construction, the female rested, and positioned herself over or next to the egg sac.

The egg sacs were disc-shaped and whitish, with an average diameter of 18.8 ± 1.1 mm ($n = 25$; range = 14–20). The egg mass had an average diameter of 9.9 ± 2.4 mm ($n = 25$; range = 8–15 mm) with a domed arrangement, and the eggs had an average diameter of 0.99 ± 0.01 mm ($n = 25$; range = 0.06–1).

Fecundity of females reared in the lab and mated once.—In this study, 180 egg sacs were obtained from 84 females from February 1996–February 1998. Three peaks of egg-laying were observed (October and December 1996, and March 1997) (Fig. 1).

Of the 84 mated females, 75 (89%) laid egg sacs. Of these, 61.1% ($n = 110$) were viable (spiderlings emerged); 21.1% ($n = 38$) were destroyed by the females (the eggs were eaten) before eclosion and in 17.8% ($n = 32$) the eggs dried out. In 41% ($n = 75$) of the spiders, only one egg sac was constructed. However many also laid between two and six egg sacs 31.1% ($n = 56$) laid two egg sacs, 22.2% ($n = 40$) laid three, 5% ($n = 9$) laid four, 1.6% ($n = 3$) laid five while one female laid a 6th
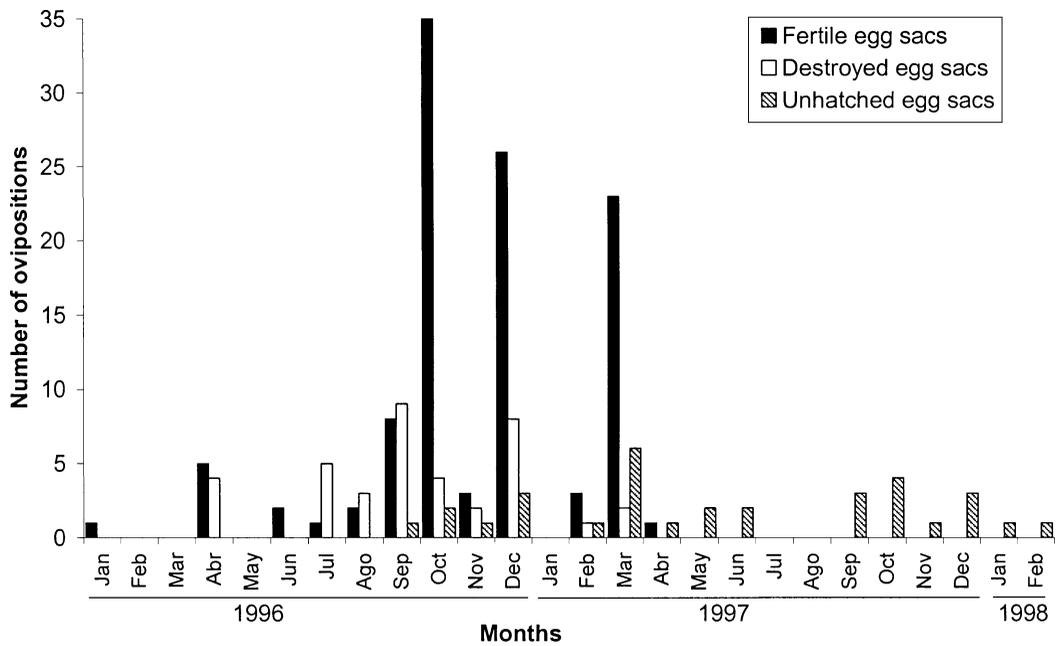
Figure 1.—Ovipositions (fertile, destroyed and non-ecloded eggs) of 75 *L. intermedia* females with known reproductive histories. The dates were obtained in the laboratory from February 1996–February 1998.

egg sac. Fertile egg sacs were not obtained in the 5th and 6th ovipositions (Table 1).

Fertile egg sacs had an average incubation time of 50.4 ± 11.7 days ($n = 110$; range = 30–106), an average number of spiderlings of 20.4 ± 21.1 ($n = 110$; range = 1–110) and an average number of non-ecloded eggs of 10.8 ± 13.8 ($n = 108$; range = 0–68). The average rate of egg viability was $70.2 \pm 30.9\%$ ($n = 108$; range = 4.2–100%). The results obtained in successive ovipositions are shown in Table 2. The number of viable eggs had a slight but significant positive correlation with the time spent in mating 1280 ± 836 sec ($n = 75$; range = 73–3757) ($r^2 = 0.123$; $P <$

0.01) and with the age of the female spider at the time of mating 490 ± 39.9 days ($n = 75$; range = 245–551) ($r^2 = 0.054$; $P < 0.05$). The period of latency (period between two ovipositions) was not correlated with the total number of eggs in any of the ovipositions.

