

DEVELOPMENT AND LIFE TABLES OF *LOXOSCELES INTERMEDIA* MELLO-LEITÃO 1934 (ARANEAE, SICARIIDAE)

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ABSTRACT. *Loxosceles intermedia* is a medically important species that is abundant in Curitiba, Paraná State, Brazil. Knowledge of the postembryonic development of this species is fundamental for preventing bites by this species and for controlling its population size. In this report, postembryonic development ($n = 212$ spiderlings) was studied in the laboratory under ambient conditions of temperature and humidity with a standardized diet. The average duration of development (from emergence from the egg sac to maturity) was 356 ± 33 days ($n = 189$; range = 213–455). Spiders matured after 5th–8th molt, although most individuals matured after 7th molt. The sex ratio was 1:1. The mortality in the laboratory was low, most pronounced in the 4th and 5th instars and was associated mainly with molting. The longevity of females (1176 ± 478 days) was significantly longer than it was for males (557 ± 88.6 days). The abundance of *L. intermedia* in Curitiba, city in the southern part of Brazil, is related to aspects of its life cycle, since a slow growth, low mortality, and greater longevity enhance the reproductive potential of the species.

Keywords: Loxoscelism, life cycle, ontogeny, longevity

The genus *Loxosceles* consists of venomous species of medical importance that are widely distributed through different parts of the world. The venom of these species, which contains powerful cytotoxins, necrotoxins and hemotoxins (Gertsch 1967), together with the tendency of many species to form large populations in urban areas, close to human constructions, has made these spiders a public health problem in Chile (Schenone et al. 1970: *L. laeta* (Nicolet 1849)) and in the city of Curitiba, a city in the southern part of Brazil and capital state of Paraná (Ribeiro et al. 1993: *L. intermedia* and *L. laeta*). Knowledge of the postembryonic development of this species is fundamental in management programs to minimize bites by these spiders and to control their population size. Postembryonic development has been described for *L. laeta* (Galiano 1967; Galiano & Hall 1973), *L. reclusa* Gertsch & Mulaik 1940 (Hite et al. 1966; Horner & Stewart 1967), *L. gaucho* Gertsch 1967 (Rinaldi et al. 1997) and *L. hirsuta* Mello-Leitão 1931 (Fischer & Marques da Silva 2001). Bücherl (1961) provided some data on the

nymphal period of *L. rufipes* (Lucas 1834) and *L. rufescens* (Dufour 1820) which, according to Gertsch (1967), are *L. laeta* and *L. gaucho*, respectively. Lowrie (1980, 1987) studied the influence of diet on the development of *L. laeta*. The number of molts required to reach maturity can vary within a species due to endogenous and exogenous factors, however it is waited that there is relationship with final body size (Foelix 1996). The maturation also may be correlated to the reproductive system in which the species is inserted as haplogynae and entelegynae spiders (Schneider 1997). In the same way, the difference between males and females in the use of resource of energy can be due the ecological role of each sex (Gary 2001).

In Brazil, cases of loxoscelism are frequent in the south and southeast of the country, especially in the state of Paraná. The city of Curitiba registers the largest number of spider bites by *Loxosceles*, with hundreds of bites each year. Two species, *L. intermedia* and *L. laeta* are found in the urban area. *Loxosceles intermedia*, found in the south and southeast

of Brazil, is abundant and is more common than *L. laeta*, the more cosmopolitan species (90% and 10% of occurrences in Curitiba, respectively) (Fischer 1994). This distribution raises the question about what factors favor an increase in the population size of the predominant species. In this study, we examined the postembryonic development and longevity of *L. intermedia* fed a standardized diet under ambient conditions of temperature and humidity.

The ontogeny of spiders is divided into three main periods: embryonic (egg fertilized until the establishment in the shape of spider body), larval (prelarva and larva unable to feed) and nympho-imaginal (nymphs or juveniles self-sufficient). Postembryonic development within the egg sac begins with rupture of the chorion (hatching) and ends with the first nymphal molt, after which the spiderlings emerge from the egg sac (Foelix 1996). The terminology used, based on Foelix (1996), was the following:

Within egg sac → emergence from egg sac

Fertilization	Emergence as 2nd instar
Eggs hatch by opening of egg membranes	(mobile stage)
Immobile stages (= 1st instar)	
First true molt to 2nd instar	

→ instars or nymphal instars → adult	
series of molts	Sexual maturity

For this study, we use the term “instar” as each stage between molts, starting with the first instar, which, along with the first true molt, occurs inside the egg sac. Maturity is reported both as time from oviposition (egg sac construction) to the maturing molt and also as emergence from the egg sac to maturing molt. In addition, we report on a measure of growth ratio, which in this study is defined as the size of a structure divided by its size in the preceding instar.

