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FEATURE ARTICLES

POSTEMBRYONIC DEVELOPMENT OF *LATRODECTUS HASSELTI* THORELL (ARANEAE, THERIDIIDAE)

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ABSTRACT

In northern Queensland the eggs of *Latrodectus hasselti* have a lower developmental temperature threshold than do postembryos which in turn have a lower threshold than first instar spiderlings prior to emergence from the egg sac. Emerged spiderlings, however, develop normally at temperatures below that which would prevent emergence from the egg sac. Arrested development of free-living first instar spiderlings may require a temperature of 10°C or less (Forster 1984). The subsequent stadia for both sexes are in general shorter than for the American species of *Latrodectus* which mature later and live longer than *L. hasselti*. For all species of *Latrodectus* for which temperature-controlled data are available males have consistently longer early stadia than do females, partly compensating for an asynchrony in time to maturity. *L. hasselti* males usually matured in the fourth instar, females in the sixth.

INTRODUCTION

The genus *Latrodectus* Walckenaer occurs widely throughout the tropical and temperate regions of the world. Since 1959 the Australian species was known as *Latrodectus mactans hasselti* and was considered conspecific with *L. mactans* Fabricius populations as far distant as the Mediterranean (Levi 1959, 1966). However, this is no longer tenable, and the taxonomy of the genus is still largely unresolved (Levi 1983). Recent investigations (Forster and Kingsford 1983, Forster 1984) uphold the view that it is a species in its own right, *Latrodectus hasselti* Thorell, and it appears to have become established in New Zealand (Forster 1984) where two related species, *L. katipo* Powell and *L. atritus* Urquhart occur (Forster and Kingsford 1983).

Being one of the few genera of spiders whose venomous bite has in some cases been fatal to humans, *Latrodectus* has been the subject of numerous clinical investigations and toxicological studies. In Australia an early survey of araneism (see Maretić 1984) reported 98 cases, including seven deaths, of envenomation by the bite of *L. hasselti*, but concluded that the mortality rate for the population at large could not be estimated (Ingram and Musgrave 1933). Cleland (1942) reported further Australian case histories and Hornabrook (1951) gave a clinical account of *L. katipo* araneism in New Zealand. Sutherland and Trinca (1978) reported 2144 cases occurring in Australia and New Zealand in the eight years to 1976.

The general and developmental biology of *Latrodectus* is best known for those species occurring in the Americas, a particularly detailed and extensive account being that of Kaston (1970). Rempel (1957) gave a comprehensive description of the embryology of *L. mactans*.

The most notable reports on the postembryonic development of *Latrodectus* are those of Deevey and Deevey (1945), Deevey (1949), McCrone and Levi (1964, 1966), Cariaso (1967), Kaston (1970), Gonzales (1979), Forster and Kingsford (1983) and Forster (1984). Developmental studies of this kind have proved to be of fundamental importance in the elucidation of complex taxonomic problems in a number of spider genera including *Latrodectus* (Seligy 1970).

Some useful data on the postembryonic development of *L. hasselti* in Australia were given by Softly and Freeth (1970); unfortunately, that study gave fewer details for females than for males, and temperature was not controlled. Forster (1984) was able to contribute significantly to our knowledge of *L. hasselti* development using specimens introduced to New Zealand from Australia. The latter study included the rearing of spiderlings to maturity at a constant temperature of 25°C, enabling direct comparison with the present data and those of some other authors.

The data presented in this report were obtained from laboratory studies conducted in 1973, 1977, 1979 and 1981. Over these years it has become apparent that although *L. hasselti* is more numerous in the field in summer, all stages of its life cycle can be found throughout the year in northern Queensland, as expected in a tropical region; field populations seemed unusually abundant in the cooler seasons (June-August) of 1973 and 1975. Regrettably, field studies, other than that of Smith (1971) which detailed the habitat preferences of *L. katipo* in New Zealand, have to date been neglected in this region.

MATERIALS AND METHODS

The laboratory conditions under which this study was conducted, unless otherwise stated, included a constant temperature of 25°C and a 14/10 hour light/dark cycle.

