# The behavioural ecology of *Latrodectus hasselti* (Thorell), the Australian Redback Spider (Araneae: Theridiidae): a review

Lyn Forster

McMasters Road, RD 1, Saddle Hill, Dunedin, New Zealand

**Abstract** – Aspects of the biogeographical history and behavioural ecology of the Australian *Latrodectus hasselti* provide support for the endemic status of this species. Cannibalism, prey stealing and short instar lengths are growth strategies for female spiders whereas early maturation, small size, hiding and scavenging are useful survival tactics for males. Moreover, male complicity is an important component of sexual cannibalism which is shown to be a highly predictable event. *Latrodectus hasselti* males hybridize with female *L. katipo* (a New Zealand species) and fertile F1 and F2 generations imply genetic relatedness. Hence, it is likely that *L. hasselti* and *L. katipo* evolved from a common ancestor in ancient Pangaea, a feasible explanation only if *L. hasselti* is endemic to Australia. It is concluded that *L. hasselti* would have been able to persist in outback Australia for millions of years, with its intraspecific predatory habits aiding subsistence and the evolution of sexual cannibalism providing a way of coping with infrequent meeting and mating opportunities.

## INTRODUCTION

Many stories and articles have been written about the redback spider (McKeown 1963; Raven 1992) with considerable attention being devoted to its venomous nature (Southcott 1978; Sutherland and Trinca 1978). But, behaviourally, this spider poses one of nature's most intriguing riddles for, instead of the North American black widow, it is actually the Australian redback female which cannibalises its mate (Fig. 1). The events preceding this deed and set in motion during courtship, are master-minded by its genes (Forster 1992a).

The redback is undoubtedly Australia's most widely known spider (Main 1965). Hence the suggestion that it could be an introduced species (Raven and Gallon 1987) aroused interest amongst the news-hungry public (Harris 1988; Mitchell 1988) as well as arachnological scientists. The main reasons for this proposition were (1) that it had not been recorded until 1870, long after many other indigenous species were known, and (2) that its preference for human-modified habitats followed a pattern known in other introduced species.

However, in 1993, Barbara York Main drew attention to the diary record and coloured illustration of a readily identifiable redback spider collected by Edward Snell from the "Adelaide Hills" in 1850 (Snell 1988). Moreover, by tracing several derivations of the words meaning "spider" in aboriginal languages, Downes (1993) raised the possibility that the redback was known to the indigenous people of Australia. While these reports do not offer "proof positive" of *L. hasselti's* indigenous status, Main (1993) notes that, (as a consequence of its supposed introduction), "the absence of *Latrodectus* in the Australian region, **prior to human habitation**, poses a curious zoogeographic dilemma". This comment raises an interesting point which will be given further attention later in this paper.

The "introduction" theory, nevertheless, gains qualified support from a paper by Cariaso (1967) about black widows in the Philippines (then believed to be *L. mactans*) in which it is stated that "after some time the male turns its abdomen towards the venomous fangs ...of the female." Later, Cariaso adds "...a majority of the males are devoured by the females." No further details are given but these comments infer that this spider cannibalises its mate in the manner described for *L. hasselti* (Forster 1992a, see below). Because this, otherwise unique, mating behaviour occurs in a Philippine *Latrodectus* species, can we assume that it **is** *L. hasselti*. If so, then did it colonise Australia at some stage, or was it introduced into the Philippines as Sloggett (1946) noted?

This paper portrays the life style and habits[1] of this spider, poses some questions and offers some possible explanations. For example, did it once eke out a living in the outback of Australia or perhaps

---

[1] Unless otherwise stated many of the new observations I describe here are the result of rearing hundreds of redback spiders in captivity but there is no reason to suppose that, if spacious enough, captive webs present any discernible differences from wild webs to their inhabitants. Observations in the field were also carried out in Queensland, Australia in 1988 and in Wanaka, New Zealand in 1981, 1983 and 1990.
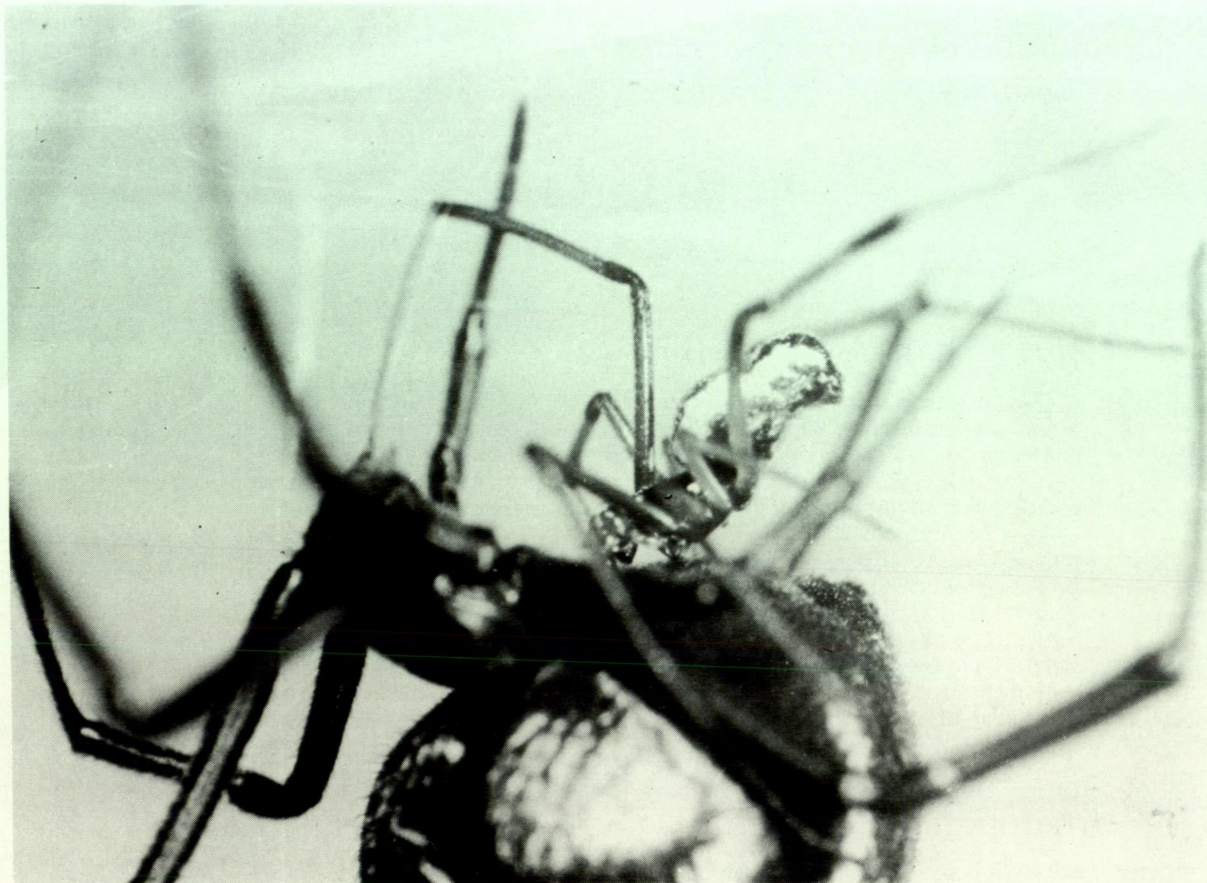
**Figure 1** Immediately after inserting his embolus into the female epigynum, the male raises himself into a headstand – shown here – then turns over in a complete somersault (see Figs 5 and 6). This highly predictable act, not known in any other *Latrodectus* species, ultimately leads to his demise. (Embolus = male reproductive organ; epigynum = female reproductive opening).

some other land and then find a comfortable livelihood in Australian suburbia? And was it perhaps a gravid female emigrating to New Zealand in somebody's luggage that led to a founding colony on the lower slopes of Mt Roy in Wanaka, central Otago, New Zealand, and thus begin the events which led to this story (Forster 1982, 1984)?