METHODS

Postembryonic development.—The spiders studied (*n* = 212) were from four egg sacs built by spiders in the laboratory. The spiderlings were reared and maintained until death. The females (*n* = 4) from which the spiderlings were obtained had already been in-

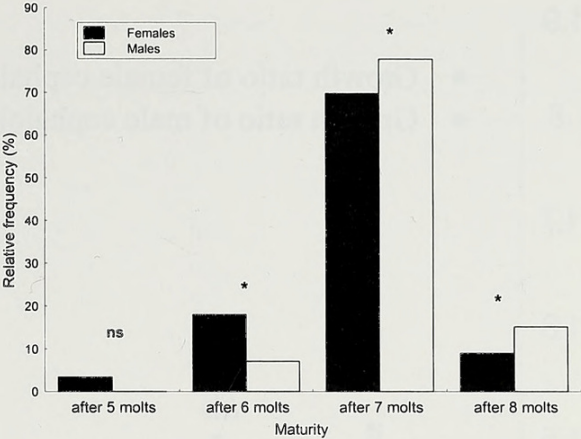


Figure 1.—Relative frequency of *Loxosceles intermedia* females and males reaching maturity after the 5th, 6th, 7th, and 8th molts. The female and male frequencies were compared using *G*-test. * = *P* < 0.05; ns = not significant.

seminated when collected in houses at different locations in Curitiba (lat. 25°25'48"S and long. 49°16'15"W). The spiders were collected in March and June of 1994.

Following their emergence from the egg sac, the spiderlings were housed individually in 120 ml plastic containers (diameter of base 4.8 cm) and, from the 4th instar onwards, were maintained in 350 ml plastic containers (diameter of base, 6 cm), before finally being transferred to 750 ml plastic containers (diameter of base, 8 cm) at adult. All containers were lined with a double sheet of paper, which provided a substratum for locomotion, web fixation, refuge, attachment, and ecdysis. The spiders were maintained under ambient conditions of temperature, humidity, and luminosity. The air temperature and relative humidity were monitored daily using a hydrothermograph. During the study, the monthly average temperature was 21.4 ± 2.3 °C (*n* = 19; range = 16.2–24.7), and the average monthly humidity was 73.9 ± 11.4% (*n* = 19; range = 57.8–95.7). Moistened cotton was supplied weekly. Juveniles up to the 4th instar were fed a standardized diet consisting of larval and adult *Drosophila melanogaster*. After the 4th instar the spiderlings were fed *Tenebrio molitor* larvae. Two fruit flies or two mealworm larvae were supplied twice a week.

The exuvia from the molt to the 2nd instar from four egg sacs were kept dry and were measured using an ocular micrometer. Fourteen exuvia (from first molt) and 20 exuvia from the 2nd to the 8th molt (10 females and