Latrodectus hasselti females of field origin in Townsville produced in the laboratory the egg sacs required for the study. For determination of hatch times and duration of early stadia, eggs were put into glass cavity blocks, the glass lids of which were separated from the rim of the blocks by a layer of non-absorbent cotton wool, with a little vaseline as adherent. This allowed for adequate aeration and easy observation while excluding mites and fungal spores. Intact egg sacs were observed simultaneously to disclose the effect, if any, that exposure of the eggs in the described manner might have on the normal course of development.

The main series of developmental studies used spiderlings that had emerged from intact egg sacs in the normal way. In all, 440 spiderlings were used, these being derived from 17 egg sacs each of which was produced by a different female parent. Each spiderling was isolated in a glass tube 50 mm x 25 mm with a perforated plastic stopper.

Insects utilized as food for the developing spiders included *Drosophila melanogaster* Meigen, *Tenebrio molitor* L. larvae (mealworms), muscoid flies and cockroach early nymphs. Prey of a size appropriate to each spider was given two or three times a week; food supply was therefore varied and adequate but not quantified. Water was not provided. Forster (1984) has confirmed that the provision of water is not only unnecessary for rearing *Latrodectus* but may be detrimental.

Weighing of food before and after feeding would be the only method of quantifying food intake and even that would not allow feeding to be rigorously correlated with development, for three reasons. First, disturbance of the spider and its web by meticulously removing food remains would be detrimental, to a varied and unknown extent, to normal development. Second, the amount of energy expended in capturing prey varies enormously between individual spiders, depending to a large degree on the extent of their webs. Third, the food provided is only assumed to be nutritionally suitable. One recent study (MacKay 1982) shows that *L. hesperus* Chamberlin and Ivie is an important predator of the ant *Pogonomyrmex rugosus* Emery, but by and large natural prey preferences and nutritional requirements are poorly understood. An instance of this is the preference shown by *L. mactans* and *L. variolus* Walckenaer for housefly maggots in the study of McCrone and Levi (1964); housefly maggots were rejected, without exception, on the numerous occasions they were offered to *L. hasselti* in the present study. *Tenebrio* larvae, however, were almost invariably eaten but they were not used extensively as food because they were not easily trapped in the web and they sometimes ate dead or weak spiders, posing a threat to spiders undergoing a molt.

Of the 440 first instar spiderlings comprising the main series, 288 subsequently provided the developmental data reported here. There were two sources of attrition. First, data for specimens that died before their sex could be determined were excluded. Second, ten specimens of each instar to maturity for each sex were taken for a morphometric study; where this involved destruction of the specimen before its sex was determined, the data on its development were excluded.

It cannot be overemphasized that the results of this and similar studies, while not invalid, can only be interpreted and compared in the light of the methodological shortcomings. Without field comparisons, laboratory results are artificial and confusing, and artificial diets have been shown to influence carapace width and number of molts in lycosid spiders (Whitcomb 1978).

RESULTS AND DISCUSSION

For the present purpose eclosion is considered to be the shedding of the chorion and to mark the close of the embryonic period. The stage following eclosion and ending with the first true integument molt is termed the postembryo and the stage following the first molt is termed the first instar. It is normally the first instar which emerges from the egg sac in *L. hasselti*. Among the most recent struggles with the terminology, since Peck and Whitcomb's (1970) exhaustive review, that of Peaslee and Peck (1983) is commendable.

The duration of development prior to emergence from the egg sac is summarized in Table 1 for four of the five temperatures used in this part of the study. Five egg sacs were incubated for four months at 15 °C but no development occurred; on transfer to 25°C for a further six months there was still no

Table 1.—Effect of temperature on the development of *Latrodectus hasselti* between oviposition and emergence from the egg sac. Figures are given as mean numbers of days, with numbers of egg sacs in parentheses (figures without (n) are derived estimates—see text). EXP = Eggs exposed for direct viewing. INT = Egg sac left intact. COMB = Combined mean. NFD = No further development. NE = No emergence from egg sac.