## HABITAT, DEVELOPMENT AND DISPERSAL

### Habitat

Primarily a ground-dwelling spider, the redback occupies a wide range of microhabitats, the main requirements being shelter from wind and rain, adequate warmth for breeding and a plentiful supply of suitable food. These conditions were more readily met in Australia with the coming of European settlers whose lighted dwellings attracted both spiders and prey, so that *Latrodectus hasselti* has prospered (Forster 1988). Within a suitable site the redback builds a conical web retreat linked by threads to a catching structure (Main 1965) which is laced with sticky globules. Together occupying an area ranging from 5 to 20 cm$^2$ they are anchored by a series of dry trap lines

to a nearby substrate. The cone retreat becomes much thicker during cooler temperatures (< 10°C) and the spider withdraws to its uppermost area (Forster, personal observations).

Despite its denser populations in warmer areas (Forster 1988), *Latrodectus hasselti* is able to tolerate a wide range of climatic conditions. In parts of Australia, temperatures fall below freezing at times; in other places redbacks have been seen in the open at 41°C (Softly and Freeth 1970). In New Zealand, snow lies on Mt Roy for short intervals during the winter but redbacks, hiding under rocks or logs, are buffered against the cold. During videotaping of females and young spiderlings moving freely about on uncovered webs, ambient temperatures from the studio lights required for such close-up work led to the death of two females although all spiderlings remained fully active. Measured at 43°C, one explanation may be that the females' heat-absorbing blackness and greater mass led to their deaths whereas the whitish sheen of the young reflected the heat and enabled them to survive (see Robinson and Robinson 1978). In the wild, dispersal could expose spiderlings to a wide range of thermal conditions, hence their pale colour not only makes them inconspicuous but may also shield them against heat extremes.
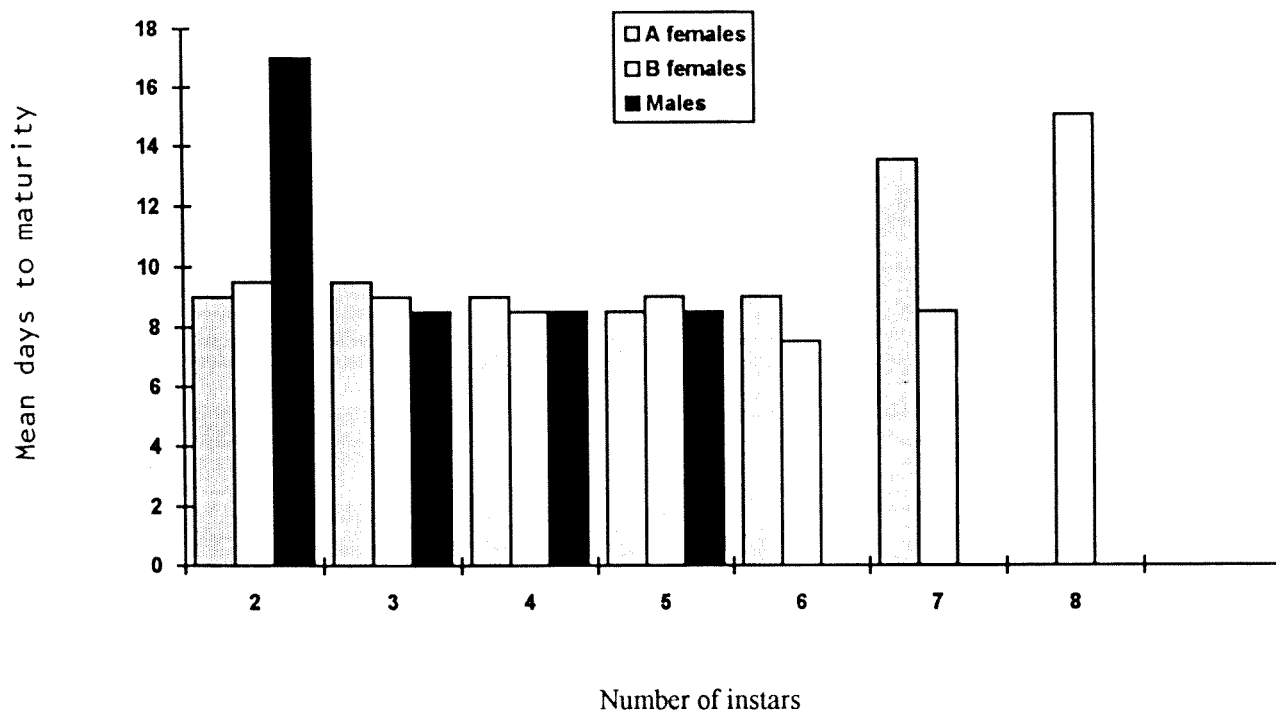
**Figure 2** Developmental trends in male and female redback spiders. Males generally mature in the 5th instar while females mature in (A) the 7th, or (B) the 8th instar. (Mean data only – for standard deviations see Forster (1984)).

## Development

Temperature has been shown (Forster 1984, Downes 1987) to influence the growth rate of these spiders. In the laboratory, males mature in 28 to 45 days and females take 45 to 74 days when kept at a constant temperature of 25°C and a light/dark regime of 12/12 hours (Forster 1984, Kavale 1986). These conditions appear to be close to optimal since Downes (1987) found that when reared at 30°C, their development rate is not markedly greater. At temperatures below 25°C, however, the time taken to reach maturity increases. Below 10°C growth apparently ceases and spiders enter a state of quiescence during which they are able to withstand cold conditions while sheltered within their now-denser conical retreats (Forster 1984).

Figure 2 shows that the duration of the second instar in females is considerably less than that of males, an advantage maintained throughout development, and a trend also noted by Downes (1987). Note that most males mature at the 5th instar and females mature at either the 7th or 8th instar (Forster 1984). Thus, although females take almost twice as long as males to reach maturity, they become larger, more quickly. Clearly this gives them the competitive edge with respect to males and smaller siblings in prey capture and cannibalism.

While *L. hasselti* has been largely regarded as a sub-tropical species, it is well adapted to endure adverse circumstances. This is no doubt why it is able to tolerate the snowy winter weather in central Otago, New Zealand. The most important factor is that, here, hot summers of 4-months or more allow them to breed. Since 1980 the population in this rather desolate uninhabited area has slowly increased and, recently, females have been discovered in the small Wanaka township some 12 km away.