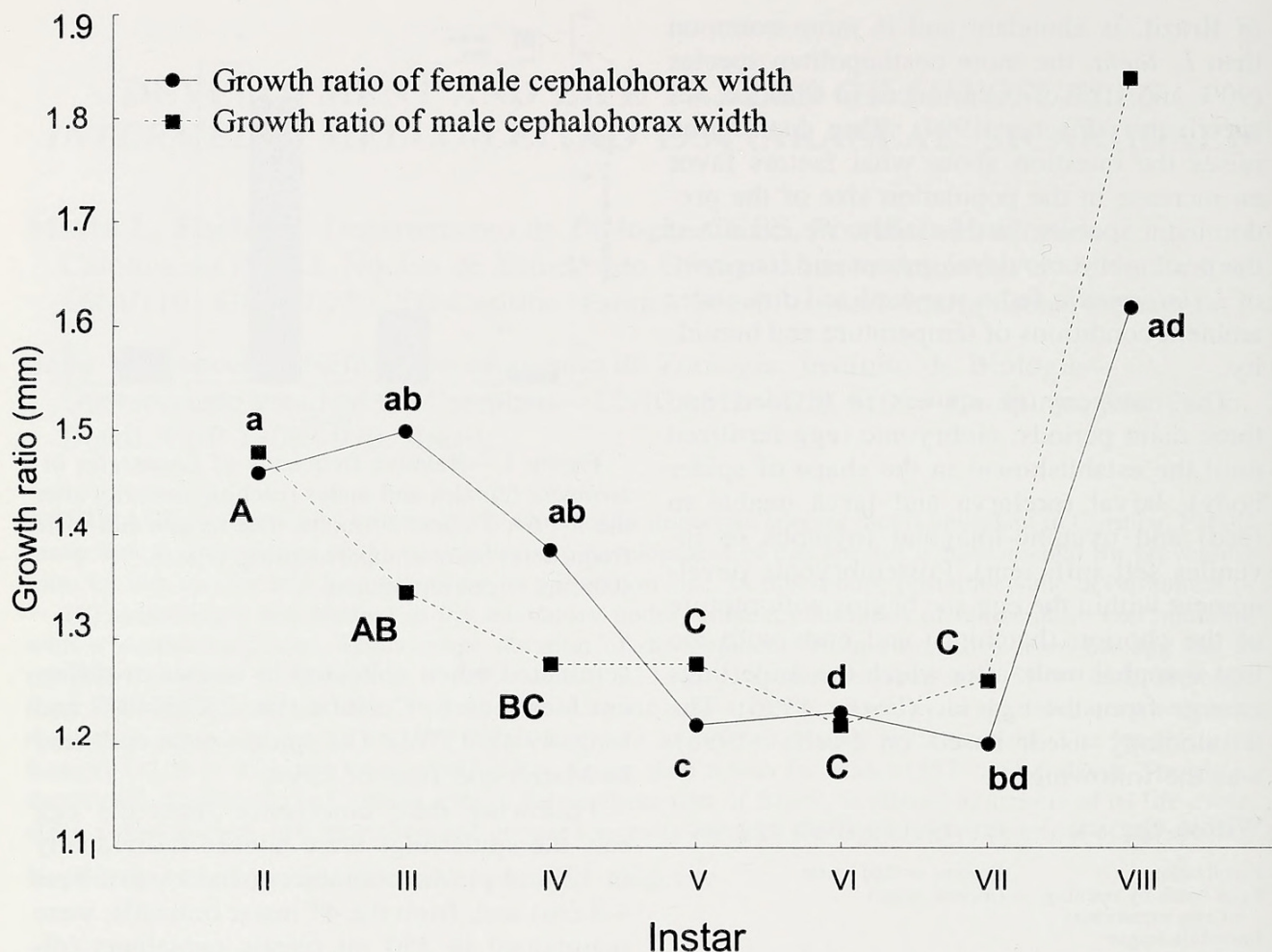


Figure 2.—Growth ratio of the cephalothorax width in successive instars of *Loxosceles intermedia* male and female (e.g., value of carapace width for instar III/ value for carapace width for instar II). The average ratios for each instar were compared using the Mann-Whitney U test. The letters (lowercase for females and uppercase for males) indicate significantly different averages ($P < 0.05$).

10 males) were examined. The sequential exuvia from all but the first molt were always from the same individuals. A thin microscope slide was placed on the exuvium to obtain measurements in the same plane. Cephalothorax width was used to compare the growth ratios of instars and adults (Huxley 1924; Hangstrum 1971; Gary 2001). The length of tibia I was used as parameter for leg growth, since total length of the leg could be affected by loss of the tarsus. To compare the size of adults that reached maturity with an additional instar, and to assess whether other body structures grew differently in males and females during postembryonic development, additional parameters were measured, including the length of the femur, tibia, metatarsus and tarsus of all legs and the femur, tibia and tarsus of the palp, the width and length of the ster-

num and chelicerae, and the length of the cephalothorax, labium and maxilla.

In adult females, the orange coloration of the sclerotized regions of the seminal receptacles is visible with maturity. However, maturity was only confirmed after insemination. The development of the palpal organs, which are characteristic of mature males, was apparent only after maturation. The fresh weight of mature females ($n = 86$) and males ($n = 57$) was measured to the nearest 0.1 mg.