The number of viable eggs decreased in successive ovipositions (H = 10.3; $P < 0.01$), and the latency period increased from the 2nd oviposition onwards (H = 71.8; $P < 0.0001$). However, the length of incubation (H = 5.3; $P > 0.05$) and the number of unhatched eggs (H = 5.1; $P > 0.05$) were not significantly different.

Fecundity of wild-caught females with

Table 1.—Relative frequency of fertile, destroyed and dried egg sacs in successive ovipositions by female *L. intermedia* fertilized only once.

Egg sacs	1st oviposition	2nd oviposition	3rd oviposition	4th oviposition	5th oviposition	6th oviposition
Fertile	63.5%	66.7%	66.7%	11.1%	0	0
	($n = 47$)	($n = 36$)	($n = 26$)	($n = 1$)		
Destroyed	27%	24%	10.2%	0	33.3%	0
	($n = 20$)	($n = 13$)	($n = 4$)		($n = 1$)	
Dried	9.5%	9.3%	23.1%	88.9%	66.7%	100%
	($n = 7$)	($n = 5$)	($n = 9$)	($n = 8$)	($n = 2$)	($n = 1$)

Table 2.—Fecundity parameters for *L. intermedia* females known to have mated only once. (The values are the mean $\pm$ s.e. with the sample size (*n*) and range in parentheses.)

Egg sacs	1st oviposition	2nd oviposition	3rd oviposition	4th oviposition	5th oviposition	6th oviposition
Incubation (days)	52.8 $\pm$ 14.5 (47; 33–106)	50.6 $\pm$ 10.3 (36; 30–80)	45.4 $\pm$ 4.7 (26; 31–53)	48 (*n* = 1)	—	—
Spiderlings	36.5 $\pm$ 21.8 (47; 1–110)	26.4 $\pm$ 22.5 (36; 2–77)	22 $\pm$ 14.2 (26; 1–59)	20 (*n* = 1)	—	—
Unhatched eggs	7.4 $\pm$ 8.8 (47; 0–42)	16.8 $\pm$ 19.4 (36; 0–68)	9.1 $\pm$ 9.4 (26; 0–35)	0 (*n* = 1)	—	—
Latency (days)	173.5 $\pm$ 81.8 (75; 25–656)	69.2 $\pm$ 45.6 (36; 11–238)	71.9 $\pm$ 50.6 (26; 10–212)	114.4 $\pm$ 66.1 (9; 32–239)	153 $\pm$ 107.1 (3; 75–203)	1142 (*n* = 1)

unknown reproductive histories.—From the 64 females collected, 36 constructed egg sacs (56.2%). Of these, 20 laid multiple egg sacs. A total of 76 egg sacs were observed between September 1994 and March 1995. Of these, 57 were viable and 19 were destroyed by the females (Fig. 2).

Oviposition was more frequent among larger females (χ^2 = 7.53; P < 0.01; df = 1) than smaller females (χ^2 = 0.95; P > 0.05; df = 1) (Fig. 3). In females with unknown reproductive histories, up to three fertile egg sacs were obtained from the same female with a third oviposition being observed only once.