## Dispersal

Prior to dispersal, neonatal spiderlings track the light and climb to the upper limits of nearby logs, stones or vegetation. Tests (Forster 1984 and unpublished data) show that this positive phototactic behaviour persists during the second instar but that subsequently spiderlings and juveniles are less likely to be attracted to light. If newly hatched spiderlings are kept in the dark, for example, they remain within 5–6 cm of the eggsac and do not climb upwards. Thus the likelihood of widespread dispersal at later instars is reduced. Perhaps this shows that, in the wild, some spiderlings may be uplifted for varying distances while others remain near their hatching site.

Under the right conditions, spiderlings are cooperative climbers. As the first echelon moves upwards, each spiderling holds a line of silk away from the substrate with a fourth leg and periodically attaches it. These primary lines are quickly climbed by other spiderlings, in turn laying still more silk. However, the 'lead' spiderlings provide the most direct path for others, and the ascent gathers momentum. Inevitably, clusters of spiderlings are formed, each cluster intent on its upward urge. Once at the summit of a rock or bush

spiderlings are ready to balloon, the aerial mode of transport usually adopted by redback spiderlings (Raven 1992). One method of 'taking off' may utilise loose strands of silk which seem to appear as spiderlings climb, somewhat similar to the 'second line' technique of airborne initiation described by Eberhard (1987). Perhaps they also take to the air in clusters since their usual refuge is within a communal network of silk (Forster 1984).

These days, however, it is most likely that larger redbacks travel by car, or boat or plane, even in Australia. The introduction of these spiders into New Zealand clearly involved sea and air transport since they were found in their dozens in containers during the early 1980s (Forster 1984). Whether, in the wild, juveniles and/or female spiders periodically leave established webs, move to another site, and build anew, has not been ascertained with certainty. But many householders in Australia testify to the sudden appearance of redbacks in a tool-shed, letter box or underneath playground equipment, for example, where none had been seen a few days earlier. In Texas, U.S.A., Gary Polis (personal communication) has observed black widows (*L. mactans*) walking on the desert sands at night.

The mobility of males is more of a mystery. Their small size and pale colouration make them inconspicuous, hence their movements go unnoticed. But finding females is not likely to be left to chance. Undoubtedly, female pheromones provide important locational signals as Ross and Smith (1979) showed for *L. hesperus* but how do males travel? Perhaps, if they balloon together as spiderlings they take up residence near a female at an early age, lurking nearby until she is mature. Laboratory studies also show that, as juveniles, males tend to hide behind twigs or under debris when communally reared with females (Forster, personal observation). Another strong possibility is that, because of their small size, adult males are still able to balloon. Perhaps larger distances are covered in this way and the male is then guided locally by pheromones. In *L. reviviensis*, for instance, Anava and Lubin (1993) found males moved from one female web to another and were probably directed by web-borne pheromones.

## PREDATORY BEHAVIOUR

### Entrapment

*Latrodectus hasselti* spiders enjoy a varied diet, trapping some 60–70% of beetles as well as other kinds of insects, spiders, small mice and occasionally lizards which blunder into their sticky trap lines (Forster 1988). When alerted by such disturbances, the redback rushes to the site, and pauses just a leg's length from the target.

Stretching out a front leg to touch it, the spider gives the impression that it is assessing the target's distance and direction and perhaps its identity and palatability. Such tactile behaviour may provide important diagnostic information for the spider which has to take the risk of turning its back before squirting a swathe of viscous silk over its target. When directed at a small house fly, for instance, this 'super glue' may instantly bind both legs and wings to its body, effectively immobilising it (Forster, personal observation). Liquid 'super glue' emanates from greatly modified aggregate glands and passes via short ducts to the posterior spinnerets (Kovoor 1987) from which it is disgorged through extra wide spigots (Coddington 1989). Perhaps a sudden increase in intra-abdominal pressure which forces liquid silk from the glands through the short duct and spigots is responsible for the swiftness of this action.

### Biting and trussing

Once restrained, the spider bites its prey repeatedly on the head, body and leg joints. Usually bites are interspersed with further bouts of both sticky and dry silk wrapping, threads being drawn from the spinnerets by the alternate movements of the hind legs. Although 'super glue' appears wet and viscous whereas sticky silk consists of globules adhering to a thread, this difference may be the result of variation in the method of application. Most often wrapping is carried out while the spider hangs vertically, its underside directed towards the victim, and abdomen bent inwards thus allowing the silk to be more carefully targeted towards the victim's body (Fig. 3) (Forster, in preparation). Prey is not rotated, hence this wrapping technique differs from that employed by araneids, for example. The effectiveness of 'glueing and biting' enables the spider to tackle large and often dangerous animals.

Provided with a torpid mealworm as prey, however, redbacks may tap it with the palps first, then bite. The bite invariably activates the mealworm and its subsequent wriggling triggers silk throwing by the spider. Silk is the primary immobilising medium used by *L. hasselti* and movement of prey the impetus for its use; the more movement from the prey, the more silk is tossed to truss it up (Forster, personal observation). Apparently, venom is only employed after the initial subjugation of prey has been achieved, except in the event of prey sluggishness.

An important function of biting and the accompanying action of the mouthparts involves the injection and infusion of digestive enzymes. These enzymes lead to the liquefaction of the internal tissues of the prey, a process which takes some time to accomplish. During biting and trussing, the spider periodically abandons its prey
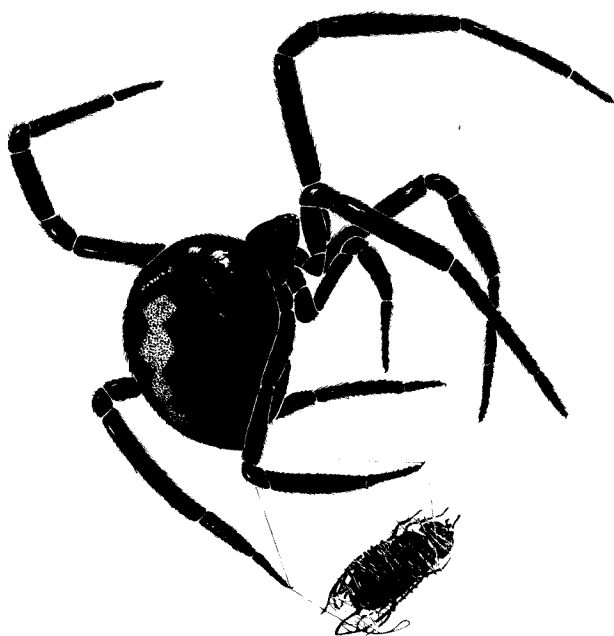
larger size, since even a slightly smaller conspecific will quickly abandon its catch as soon as the marauder is within touching distance. The victor may gather up several extra items in this way, cutting them free and transporting them all back to its lair. Occasionally, if the seized item is left unattended while the marauding spider steals another, the original owner may steal it back (Forster in prep.).

There are considerable advantages to this strategy. The larger spider gains extra food at a much lower cost, there being less energy expenditure and a greatly reduced use of silk. The spider will consume most of this food over the next few days, items such as meal worms often requiring 24 hours or more to ingest. During this time, the spider swells visibly, its black velvet sleekness being replaced by a dull brownish-orange hue. Mealworms and other larvae, in particular, affect the colour of the spider if large quantities are consumed (Forster, personal observation).