Stage of Development		Temperature (°C)			
		18	20	25	30
Oviposition to hatching	EXP	41 (3)		11 (9)	9 (4)
	INT	44 (9)	34 (5)	13 (21)	11 (3)
	COMB	43 (12)	34 (5)	12 (30)	10 (7)
		NFD—(11)			
Hatching to first molt	EXP	25 (1)		10 (9)	5 (4)
	INT		17 (5)	7 (3)	5 (3)
	COMB	25 (1)	17 (5)	10 (12)	5 (7)
		NE—(1)	NE—(5)		
First molt to emergence	EXP				
	INT				
	COMB			11	6
Total (Oviposition to emergence)	EXP				
	INT			33 (47)	21 (19)
	COMB			33 (47)	21 (19)

development although some of the eggs had not dehydrated. Development rarely proceeded beyond the postembryo stage at 18°C and first instar spiderlings did not emerge from the egg sac at 20°C; but after four months (from oviposition) at these temperatures the spiderlings were still viable. Despite these effects, first instar spiderlings that had hatched and emerged at 25°C developed normally, at a reduced rate, at 18°C (see Table 2). In Western Australia *L. hasselti* eggs failed to hatch at 9°C but spiderlings that had hatched at higher temperatures withstood periods of 56 days at 7-9°C, emerging from their egg sacs and thriving on return to room temperature (Softly and Freeth 1970). Similarly, Forster (1984) reported tolerance of temperatures less than 10°C in first instar *L. hasselti* spiderlings.

Whether these temperature tolerances are related to or comparable with the seasonal overwintering that occurs in other *Latrodectus* species is unknown. Smithers (1944) recorded overwintering of up to 212 days in egg sacs of *L. indistinctus* O. P. Cambridge (also synonymized with *L. mactans* by Levi (1959)). In Tasmania, where a similar phenomenon might be expected to occur, the oviposition—emergence period for *L. hasselti* is 50 days in January (summer) and 70 days in November (spring) (Hickman 1967). Data for the winter months would be interesting.

The upper limit of temperature tolerance for development to emergence is close to 30°C (Table 1). Only 10 to 20 spiderlings emerged from four of the egg sacs and the first instar spiderlings of one sac failed to emerge at all. 30°C would not be an unusually high temperature in the field in Townsville; it seems likely that *L. hasselti* web sites are normally positioned to preclude any prolonged exposure to temperatures of 30°C or higher. However, Softly and Freeth (1970) reported that at 37°C *L. hasselti* eggs hatched in eight days and the first instar spiderlings emerged from the egg sac seven days later.

Table 2.—Postembryonic development of *Latrodectus hasselti* at temperatures above and below optimum. Figures are given as mean numbers of days with numbers of individuals in parentheses. First stadium does not include the portion spent in the egg sac.

Temp. (°C)	Sex	Stadium 1	Stadium 2	Stadium 3	Stadium 4
30	Male	14 (7)	10 (7)	15 (7)	12 (4)
	Female	10 (9)	7 (9)	12 (9)	11 (5)
18	Male	29 (5)	27 (5)	47 (4)	
	Female	24 (6)	23 (6)	21 (6)	39 (6)

It is difficult to determine the point of hatching and that of the first molt in intact egg sacs of *L. hasselti.* The former was judged largely as the point at which the mass of eggs ceased to roll freely in the sac, and the latter involved a darkening of the sac contents due to pigment development in the first instar spiderlings. Table 1 clearly shows that either the incubation period prior to hatching is overestimated by the above method or exposure of the eggs shortens the time of incubation. Cariaso (1967) found the reverse: *L. hasselti* eggs, judged from observation of intact egg sacs to hatch in 7.5 days at 27-29°C, took 9-13 days to hatch when exposed.

Since the time of emergence from the egg sac is not applicable in the case of exposed eggs, the time between the first molt and emergence is given as a single value derived by subtraction of the oviposition—first molt time from the mean oviposition—emergence time.

Cariaso (1967) found a wider range (16-44 days) of times from oviposition to emergence at 27-29°C than the corresponding ranges of the present study at 25°C and 30°C which were 26-43 days and 17-24 days respectively. His mean of 28.7 days is reasonably consistent with the results in Table 1.

The three American species of *Latrodectus* studied by Kaston (1970) have exactly corresponding hatch times at 25°C to that of *L. hasselti* given in Table 1; however, subsequent development up to emergence must be faster than it is in the Australian species, emergence taking place between 26 days (*L. variolus*) and 30 days (*L. hesperus*). This is peculiar in view of development rates after emergence.