Statistical analyses.—G-tests were used to compare the maturation rates of the different instars and the sex ratios. Since the data were not normally distributed (Shapiro-Wilks W test), the non-parametric Kruskal-Wallis (H test) were used to compare the average period between successive ecdysis and the average growth ratio of the different morphological

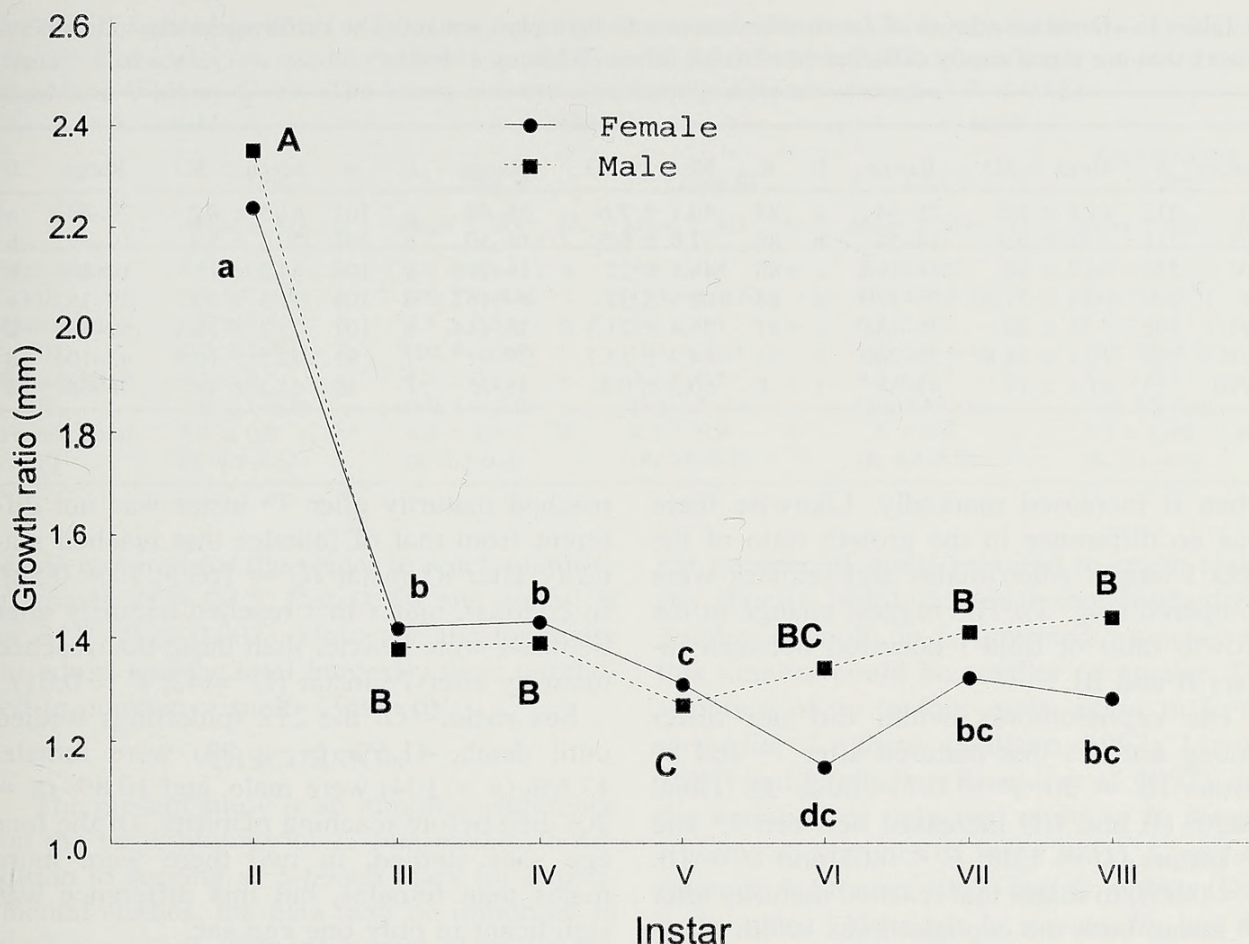


Figure 3.—Growth ratio of tibia I length in successive instars of male and female *Loxosceles intermedia* (e.g. value of tibia I length for instar III/value for tibia I length for instar II). The average ratios for each instar were compared using the Mann-Whitney U test. The letters (lowercase for females and uppercase for males) indicate significantly different averages ($P < 0.05$).

structures. The Mann-Whitney U test was used to compare the average interval between molts, the growth ratios, spider weights, and the longevity of males and females, and of spiders that reached the maturity after 7 and 8 molts.

