Web site characteristics, dispersal and species status of New Zealand's katipo spiders, *Latrodectus katipo* and *L. atritus*

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Over the last 30 years, *Latrodectus katipo* Powell 1870 and *L. atritus* Urquhart 1890 numbers have declined and these species are now absent from many dune systems where they were once common. The cause of the decline in *L. katipo* and *L. atritus* numbers is not certain and little is known about their ecology. This thesis examined *L. katipo* and *L. atritus* web site characteristics, dispersal, species status and the probable implications of habitat modification on their ecology. The thesis focused on these aspects of *L. katipo* and *L.atritus* in order to provide information that might be used to conserve these species.

Results showed that *L. katipo* and *L. atritus* web sites are defined by similar characteristics. Both species were commonly found in *Muehlenbeckia complexa* A. Cunn. 1838, *Coprosma acerosa* A. Cunn. 1839, and *Desmoschoenus spiralis* (A. Rich.), but were also found in driftwood, *Spinifex sericeus* (R. Br. 1810) and *Ammophila arenaria* Link 1827. Web sites were most commonly associated with dune regions defined by 33-66 % ground cover, northerly, easterly or westerly aspect, sloping ground and the absence of detritus.

Using habitat classification trees, a model was constructed that was useful for predicting *L. katipo* and *L. atritus* presence and absence. The model accurately predicted *L. katipo* or *L. atritus* absence at > 90% of points sampled, but less accurately predicted *L. katipo* or *L. atritus* presence at 33 – 38 % of points sampled. It is argued that model was less able to predict *L. katipo* or *L. atritus* presence because intra-specific competition among the two species or inter-specific competition with *Steatoda capensis* Hann 1990 might prevent greater use of potential web sites in optimal habitat. Alternatively, the model may not accurately define web sites. This assertion is supported by results that suggest web sites might be associated with patches of open sand rather than ground cover *per se* and that the web site association with northerly, easterly or westerly aspect might be related to temperature rather than aspect.

The association between web sites and patches of open sand and northerly, easterly or westerly aspect was examined in the laboratory. Results showed that all catching-webs built by *L. katipo* and *L. atritus* were positioned over open sand and that no catching-webs were built within dense *A. arenaria* clumps. These results suggests the structural requirements of the catching-web are not met by dense dune grasses, which would explain why *L. katipo* and *L. atritus* are rarely present in dune regions dominated by dense *A. arenari*, or other dune grasses, such as *Pennisetum clandeestinum* Chiou 1903 and *Stenotaphrum secundatum* Kuntze 1891 that also have a dense growth habit. That the majority of spiders included in the experiment favoured web sites at the warmer well-lit end of a temperature and light gradient supported the hypothesis that the association between web sites and aspect may be linked to temperature.

L. katipo and *L. atritus* spiderlings were found to disperse by 'ballooning' and adult females are able to tolerate exposure to salt water for up to nine days, indicating that they may be capable of travelling substantial distances at sea on driftwood. These results suggest that both species are good dispersers, as evidenced by their current distributions, which span numerous geographic barriers, such as open sea, estuaries and large rivers. This assertion was further supported by molecular analysis that revealed low intra-specific pairwise distances between *L. katipo* and *L. atritus* populations in the ND1 gene region, indicating that intra-specific gene flow has recently occurred, and may still occur throughout the distributions of these species. Molecular analysis also revealed low inter-specific pairwise distances between *L. hasselti* and New Zealand's widow spiders suggesting that gene flow has recently occurred between the endemic Australian and New Zealand widow fauna and raises questions about the accuracy of their current taxonomy.

Overall, my results suggest that the likely cause of *L. katipo* and *L. atritus* decline is the increasing dominance of dense exotic dune grasses in New Zealand's coastal dune systems, as these do not appear to meet the structural requirements of either species' webs. Moreover, that *L. katipo* and *L. atritus* are rarely recorded from dunes modified by urban or rural development indicates that these types of development may also fail to provide suitable habitat for these species. Although results showed that *L. katipo* and *L. atritus* are good dispersers, the introduction of exotic plants and/or urban or rural development may result in the reduction and fragmentation of these species' habitat, inhibiting dispersal. This would reduce both species' capacity to re-colonise dune regions from which they have been displaced. Consequently, both species may be vulnerable to local extinction in areas where their habitat has been extensively modified.

Key words - redback, ballooning, bridging, web, dispersal, habitat, katipo, *Latrodectus, L. hasselti,L. atritus,* retreat, spider, taxonomy.

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General Introduction

Thesis context

Latrodectus katipo Powell 1870 and *L. atritus* Urquhart 1890 are the two southern-most species of the genus *Latrodectus* Walckenaer 1805 (Araneae: Theridiidae), commonly referred to as widow spiders after the female *L. mactans* (Fabricius 1775) (black widow) (Forster 1995). Both species are endemic to New Zealand and inhabit vegetation, driftwood and flotsam in coastal dune systems. *L. katipo* is currently found in the lower North Island of New Zealand and the upper half of the South Island, whereas *L. atritus* distribution is restricted to the upper half of the North Island. Currently, *L. katipo* and *L. atritus* distributions overlap around the middle of the North Island of New Zealand (pers. obs.). According to Forster and Forster (1999), they do not appear to interbreed.

Over the last 30 years, a marked decline in *L. katipo* numbers has occurred in many dune systems (Lyn Forster 1999, pers. com.) and museum records indicate the species' range may have contracted, as it has been recorded from the Coromandel Peninsula and the Auckland region (Patrick, in press). If *L. katipo* numbers continue to decline at the current rate, the species may become extinct. *L. katipo* is already absent from many dune systems where it was once very common (Smith 1971; Lyn Forster 1999, pers. com; Brian Patrick 2001, pers. com; pers. obs.). It is not clear whether *L. atritus* has also declined in numbers or undergone a range contraction, but anecdotal evidence indicates that it is absent from many sites where it was previously recorded, and that it is generally much less abundant than it was in the past (Andrea Booth 2000, pers. obs.). Consequently, *L. atritus* may also be vulnerable to extinction.

Although the cause of the decline in *L. katipo* numbers is not yet evident, it has been suggested that *Steatoda capensis* Hann 1990 (Araneae: Theridiidae), an introduced South African spider species, may be displacing *L. katipo* in some dune regions (Hann 1990). *L. katipo*, however, has declined in many dune systems from which I have not recorded *S. capensis* indicating that other factors may be responsible for the decline in *L. katipo* numbers.

General aim

This thesis aims to develop a greater understanding of *L. katipo* and *L. atritus* web site preferences, dispersal and species status in order provide information that can be used to conserve these species. Furthermore, the thesis also aims to add to the body of knowledge pertaining to New Zealand's native dune communities.

Objectives

The thesis aim is addressed in the following objectives:

1. To identify micro-habitat characteristics associated with *L. katipo* and *L. atritus* web sites and to develop a model that defines both species web sites,
2. To determine how micro-habitat structure and aspect influence *L. katipo* and *L. atritus* web structure, web site preferences and prey capture,
3. To determine how *L. katipo* and *L. atritus* disperse,
4. To examine intra-specific and inter-specific genetic relationships between *L. katipo*, *L. atritus* and *L hasselti* Thorell 1870 (Australian redback) in order to infer likely levels of gene flow between and within the species.

Structure of thesis

To address the above objectives, this thesis will focus on the distribution of *L. katipo* and *L. atritus* at different spatial levels. At the smallest spatial scale, the thesis examines *L. katipo* and *L. atritus* micro-habitat characteristics in terms of the immediate biotic and abiotic context of the web, whereas, the dispersal mechanisms employed by *L. katipo* and *L. atritus* are investigated to better understand these species' distributions at a regional and national scale. Examination of the intra and inter-specific differences between *L. katipo, L. atritus* and *L. hasselti* in the ND1 gene region provide further information about the national distributions of *L. katipo* and *L. atritus*, but also address questions relating to the international distribution of these species arising from uncertainty surrounding *Latrodectus* taxonomy.

This thesis is structured as a series of interconnecting chapters. To avoid unnecessary repetition, chapters 3-6 rely on information provided in the taxonomic, biological and ecological overview (Chapter two) and, to some degree, chapters four to six depend on information provided in earlier chapters. With the exception of chapters one, two and seven, it is intended that all chapters will be published but, since they are yet to be submitted for publication, all chapters follow a similar format.

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Chapter Two
Taxonomic, biological and ecological overview

In this chapter, I present a précis of *L. katipo* and *L. atritus* taxonomy, biology and ecology to familiarise the reader with the species central to this thesis. I discuss a recent decline in *L. katipo* and *L. atritus* numbers, and examine probable causes of the decline, particularly the modification of coastal dune systems inhabited by these species.

Taxonomy

L. katipo and *L. atritus* are endemic to New Zealand and are currently designated as distinct species within the cosmopolitan genus *Latrodectus* (Forster and Forster 1999). Current *Latrodectus* taxonomy, however, is uncertain. Though *Latrodectus* spp. vary in colour and patterning, they have similar genital morphology and behavioural traits (Levi 1959; Levi, 1983; Forster and Forster 1999). These similarities have made the taxonomy of *Latrodectus* spp. difficult (Levi 1959; Forster and Kingsford 1983; Forster and Forster 1999).

In 1958, Levi revised the entire *Latrodectus* genus, reducing 35 or so species to six (Levi 1958; Levi 1959; Forster 1995; Forster and Forster 1999). Through this revision, *L. katipo*, *L. atritus*, *L. hasselti* and other *Lactrodectus* spp. found around the western Pacific were designated as a subspecies (*Latrodectus mactans hasselti*) of *L. mactans* (*ibid*). Recent research, however, has identified significant differences in the stereotype behaviour of *L. katipo* and *L. hasselti* (Forster and Kingsford 1983; Forster 1995). *L. hasselti* males, for example, may mate with female *L. katipo* to produce viable F1 hybrids, but male *L. katipo* mating attempts with female *L. hasselti* fail. Heavier than their *L. hasselti* counterparts, male *L. katipo* trigger a predatory response in female *L. hasselti* and are eaten. Although *L. hasselti* males are also devoured by female *L. hasselti* after mating, when they mate with *L. katipo* they are released without being eaten. Forster and Forster (1999) contended that there are also apparent differences between *L. atritus* and *L. katipo*. Records and more recent observations suggest that *L. katipo* and *L. atritus* have co-existed at several beaches in the central North Island of New Zealand, but they do not appear to interbreed (*ibid*). This observation is supported by laboratory studies that show *L. katipo* and *L. atritus* seldom mate and that mating does not result in the production of fertile eggs (Forster and Forster 1999). These findings encouraged Forster and Kingsford (1983) to advocate that *L. katipo*, *L. atritus* and *L. hasselti* should be recognised as distinct species. In 1983, Levi acknowledged that his revision of the *Latrodectus* taxonomy had been flawed (Levi 1983). Subsequently, most of the original *Latrodectus* taxa have been tentatively re-accepted (Forster 1995; Forster and Forster 1999).