**Figure 3** After spurting sticky silk at prey, the redback spider throws more silk and partially wraps it before biting.

some 6 to 10 times, these egresses gradually increasing in duration from two to three seconds to up to 10 minutes. The interval between first bite and ingestion may be from 5 to 20 mins, this variability depending to a large extent on the relative size of prey and spider as well as the degree of prey resistance (Forster in prep.). This 'elapsed time' is assumed to be a measure of the venom and enzyme reaction time required prior to ingestion.

## CANNIBALISM

Often cannibalism is regarded as an artefact of captivity. But in a web-building spider, captivity is less likely to influence behaviour than in, say, hunting spiders because a web is always the spider's natural environment wherever it is constructed. This is demonstrated by the fact that redbacks appear equally at home in the glove box of a car (Forster 1985) as they are under a log well away from human habitation. Moreover, cannibalism has never been observed in *Steatoda grossa* (Theridiidae), a related genus with similar appearance and habits, when maintained in equivalent captive conditions. It is likely, therefore, that *L. hasselti* is innately predisposed towards cannibalistic behaviour.

### Transport and Ingestion

When trussing and biting have been completed the spider cuts its well-wrapped prey free from the surrounding web. Then, with its prey securely supported with a thread from its spinnerets and held between the back legs, the spider climbs back to its lair. Feeding commences at once, the spider ingesting the contents from several places around the head, body and leg joints. All available nutrients are extracted, leaving the carcase completely desiccated.

### Prey stealing

Sneak feeding by spiderlings (see below) and prey stealing amongst larger females are common occurrences (N>25). Gravid females are particularly assiduous in gathering up as much food as possible and storing it within their retreats. When prey is readily available, the spider will truss and bite its own victim and then, alerted by a nearby spider's activity, it will move through the web and seize this spider's already trussed and bitten prey. Its success is mainly by reason of its

### First meals

Most redback spiderlings emerge from the eggsac within 12 hours of each other but up to 10% remain within the sac for 2–5 days. This latter group tend to be the "stay-at home" spiderlings who do not disperse with the others (Forster 1984). First meals for some of these may consist of siblings or they may "sneak feed" from the female's catch. As the female begins to devour her catch, two or three spiderlings approach cautiously, usually assuming feeding positions on the far side of her prey. Sneak feeding is not condoned by the female who periodically conducts exploratory sweeps with her front legs, actions which often deter them. Some of the "super glue" thrown by the female may miss its target and can be seen in globular form attached to a silk thread. These globules are frequently imbibed by spiderlings still in the female web (Forster 1992b).

In captivity, spiderlings readily catch *Drosophila* but initially the direction and distance needed for swathing prey may be astray. Accuracy quickly improves. Since several spiderlings may attack a single fruit fly it is almost inevitable that some fall victim to the "super glue" attacks of others. A bundle consisting of one *Drosophila* and two to three spiderlings may ensue and this food parcel is then shared by several spiderlings, not necessarily those which initiated the attack. Indeed, those first on the scene are more likely to be victims.

First meals for spiderlings dispersed in the wild have not been observed but it is reasonable to suppose that midges and other small insects form the basis of such meals. Since spiderlings quickly construct a communal silk network it is probable that opportunistic cannibalism is also a feature of their wild existence. In captivity, cannibalism of sluggish individuals by more active spiderlings is a frequent occurrence but does not generally take place until neonatals are more than ten days old (Forster 1992b).

## Juvenile cannibalism

In captivity, juvenile cannibalism is a regular feature (Forster 1984) regardless of the starvation level (Forster and Kavale 1989) exhibited by the cannibal. While it is more common that larger spiders prey upon smaller companions, the reverse situation has also been observed. The victim of a cannibalistic attack is treated as prey. Initially, there is an encounter between spiders from adjoining webs. Each spider may attempt to immobilise the other with silk but the larger one is more likely to be successful. After wrapping, injecting and the 'venom/digestive time-lapse', the hapless spider is consumed, its carcase cut from the web and discarded. Should the target spider flee after first being struck with sticky silk, it is able to remove this silk by first wiping its legs with the mouthparts and then using its legs to clear the abdomen of silk (Forster, personal observation).

Studies have shown (Forster 1992b) that cannibalism is a growth strategy for female *Latrodectus* spiders. From the neonatal stage to adulthood, cannibalistic females grow more quickly and reach maturity earlier than less cannibalistic siblings. Once a particular female gains the advantage, she will prey on smaller individuals and steal their catches. In this competitive environment young males are disadvantaged. However, by hiding and feeding on prey remains, many survive. Moreover, because they soon need much smaller food items than the female, they are no longer competing, nor in danger. As adults, males do not catch prey although they often imbibe water and have been seen on discarded prey carcases.

## Adult cannibalism

Despite the prevalence of juvenile cannibalism, adult females may be surprisingly tolerant of some younger females in the same web structure, preferring to steal their prey rather than cannibalise them. It could be argued that space and hunger are limiting factors and that once a population equilibrium has been reached, cannibalism is minimised (Forster 1984). Experiments with *L. mactans* (Forster 1992b) show that conspecifics and prey items less than 15% the size of a female are mostly ignored. This means that a juvenile spider the size of an adult male is not treated as prey. Close scrutiny reveals that females are unresponsive to small movements in the web. This observation has important implications for interpreting the behaviour of a male in the female web.

## SEXUAL CANNIBALISM

### Pheromonal cues

For 2–3 days before moulting, sub-adult females may be courted by mature males. Most of this activity consists of pre-copulatory behaviour (see Forster 1992a) and is conducted in the vicinity of the epigynum. Prior to this, resident males subsist around the perimeter of the female web. Moulting females were not observed to attract males and male courtship did not generally begin until at least 24 hours after this moult. However, males performed courtship in fresh webs made by females which had been removed as Anava and Lubin (1993) also found in *L. reviviensis*.

### Functions of courtship

In *Latrodectus hasselti*, the onset of courtship precedes copulation by several hours (5.03 ± 0.84h). A number of acts peculiar to *Latrodectus* courtship (Forster 1992a; Anava and Lubin 1993) are performed by males, these eliciting leg-flicking, lunging and/or chasing from females. Most male acts relate to particular stages of courtship, e.g, (i) when he first enters the web (ii) after contact with the female and (iii) upon mounting the female venter (Forster 1992a). Female rejection responses usually diminish with time and ultimately she adopts a suspended docile posture in or near her retreat.

Platnick (1971) suggested that the principal functions of courtship are to (i) reduce the likelihood of the male being attacked by the female (ii) provide signals indicating the male's potential reproductive status and (iii) allow for physiological priming in both partners. Experimental studies reveal some modifications to the first of these notions. Like *L. mactans*, *L. hasselti* females are similarly unresponsive to small prey judged to be

less than or equal to the body weight of males (mean 6.83 ± 2.41 mg, n = 85) (Kavale 1986). Moreover, during trials in which 17 females were each courted by one male it was found that, in all cases, males were only assaulted after copulation and somersaulting (Forster 1992a). Of 13 males introduced into non-virgin female webs 96 h after females had mated, two mated within 24 h and were also cannibalised. The other 11 males did not court or mate after this 96 h period, were not attacked by females and were removed unharmed after 14 days (Forster, unpublished data). Hence it appears that mated females become unresponsive to males in the web within four to five days after mating regardless of whether such males are, or are not courting, the inference being that redback males in the web are not in danger of being treated as prey.