Voucher specimens are deposited in arachnological collection Dra. Vera Regina von Eickstedt in session of poisonous arthropods of Immunologic Production and Research Center (SESA-PR).

RESULTS

Number of molts and instars.—Females matured after 5–8 molts whereas males matured after 6–8 molts (Fig. 1). In both males and females, the highest frequency of maturity was after 7th molt (females: G -test = 44; $P < 0.001$; $df = 3$; males: G -test = 42; $P < 0.001$; $df = 2$). The frequency of maturation after 5th, 6th, 7th and 8th molts was different between males and females (G -test = 10.5; $P < 0.05$;

$df = 3$). The highest frequency of maturity after 6th molt was observed in females, and after 7th and 8th molt in males (Fig. 1).

Duration of stages or instars.—There was no pattern of increasing or decreasing the duration of the interval between molts during development. However, the duration of the instars was different in females ($H = 380$; $P < 0.001$) and males ($H = 423.2$; $P < 0.001$) (Table 1) in the 4th to 8th instars (for 5th instar, $U = 28530.5$; $P < 0.001$; and 7th instar $U = 2215$; $P < 0.01$). The time (days) until adulthood was not significantly different between males and females ($U = 3334.5$; $P = 0.15$) (Table 2).

Growth.—A comparison of the growth ratio of the cephalothorax width showed the same pattern between males and females (Fig. 2). A growth ratio of 1.5 shows that the carapace width was 1.5x greater in one instar than the previous instar. The growth ratio decreased with each instar until the VIII instar,

Table 1.—Duration (days) of *Loxosceles intermedia* nymphal instars. The different letters indicate averages that are significantly different ($P < 0.05$; Mann-Whitney U test).

Instars	Total				Females				Males			
	n	Mean \pm SD	Range	U	n	Mean \pm SD	Range	U	n	Mean \pm SD	Range	U
II	212	41.1 \pm 7.8	25–64	a	88	40.1 \pm 7.6	25–64	a	101	41.5 \pm 8.2	29–64	a
III	211	31 \pm 6.2	14–57	b	88	31.6 \pm 6.5	14–50	b	101	30.3 \pm 5.4	19–57	b
IV	210	46.9 \pm 22	14–198	c	88	48.1 \pm 27	16–198	c	101	44.2 \pm 15	14–105	a
V	200	99.5 \pm 31.8	39–170	d	88	108.5 \pm 32	49–167	d	101	91.3 \pm 30	39–162	c
VI	192	74 \pm 20	36–188	e	87	75.4 \pm 21.3	36–144	e	101	73.2 \pm 18.4	50–188	d
VII	164	70.1 \pm 18.8	39–200	e	72	64.7 \pm 13.7	39–91	f	91	72.3 \pm 12.9	43–104	d
VIII	23	61.5 \pm 14	45–84	f	8	60.5 \pm 9.8	45–75	f	16	61.2 \pm 49	45–84	e

when it increased markedly. Likewise there was no difference in the growth ratio of the tibia I length when males and females were compared (Fig. 3). The biggest change in the growth ratio of tibia I occurred between instars II and III.

The cephalothorax width did not differ among females that matured after 7th and 8th instars ($U = 20$; $P = 0.7$) (Table 3). Tibial length (II and III) increased between 7th and 8th instars ($U = 13.5$; $P < 0.01$ and $U = 16$; $P < 0.05$). In males that reached maturity after 8th instar, both the cephalothorax width ($U = 0.1$; $P < 0.001$) and tibial length of all legs (I: $U = 14$; $P < 0.01$; II: $U = 18$; $P < 0.05$; III: $U = 17.5$; $P < 0.01$; IV: $U = 9.5$; $P < 0.0001$) were significantly greater than in males that matured after the 7th instar (Table 3). The cephalothorax width did not differ between males and females that reached maturity after 7th and 8th instars. However, the tibial length was longer in males in both situations (Table 3).