Morphology

Despite taxonomic uncertainty, adult female *L. katipo* and *L. atritus* are easy to distinguish. Adult female *L. katipo* are primarily velvet black with the exception of a bright red dorsal stripe that runs from the thorax to the spinnerets (Plate 2.1). Many adult females also have faint white lines on the front of the abdomen, although these may be entirely absent in some individuals (pers. obs.). The underside of the abdomen is black with a distinctive red hourglass shaped marking. The body is approximately 8-10 mm long (pers. obs.), most of which is accounted for by the abdomen, which is about the size of a garden pea. Adult *L. atritus* females are almost identical in size and colouration except they lack the red dorsal stripe (Plate 2.2) and the red hourglass on the underside of their abdomen is less distinct. The abdominal colouration of *L. atritus* is also generally lighter than in *L. katipo* (Plate 2.2)

Plate 2.1. Adult female *L. katipo* on marram grass

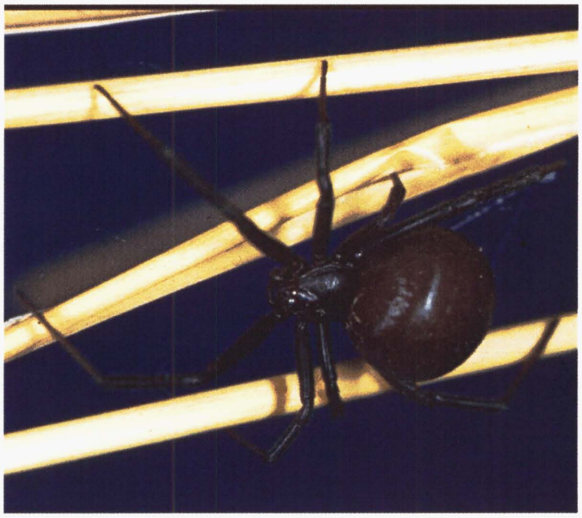

Plate 2.2. Adult female *L. atritus* on marram grass

In contrast, mature male *L. katipo* (Plate 2.3) and *L. atritus* (Plate 2.4) are predominantly white with a series of red-orange diamonds running from the thorax to the spinnerets along the dorsal region of the abdomen. These are bordered on either side by irregular black lines. The adult male abdomen is more elongate than in the female and the palps are noticeably bigger, so that it appears as though the male is equipped with a pair of boxing gloves. When fully mature, males are approximately one sixth the size of a mature female (Forster and Forster 1999). Inter-specific differences between mature males are much less obvious than between females, but mature *L. atritus* males can apparently be distinguished from mature *L. katipo* males through examination of the abdominal colouration and patterning which is noticeably paler and less continuous in *L. atritus* males than in *L. katipo* males (Forster and Kingsford 1983). As considerable intra-specific variation occurs amongst *L. katipo* and *L. atritus* (pers. obs.), however, this distinction may not be useful.

Plate 2.3. Adult male *L. katipo* on marram grass

Plate 2.4. Adult male *L. atritus* on driftwood

Before the third instar, morphological differences between species and sexes are not evident in the field. Male and female spiderlings of both species have red-brown legs with darkened areas around the leg joints (Plate 2.5). After the third instar, differences between sexes and species become increasingly evident as the spiders mature (Plate 2.6).

Plate 2.5. Juvenile *L. atritus* on marram grass

Plate 2.6. Sub-adult female *L. katipo* on driftwood

Origins

It is not certain how or when *L. katipo* and *L. atritus* arrived in New Zealand, but Forster (1995) argued that all *Latrodectus* taxa are probably derived from a common theridiid ancestor that evolved on Pangea. As portions of the landmass gradually broke away under the pressure of continental plate movement 400 million years ago, groups of theridiid spiders became separated from one another (Stevens 1985; Forster 1995). Evolving in isolation, these groups developed unique physiological and behavioural attributes. The more recent separation of New Zealand from Gondwana 80 million years ago explains the physiological and behavioural similarities between *L. katipo* and *L. hasselti* (Stevens 1985; Forster 1995). Although Forster's (1995) hypothesis appears to explain the similarities between some *Latrodectus* spp. and accounts for the global distribution of this genus, it assumes that current *Latrodectus* distribution results solely from the fragmentation of Gondwana. Forster did not consider the possibility that *L. katipo* and *L. atritus* may have colonised New Zealand more recently.

Spiders are well known for their ability to balloon, an aerial dispersal mechanism that facilitates travel over large distances (>300 km) (Greenstone 1982; Greenstone *et al.*1987; Nentwig 1987; Crawford *et* *al.*1995; Crawford 1996; Foelix 1996). Furthermore, some spiders or spider eggsacs can withstand periods at sea attached to driftwood or flotsam suggesting they may travel substantial distances on ocean currents (Nentwig 1987). Presumably employing either of the above dispersal mechanisms, spiders are often recorded among the first arthropod colonists of newly formed volcanic islands (Decae 1987; Greenstone *et al.*1987; Crawford 1996). It is not known whether *L. katipo*, *L. atritus* or other *trodectus* can balloon or disperse by sea, but current *L. katipo* and *L. atritus* distribution indicates that they are probably able to travel across geographical barriers such as headlands, rivers, estuaries and lengths of coastline where suitable habitat is absent.

Distribution

L. katipo and *L. atritus* are found in dune systems around much of the New Zealand coastline. Although records suggest that *L. katipo* once had a scattered distribution around Auckland and Northland (Patrick in press), currently, *L. katipo* is found only from New Plymouth and East Cape in the middle of the North Island as far south as Karamea and Dunedin in the South Island (Figure 2.1)(Forster and Forster 1999); Brian Patrick, 2001, pers. com.; pers. obs.). In contrast, *L. atritus* inhabits dune systems from New Plymouth and East Cape to Cape Reinga (Figure 2.1). Some overlap in distribution currently occurs around East Cape and New Plymouth (Forster and Forster 1999). Forster (1999) postulated that the differences between *L. katipo* and *L. atritus* distribution may be related to differences in the temperature requirements of *L. katipo* and *L. atritus* embryos. *L. atritus* embryos require temperatures > 22°C for development, whereas *L. katipo* embryos appear to develop at temperatures > 17 $^{\circ}$C. Consequently, *L. atritus* is unable to maintain populations in cooler regions of New Zealand (Forster and Forster 1999). It is not clear why *L. katipo* is no longer found in Northern regions of New Zealand, but it is possible that they may have been out competed by *L. atritus* that according to Forster and Forster (1999) appear to be adapted to higher temperature. Alternatively, interbreeding between *L. katipo* and *L. atritus*, if it occurs, may have reduced colour variation between the two species, confounding *L. katipo* identification.

Figure 2.1. The distribution of *L. katipo* and *L. atritus* on the New Zealand coastline (*L. katipo* distribution = 🟥, *L. atritus* distribution = 🟦, distribution overlap = 🟩)

Plate 2.7. Adult female *L. katipo* and eggsacs in pingao

Female *L. katipo* and *L. atritus* web sites are generally located at the base of dune grasses and low growing shrubs such as marram (*Ammophila arenaria* Link 1827), pingao (*Desmoschoenus spiralis* (A. Rich.)), spinifex (*Spinifex sericeus* (R. Br. 1810)), mingimingi (*Muehlenbeckia complexa* A. Cunn. 1838), sand coprosma (*Coprosma acerosa* A. Cunn. 1839), *Cassinia leptophyllla* A. Cunn. 1839 and *Pimelea arenaria* A. Cunn. 1833, but are also common in driftwood and in flotsam. Sub-adult males are also thought to build small catching-webs amongst vegetation and flotsam, but observations by Forster and Forster (1999) suggest that once they reach maturity males cease to establish catching-webs. Instead, they search for mates and are often found within the retreat of an adult female (pers. obs.) where they may feed on prey caught by the resident adult female (Lyn Forster, 1999, pers. com.). Currently, both species are most commonly found within a few hundred metres of the high tide mark (Smith 1971; Forster and Forster 1999), however, they have been recorded from dune systems several kilometres from the sea (Powell 1871).

Lifecycle

During November and December, adult female *L. katipo* and *L. atritus* construct one to three cream-coloured eggsacs from strong viscous silk (Forster and Forster 1999). Within each eggsac, fertilised eggs are laid in a small antechamber also constructed of silk. The antechamber protects the spider embryos from temperature and humidity fluctuations (Nentwig 1987; Foelix 1996). *L. katipo* lays ≈70-90 eggs in each eggsac, whereas *L. atritus* lays ≈ 40-60 (Forster and Kingsford 1983). Additional protection for developing embryos and spiderlings is provided by the adult female's retreat in which the eggsacs are stored, usually in the upper region of the retreat, where they appear to be sheltered from the wind, rain and solar radiation (pers. obs.). The retreat may also protect eggsacs from temperature and humidity fluctuations (Nentwig 1987).

When the spiderlings hatch, usually after 20-25 days, they move into the main body of the eggsac where they continue development (pers. obs.), each sustained by an internal yolk reservoir (Nentwig 1987)). They remain in the eggsac until they reach the second instar then they gradually ingest the silken wall of the eggsac, which becomes thin and transparent (Plate 2.8) (pers. obs.). Between January and February, after approximately four to six weeks of incubation and development, spiderlings emerge by eating a small hole in the eggsac wall (pers. obs.). *L. katipo* juveniles generally take about 30 days to emerge at 15-25°C and *L. atritus* juveniles take approximately 40 days at 15-25°C (Forster and Kingsford 1983; Forster and Forster 1999). Incubation times, however, vary depending on temperature (Forster and Kingsford 1983; Forster and Forster 1999).

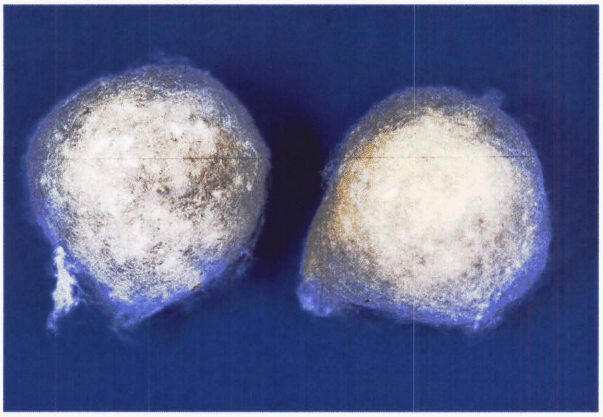

Plate 2.8. *L. atritus* eggsacs (spiderlings in the eggsac on the left have begun to ingest the eggsac wall)

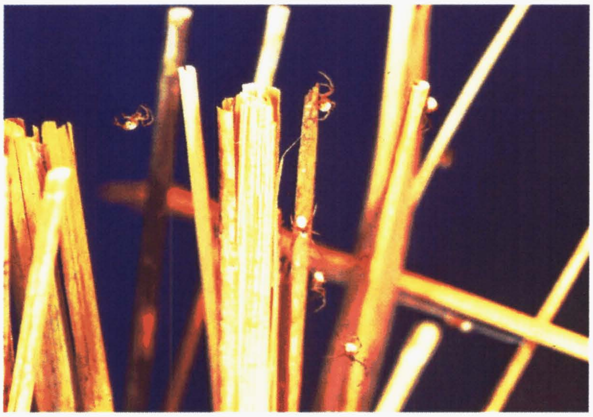

Plate 2.9. Post-emergent *L. katipo* spiderlings clustered at the top of marram tillers

Little is known about the post-dispersal phase of *L. katipo* or *L. atritus* development, probably because cryptic colouration and small size make sub-adult individuals difficult to find. Research undertaken on other *Latrodectus* spp., and laboratory observations of *L. katipo* and *L. atritus,* however, suggest that after dispersing from the nest, female spiderlings establish a web and retreat (Kaston 1970; Lubin 1993; Forster and Forster 1999; pers. obs.). Although juveniles may occasionally relocate web sites, once spiderlings mature, relocation is likely to be infrequent, probably due to the energy cost associated with leaving an established web (Tanaka 1989; Lubin 1993; pers. obs.). *L. katipo* and *L. atritus* invest relatively large quantities of silk in web and retreat construction compared with many other web-building spiders (Tanaka 1989; pers. obs.). Field observations suggest they do not recycle the web so the cost of relocation is unlikely to be subsidised by proteins and other foodstuffs ingested when recycling the web, as found in other spider species (Tanaka 1989; Wise 1993; Foelix 1996). Consequently, the cost of relocation is likely to be relatively high.