Figure 1 shows the results of the main series of developmental studies for which 288 spiders, whose sexes were determined, provided data on the duration of the post-emergence stadia. Mortality, to the extent it is meaningful in the artificial conditions of the study, can be taken to be 20-25% (see Methods).

The appropriate data for the earlier (unsexed) stages are included to give a complete picture of the ranges in the duration of all life-history stages; only the period from the first molt to emergence from the egg sac is a derived estimate, without a range, for the reasons given above.

Despite uncontrolled temperature the results of Softly and Freeth (1970) can be reconciled with the ranges of the present data, except that Fig. 1 shows that some *L. hasselti* males molt six times, once more than found for *L. hasselti* in Western Australia. Five was the maximum number of molts undergone by *L. hasselti* males in the study of Forster (1984), while Cariaso (1967) found a maximum of but four molts for *L. hasselti* males in the Philippines.

Two features of the data in Fig. 1 are of particular interest when compared with the results of those studies on the same or related species of *Latrodectus*

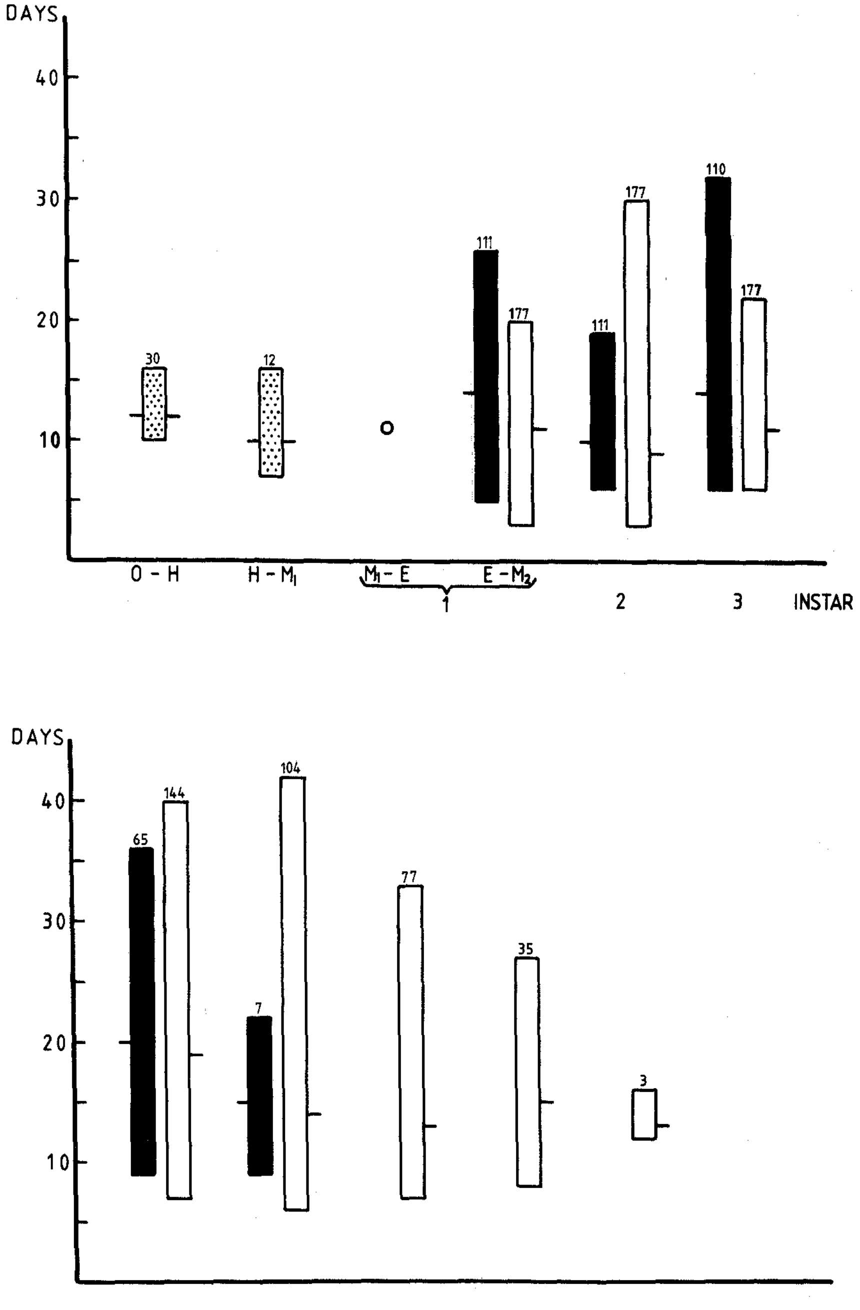

Fig.1.—Mean and range of stadia of *Latrodectus hasselti* at 25°C. Dark columns, males; light columns, females; stippled columns, both sexes combined. O is a derived estimate (see text). Numbers above columns are numbers of individuals. O = oviposition; H = hatching; M = molt; E = emergence from egg sac.

which were carried out at constant and comparable temperature (Cariaso 1967, Forster 1984, Forster and Kingsford 1983, Kaston 1970, McCrone and Levi 1964, 1966). The first is that the two studies on *L. hasselti* show stadia durations comparable with those given in Fig. 1, especially with regard to the absence of any tendency towards significantly longer duration of the later stadia. By contrast, Kaston's (1970) results, and particularly those of McCrone and Levi (1964, 1966), show that much longer periods of time are spent in the later instars in the American species of *Latrodectus*. The results of Gonzales (1979), although for specimens reared at a temperature that varied between 20-25°C, show the same feature. A similar, though less marked, pattern of longer late stadia is found in the New Zealand species (Forster and Kingsford 1983). The second notable feature is that all six of these comparable studies consistently show, as does Fig. 1, that males spend longer in the early instars than do females. Again, the data of Gonzales, though not constant temperature data, show precisely the same feature. It has been suggested (Downes 1981) that this tendency compensates for their having fewer instars to maturity than females, the latter phenomenon being a direct result of the sexual dimorphism in size that has evolved in this genus.