The average number of days between consecutive ovipositions was 68.8 $\pm$ 26 days (*n* = 20; range = 18–136 days). In our sample, 36.8% of the ovipositions showed 100% hatching, with the average percentage of nonviable eggs per egg sac being 17.5 $\pm$ 28.5% (*n* = 57; range = 0–97%). The average *L. intermedia* egg viability (proportion of hatching eggs per egg sac) was 81.4 $\pm$ 30.9% (*n* = 57; range = 1–100%) (Tables 3, 4). The number of eggs (t = 1.6; P > 0.05; df = 54), spiderlings (t = 1.1; P > 0.05; df = 54) and non-viable eggs (t = 0.53; P > 0.05; df = 54) did not significantly differ between the first
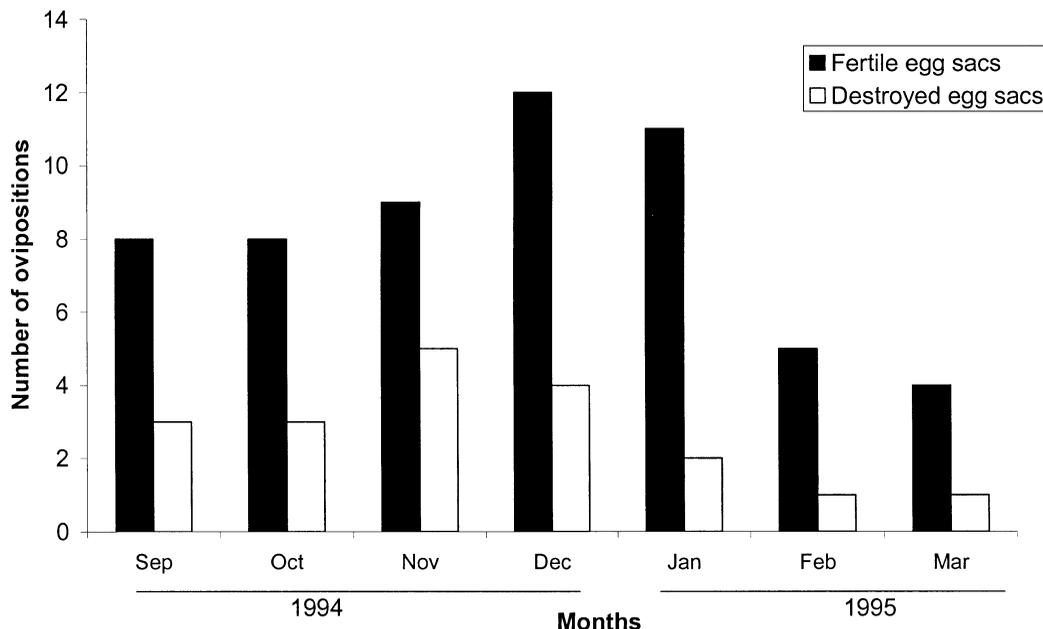

Figure 2.—Ovipositions by 36 *Loxosceles intermedia* females of unknown reproductive histories in the laboratory, from September 1994–March 1995.
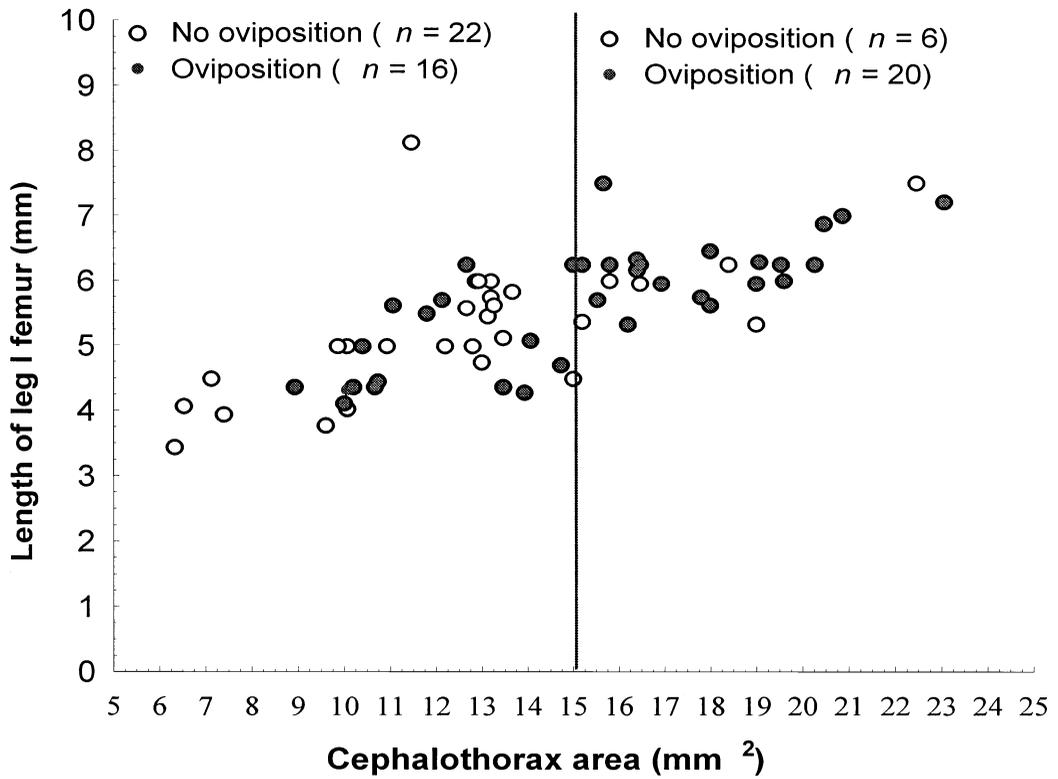
Figure 3.—Relationship between the sizes of female *Loxosceles intermedia*, leg I femur length and cephalothorax area with an unknown reproductive history and the tendency to lay eggs.