Sub-adult males are also believed to establish a web and retreat, although once they reach maturity they are thought to abandon web building. Instead, they search for mates, an endeavour that may be guided by pheromones in the female web (Forster 1995), as found in *L. hesperus* Chamberlin & Ivie 1935 (Ross and Smith 1979; Nentwig 1987). Upon finding an adult female, male *L. katipo* and *L. atritus* begin gently vibrating the female's web, presumably to communicate that they are prospective mates and not prey. If the female does not chase him away, the male will slowly advance and tap her abdomen as she hangs upside down in the web. If the female accepts him as a mate, he will move on to her ventral abdomen and insert his sperm-charged palps one at a time into her epigyna (Forster and Forster 1999). Copulation usually lasts about 10-15 minutes after which the male retreats to groom himself (Forster and Forster 1999).

The catching-web, prey capture and retreat

Catching-webs constructed by female *L. katipo* and *L. atritus* comprise a hammock-like structure built from a tangled mass of strong, non-sticky threads usually positioned ≈50 mm above the ground. From this platform, up to 50 catching threads are attached to the substrate (Court 1971). Each catching line is armed with a series of very sticky globules usually positioned within ≈10 mm of the ground. These sticky globules act like unbaited fishing hooks, snaring ground-dwelling invertebrates that crawl into catching lines. Vibrations emanating from struggling prey alert the resident spider, which quickly locates and subdues the prey with a mass of strong sticky silk (Court 1971; Forster and Forster 1999; pers. obs.). The method by which *L. katipo* and *L. atritus* subdue prey is facilitated by a series of curved bristles on the tarsi of the hind legs. This comb-like bristle arrangement, a synapomorphy for Theridiidae, is used to card silk into a mass of very strong sticky strands that are thrown over struggling prey. Once subdued, prey is reeled into the web and bitten, often a number of times. The purpose of the bite, usually administered at a leg joint where there is a gap in the exoskeleton, is to inject both a toxin and enzyme. The toxin immobilises the prey and the enzyme breaks down the internal organs so that they may be sucked out. If the prey is particularly active, further catching lines are attached to the prey to ensure it does not escape before it is reeled into the main body of the web (Forster and Forster 1999).

During periods of inactivity, *L. katipo* and *L. atritus* are commonly found within a retreat, which is usually located at the edge of the catching-web in prostrate shrubs, driftwood or the base of dune grasses. The retreat is a densely woven sock-like structure constructed from strong viscous silk. It is positioned so the closed end, or toe, is higher than the opening (2-4 cm diameter), presumably to protect the resident spider from rain, direct insolation and exposure to wind. Spider retreats regulate temperature and humidity fluctuations (Nentwig 1987) and, therefore, may enable *L. katipo* and *L. atritus* to inhabit dune regions with micro-climates that are not optimal.

Prey

Analysis of prey exoskeletons ensnared in *L. katipo* and *L. atritus* webs showed that both species feed on a wide range of invertebrates, and that prey differs between sites (Smith 1971; Hann 1990). Hann (1990) found that the proportion of prey species in *L. katipo* webs at two neighbouring sites at Motueka was markedly different. At site A, predominant prey species comprised the coleopteran *Cecyropa jucunda* Broun 1917, 43 %, the isopodan *Talorchestia quoyana* Stephenson 1938, 36 %, the dermapterans *Forficula* spp. L. 1758, 4 % and the coleopteran *Mimopeus elongates* Breme 1842, 9 %, whereas at site B, predominant prey species comprised the isopodan *T.quoyana*, 70 %, the coleopterans *C. jucunda*, 17 % and *Mitophyllus irroratus* Parry 1845, 2 %. In contrast, at South Brighton Beach, Smith (1971) found the predominant prey of *L. katipo* comprised the coleopterans *Cecyropa modesta* Fabricius 1781, 56 %, *Mimopeus thoracicus* Bates 1873, 17 % and *Xylotoles griseus* Fabricius 1775, 9 % and the isopodan *T. quoyana*, 6 %. These results suggest, that like many web building spider species, *L. katipo* and *L. atritus* are generalist feeders and will prey on most invertebrates that become ensnared in the web (Savory 1977; Nentwig 1987; Hann 1990). Due to the web structure, however, the predominant prey species caught in webs are active ground dwelling invertebrates, presumably because these characteristics enhance the probability of capture. Differing proportions of invertebrate species found in *L. katipo* and *L. atritus* webs, therefore, probably reflect prey availability and predisposition to capture rather than active selection on the part of the spider.

Metabolism

Most spiders, especially those that rely on webs to capture prey, can withstand long periods of starvation between prey capture events (Nentwig 1987). For example, the adult wolf spider, *Hogna lenta* (Hentz 1844), can survive up to 208 days under starvation conditions, whereas, the webbuilder *Kukulcania hibernalis* (Hentz 1842) survived 305 days under similar conditions (Nentwig 1987). The reason spiders are able to endure long periods between capture of prey is principally related to their low metabolic rate and relative inactivity, but may also be related to their ability to ingest web silk. Web silk, having been exposed to air movement over time, is often covered with pollen dust and microscopic organisms rich in protein. Thus, through recycling web silk, spiders may gain valuable protein in times of prey shortage, both through ingesting pollen and micro-organisms adhered to the silk and through ingesting the silk, which is also very high in protein (Smith and Mommsen 1984; Nentwig 1987). No formal studies have been undertaken on *L. katipo* or *L. atritus* metabolism, but adult female *L. katipo* and *L. atritus* I reared in the laboratory have survived up to eight weeks without food. Furthermore, starvation experiments undertaken by Forster and Kavale (1989) showed that adult *L. hasselti* are able to withstand up to 12 weeks of starvation and recover after feeding. The ability to withstand prolonged starvation may enable *L. katipo* and *L. atritus* to survive periods when prey is scarce or when low temperatures inhibit activity. In addition, the capacity to persist during food shortages may aid *L. katipo* and *L. atrtitus* dispersal on driftwood, in the same way it has enabled *L. hasselti* and *L. mactans* to reach New Zealand in container freight (Forster 1984).

Decline

Anecdotal evidence suggests that over the last 20 years a dramatic decline in *L. katipo* numbers has occurred in many of New Zealand's dune systems (Hann 1990; Brian Patrick 2000, pers. com.). More recent evidence, suggests *L. atritus* numbers may also be declining (Andrea Booth 1999, pers. com.; pers. obs.). Although the cause of these declines is not yet certain, it is hypothesised that an introduced South African spider, *S. capensis*, may be displacing *L. katipo* in some areas (Hann 1990) and that dune modification may result in the reduction and fragmentation of *L. katipo* and *L. atritus* habitat.

Steatoda capensis

S. capensis is found in many dune systems where *L. katipo* was historically abundant leading to the belief that it is associated with the decline in *L. katipo* numbers. *S. capensis* can produce approximately twice as many eggs per year as *L. katipo* and is able to reproduce throughout the year, whereas *L. katipo* reproduces only during late spring and early summer (Hann, 1990). Furthermore, *S. capensis* appears to have much less specific habitat requirements than *L. katipo* (pers. obs.), and, consequently, may be more likely to persist in areas adjacent to dune regions subject to perturbation.

Due to these biological and ecological factors *S. capesis*, may be more readily able to recolonise disturbed dune regions after perturbation.

Although *L. katipo* appears to dominate in aggressive encounters with *S. capensis* outside the web, *L. katipo* seems unable to displace *S. capensis* once it is established in a web (Hann 1990). For the above reasons, and because the coastal environment is prone to frequent disturbances, Hann (1990) argued that *S. capensis* may pose a significant threat to *L. katipo*. In a preliminary survey conducted on the Canterbury Coast, however, I found that *L. katipo* also appeared to be declining in dune systems in which few or no *S. capensis* were present. This finding suggests other factors may also be implicated in *L. katipo* decline.

Changes to dune structure and plant species composition

When European settlers arrived in New Zealand, they altered the composition and structure of the landscape considerably (Johnson 1992; Partridge 1992; Wilson 1992). In coastal sand dunes, a number of sand-binding plants such as marram, kikuyu (*Pennisetum clandestinum* Chiou 1903), buffalo grass (*Stenotaphrum secundatum* Kuntze 1891), ice plant (*Disphyma* spp. N.E.Br. 1930) and lupins (*Lupinus* spp. L. 1753) were introduced (Partridge 1995). In most cases, these introduced species have displaced endemic plants that were once the dominant component of New Zealand's dune flora (*ibid*). Currently, there are few substantial areas (>5 km^2) of native dune vegetation remaining (*ibid*). Without management, it is likely that remaining fragments of native dune vegetation will also be displaced (David Given 2000, pers. com.).

With the introduction of exotic plant species, the physical character of most dune systems has been modified (Partridge 1995). Marram grass, kikuyu, buffalo grass, iceplant and lupins have excellent sand binding properties and have stabilised dune systems that were historically fluid (Partridge 1995). Dune stabilisation has resulted in increased vegetation cover that, because of its sand trapping qualities, has encouraged the formation of steep high dune systems (McKelvey 1999). Conversely, native dune vegetation, that is relatively sparse, is most commonly associated with low, gently sloping dunes because sand movement is less inhibited (Partridge 1995; McKelvey 1999).

As a consequence of changes to dune structure and plant composition, micro-sites that possess micro-climatic conditions and structural characteristics favoured by *L. katipo* or its prey species may be less abundant. This hypothesis is supported by evidence suggesting that *L. katipo* numbers have declined in dune regions that have been subject to significant changes in habitat structure and plant species composition, but where *S. capensis* has not yet been recorded (Smith 1971; Hann 1990; pers. obs.). Smith (1971) estimated that *L. katipo* density at South Brighton Beach was ≈1.1 spiders/m^2 in 1969. A similar survey I conducted at South Brighton Beach in 1999 produced only one male and two female *L. katipo* (≈0.004 spiders/m^2). Although the apparent decline in *L. katipo* abundance between the two surveys might be partly explained by differences in the methodology, I believe it is unlikely that methodological differences account for such a marked reduction in *L. katipo* numbers. Changes in plant species composition and dune structure, however, may have contributed to the decline in *L. katipo* numbers at the site surveyed.

When Smith surveyed the South Brighton Beach for *L. katipo* in 1969, marram had only recently been introduced to the dunes at South Brighton (Smith 1971). Although there were relatively few patches of pingao remaining, (≈ 8 % of vegetation surveyed) marram was still predominantly sparse (≈ 66 % of marram surveyed comprised distinct tussocks interspersed with open sand) (Smith 1971). In contrast, when the area was resurveyed in 1999, no pingao remained and dense marram (tussocks indistinct and no sand visible) was the most common vegetation type (≈ 89 % of vegetation types surveyed).

Changes to disturbance regimes

In addition to changes in dune structure and composition, dune systems are currently subjected to disturbance regimes that differ from those that occurred historically. Frequent and sustained perturbation resulting from mechanical alteration of dune shape for dune stabilisation, the collection of driftwood by local residents, sand extraction and off-road vehicles may affect the quality and abundance of suitable *L. katipo* habitat (Smith 1971, pers. obs.).