It is likely, therefore, that *L. hasselti* courtship is not designed to enable the male to approach the female with caution but rather to attract her attention, since his normal web movements do not. No doubt, male acts such as abseiling, running away, web-cutting and web bouncing led observers to interpret this behaviour as constituting a prudent approach. Whereas it may be that certain facets of male courtship are designed as deterrents or distractions to competing males. If, for instance, a potential mate has less chance of a successful copulation in the presence of other males, how, then, can this competition be minimised?

Since courtship is a genetically programmed event, activated by web pheromones (Ross and Smith 1979; Anava and Lubin 1993) would it not be selectively advantageous to have male-impedance components incorporated within it? Moreover, because there are several reports of two or more males being seen in the periphery of a female's web in the wild (e.g. McKeown 1963, Forster, personal observation) it makes evolutionary sense for male courtship to cater for this probability. Hence, it may be erroneous to describe courtship as being directed solely at the female. Rather, some elements, such as web cutting and web-bundling, may delay or impede the activities of another male. Once selected by the female, elements that disadvantage other males and hence benefit the "successful" suitor, will persist regardless of whether other males are actually in the web or not during courtship.

The fact that courtship is almost always a lengthy procedure supports the contention that physiological priming is one objective. Female choice may be another (Forster 1992a). Moreover, male web activities, such as bouncing, jerking, leg waving stimulate the female either into activity or docility. Female responses to male acts include flicks of the legs, lunges or short chases. But, during courtship, females never throw silk at conspecific males or behave in a distinctly predatory fashion. Males may repeat their web-related acts for many hours until female priming/choice is achieved, probably demonstrated when females adopt the mating posture. Once complaisance occurs and males make contact with the female, she submits to having silk, usually referred to as the 'bridal veil', thrown over legs and body. Videotaping of *L. hasselti* females show, however, that part of this "bridal veil" actually forms a cradle beneath the abdomen and, as we shall see, provides leverage for both male and female during subsequent events.

## Precopulatory events

Males add a number of acts to their repertoire once they climb on the venter of a submissive female (Forster 1992a). Many of these utilise movements of the palps which tap vigorously in the vicinity of the epigynum. For example, "knocking" with the `selected intromittent' palp (usually the left one first) against the epigynum may have a stimulatory effect on the female. "Scraping" the edge of this palp at the epigynal rim eventually leads to the `freeing' of the embolus tip (video obs.) from its protected position (Fig. 4). Perhaps "rubbing" the distal parts of the palps together conditions the emboli for insertion. "Nibbling" at the epigynal orifice with the mouthparts coincides with the appearance of fluids
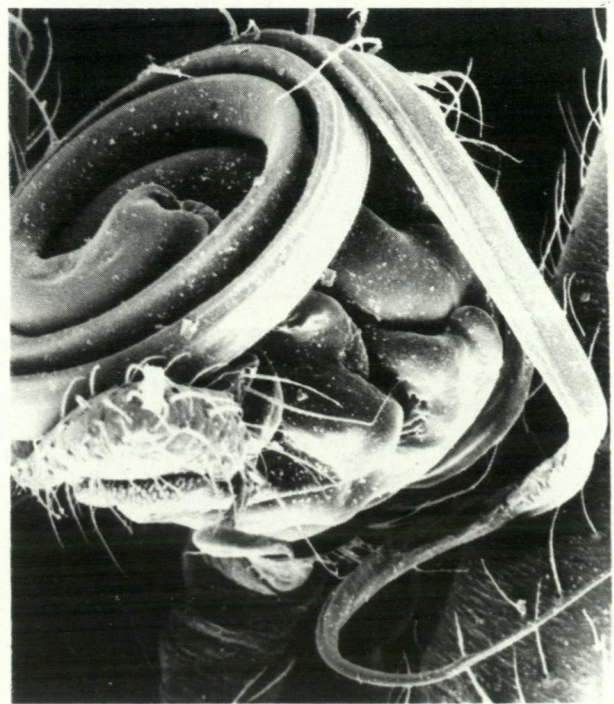


**Figure 4**  Lateral SEM view of palp of an unmated male *Latrodectus hasselti* (courtesy of J. Kavale, 1986). The distal portion of the embolus is tucked protectively behind the cymbium and must be "sprung" before intromission can take place.

which flow over the epigynum and seem likely to have originated from the male (video obs.). Are they digestive juices and is their function a lubricative one?

During these episodes of palpal foreplay, the male pauses periodically while the abdomen vibrates rapidly up and down (8–12 cycles/sec) for 10–15 secs. Intervals of 30–120 secs separate these intense vibratory phases (Forster, unpublished data) which accompany a gradual mid-abdominal constriction and shrinkage of the posterior abdomen. This pre-copulatory phenomenon is not known in any other *Latrodectus* species. Apparently, abdominal constriction and release of the embolus tip foreshadow penetration of the epigynal duct and the associated hematodochal inflation (Forster 1992a).

## Copulation and somersaulting

Up to this stage, the copulatory posture of the male is as for other *Latrodectus* species (see Kaston 1948, fig. 2009). But then, a unique event occurs. The male raises himself into a headstand position (see Fig. 1) and somersaults towards the female's sternum. The somersault is conditional upon hematodochal inflation and is apparently initiated by this event (Forster 1992a). But it is also assisted

by an upward push from the female abdomen which is supported by the web cradle below (video obs.). This somersaulting behaviour has occurred in all observed trials (n = 86) (Forster 1992a and unpublished data).

The male comes to rest with his abdomen against the female's mouthparts (Fig. 5) from which digestive fluids are exuded at once; his surrender is complete when the female secures his abdomen with her fangs. Although it has not been possible to determine whether the female injects poison at this time, it seems unlikely. One reason is, that for the female to benefit from a second insemination, the male must survive the first one. Second, in mating observations involving just a single intromission (n = 11), the male remained active for periods of up to 24 hours (Forster 1992a).