Table 3.—Fecundity in the laboratory for *Loxosceles intermedia* with an unknown reproductive history (the values are the mean ± SD with the sample size (*n*) and range in parentheses).

	1st oviposition		2nd oviposition		3rd oviposition		Total	
	n	Average	*n*	Average	*n*	Average	*n*	Average
	48		27		1		76	
# of egg sacs								
# of fertile egg sacs	36		20		1		57	
# of destroyed egg sacs	12		7		—		19	
Total number of eggs	1908	53 ± 23.3 (36; 6–92)	62	43.1 ± 19 (20; 8–84)	—	47 (*n* = 1)	2823	49.4 ± 21.9 (57; 6–92)
Spiderlings	1591	44.2 ± 17 (36; 2–92)	30	36.5 ± 21 (20; 7–84)	—	30 (*n* = 1)	2351	41.2 ± 25 (57; 2–92)
Egg viability (%)	—	80.3 ± 31 (36; 2–100)	—	85.7 ± 25 (20; 15–100)	—	64 (*n* = 1)	—	81.8 ± 28 (57; 2–100)
Undeveloped eggs	317	8.2 ± 15.9 (36; 0–80)	32	6.6 ± 11.8 (20; 0–41)	—	36 (*n* = 1)	466	8.5 ± 14.9 (57; 0–80)
Incubation time (days)	—	46.2 ± 9.5 (32–45)	—	47.9 ± 14.1 (20; 37–92)	—	65 (*n* = 1)	—	47.1 ± 11.4 (57; 32–92)

Table 4.—Variables for fertile egg sacs from *L. intermedia* with unknown reproductive histories maintained in the laboratory (September 1994–March 1995). (The values are the mean ± SD with the sample size (*n*) and range in parentheses.)

	n	Mean ± SD	Range
Female cephalothorax area (mm^2)	57	15.5 ± 3.7	8.9–23.1
Female weight (mg)	57	103.9 ± 53.4	34.6–264
Spiderling weight (mg)	57	0.078 ± 0.048	0.001–0.0024
Temperature during the incubation period (°C)	57	23.8 ± 2.1	20.9–29.2
Air humidity during the incubation period (%)	57	72.6 ± 5.5	63.3–88.7
Latency between ovipositions (days)	20	68.8 ± 25.8	18–136

and second ovipositions (Tables 3, 4), despite a tendency to increase.

The length of incubation appeared to be related to air temperature and relative humidity. Most of the fertile ovipositions were incubated at 21 °C to 27 °C at a relative air humidity of 64–76%. Larger females tended to deposit more eggs ($r^2 = 0.062$; $P = 0.06$; $n = 57$; df = 56), with a slight but significant correlation between female weight *vs* the number of eggs ($r^2 = 0.072$; $P < 0.05$; $n = 57$; df = 56).

There was no correlation between spiderling weight or latency to oviposition and the total number of eggs, spiderlings or non-viable eggs. ($r^2 = 0.008$, $P = 0.4$, df = 105; $r^2 = -0.0003$, $P = 0.3$, df = 105; $r^2 = -0.018$, $P = 0.9$, df = 105 and $r^2 = 0.003$; $P = 0.2$, df = 105; $r^2 = 0.003$; $P = 0.2$; df = 105; $r^2 = 0.009$; $P = 0.9$; df = 105, respectively).

In the case of destroyed egg sacs, the average time in which they remained intact was 8 ± 8.3 days ($n = 19$; range = 0–26 days). Five eggs which fell from destroyed egg sacs, developed normally. Their temperature and relative humidity during the incubation period are shown in Table 5.

Females remained close to the egg sac throughout the whole incubation period. Four females opened the egg sac about six days before the eggs hatched. In one of these cases, the female spider ate the spiderling.