Implications of micro-habitat modification

Spiders commonly establish in micro-habitats that provide protection against climatic conditions to which they and their prey are physiologically ill-adapted (Savory 1977; Foelix 1996). Habitat structure is also particularly important for web-spinning spiders that require certain structures on which to construct a web (Shear 1986; Nentwig 1987; Foelix 1996). In some cases, dependence on particular structural or micro-habitat types is so strong that certain spiders species may be found on only one plant species or at one location (Savory 1977; Nentwig 1987; Wise 1993; Foelix 1996). Though habitat specificity may afford spiders some protection against normal climatic variations and enhance the potential for prey capture, dependence on strict micro-habitat criteria may increase spiders' vulnerability to changes in habitat structure or composition (*ibid*). If, for example, increased vegetation density associated with the introduction of exotic plants does not meet the structural requirements of *L. katipo* or *L. atritus* catching-webs, both species may be excluded from large sections of New Zealand's coastal dunes that have been modified by introduced plants (Shear 1986; Nentwig 1987; Foelix 1996). Similarly, changes in microclimatic conditions caused by habitat modification could exclude *L. katipo* or *L. atritus* from modified dune systems.

The reduction and fragmentation of *L. katipo* and *L. atritus* habitat could also impede dispersal, reducing the likelihood that either species could recolonise dune regions from which they have been displaced by stochastic events, such as storms or fires. In turn, this might increase the probability that *L. katipo* or *L. atritus* could be permanently displaced from some dune systems and might reduce gene flow between populations decreasing genetic diversity.

Conclusions

Although considerable debate surrounds the current taxonomic classification of *Latrodectus* spp., New Zealand's endemic widow fauna is considered to comprise two species: *L. katipo* and *L. atritus.* Both species inhabit coastal dunes, and are found amongst dune vegetation, driftwood and flotsam. They primarily prey on ground-dwelling invertebrates. *L. katipo* is found in coastal dunes in the upper half of the South Island of New Zealand and the lower half of the North Island, whereas *L. atritus* inhabits dune systems in the upper half of the North Island. The difference between *L. katipo* and *L. atritus* distribution may be related to different temperature requirements for embryonic development.

Over the last 30 years, *L. katipo* numbers have declined dramatically. *L. katipo* is now absent from many dune systems in which it was historically abundant. Recent evidence suggests that *L. atritus* numbers may also be declining. It has been hypothesised that the decline in *L. katipo* abundance may be related to the introduction of a South African spider, *S. capensis,* which has higher fecundity than *L. katipo* and appears to have less specific habitat requirements. Consequently, it can colonise sites from which *L. katipo* has been displaced during perturbation. Once *S. capensis* becomes established, *L. katipo* appears unable to reclaim web sites and is displaced. Recent surveys, however, show that *L. katipo* has declined in dune systems from which *S. capensis* has not been recorded. This suggests that other factors may be responsible for the decline in *L. katipo* numbers.

Over the last 50 years, New Zealand's dune systems have been extensively modified through the introduction of exotic sand-binding plants and the reclamation of dune systems for urban and rural development. These changes have affected the physical and biological character of many dune systems and may have reduced the availability of suitable *L. katipo* and/or *L. atritus* habitat. Habitat fragmentation and truncation associated with these changes may have reduced the probability that *L. katipo* and *L. atritus* could recolonise sites from which they have been displaced during stochastic events. Moreover, gene flow between *L. katipo* and *L. atritus* populations may also have been reduced.

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Chapter Three
Micro-habitat characteristics of adult female *L. katipo* and *L. atritus* webs sites

Introduction

A survey of *L. katipo* at South Brighton Beach on the Canterbury coast conducted by Smith (1971) revealed that *L. katipo* web sites were most commonly associated with dune regions characterised by steep slopes (30-45°), westerly aspect and the absence of detritus. Webs were most commonly found in pingao, and marram where it was present at sparse and medium densities (plants distinct with 1-100 stalks per tussock) (Chapter two). Few *L. katipo* web sites were associated with dense marram or other exotic vegetation such as iceplant or lupins (Chapter two). These results suggest that *L. katipo* may have specific micro-habitat requirements (Smith 1971; Forster and Forster 1999) and that dense marram, which now covers large tracts of New Zealand's dune systems (Trevor Partridge 2001, pers. com.; pers. obs.), and other exotic vegetation do not provide optimal *L. katipo* habitat (Chapter two). With the exception of Smith's study, however, little is known about the micro-habitat requirements of *L. katipo,* and there have been no studies conducted on the micro-habitat requirements of *L. atritus*. Consequently, it is not known whether the *L. katipo* web site characteristics identified by Smith are generic to *L. katipo* populations around New Zealand, or if *L. atritus* web sites are also defined by these characteristics. Moreover, the implications of dune modification for the ecology of *L. katipo* and *L. atritus* have not been explored.

In this chapter, I examine the micro-habitat characteristics associated with *L. katipo* and *L. atritus* web sites throughout their distributions. I also investigate the probable effects of dune modification on the ecology of *L. katipo* and *L. atritus*. The chapter comprises two sections because two methodologies were used. Transect sampling (Section one) was employed to conduct intensive surveys of *L. katipo* in Canterbury and *L. atritus* in Northland (figure 3.1). In contrast, stratified sampling (Section two) was used to determine whether the micro-habitat characteristics of *L. katipo* and *L. atritus* web sites, as identified through transect sampling, were generic throughout both species' national distributions (Figure 3.1). Stratified sampling was also used to gain additional information on the relationship between *L. katipo* and *L. atritus* web sites and habitat structure.

Methods - Section One

Transect sampling was undertaken at a total of 19 sites from Kaitorete Spit to Leithfield Beach in the Canterbury region of the South Island and at 28 sites from Pouto Point and Waipu Cove to Cape Reinga in Northland (Figure 3.1). As *L. katipo* distribution is currently limited to areas south of East Cape and New Plymouth and *L. atritus* distribution is currently restricted to the northern half of the North Island (Forster and Forster 1999), sampling conducted in the Canterbury region taregeted *L. katipo*, whereas sampling undertaken in the upper North Island focused on *L. atritus.*

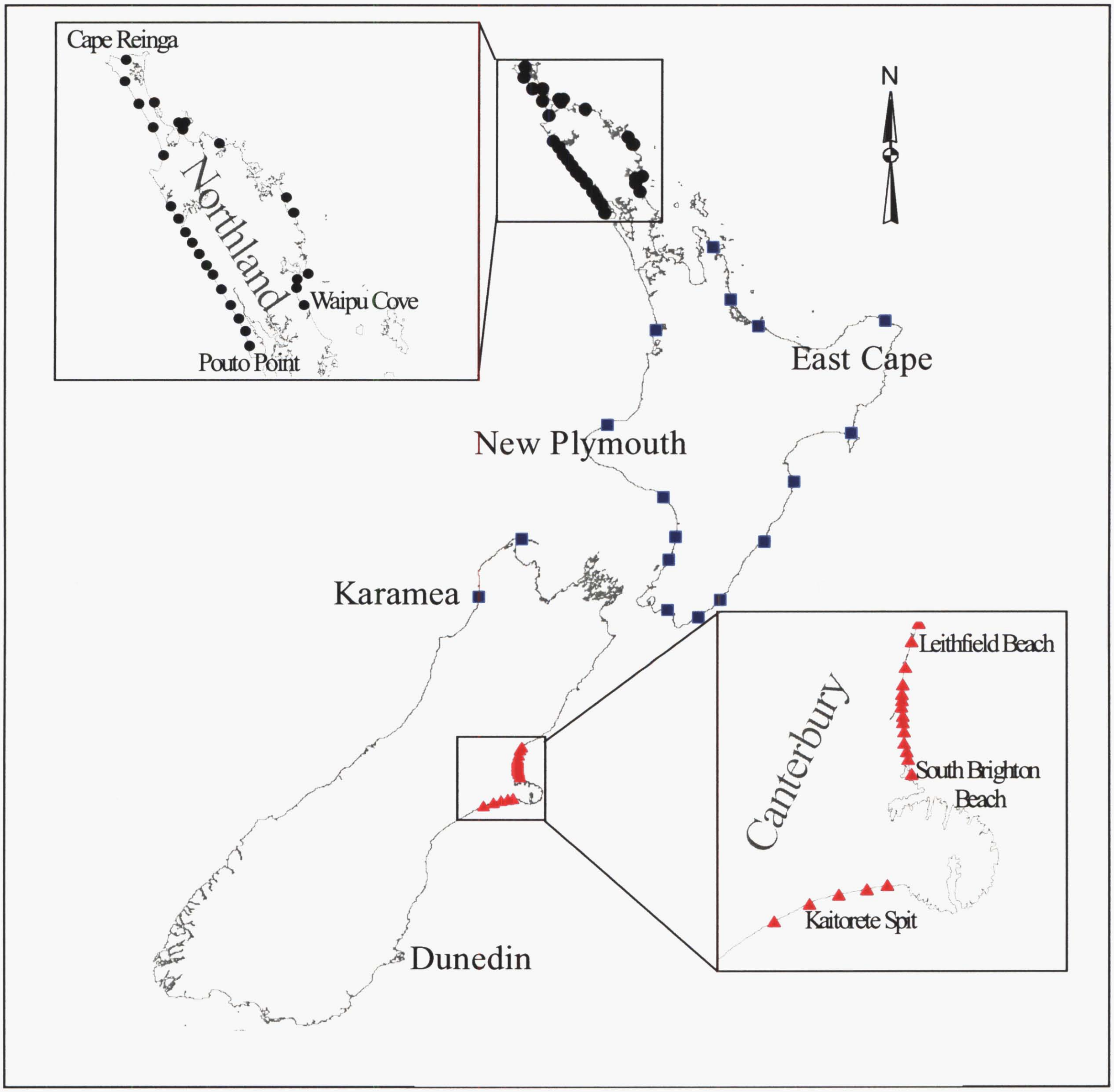

Figure 3.1 Sites at which transect sampling and stratified sampling were conducted around the New Zealand coastline (● = transect sampling sites *L. atritus* ▲ = transect sampling sites *L. katipo* ■ = stratified sampling sites)

In each region, the coastline was sampled at 1–20 km intervals because this scale was considered necessary to attain a representative sample of the range of climatic conditions, dune modification and vegetation types present. Extensive dune systems with little variation in vegetation type were sampled at ≈ 10-20 km intervals, whereas less extensive dune systems that were characterised by a range of vegetation types were sampled at ≈ 1-5 km intervals. All sites surveyed were located in dune systems because *L. katipo* and *L. atritus* have not been recorded from other ecosystems. Because large sections of east coast of northern New Zealand are characterised by estuaries, cliffs and rocky beaches larger distances separated some of the sites surveyed in this region than elsewhere (Figure 3.1)

To accommodate the aggregated nature of many *L. katipo* and *L. atritus* populations and the variety of micro-habitats found in sand dunes, large study sites of 5000 m^2 (50 m x 100 m) were used. These were positioned so that the shorter edge of study sites ran parallel to the high tide mark, whereas the longer edge ran inland. Within each 5000 m^2 study site, six 100 m transects running perpendicular to the shoreline, were spaced at 20 m intervals along the high tide mark. At 10 m intervals along each transect, plants, driftwood and flotsam within a circle (1.5 m radius) were searched for *L. katipo* or *L. atritus*. At each point where searching was conducted, the presence or absence of established (denoted by the presence of extensive webbing and/or the presence of eggsacs) mature female *L. katipo* and *L. atritus* was noted. Sampling targeted established adult females because they were considered to have a higher degree of web site specificity than males or sub-adult females (Chapter two), and because web site selection among adult female *L. katipo* and *L. atritus* was considered more likely to be closely related to levels of fecundity than male or sub-adult female web site selection (Chapter two). Although the presence of male and sub-adult female *L. katipo* or *L. atritus* was also noted, these individuals were excluded from analysis. The following were recorded at each transect point: plant type or driftwood and flotsam present, the estimated percent ground cover (% of the ground covered by dune plants or driftwood and flotsam), aspect, slope, the presence or absence of detritus, elevation relative to the high tide mark (low, medium or high), the distance from the high tide mark and ground-level temperature (sampled with a Digitherm© temperature probe ≈5 cm above the substrate underneath the retreat). The location (plant type or driftwood and flotsam) of *L. katipo* and *L. atritus* retreats was also recorded.