The first signs, some 5 to 20 mins later, that male withdrawal is imminent come when he begins to flex and jerk his legs. These movements accentuate and eventually the female releases him. Sometimes she restrains him with a single fang and at other times she seizes a leg. Once the male achieves some purchase against the female abdomen with three or four legs, he is able to tug his embolus free. The male's release is usually accompanied by the appearance of a pellet of white guanine at the
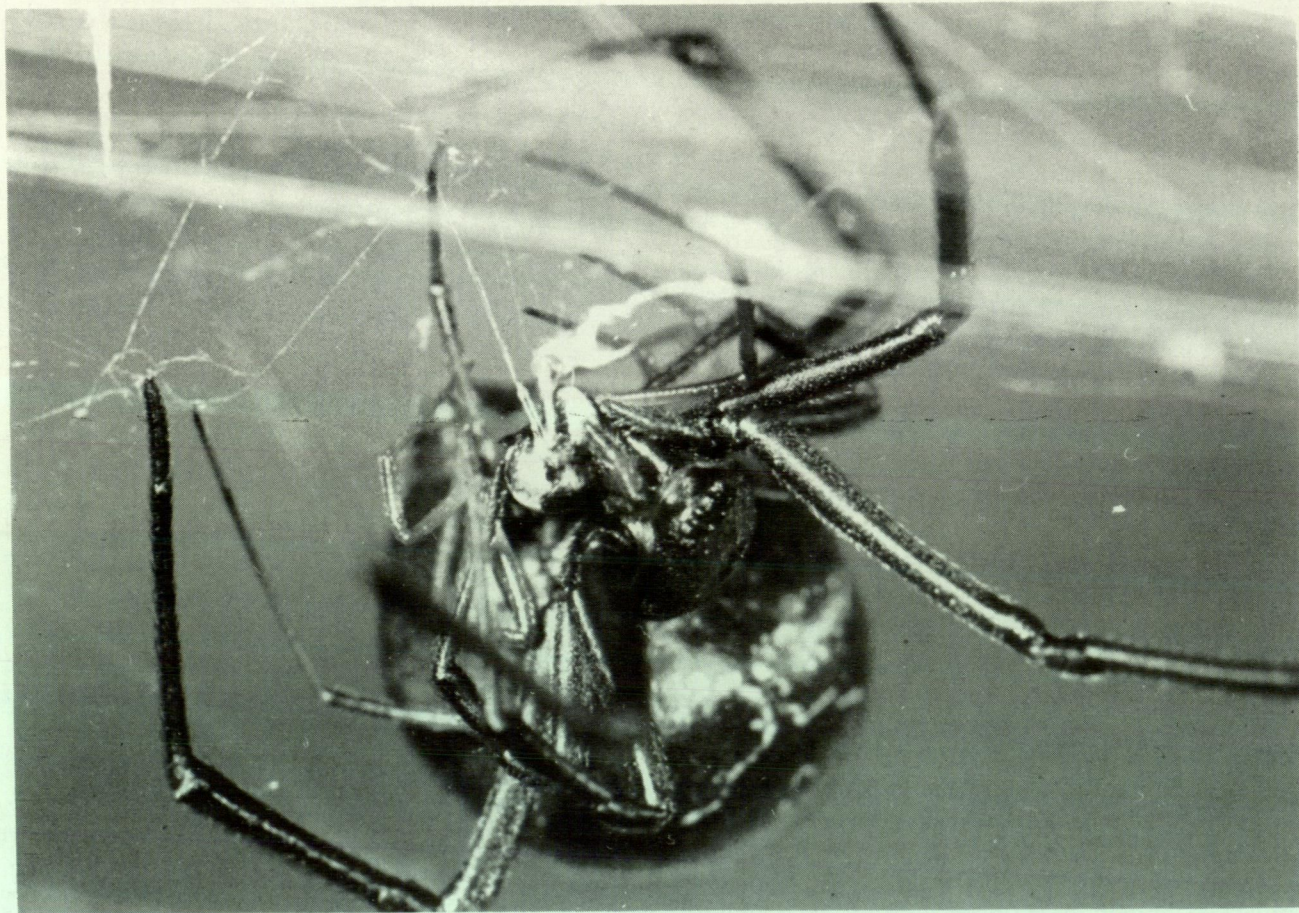


**Figure 5**   The "somersault" results in the redback male falling backwards against the female's mouthparts (also see Fig. 1). Immediately she grasps him and exudes digestive juices onto his abdomen.

female's mouthparts (Forster 1992a). This happens because the first digestive phase consists of the dissolution of the outer chitin and sub-dermal guanine layers of a portion of the male's dorsal abdomen. These particles are too large to be ingested and are filtered out by a "palate plate" and regurgitated (Bartels 1930). Perhaps it is the need for the disposal of this pellet that induces the female to liberate the male. Moreover, this intermission also provides for pre-digestive processing, the male normally returning for the

second insemination in about 10 to 15 minutes (Forster 1992a).

### Sexual cannibalism

After the next somersault the female begins to suck up his internal body fluids, and the male generally becomes too weak to escape a second time. Timing is critical, with two different digestive phases being controlled by distinctive behaviours. But "slip-ups," occur; males sometimes do not, or cannot, return for a second insemination,
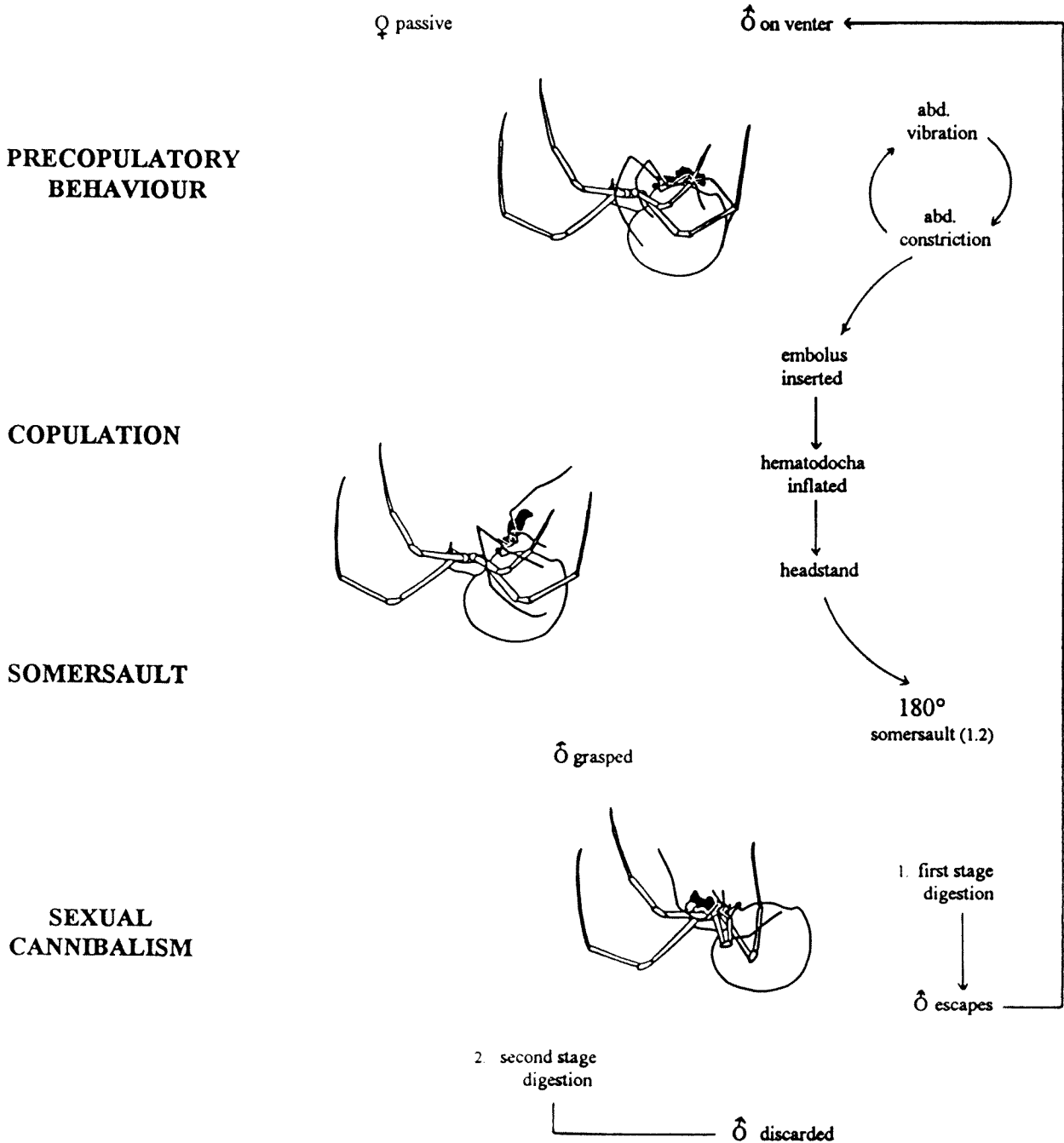


**Figure 6**   Key events which determine the fate of the male *L. hasselti*. Abdominal vibration (abd.vib) appears to be linked to abdominal constriction (abd. constr), the latter probably ensuring that vital organs are not initially damaged (see Forster 1992a). This process only occurs during the first precopulatory stage. Each of the two somersaults (1, 2) presages a particular digestive phase. Each digestive phase accompanies an insemination, most commonly with the left palp first and the right palp second. See text for details.

sometimes they escape after the second intromission although the female may later find, wrap and devour her wounded mate (Forster 1992a).