Not surprisingly, lower and higher temperatures retard and accelerate development respectively. Table 2 shows these effects. It is apparent that stadia remain longer for males than for females regardless of temperature.

The shortest time between oviposition and maturity for a female *L. hasselti* was 58 days. Females usually matured in the sixth instar, males in the fourth. The greatest longevity observed for a female *L. hasselti* was for a specimen that was collected mature in the field and died 229 days later in the laboratory (a lifespan well in excess of 300 days can be inferred from this). For a male, 136 days from emergence was the maximum recorded longevity at 25°C, and 211 days from emergence at 18°C. The American species of *Latrodectus*, then, develop more slowly, mature later and live longer than *L. hasselti* of the Philippines and Australia.

The development of the palpal organs, characteristic of maturing males, was sometimes apparent in the second instar but was occasionally not evident even in the third instar. Those individuals that died before their fourth instar, therefore, unless clearly males, were excluded from the study. Of the remaining individuals 111 were male and 177 female. Males tended to construct inferior webs and expend more energy in trapping prey than did females; more males than females may therefore have died before maturity. A similar situation may have influenced the observations of Softly and Freeth (1970) who reported a male:female sex ratio of 1:5 for *L. hasselti*. There is no reliable report of a sex ratio other than 1:1 in the literature on *Latrodectus*.

There remains, in this and other similar studies, a marked variability in the number and duration of the stadia in *Latrodectus* (see Kaston 1970), despite stringent efforts to apply uniform conditions. Apart from the difficulties (discussed above) of controlling food supply and feeding there is another factor, other than inherent genetic variability, contributing to this: the production and use of trophic eggs (Downes 1985). Reports of the occurrence of this phenomenon continue to accumulate and it occurred in the present study as it did in Kaston's (1970) study of *Latrodectus* in the United States. Its effects, investigated by Schick (1972) and Valerio (1974), may influence subsequent development more than has hitherto been recognized. An extensive investigation has been made of egg-feeding in *Theridion rufipes* Lucas, one of four Townsville theridiid spiders, including *L. hasselti,* whose first instar spiderlings have been seen to feed on inviable eggs prior to emergence from the egg sac. The results of that study will be available in the near future.

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