Transect sampling was undertaken in the Canterbury region between October 1998 and March 1999 and in the upper North Island during January and February 2000. All sampling was conducted during daylight hours to minimize the risk of being bitten by *L. katipo* or *L. atritus* and to maximise the probability that *L. katipo* and *L. atritus* web sites situated along transects would be located.

Analysis

Before analysis, ground-level temperature records were converted to standard deviations from the site mean to avoid confounding due to temporal variation in temperature. Data were then analysed using χ^2 tests (Minitab version 13) to determine whether there was a significant difference ($P = <0.05$) between sampled variables at sites where adult female *L. atritus* or *L. katipo* were present and those where they were absent. Habitat classification trees (Clarke and Pregibon 1993) were used to identify which variable ranges, or combination of variable ranges, best predicted *L. katipo* and *L. atritus* presence or absence. Initially, all data points from which no plants, driftwood or flotsam were recorded were removed from the data set, as *L. katipo* and *L atritus* web sites were not associated with sites characterised exclusively by open sand. The data set was then divided by plant type or driftwood and flotsam, and the filter option in Microsoft Excel 2000 used to examine the predictive capacity of all variable ranges. Ground-level temperature was excluded from analysis, because it was an unreliable predictor of *L. katipo* and *L. atritus* presence or absence[1]. Predictors were selected for plant type or driftwood and flotsam in a stepwise manner, on the basis that they offered the greatest predictive power per step and that they predicted *L. katipo* or *L. atritus* presence 10 % more accurately than the previous step. If fewer than five *L. katipo* or *L. atritus* were associated with a particular plant or flotsam type, no predictors were sought, as the sample size was considered too low to accurately identify useful predictors. Predictors identified through this approach were incorporated in a model predicting both *L. katipo* and *L. atritus* presence and absence. The model was subsequently applied to *L. katipo* and *L. atritus* transect survey data and examined as percentages to determine its validity and was later used to divide dune systems into strata for stratified sampling.

Mapping

At all beaches where transect sampling was undertaken, northing and easting co-ordinates were recorded. These were entered into ArcView GIS 3.05 for mapping and associated with data on *L. katipo* and *L. atritus* abundance (*L. katipo* or *L. atritus* found/number of transect points x Π x 75cm^2) and degree of dune modification. The degree of dune modification was estimated based on the number of transect points containing exotic plants; no modification = exotic vegetation at 0% of points sampled, low modification = 1-25% of points sampled contained exotic vegetation, moderate modification 26-50% of points sampled contained exotic vegetation, high modification = 51-75% of points sampled contained exotic vegetation, very high modification = 76-100% of points sampled contained exotic vegetation.

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[1] On cloudy days ground-level temperature is relatively uniform throughout dune systems (pers. obs.). Consequently, it was not possible to use ground-level temperature to predict *L. katipo* or *L. atritus* presence or absence on cloudy days.

Results - Section One

Transect sampling

Transect sampling results revealed that adult female *L. katipo* and *L. atritus* web sites were not randomly distributed throughout dune systems surveyed, but were associated with specific structural and microclimatic conditions. Adult female *L. katipo* web sites located during transect sampling were most frequently associated with *M. complexa* and pingao, but were less frequently associated with driftwood and flotsam or marram, the dominant vegetation type found along the Canterbury coast (Figure 3.2). Although they are also known to inhabit other vegetation, no *L. katipo* webs were found in other plant types during this survey. In contrast, *L. atritus* web sites were most frequently associated with *C. acerosa*, pingao and marram (Figure 3.3), but were also associated with *M. complexa*, spinifex, *C. lyptophylla* and driftwood or flotsam. No web sites were found in other plant types, which primarily comprised exotic weeds such as kikuyu and buffalo grass, but also included a range of other plants species encountered at low numbers (1-5/total transect points sampled).

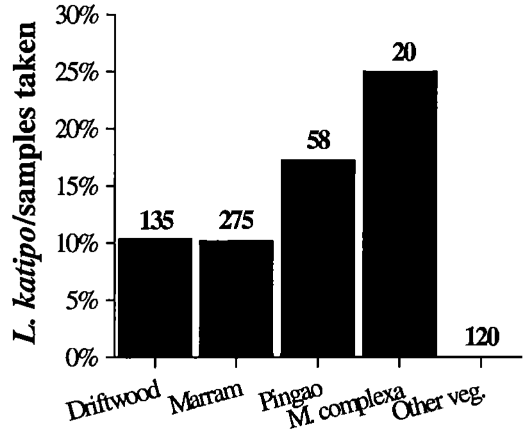

Figure 3.2 ***L. katipo*** **as a percentage of plant types and driftwood or flotsam present at points sampled** [2,3] **(Chi^2 = 22. 295, df = 4, p = 0.001)**

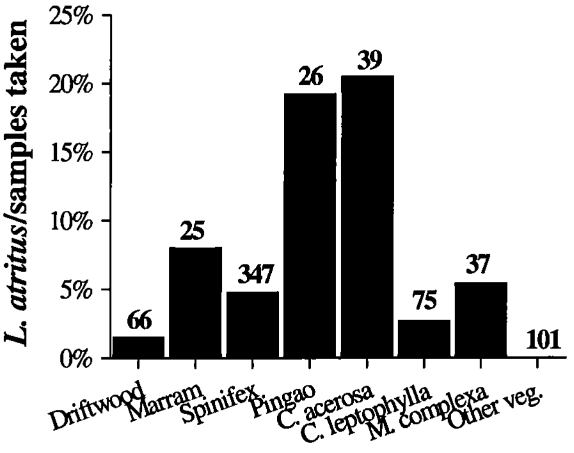

Figure 3.3 ***L. atritus*** **as a percentage of plant types and driftwood or flotsam present at points sampled (Chi^2 = 33.959, df = 7, p = 0.001)**

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[2] All graphs illustrate the number of *L. katipo* or *L. atritus* as a percentage of samples taken per category (e.g., *L. katipo* were present at 10 % of points sampled in driftwood in Canterbury).

[3] The numbers above the bars represent the number of points at which a particular plant type or driftwood and flotsam was present (e.g., driftwood was present at 135 points sampled in Canterbury)

Web sites of both species were most commonly associated with dune regions characterised by 34-66 % ground cover (Figure 3.4 &Figure 3.5), northerly aspect (Figure 3.6 & Figure 3.7), sloping ground (Figure 3.8Figure 3.9) and the absence of detritus (Figure 3.10Figure 3.11). Although *L. katipo* web sites were most frequently located at transect points within 20 m of the high tide mark at elevated sites, *L. atritus* web sites were not associated with a particular distance from the high tide mark or relative elevation (Figure 3.12 -Figure 3.15). Analysis of standardised temperature samples revealed that both species were located at sites in dune regions that were cooler (Figure 3.16Figure 3.17) than the mean ground-level temperature recorded at each site.

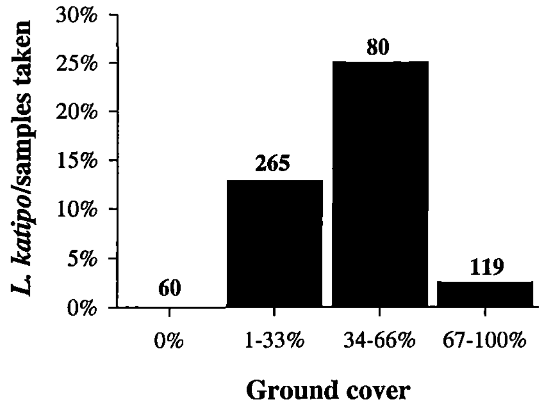

Figure 3.4. ***L. katipo*** **presence as % of samples taken/ground cover category (Chi^2 = 33.395, df = 3, p = 0.001)**

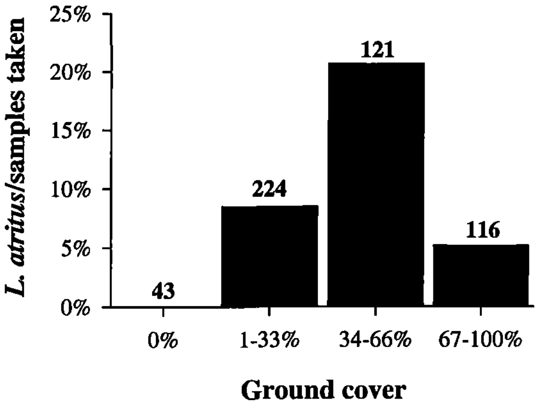

Figure 3.5. ***L. atritus*** **presence as % of samples taken/ground cover category (Chi^2 = 23.729, df = 3, p = 0.001)**

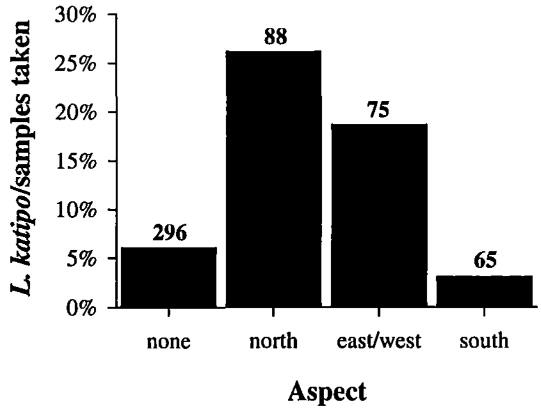

Figure 3.6. ***L. katipo*** **presence as % of samples taken/aspect category (north = <59°/ > 301°, east/west = 60° – 120° /240° – 300°, south = 119° – 239°) (Chi^2 = 36.932, df = 3, p = 0.001)**

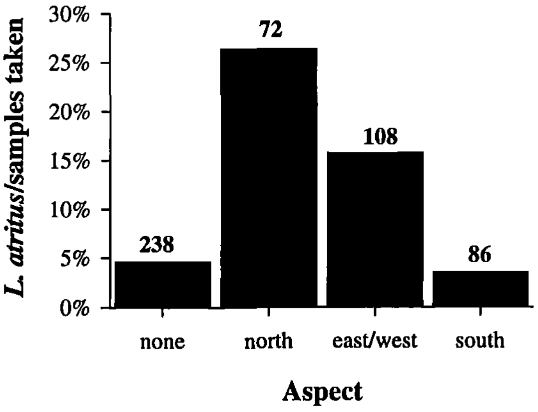

Figure 3.7. ***L. atritus*** **presence as % of samples taken/aspect category (north = <59°/ > 301°, east/west = 60° – 120° /240° – 300°, south = 119° – 239°) (Chi^2 = 37.251, df = 3, p = 0.001)**