The sequence of events described here reveals a finely tuned strategy during which the mating obligations of these two spiders and the pre-digestive conditions of female predation are intricately interwoven (Fig. 6). Thus, sexual cannibalism by *L. hasselti* females incorporates predictable elements of male complicity, a genetic state of affairs (Forster 1992a) found in relatively few other species[2].

## HYBRIDIZATION

### Cross-mating experiments

New Zealand has two indigenous *Latrodectus* species, one of which is *L. katipo*. When *L. katipo* males were introduced into *L. hasselti* webs, the resident redback female always attacked the katipo male (n = 10) (Forster 1992a). Mating was not induced even when several ploys, such as "switching males and/or webs" and "waxing the tarsi to prevent female attack", were attempted (Kavale 1986). A likely explanation relates to the fact that a katipo male weighs some 12 ± 2.78 mg (n = 50), twice that of a redback male (loc. cit.). Hence his greater "noise" in the web sends prey signals to the redback female which reacts accordingly.

However, redback males readily mated with female katipos (100% success, n = 22)(Forster 1984, Kavale 1986), a unidirectional reproductive phenomenon noted in some other species, e.g. *Phidippus* spp. (Edwards 1980). Apparently, their almost identical courtship regime overcomes an otherwise, relatively "noiseless" approach, thereby deceiving the katipo into mate acceptance. As in conspecific matings, redback males somersault and lie against the katipo mouthparts but are not cannibalised (Forster 1992a).

These interspecific matings produced viable F1 hybrids from which F2 generations were bred (Kavale 1986). Fecundity in hybrids was found to be intermediate between the parent stock (Fig. 7) indicating a genetic 'bias', although it is known that factors such as nutritional state of the female, temperature and adult size (Kavale 1986) are also influential. There was, moreover, a skewed ratio (*ca.* 3:1) of females to males in the F1 generation. Visually, hybrids looked more like katipos but
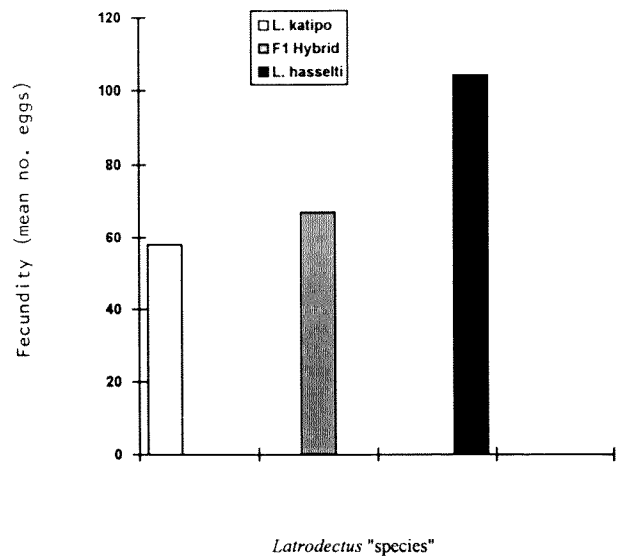
*Latrodectus* "species"

**Figure 7**  Comparison of mean fecundity data in *L. katipo* (n = 56), F1 hybrid (n = 36) and *L. hasselti* (n = 16). (For original data and standard deviations see Kavale (1986)).

other characters such as leg length, hair type and density, etc., were quite variable. Fertility was very low (3%) in the F1 generation but improved substantially (83%) in the F2 generation (Kavale and Forster, in prep.). This high F2 fertility rate means that the hybrids must have been capable of exchanging genes which, in turn, implies that their allopatric biparental stock possess common fertilization systems, and hence a high degree of genetic relatedness. (For more details of this argument, see Templeton 1992 and Paterson 1993.)

Perhaps these findings are best explained by proposing a common origin for these two species arising from the juxtaposition of Australian and New Zealand land masses during the "gondwana" era some 150 million years ago (Stevens 1985). If, therefore, *L. hasselti* and *L. katipo* are sibling species, their long geographical isolation has led to specific changes in mating behaviour, habits and some morphological characters (Kavale 1986) but not to other heritable features. Such an explanation is only tenable if we accept that redbacks are indigenous to the Australian region and not a recently introduced species. In which event, Sloggett's (1946) account of the introduction of *L. hasselti* into the Philippines in boxes and crates from Australia is supported.

## BIOGEOGRAPHICAL PERSPECTIVES

Only a few spider genera are as widely distributed as *Latrodectus*. Relatively minor differences occur in their general appearance, their overall habitat requirements, their behaviour and, quite significantly, their genitalia. Understandably,

---

[2] Elgar (1992) lists some 87 invertebrate species in which sexual cannibalism has been recorded, but in many of these the event does not appear to be stereotyped and predictable. Moreover, there is little evidence relating to the circumstances, e.g. starvation, misadventure, mistaken identity, etc., under which such predation occurred.

these resemblances led Levi (1958, 1959) to group 35 species into six, a finding which, in 1983, he acknowledged to be incorrect.

The belief, now, that most of the earlier species are valid taxa raises as interesting point. Since there is no longer a case for six taxa to have been introduced into various host countries by human agency or other mechanisms, we must assume that most are endemic to their present countries. Their evident affinities imply that all these species have sprung from a common ancestor. The only conceivable explanation is that this common ancestor, a theridiid, must have evolved in Pangaea before its breakup into separate land entities at the end of the Palaeozoic, about 400 million years ago (Stevens 1985). Moreover, another theridiid genus, *Steatoda*, also widespread and with many similar characteristics, can be linked to this common ancestor. The conclusion reached here is that theridiids have an ancient history, a view which may be inconsistent with that of Coddington (1986) who considers that this family derived its cobweb from the orbweb group.

Perhaps the key to the question of *L. hasselti's* indigenous status lies in Barbara York Main's comment (loc.cit.) about the zoogeographic dilemma of the Australian region if this spider was proved to be introduced. Given Australia's biogeographical history, it would be extraordinary if that country had not spawned its own endemic species especially since *Latrodectus* occurs in all other continents as well as there being two species (*L. katipo* and *L. atritus*) in New Zealand. The close genetic relationship suggested between *L. hasselti* and *L. katipo* adds weight to this argument. Moreover, it has been shown here that *L. hasselti* has an adaptable lifestyle, one which permits it to live in a range of habitats and climatic conditions. Hence, it would have been able to subsist in outback Australia for millions of years, with its intraspecific predatory habits aiding subsistence and the evolution of sexual cannibalism providing a way of coping with infrequent meeting and mating opportunities.