The average weight of the wild-caught females (105.3 ± 57 mg [$n = 36$; range = 39.7–264.8]) did not differ of the spiders reared at laboratory (107.8 ± 5.1 mg [$n = 75$; range = 101–118]) ($t = -0.3$; $P = 0.7$; df = 108). In egg sacs from females with unknown reproductive histories, the average number of spiderlings (41.2) (U = 2151; $P < 0.01$), the total number of eggs (49.5) (U = 2788.5; $P < 0.01$) per egg sac, and the average percentage of egg viability (82.7%) (U = 2120.5; $P < 0.001$) were greater than in females subjected to only one mating (29.4, 36.5 and 70.2%, respectively). Nevertheless, the average number of unhatched eggs per egg sac (U = 2323.5; $P < 0.01$) and the duration of incubation (U = 2033; $P < 0.001$) were greater in females with one mating than in those with unknown reproductive histories.

DISCUSSION

The egg sac construction of *L. intermedia* (behavior and time), and oviposition of the egg in the number of sacs agree with the reported patterns for the genus (Galiano 1967 for *L. laeta*; Hite et al. 1966 and Horner & Stewart 1967 for *L. reclusa* and Rinaldi et al. 1997 for *L. gaucho*). Only Delgado's (1966) description for *L. rufipes* was different. This author noted that oviposition required one to

Table 5.—Variables related to egg sacs destroyed by *L. intermedia* with unknown reproductive histories in the period from September 1994–March 1995. (The values are the mean ± SD with the sample size (*n*) and range in parentheses.)

	n	Mean ± SD	Range
Incubation period (days)	19	8.42 ± 8.3	0–26
Temperature during the incubation period (°C)	19	22.3 ± 2.3	18–25.3
Air humidity during the incubation period (%)	19	69.6 ± 1	51.9–87

two weeks and that the female positioned herself over the egg sac within a silk covering.

Females with unknown reproductive histories produced up to three fertile consecutive egg sacs and the period of egg-laying was restricted to seven out of the 18 months observed. On the other hand, females with only one insemination constructed up to four fertile egg sacs during 26 of 48 months of observation. Hite et al. (1966) reported similar results for *L. reclusa*, in which already mated females produced a smaller number of egg sacs than females mated only once in the laboratory. However, the possibility that the females deposited other egg sacs could account for the results of the latter study, the difference between our results and those of Andrade et al. (2000). In these studies already fertilized *L. intermedia* oviposited up to five times. Despite the probable relationships between spider weight and size and the number of eggs produced, the number of egg sacs is very similar among many species of the genus. For *L. hirsuta*, up to the three fertile egg sacs have been reported (Fischer & Marques da Silva 2001). For *L. gaucho*, 56.5% of the females that constructed more than one egg sac oviposited three or four times (Rinaldi et al. 1997) and Bücherl (1961) also reported that *L. laeta* and *L. gaucho* laid up to three egg sacs. For *L. reclusa* (Hite et al. 1966) and *L. laeta* (Galiano & Hall 1973), 5–15 ovipositions per female have been observed. However, these data were not confirmed by later studies of *L. reclusa* (up to three egg sacs) (Horner & Stewart 1967) and *L. laeta* (up to four egg sacs) (Andrade et al. 2000).

The total number of eggs and number of fertile eggs was significantly greater in females with unknown reproductive histories, suggesting that these spiders may have been fertilized more than once or were healthier from living in the wild. It is possible that multiple matings can favor reproductive success resulting in a larger number of fertile eggs than females that copulated once. The same point can be made about multiple egg sacs. According to Horner & Stewart (1967), female *L. reclusa* that mated repeatedly during the season were more fertile since additional mating protected against the gradual loss of sperm viability and inadequate storage capabilities.