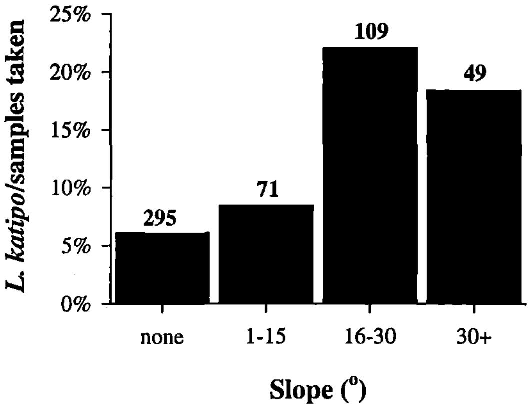

Figure 3.8. ***L. katipo*** **presence as a % samples taken/slope category (Chi^2 = 24.162, df = 3, p = 0.001)**

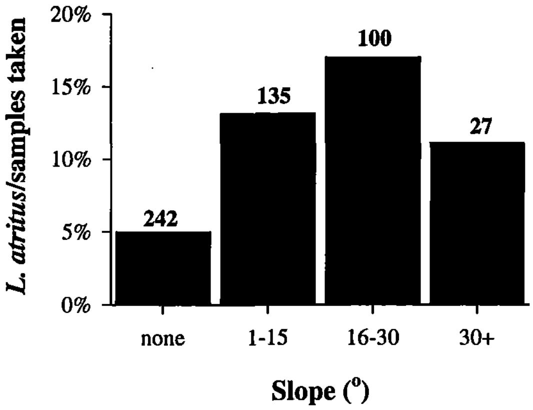

Figure 3.9. ***L. atritus*** **presence as a % samples taken/slope category (Chi^2 = 12.233, df = 3, p = 0.007)**

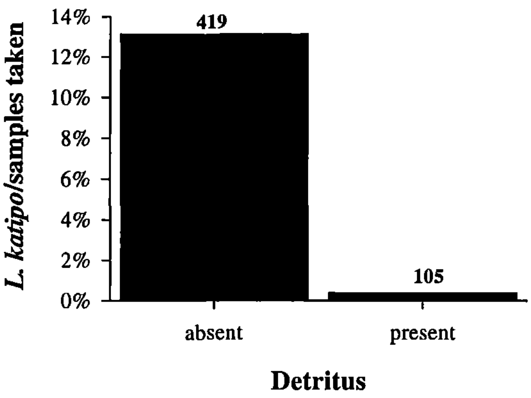

Figure 3.10. ***L. katipo*** **presence as % of samples taken with detritus present and absent (Chi^2 = 10.906, df = 1, p = 0.001)**

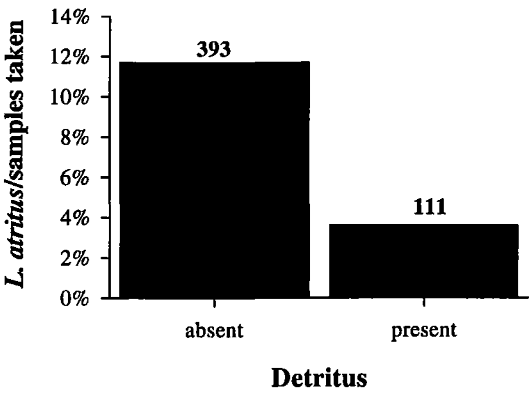

Figure 3.11 ***L. atritus*** **presence as % of samples taken with detritus present and absent (Chi^2 = 6.389, df = 1, p = 0.011)**

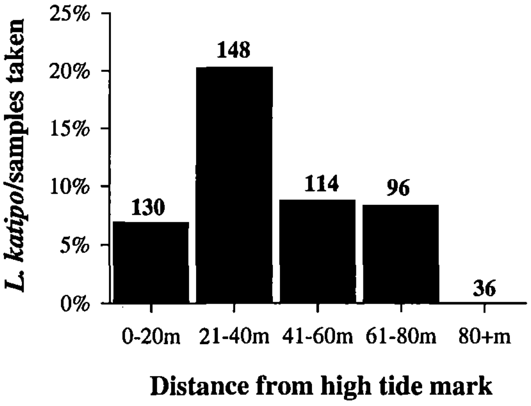

Figure 3.12 ***L. katipo*** **presence as a % of samples taken/distance from the hightide mark (Chi^2 = 21.121, df = 4, p = 0.001)**

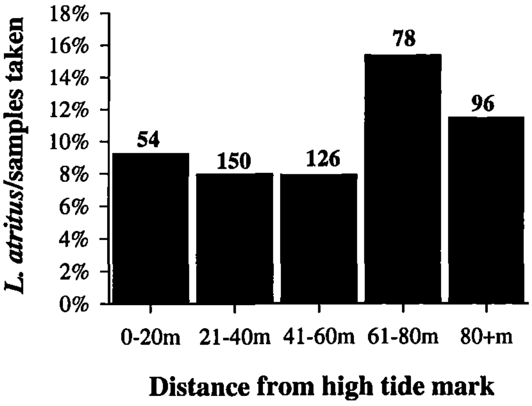

Figure 3.13 ***L. atritus*** **presence as a % of samples taken/distance from the hightide mark (Chi^2 = 4.041, df = 4, p = 0.401)**

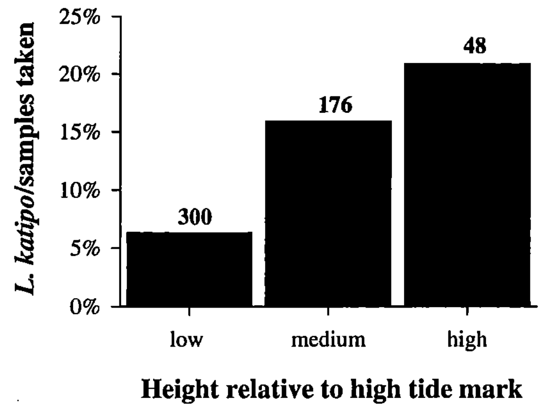

Figure 3.14 *L. katipo* **presence as a % of samples taken/relative elevation category (Chi^2 = 15.894, df = 2, p = 0.001)**

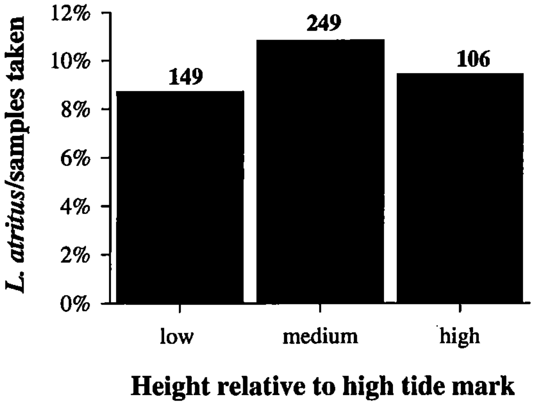

Figure 3.15 *L. atritus* **presence as a % of samples taken/relative elevation category (Chi^2 = 0.478, df = 2, p = 0.787)**

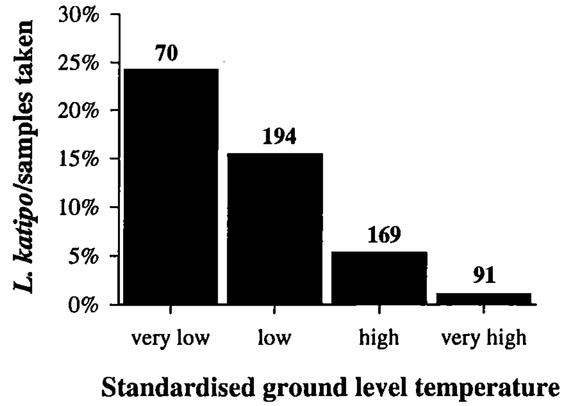

Figure 3.16 *L. katipo* **presence as a % of samples/standardised ground level temperature category (very low = -2 sdv (standard deviations from the mean), low = -1 sdv, high = +1 sdv, very high = +2 sdv,) (Chi^2 = 31.540, df = 3, p = 0.001)**

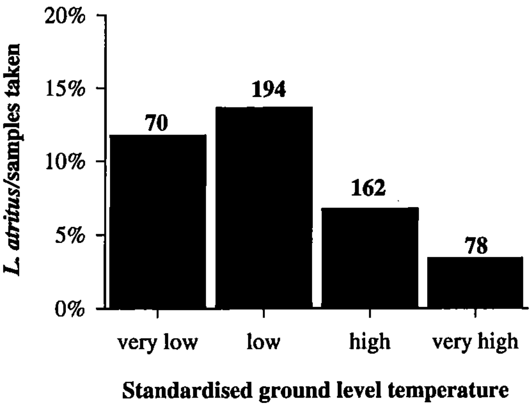

Figure 3.17 *L. atritus* **presence as a % of samples/standardised ground level temperature category (very low = -2 sdv (standard deviations from the mean), low = -1 sdv, high = +1 sdv, very high = +2 sdv,) (Chi^2 = 10.341, df = 3, p = 0..016)**

Habitat classification trees

Habitat classification trees constructed using the filter option in Microsoft Excel 2000, revealed that predictors of *L. katipo* presence varied depending on plant type and driftwood or flotsam. *L. katipo* web sites in marram, for example, were best defined by 34-66 % ground cover and northerly, easterly or westerly ($<120^\circ$ or $>240^\circ$) aspect, whereas web sites found in pingao and prostrate native shrubs were most accurately defined by northerly, easterly or westerly aspect alone. In contrast, *L. katipo* web sites in driftwood or flotsam were defined exclusively by 34-66 % ground cover (Figure 3.18). As with *L. katipo*, predictors of *L. atritus* presence or absence also varied with habitat type. *L. atritus* web sites in spinifex, for example, were best defined by 34-66 % ground cover and northerly, easterly or westerly aspect, but web sites found in *C. acerosa,* a prostrate native, were most commonly found at sites characterised by northerly, easterly or westerly aspect and the absence of detritus (Figure 3.19).