## ACKNOWLEDGEMENTS

## REFERENCES

Anava, A. and Lubin, Y. (1993). Presence of gender cues in the web of a widow spider, *Latrodectus reviviensis*, and a description of courtship behaviour. *Bulletin of the British arachnological Society* **9**: 119–122.

Bartels, M. (1930). Über den Fressmechanismus und chemischen Sinneinger Netzspinnen. *Revue Suisse de Zoologie* **37**:1–42.

Cariaso, B.L. (1967). A biology of the black widow spider, *Latrodectus hasselti*, Thorell (Araneae: Theridiidae). *Philippine Agriculturist* **51**: 171–180.

Coddington, J.A. (1986). The monophyletic origin of the orb web. *In* Shear, W.A. (ed.), *Spiders: Webs, Behavior, and Evolution*: 319–363. Stanford University, Stanford.

Coddington, J.A. (1989). Spinneret spigot morphology: evidence for the monophyly of orb-weaving spiders, Cyrtophorinae (Araneidae), and the group Theridiidae plus Nesticidae. *Journal of Arachnology* **17**: 71–95.

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

Downes, M.F. (1993). More on the redback status question. *Australian Arachnology* **47**: 3.

Eberhard, W.G. (1987). How spiders initiate airborne lines. *Journal of Arachnology* **15**: 1–9.

Edwards, G.B. (1980). Taxonomy, ethology and ecology of *Phidippus* (Araneae: Salticidae) in eastern North America. Ph.D. thesis, University of Florida, 354 pp.

Elgar M.A. (1992). Sexual cannibalism in spiders and other invertebrates. *In* Elgar, M.A. and Crespi, B.J. (eds), *Cannibalism. Ecology and Evolution among Diverse Taxa*: 128–155. Oxford University Press, Oxford, New York, Tokyo.

Forster, L.M. (1982). The Australian redback spider – an unwelcome immigrant to New Zealand. *Weta* 5(2): 35.

Forster, L.M. (1984). The Australian redback spider (*Latrodectus hasselti*): its introduction and potential for establishment and distribution in New Zealand. *In* Laird, M. (ed.), *Commerce and the Spread of Harmful Pests and Disease Vectors*: 273–289. Praegar Press, New York.

Forster, L.M. (1985). Is the redback spider here to stay? *New Zealand Journal of Agriculture* **150**(6): 58–59.

Forster, L.M. (1988). Report on *Latrodectus hasselti* (Redback spider). Royal Society of New Zealand, Science House, Wellington, New Zealand.

Forster, L.M. (1992a). The stereotyped behaviour of sexual cannibalism in *Latrodectus hasselti* (Araneae:

Theridiidae), the Australian redback spider. *Australian Journal of Zoology* **40**: 1–11.

Forster, L.M. (1992b). Cannibalism: a growth strategy for *Latrodectus* female spiders (Theridiidae: Araneae). Paper presented at the XIIIth International Congress of Arachnology, July 1992, Brisbane, Australia.

Forster, L.M. and Kavale, J. (1989). Effects of food deprivation on *Latrodectus hasselti* Thorell (Araneae : Theridiidae), the Australian redback spider. *New Zealand Journal of Zoology* **16**: 401–408.

Harris, A (1988). Redbacks may not be true blue. *The West Australian*, 25 March 1988: 3.

Kaston, B.J. (1948). *Spiders of Connecticut*. State Geological and Natural History Survey Bulletin No. 70. Hartford, Connecticut, USA.

Kavale, J. (1986). The comparative biology of two *Latrodectus* species. M.Sc dissertation, University of Otago, Dunedin, New Zealand.

Kovoor, J. (1987). Comparative structure and histochemistry of silk-producing organs in arachnids. *In* Nentwig, W. (ed.), *Ecophysiology of Arachnids*: 160–186. Springer-Verlag, Berlin, Heidelberg.

Levi, H.W. (1958). Number of species of black widow spiders (Araneae: Theridiidae). *Science* **127**: 1055.

Levi, H.W. (1959). The spider genus *Latrodectus* (Araneae: Theridiidae). *Transactions of the American Microscopical Society* **78**: 7–43.

Levi, H.W. (1983). On the value of genitalic structures and coloration in separating species of widow spiders (*Latrodectus* sp.) (Araneae: Theridiidae). *Verhandlungen naturwissenschaften vereins Hamburg* (NF) **26**: 195–200.

Main, B.Y. (1965). *Spiders of Australia*. Jacaranda Press, Brisbane.

Main, B.Y. (1993). Redbacks may be dinky-di after all: an early record from South Australia. *Australasian Arachnology* **46**: 3–4.

McKeown, K.C. (1963). *Australian Spiders: their Lives and Habits*. Angus and Robertson, Sydney.

Mitchell (1988). In Bustards of the Bush. *The Weekend Australian, 26–27 March 1988: 20.*

Paterson, H.E.H. (1993). *Evolution and the Recognition Concept of Species*. Collected Writings, McEvey, S.F. (ed.). The John Hopkins University Press, Baltimore and London.

Platnick, N.I. (1971). The evolution of courtship behaviour in spiders. *Bulletin of the British Arachnology Society* **2**: 40–47.

Raven, R.J. (1992). Redback spiders, black widows and their kin. Presidential address. *News Bulletin of the Entomological Society of Queensland* **20**: 4–8.

Raven, R.J. and Gallon, J. (1987). The Redback Spider. *In* Covacevich, J., Davie, P. and Pearn, J. (eds), *Toxic Plants and Animals. A Guide for Australia*: 306–311. Queensland Museum, Brisbane.

Robinson, M.H. and Robinson, B. (1978). Thermoregulation in orb weavers. New descriptions of thermoregulatory postures and experiments on the effects of posture and coloration. *Zoological Journal of the Linnean Society* **64**: 87–102.

Ross, K. and Smith, R.L. (1979). Aspects of the courtship behaviour of the black widow spider, *Latrodectus hesperus* (Araneae: Theridiidae), with evidence for the existence of a contact sex pheromone. *Journal of Arachnology* **7**: 69–77.

Sloggett, B.M. (1946). Introduction of *Latrodectus* to the Pacific Islands. *Victorian Naturalist* 62(9): 165

Snell, E. (1988). *The Life and Adventures of Edward Snell. The Illustrated Diary of an Artist, Engineer and Adventurer in the Australian Colonies 1849 to 1859.* Griffiths, T. (ed.). Angus and Robertson, and the Library Council of Victoria.

Softly, A. and Freeth, G.E. (1970). The laboratory maintenance of *Latrodectus mactans* (known in Australia as the Redback spider). *Journal of the Institute of Animal Technicians* **21**: 117–126.

Southcott, R.V. (1978). *Australian harmful arachnids and their allies*. Griffen Press, South Australia.

Stevens, G. (1985). *Lands in Collision*. Science Information, DSIR Publishing Centre, Wellington, New Zealand.

Sutherland, S.K. and Trinca, J.C. (1978). Survey of 2144 cases of red-back spider bites. *Medical Journal of Australia* **2**: 620–623.

Templeton, A. (1992). Meaning of species, speciation – a genetic perspective. *In* Ereshefky, M. (ed.), *The Units of Evolution. Essays on the Nature of Species*: 159–183. MIT Press, Cambridge, MA, USA.