Oviposition was more frequent in larger females which also tended to lay a greater total number of eggs and more eggs per egg sac. These observations indicate the importance of foraging success on fertility. Interspecific variations have been recorded for *L. laeta* and *L. intermedia* (Andrade et al. 2000) with the former species laying a greater number of eggs because of its greater size and weight. The average number of eggs per egg sac varies considerably in *Loxosceles*, e.g. 50.1 in *L. reclusa* (Hite et al. 1966), 61.3 in *L. gaucho* (Rinaldi et al. 1997), 33.7 in *L. hirsuta* (Fischer & Marques da Silva 2001), and 88.4 in *L. laeta* (Galiano 1967). Various factors, including the female's physiological state, can influence those results since an average of only 23 eggs per egg sac has been reported for *L. reclusa* (Horner & Stewart 1967). Rinaldi et al. (1997) attributed the low values reported by Bücherl (1961) for *L. laeta* and *L. gaucho* (12–15 eggs per egg sac) to the construction of egg sacs during female senescence. The existence of morphological and numerical variations in the seminal receptacles of *L. intermedia* females must also be considered (Buckup 1980; Fischer 1994), with the relationships between the number of receptacles, their functionality and female fecundity requiring further detailed studies. For the females reared in the laboratory, the number of viable eggs of *L. intermedia* correlated with the duration of mating and female age. According to Rinaldi et al. (1997), if the first mating in *L. gaucho* females lasted more than double the female's age, number of offspring per oviposition was lower. In the Lyniphiidae, the relationship between the duration of mating and egg viability was related to the time required for the transfer of sufficient sperm for the construction of three egg sacs (Suter & Parkhill 1990).

The length of incubation in *L. intermedia* appeared to be related to the air temperature and relative humidity, and these factors appeared to influence how long the spiderlings remained within the egg sac. Similar studies have reported values of 36.7 days for *L. reclusa* (Hite et al. 1966), 40.1 days for *L. gaucho* (Rinaldi et al. 1997) and 56.9 days for *L. hirsuta* (Fischer & Marques da Silva 2001), and these appear to be little affected by variations in the environmental conditions. The time interval between consecutive ovipositions may also be influenced by the spiders'

nutritional state, sperm storage and stress since there was an increase in this interval after the second oviposition. In the present study, females with unknown reproductive histories had smaller intervals (68.8 days) than females with one mating (116.7 days), although a greater number of egg sacs were observed in the former

Loxosceles intermedia thus has a greater interval between oviposition than *L. gaucho* (39.2 days) (Rinaldi et al. 1997) and *L. reclusa* (32 days) (Horner & Stewart 1967).

The average number of non-viable eggs did not differ between the two groups, although non-viable eggs were seen in 63.2% of the egg sacs produced by female *L. intermedia* with unknown reproductive histories compared to 83.5% in females with only one mating. The presence of non-viable eggs could reflect a lack of fertilization, the interruption of development because of environmental or biological conditions and the possibility that these eggs were eaten by older spiderlings. Non-viable eggs have also been reported for *L. hirsuta* (42.7% of cases: Fischer & Marques da Silva 2001) and for other spider groups (Valério 1974; Anderson 1978; Christenson et al. 1979; Downes 1985; Gonzales 1989).

The decrease in the number of viable eggs in successive egg sacs was insignificant in females fertilized only once. Contrary to the findings of Eberhard (1979), a reduction in the number of eggs in successive ovipositions has also been observed in *L. hirsuta* (Fischer & Marques da Silva 2001), *L. gaucho* (Rinaldi et al. 1997) and other spiders (Downes 1985; Gonzales 1989; Willey & Adler 1989; Suter 1990; Wheeler et al. 1990).

The destruction of egg sacs may have been influenced by various factors. In females which did not oviposit more and which later destroyed their egg sac, this behavior may have been influenced by physiological conditions such as infertility, age, nutrient shortage or stress. Also, since sperm storage was not an important factor in egg sac destruction, the influence of air temperature, relative humidity and stress must be considered. Although the relationship between the incubation length and the air temperature and relative humidity was low, there nevertheless appeared to be some minimum requirements for oviposition and egg development to occur. The destruction of egg sacs by females has been recorded for *L.*

reclusa (Hite et al. 1966) in which the females sometimes ate their own eggs and the eggs in some egg sacs did not eclode. In *L. hirsuta*, 55.6% of the females that destroyed their egg sacs constructed other fertile sacs. A similar behavior was observed in *Lycosa malitiosa* Tullgren 1905 (Lycosidae) (Capocasale et al. 1984) and was attributed to the peak of synchronization between the spontaneous opening of the egg sac by the mother and spiderling development. As observed here, Horner & Stewart (1967) also noted that *L. reclusa* spiderlings did not need help to leave the egg sac, but if the mother was present, she helped to tear the egg sac.