The average weight of adult females was 127.4 \pm 5.03 mg ($n = 86$; range = 30–240) and that of adult males was 68.6 \pm 23.7 mg ($n = 57$; range = 10–110). Females were thus significantly heavier than males ($U = 649.5$; $P < 0.001$). The weight of females that

reached maturity after 7th instar was not different from that of females that reached maturity after 8th instar ($U = 163.5$; $P = 0.58$). In contrast, males that reached maturity after 8th instar were heavier than those that reached maturity after 7th instar ($U = 42$; $P < 0.01$).

Sex ratio.—Of the 212 spiderlings studied until death, 41.5% ($n = 88$) were female, 47.6% ($n = 104$) were male, and 10.8% ($n = 20$) died before reaching maturity. Of the four egg sacs studied, in two there were more males than females, but this difference was significant in only one egg sac.

Longevity.—*Loxosceles intermedia* reared in the laboratory had a low overall mortality rate. Mortality which was greatest in the 4th and 5th instars and was associated mainly with molting (immediately prior to ecdysis). The spiders sometimes remained attached to the old exoskeleton and died 1–4 days after molting. The initial instars had the greater life expectancies (ex), which then decreased during development (Table 4).

Adult longevity and total longevity post emergence was significantly greater in females than in males ($U = 589.5$; $P < 0.001$ and $U = 527$; $P < 0.001$) (Table 5). The time required for growth from oviposition to the adult stage increased with the number of ec-

Table 2.—*Loxosceles intermedia* maturation times.

Time (days)	Total			Female			Male		
	n	Mean \pm SD	Range	n	Mean \pm SD	Range	n	Mean \pm SD	Range
Oviposition to maturity	189	409 \pm 33	269–506	88	404 \pm 56	112–506	101	410 \pm 46	269–744
Emergence of egg sac to maturity	189	356 \pm 33	213–455	88	359 \pm 35.7	241–455	101	354.7 \pm 31.1	258–431

Table 3.—Average tibia I length (mm) and cephalothorax width (mm) in successive instars of male and female *Loxosceles intermedia* (sample size and range in parentheses). The averages were compared using the Mann-Whitney *U* test. The letters indicate significantly different averages (*P* < 0.05).

	Tibia I			Tibia II			Tibia III			Tibia IV			Cephalothorax width		
	Mean ± SD		<i>U</i>	Mean ± SD		<i>U</i>	Mean ± SD		<i>U</i>	Mean ± SD		<i>U</i>	Mean ± SD		<i>U</i>
Male instar VII	5.9 ± 0.6 (10; 4.7–6.9)		a	7.0 ± 0.8 (10; 5.9–8.4)		a	4.8 ± 0.4 (10; 4.1–5.6)		a	5.4 ± 0.62 (10; 4.7–6.3)		a	3.0 ± 0.3 (10; 2.4–3.3)		a
Male instar VIII	6.6 ± 0.6 (10; 5.1–7.5)		b	9.3 ± 0.5 (10; 8.1–9.7)		b	5.2 ± 0.1 (10; 5–5.3)		b	6.3 ± 0.2 (10; 5.6–6.4)		b	3.8 ± 0.2 (10; 3.4–3.9)		b
Female instar VII	4.3 ± 0.7 (10; 3.1–5.3)		c	4.7 ± 0.8 (10; 3.4–5.6)		c	3.4 ± 0.6 (10; 2.3–4.4)		c	4.4 ± 0.7 (10; 3.4–5.6)		c	3.1 ± 0.3 (10; 2.5–3.6)		a
Female instar VIII	5.2 ± 0.9 (8; 4.5–6.6)		c	6.5 ± 1.8 (8; 5.2–9.4)		d	4.3 ± 0.8 (8; 3.6–5.9)		d	5 ± 0.6 (8; 4.4–5.9)		c	3.5 ± 0.45 (8; 3.1–4.4)		ab

dysis required for the spider to reach maturity (females: *H* = 24.5; *P* < 0.001 and males: *H* = 31.2; *P* < 0.001). However, the longevity as adults and the total longevity were unrelated to number of molts (Table 6).

DISCUSSION

The present study is an important reference on the basic biology of *L. intermedia*. In addition to serving as a bench mark for experimental studies, the data may be important in the preparation of management plans for the species. The observation of the 212 spiders for more than six years allowed the characterization of the postembryonic development evidencing long time to maturity, similar growth of different parts of the body in males and females, similar proportion of the sexes, little mortality and long-lived spiders in spite of their small size.