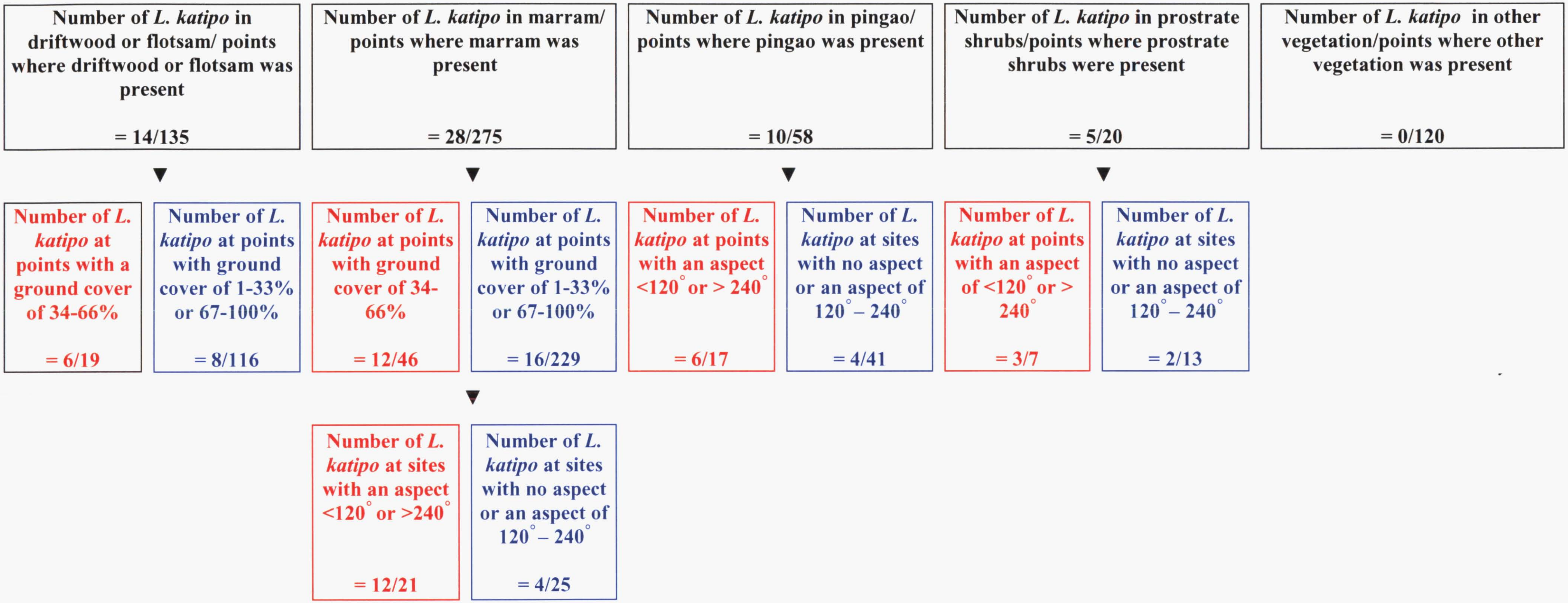

Figure 3.18 Habitat classification tree for *L. katipo* • = Raw data before analysis • = Predictors of *L. katipo* presence • = Predictors of *L. katipo* absence

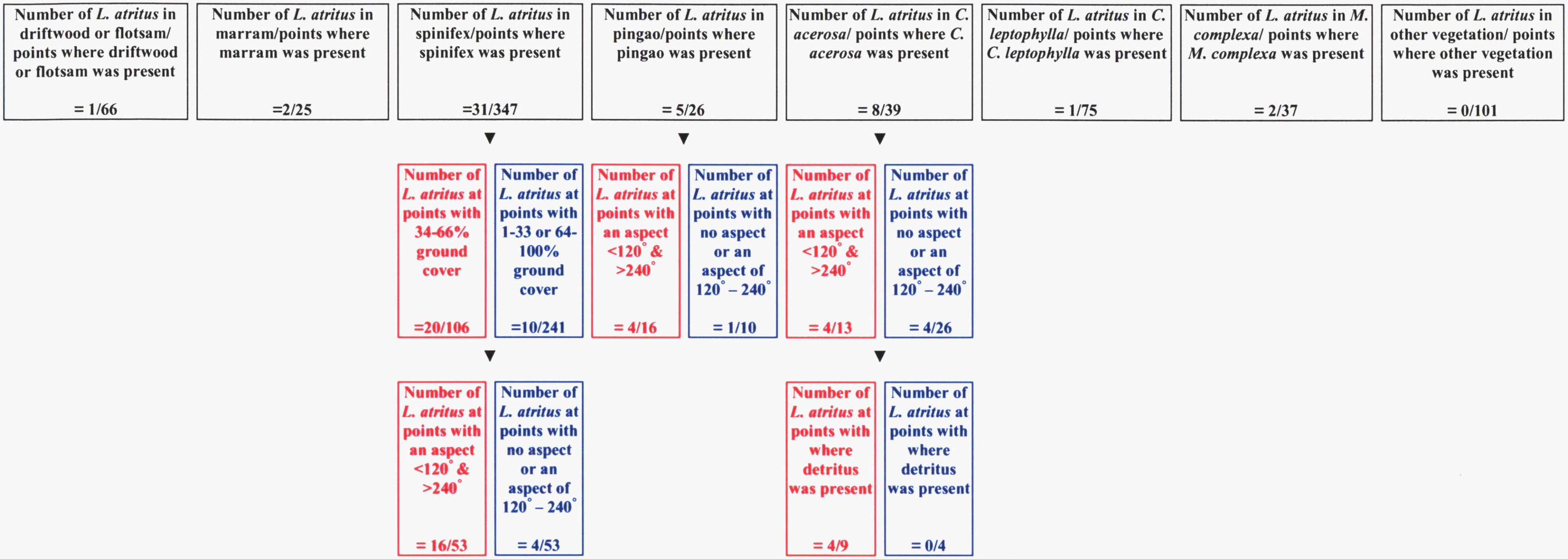

Figure 3.19. Habitat classification tree for *L. atritus* □ = Raw data before analysis □ = Predictors of *L. atritus* presence □ = Predictors of *L. atritus* absence

Predictors of *L. katipo* and *L. atritus* web sites were subsequently incorporated in a model dividing dune systems into two strata, optimal and sub-optimal habitat (Table 3.1). Model designations (optimal and sub-optimal habitat), when applied to transect data, predicted *L. katipo* absence at 94% of data points and *L. katipo* presence at 49% of data points (Table 3.2). Similarly, when applied to *L. atritus* data, the model predicted *L. atritus* absence at 95% of data points and presence at 31% of data points (Table 3.3).

Table 3.1. Habitat strata used in stratified sampling

	Plant type and driftwood or flotsam	**Ground cover**	**Aspect**	**Detritus**
Frequently present	Marram/spinifex	34 – 66%	<120° & >240°	N/A
	Pingao	N/A	<120° & >240°	N/A
	Prostrate natives	N/A	<120° & >240°	Absent
	Driftwood/Flotsam	34 – 66%	N/A	N/A
Infrequently present	Marram/spinifex	1-33% & 67-100%	None or 120° – 240°	N/A
	Pingao	N/A	None or 120° – 240°	N/A
	Prostrate natives	N/A	None or 120° – 240°	Present
	Driftwood/Flotsam	1-33% & 67-100%	N/A	N/A

Table 3.2. Predicted *L. katipo* presence and absence

		Predicted presence	
		Infrequently present	**Frequently present**
Observed	**Absent**	% = 93.79 438/467[4]	% = 50.88 N = 29/57
	Present	% = 6.21 29/467	% = 49.12 N = 28/57

Table 3.3. Predicted *L. atritus* presence and absence

		Predicted presence	
		Infrequently present	**Frequently present**
Observed	**Absent**	% = 94.69 392/414	% = 68.89 62/90
	Present	% = 5.31 22/414	% = 31.11 28/90

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[4] Number of sites at which *L. katipo* and *L. atritus* were observed to be present or absent over the number of sites sampled in sub-optimal and optimal habitat

Mapping

Although *L. katipo* and *L. atritus* inhabit dune regions modified by exotic vegetation, both species were generally more abundant in unmodified dune regions. Dune systems in Canterbury have undergone greater modification through the introduction of exotic vegetation than dune systems in Northland. This is particularly evident when comparing dune systems between South Brighton Beach and Leithfield Beach in Canterbury with the West coast of Northern New Zealand (Figure 3.20 - Figure 3.23)

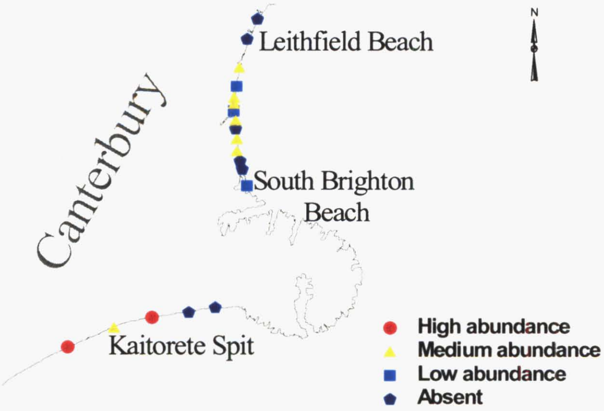

Figure 3.20. ***L. katipo*** **abundance on the Canterbury coast**

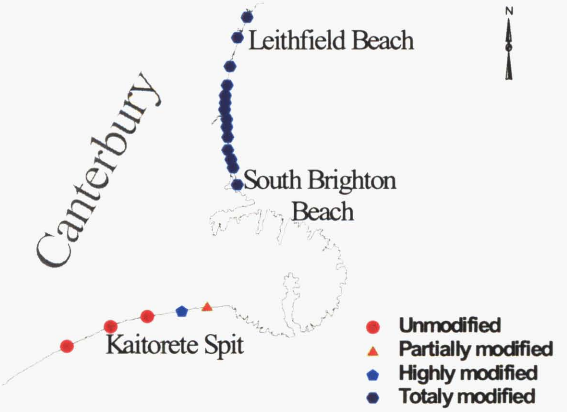

Figure 3.21. Dune modification on the Canterbury coast

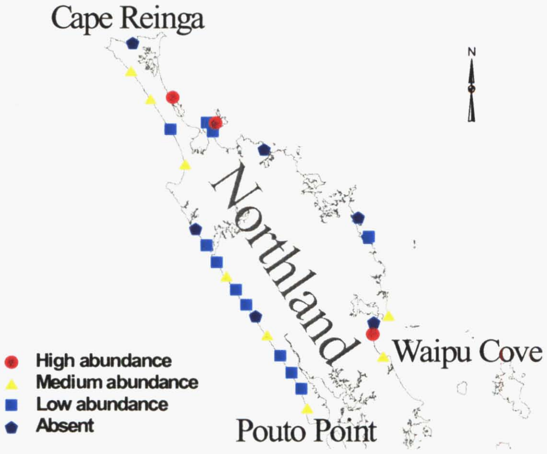

Figure 3.22. ***L. atritus*** **abundance on the northern New Zealand coastline**

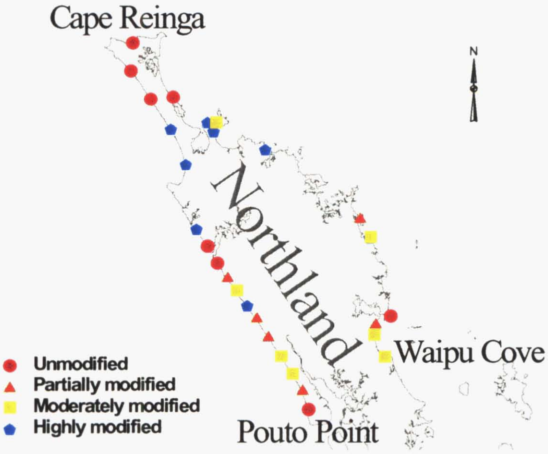

Figure 3.23. Dune modification on the northern New Zealand coastline

Discussion – Section One

Although results from transect sampling conducted on the Canterbury coastline generally supported Smith's findings (Smith 1971), there were discrepancies between the two studies. Smith found that *L. katipo* web sites were most frequently associated with marram and pingao, but less frequently (1% of *L. katipo* found) with other vegetation. Smith also found that most web sites were associated with steep slopes (30°-45°) and westerly aspect. In contrast, the current study revealed that *L. katipo* web sites were most frequently located in prostrate shrubs, driftwood or flotsam and pingao. They were less frequently associated with marram. Web sites were most common in dune regions characterised by medium (34-66 %) ground cover, sloping ground (1-30°), northerly (<60°/ >300°) aspect and the absence of detritus. In addition, this survey indicated that *L. katipo* web sites were frequently associated with dune regions situated within 20 m of the high tide mark that were higher than surrounding dune areas and at which ground-level temperature was lower than the site mean. Discrepancies between the two studies, however, may be attributed to differences in the range of dune systems surveyed, variation in dune geomorphology, and the way in which aspect was classified.