Reproductive success in *L. intermedia* is influenced by numerous factors that can affect spider fertility, including: air temperature, relative humidity, length of mating, female weight, and female age. These factors are relevant for *L. intermedia* since these spiders live in and around buildings and are, therefore subject to smaller oscillations of environmental conditions, have food in abundance, have large populations with numerous males that can potentially inseminate any given females, the fecundity is likely to be high and could explain the abundance of this species in Curitiba.

ACKNOWLEDGMENTS

LITERATURE CITED

Anderson, J.F. 1978. Energy content of spiders eggs. Oecologia 37:41–57.

Andrade, R.M.G., W.R. Lourenço & D.V. Tambourgi. 2000. Comparison of the fertility between *Loxosceles intermedia* and *Loxosceles laeta* spiders (Araneae, Sicariidae). Journal of Arachnology 28:245–247.

Begon, M.J., L. Harper, & C.R. Towsend. 1990.

Ecology of Individuals, Populations and Communities. Cambridge: Blackwell Scientific Publications.

Bücherl, W. 1961. Aranhas do gênero *Loxosceles* e loxoscelismo na América. Ciência e Cultura 13:213–224.

Buckup, E.H. 1980. Variação interpopulacional dos receptáculos seminais em aranhas do grupo Spadicea do gênero *Loxosceles* Heinecken & Lowe, 1832 (Araneae; Scytodidae). Hieringia série Zoologia 55:137–147.

Capocasale, R.M., F.G. Costa & J.C. Moreno. 1984. La produción de ootecas de *Lycosa malitiosa*, Tullgren (Araneae, Lycosidae). II Analisis cuantitativo de hembras virgenes e copuladas. Aracnologia 3:1–7.

Christenson, T.E., P.A. Wenzl & P. Legum. 1979. Seasonal variation in egg hatching and certain egg parameters of the golden silk spider *Nephila clavipes* (Araneae). Psyche 2:137–147.

Christenson, T.E. & P.A. Wenzl. 1980. Egg laying of the golden silk spider, *Nephila clavipes* L. (Araneae, Araneidae): functional analysis of the egg sac. Animal Behaviour 28:1110–1118.

Cooke, J.A.L. 1965. A contribution to the biology of the British spiders belonging to the genus *Dysdera*. Oikos 6:20–25.

Costa, F.G. & R.M. Capocasale. 1984. La produción de ootecas de *Lycosa malitiosa* Tullgren (Araneae:Lycosidae). Importancia de la muda de maturacion sobre la primera oviposición. Aracnologia 2:1–8.

Delgado, A. 1966. Investigación ecológica sobre *Loxosceles rufipes* (Lucas), 1834 en la región costera del Perú. Memórias do Instituto Butantan 33:683–688.

Downes, M.F. 1984. Egg sac ''theft'' among *Latrodectus hasselti* females (Araneae, Theridiidae). Journal of Arachnology 12:244.

Downes, M.F. 1985. Fecundity and fertility in *Latrodectus hasselti*. Australian Journal of Ecology 10:261–264.

Downes, M.F. 1987. Postembryonic development of *Latrodectus hasselti* Thorell (Araneae, Theridiidae). Journal of Arachnology 14:293–301.

Downes, M.F. 1988. The effect of temperature on oviposition interval and early development in *Theridion rufipes* Lucas (Araneae, Theridiidae). Journal of Arachnology 16:41–45.

Eberhard, W.G. 1979. Rates of egg production by tropical spiders in the field. Biotropica 11:292–300.

Enders, F. 1976. Clutch size related to hunting manner of spider species. Annals of the Entomological Society of America 69:991–998.

Figueira, J.E.C. & J. Vasconcellos-Neto. 1993. Reproductive success of *Latrodectus geometricus* (Theridiidae) on *Paepalanthus bromelioides* (Er-

iocaulaceae): rosette size, microclimate, and prey capture. Ecotropicos 5:1–10.

Fink, L.S. 1986. Costs and benefits of maternal behaviour in the green lynx spider (Oxyopidae, *Peucetia viridans*). Animal Behaviour 34:1051–1060.

Fischer, M.L. 1994. Levantamento das espécies do gênero *Loxosceles* Heinecken & Lowe, 1832 no município de Curitiba, Paraná, Brasil. Estudos de Biologia 38:65–86.

Fischer, M.L. & E. Marques da Silva. 2001. Oviposição e desenvolvimento de *Loxosceles hirsuta* Mello-Leitão, 1931 (Araneae; Sicariidae). Estudos de Biologia 47:15–20.