Variations in final body size of the *Loxosceles* species (Gertsch 1967) reflect the differ-

ent number of molts required to reach maturity (Foelix 1996). Although the standardized number of molts in *L. intermedia* was seven, this number could be smaller or greater. The variation of up to four molts occur in *L. intermedia*, *L. laeta* (Galiano 1967; Lowrie 1987) and *L. gaucho* (Rinaldi et al. 1997), and the variation of only two molts in *L. hirsuta* (Fischer & Marques da Silva 2001), *L. reclusa* (Horner & Stewart 1967) and *L. rufipes* (Delgado 1966). Although *L. intermedia* has the same number of molts or more than other species, this species required more time to reach maturity (7 molts; 357 days) compared to *L. laeta* (6–9 molts; 315.3 days) (Galiano 1967) and *L. reclusa* (7 molts; 303.3) (Hite et al. 1966); *L. rufipes* (3–4 molts; 357 days) (Delgado 1966) had smaller number of molts but required the same time as *L. intermedia*.

The maturation period and the number of molts until maturity can vary within the same species when spiders are maintained in different conditions. In spiders, this variation is attributed to the feeding regime (Turnbull 1962, 1965; Levy 1970), temperature (Downes 1988), predation of infertile eggs by spiderlings within the egg sac (Galiano 1967; Valerio 1974) and genetic variation (Muniappan & Chada 1970; Wise 1976; Downes 1987). For *Loxosceles* the time and number of molts was attributed to the amount and composition of food (Lowrie 1980, 1987; *L. laeta*), temperature during development (Horner & Stewart 1967; *L. reclusa*) and season when the egg sac was deposited (Hite et al. 1966; *L. laeta*).

The maturation also may be correlated to the mating system, which is in turn influenced by spermathecal morphology and the pattern

Table 4.—Life table of *Loxosceles intermedia* reared in the laboratory (*l_x* = number of survivors at the start of the instar; *d_x* = number of deaths in the interval *x* and *x* + 1; *q_x* = mortality rate; *e_x* = average life expectancy for an individual alive at the beginning of the interval; *L_x* = average number of individuals alive in the interval *x* and *x* + 1; *T_x* = individuals for unit of time).

Instar	<i>l_x</i>	<i>d_x</i>	<i>q_x</i>	<i>e_x</i>	<i>L_x</i>	<i>T_x</i>
II	164	1	0.006	5.18	163.5	847
III	163	1	0.006	4.21	162.5	683
IV	162	10	0.006	3.32	157	521
V	152	6	0.66	2.44	149	364
VI	146	4	0.41	1.49	144	215
VII	142	142	1	1.01	71	144

Table 5.—Average longevity (days) of female and male *Loxosceles intermedia* reared in the laboratory. The values are the mean \pm SD. The number of spiders and the range are shown in parentheses.

	Total	Female	Male
Longevity as adults (last molt to death)	493.7 \pm 455 (175; 0–181)	816.9 \pm 478.1 (83; 124–1810)	202 \pm 92 (92; 0–483)
Longevity total (emergence from egg sac to death)	850.6 \pm 455.8 (175; 368–2195)	1176 \pm 478 (83; 465–2195)	557 \pm 88.6 (92; 368–795)

of use of stored sperm (Schneider 1997). In species in which the sperm package deposited first will also be the first to leave the spermathecae (conduit spermathecae), the males should reach maturity before females, and should compete for a mate, guarding the females in order to maximize their fertilization rates. In this system (strong male-male competition) a larger body size for males is important. In *Loxosceles*, there is a single opening to the spermathecae (Gertsch 1967; Fischer 1994) and the spiders are considered haplogynae since the copulatory duct also serves as the fertilization duct (Foelix 1996). Such species are considered to have last male priority, since the sperm deposited last in the spermathecae will be the first to reach the eggs (Schneider 1997). Hence, the males reach maturity at the same time as the female, as observed in *L. intermedia* (this study) and *L. gaucho* (Rinaldi et al. 1997), or a little later, as in *L. laeta* (Galiano 1967; Galiano & Hall 1973; Lowrie 1980, 1987) and *L. hirsuta* (Fischer & Marques da Silva 2001). Experimental studies should be conducted with other *Loxosceles* to confirm this trend.