Fischer, M.L. & J. Vasconcelos-Neto. 2000. Comportamento sexual de *Loxosceles intermedia* Mello-Leitão, 1934 (Araneae; Sicariidae). Revista de Etologia 2:31–42.

Foelix, R.F. 1996. Biology of Spiders. New York. Oxford University Press.

Fritz, R.S. & D.H. Morse. 1985. Reproductive success and foraging of the crab spider *Misumena vatia*. Oecologia 65:194–200.

Galiano, M.E. 1967. Ciclo biologico e desarollo de *Loxosceles laeta* (Nicolet,1849). Acta Zoologica Lilloana 23:431–464.

Galiano, M.E. & M. Hall. 1973. Datos adicionales sobre el ciclo vital de *Loxosceles laeta* (Nicolet) (Araneae). Physis 32:277–288.

Gonzalez, A. 1989. Analisis del comportamiento sexual y producción de ootecas de *Theridion rufipes*. Journal of Arachnology 17:129–136.

Hite, M.J., W.J. Gladney., J.L LancasterJR, & W.H. Whitcomb. 1966. Biology of brown recluse spider. Arkansas Agriculture Experimental Station Bulletin 711:2–26.

Hoffmaster, D.K. 1982. Predator avoidance behaviors of five species of Panama orb-weaving spiders (Araneae; Araneidae, Uloboridae). Journal of Arachnology 10:69–73.

Horner, N.V. & K.W. Stewart. 1967. Life history of the brown spider, *Loxosceles reclusa* Gertsch and Mulaik. Texas Journal of Sciences 19:333–347.

Jackson, R.R. 1978. Life history of *Phidippus johnsoni* (Araneae, Salticidae). Journal of Arachnology 6:1–29.

Killebrew, D.W. & N.B. Ford. 1985. Reproductive tactics and female body size in the green lynx spider *Peucetia viridans* (Araneae, Oxyopidae). Journal of Arachnology 13:375–382.

Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15–66. *In* Spider Communication: Mechanisms and Ecological Significance (P.N. Witt & J. S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.

Levy, G. 1970. The life cycle of *Thomisus onustus* (Thomisidae: Araneae) and outlines for the clas-

sification of the life histories of spiders. Zoology 160:523–536.

Miyashita, K. 1987. Development and egg sac production of *Achaearanea tepidariorum* (C.L. Koch) (Araneae; Theridiidae) under long and short photoperiods. Journal of Arachnology 15: 51–58.

Muniappan, R. & H.L. Chada. 1970. Biology of the crab spider, *Misumenops celer*. Annals of the Entomological Society of America 63:1718–1722.

Nuessly, G.R. & R.D. Goeden. 1984. Aspects of the biology and ecology of *Diguetia mojavea* Gertsch (Araneae, Diguetidae). Journal of Arachnology 12:75–85.

Opell, B.D. 1984. A simple method for measuring desiccation resistance of spider egg sacs. Journal of Arachnology 12:245.

Rinaldi, I.M.P., L.C. Forti, & A.A. Stropa. 1997. On the development of the brown spider *Loxosceles gaucho* Gertsch (Araneae; Sicariidae): the nympho-imaginal period. Revista Brasileira de Zoologia 14:697–706.

Ruttan, L.M. 1991. Effects of maternal presence on the growth and survival of subsocial spiderlings (Araneae: Theridiidae). Insect Behaviour 4:251–257.

Suter, R.B. 1990. Courtship and the assessment of virginity by male bowl and doily spiders. Animal Behaviour 39:307–313.

Suter, R.B. & V.S. Parkhill. 1990. Fitness consequences of prolonged copulation in the bowl and doily spider. Behaviour, Ecology, and Sociobiology 26:369–373.

Turnbull, A.L. 1962. Quantitative studies of the food of *Linyphia triangularis* Clerk (Araneae; Linyphiidae). Canadian Entomology 91:1233–1237.

Wheeler, G.S., J.P. McCaffrey, & J.B. Johnson. 1990. Developmental biology of *Dictyna* spp (Araneae: Dictynidae) in the laboratory and field. American Midland Naturalist 123:124–134.

Willey, M.B. & P.H. Adler. 1989. Biology of *Peucetia viridans* (Araneae, Oxyopidae) in South Carolina, with special reference to predation and maternal care. Journal of Arachnology 7:275–284.