The linear growth of different parts of the body (e.g. cephalothorax width and abdomen length) means that there was no difference in the allocation of resources to specific body parts, also shown by Gary (2001) for males and females of *Linyphia triangularis* (Clerck 1757) (Linyphiidae). Although the abdomen of *L. intermedia* was not measured here, the existence of resource allocation is seen in the larger weight of the females, and the longer walking legs of the males. The female probably uses energy resources for egg production, while males have a more wandering lifestyle (mate-searching in adult life) and maximize mating with a larger number of females. On the other hand, the similar size of the cephalothorax width may indicate that there is intraspecific competition in both sexes, selecting

the largest size. A larger size in females would favor a greater production of eggs, while in males a larger size would be important for competition during mating opportunities and possibly for fighting.

The long time to maturity and the similar growth of different parts of the body in males and females indicate that rapid growth mechanisms do not exist in *L. intermedia*. The rapid growth registered in *Nephila clavipes* (Linnaeus 1767) (Tetragnathidae) has ecological costs (increase in mortality) that are related to the risk of predation and parasitism (associated with increased foraging), and an inherent physiological cost because of the high food consumption (Higgins & Rankin 2001).

The lack of difference in the body size of juvenile male and female *L. intermedia* has also been observed in *L. gaucho* (Rinaldi et al. 1997) and *L. laeta* (Galiano 1967). According to Galiano (1967), instar VI was the earliest age for accurate recognition of the sexes. Again, this pattern is evidence of a similar allocation of energy resources during development in order to produce adults of similar body sizes (cephalothorax width). Although a larger size benefits both sexes, the additional molt was significant only for male *L. intermedia* and *L. hirsuta* (Fischer & Marques da Silva 2001) and reflected advantages in the accumulation of energy (Wheeler et al. 1990). In females an 8th molt probably does not influence the reproductive potential since body weight and size did not differ.

There was little mortality during development of *L. intermedia* and *L. hirsuta* (Fischer & Marques da Silva 2001). The correlation between deaths and molting (before, during or after) indicates that this is a time of great stress and a very vulnerable phase in the life history of spiders (Galiano 1967, *L. laeta*; Turnbull 1965, Agelenidae; Nuessly & Goeden 1984, Diguettidae; Downes 1993, Amaurobidae). According to Galiano (1967), the de-

Table 6.—Time (days) from emergence to adult hood, adult longevity, and longevity after emergence of female and male *L. intermedia* that reached maturity after 5th, 6th, 7th, and 8th instar. The values are the mean ± SD. The number of spiders and the range are shown in parentheses. The averages were compared using the Mann-Whitney *U* test. The letters indicate significantly different averages (*P* < 0.05).

Instar	Females			Males		
	Time to maturity	Adult longevity	Total longevity	Time to maturity	Adult longevity	Total longevity
V	258 ± 24 (4; 241–275) a	321 ± 68 (4; 273–369) a	579 ± 43.8 (4; 548–610) a	—	—	—
VI	334 ± 42.2 (16; 263–192) b	1045 ± 400 (16; 128–1577) ab	1385 ± 396 (16; 465–1894) ab	306 ± 39.7 (7; 261–367) a	242 ± 120 (7; 146–461) a	547 ± 100 (7; 45–729) a
VII	365.3 ± 27 (62; 271–435) c	779 ± 482 (62; 124–1810) ac	1143 ± 482 (62; 495–2195) b	354 ± 23.5 (77; 258–403) b	199 ± 91 (77; 2–483) a	554 ± 88 (77; 368–795) a
VIII	382.4 ± 14.3 (8; 363–405) d	825 ± 520 (8; 18–1558) a	1204 ± 511 (8; 568–1935) ab	387 ± 22.6 (15; 331–431) c	197 ± 89 (15; 0–293) a	585 ± 91 (15; 368–705) a

lay in growth and the difficulty in molting results from an increase in the time between successive feedings. Higgins & Rankin (2001) observed that spiders fed large amounts of food were more likely to die at or immediately before the next molt.

The abundance of *L. intermedia* in Curitiba is associated with aspects of this species' life cycle. The long period until maturity is reached results in large body size and a low mortality rate. The fertilization of a larger number of females by males is favored by the greater longevity and larger body of the males. Likewise, the life span of up to five years in adult females maximizes their reproductive potential by allowing than to be fertilized by successive generations of males.

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