At the time of Smith's 1971 study, South Brighton was characterised by a gently shelving beach with little driftwood or flotsam (Plate 3.1). The beach was backed by dunes that were becoming steeper as marram was becoming increasingly dominant (Plate 3.3)(Chapter two). In contrast, the current study sampled a range of dune systems that included: Kaitorete Spit, which is characterised by a steeply shelving beach with abundant driftwood and flotsam (Plate 3.2) and low undulating dunes dominated by native vegetation (Plate 3.4), a range of sites along the Pegasus Bay coastline similar to South Brighton, and a number of comparatively flat dune systems with a mixture of native and exotic vegetation. Thus, although Smith found that *L. katipo* web sites were most frequently associated with marram and were not associated with driftwood, because prostrate shrubs, pingao and driftwood were not abundant at South Brighton, *L. katipo* web sites located during Smith's study are unlikely to reflect

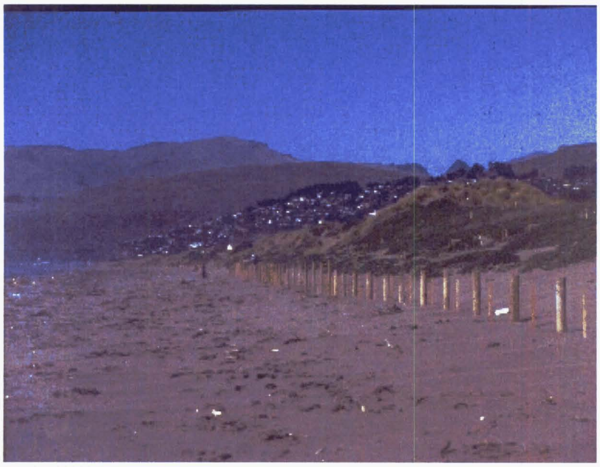

Plate 3.1. Driftwood at South Brighton Beach (note gently shelving beach)

Plate 3.2. Driftwood at Kaitorete Spit (note steeply shelving beach)

Plate 3.3. Marram dominated dunes at South Brighton Beach (note dark green patch of newly planted ice-plant and the absence of open sand)

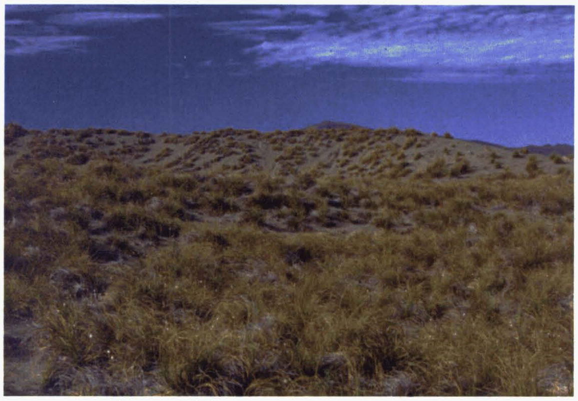

Plate 3.4. Pingao dominated dunes at Kaitorete Spit (note the presence of open sand between pingao clumps)

the habitat characteristics of this species in dunes containing a wider range of plants or driftwood and flotsam. Moreover, at the time of Smith's (1971) study marram had only recently been introduced at South Brighton and, consequently, was present at low densities. As a result, marram surveyed during Smith's study may have provided better *L. katipo* habitat than marram surveyed during the current study, which was established on the Canterbury Coast over 40 years ago and now forms a dense swathe over most dunes in the Pegasus Bay region (pers. obs.).

Geomorphological differences between South Brighton and the dune systems sampled during the current study may also account for discrepancies between the two studies. The gentle shelving beach at South Brighton allows the sea to wash over driftwood during high tides. As a result, *L.katipo* may be unable to inhabit driftwood at South Brighton. In contrast, driftwood at Kaitorete Spit is infrequently swamped by high tides because of the protection afforded by the steeply shelving beach, which may explain why *L. katipo* frequently inhabit driftwood at Kaitorete Spit (Plate 3.2) (pers. obs.). Variation in the slope range most commonly associated with web sites between the two studies might also be related to geomorphologic differences between dune systems sampled. Smith's study was conducted in a dune system that was dominated by steep dunes, whereas the current study examined *L. katipo* web site characteristics in a range of dune types, which included low flat dune systems and low undulating dunes. Thus, although steep marram dominated dunes were sampled during this study, because a range of other dune types were also sampled, the current study reflects *L. katipo* web site characteristics along a large section (≈150km) of the Canterbury coast. In contrast, Smith's study was confined to a dune system modified through the introduction of marram and truncated by urban development.

Unlike the discrepancies between the two studies outlined above, variation in the aspect associated with *L. katipo* web sites between the studies is likely to have resulted from methodological differences. Smith classified aspect into four categories (north, east, west & south), whereas this survey recognised only three aspect classifications (northerly = $<60^\circ/>300^\circ$, easterly/westerly = 60°-$120^\circ/240^\circ$ - 300° and southerly =120° – 240°). Consequently, many web sites that Smith would have classified as westerly aspect were classified as northerly aspect in this survey.

Transect sampling conducted in northern New Zealand revealed that *L. atritus* web sites are defined by similar characteristics to those of *L. katipo*. *L. atritus* web sites were most commonly associated with dune regions characterised by medium ground cover, sloping ground (1-30°), northerly aspect, the absence of detritus and low standardised ground-level temperature. Although there were inter-specific differences between the habitat types in which *L. katipo* and *L. atritus* web sites were located and their distance and relative elevation from the high tide mark, these differences may be explained by regional variation in habitat availability and dune geomorphology. For example, in northern regions of New Zealand, where *C. acerosa* is relatively common, *L. atritus* was most frequently found in *C. acerosa,* whereas in the lower North Island and South Island, where *C. acerosa* is rare (Johnson 1992; Partridge 1992) *L. atritus* and *L. katipo* most frequently inhabited *M. complexa* and pingao (pers. obs.). Similarly, at Kaitorete Spit, where driftwood or flotsam was abundant and protected from the sea by a steeply shelving beach, *L. katipo* was commonly found in driftwood or flotsam. In contrast, *L. katipo* and *L. atritus* were rarely found in driftwood or flotsam in other dune systems where driftwood or flotsam was generally less abundant and more prone to flooding during high tides.

Structural differences between dune systems dominated by marram and those dominated by native vegetation may account for differences between *L. katipo* and *L. atritus* web site position in relation to the high tide mark and relative elevation within dunes. Most dune systems dominated by marram are principally characterised by dense ground cover, with the exception of a narrow band (< 20 m wide) of sparse to medium marram situated along the top of the foredune (pers. obs.). Presumably, because it is unable to colonise dense marram, *L. katipo* is frequently found in this band of sparse to medium marram, which is apparently unable to reach higher densities because its growth is inhibited by large amounts of wind deposited sand. This may explain why *L. katipo*, which inhabits marram-dominated dune systems throughout much of its distribution, was most commonly found < 20 m from the high tide mark[5] at relatively elevated sites. In contrast, native-dominated dunes are characterised by comparatively sparse ground cover. Thus, *L. atritus,* which principally inhabits dune systems dominated by native vegetation, was not associated with a particular distance from the high tide mark or relative elevation. (Figure 3.9Figure 3.11), individually, variable ranges were not useful predictors of *L. katipo* and *L. atritus* presence or absence. For example, although transect surveys indicated that northerly aspect was the variable range most frequently associated with *L. katipo* and *L. atritus* presence, *L. katipo* and *L. atritus* were present only at 11% and 13% of sites that were not characterised by northerly aspect, which represented over half the *L. katipo* and *L. atritus* found (Figure 3.5). Furthermore, because the proportion of *L. katipo* or *L. atritus* web sites associated with a particular variable range varied, depending on plant type and driftwood or flotsam (Figure 3.18Figure 3.19), the predictive capacity of variable ranges was unreliable.

Using the filter option in Excel, a model was created from variable ranges that best predicted *L. katipo*

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[5] This result may also have been influenced by *L. katipo* inhabiting driftwood (10 % of *L. katipo* web sites located)(Results – Section One)

3.19), the predictive capacity of variable ranges was unreliable.

Using the filter option in Excel, a model was created from variable ranges that best predicted *L. katipo* and *L. atritus* presence or absence in each plant type and driftwood or flotsam. When re-tested on the dataset, the model predicted *L. katipo* and *L. atritus* presence and absence more accurately and reliably than individual variable ranges, irrespective of plant type and driftwood or flotsam (Table 3.2 & Table 3.3). Moreover, as the model was based on the results of both the Canterbury survey of *L. katipo* and the northern New Zealand survey of *L. atritus,* it was possible to identify predictors for all plant types and driftwood of flotsam, including those that were excluded from analysis due to low sample sizes. For example, although low sample size prevented the identification of predictors for *L. atritus* presence or absence in driftwood or flotsam, results from the Canterbury survey, that showed *L. katipo* was most likely to be found in driftwood or flotsam at sites characterised by 34-66% ground cover, were also used to predict *L. atritus* presence in driftwood or flotsam.

Methods – Section Two

Stratified sampling was conducted at 17 dune systems between Karamea and Auckland during May and July 2000 (Figure 3.1). Dune systems where stratified sampling was undertaken were selected on the basis that they were separated by ≈ 100 km, so that a representative range of dune systems and climatic conditions found on the New Zealand coastline was sampled. A further selection criterion was that *L. katipo* and *L. atritus* were found within 15 minutes of directed searching in dune regions designated as optimal habitat on the basis of transect survey results (Table 3.1).

Selected dune systems were divided into two strata (Table 3.1), dune regions in which *L. katipo* or *L. atritus* were predicted present and dune regions in which *L. katipo* or *L. atritus* were predicted to be absent. Sampling was conducted at an equal number of points within each stratum. These were selected as they were encountered on the basis that they were ≈ 5 m from other points sampled At each point, a circle (1.5 m radius) was searched for *L. katipo* or *L. atritus* and their presence or absence noted. The position of the catching-web in relation to open sand and the distance (cm) between the retreat and open sand were also noted. Each dune system surveyed was sampled for up to one hour or until all potential sampling points in either strata had been searched.

Analysis

Stratified sampling data were analysed as percentages to determine whether the model designations, optimal and sub-optimal *L. katipo* and *L. atritus* habitat, fitted the data. Data relating to the position of the catching-web and the retreat were also examined as percentages.

Results – Section Two

Stratified sampling revealed that the model constructed on the basis of transect survey results fitted the data well. The model correctly predicted *L. katipo* presence at 23% of points sampled and predicted absence at 95% of sites sampled. Similarly, the model correctly predicted *L. atritus* presence at 38% of points sampled and predicted *L. katipo* absence at 91% of sites sampled.

Table 3.4. Predicted *L. katipo* presence and absence

		Predicted presence	
		Infrequently present	**Frequently present**
Observed	**Absent**	% = 94.74 72/76	% = 76.92 60/78
	Present	% = 5.26 4/76	% = 23.08 18/78

Table 3.5. Predicted *L. atritus* presence and absence i

		Predicted presence	
		Infrequently present l	**Frequently present**
Observed	**Absent**	% = 91.30 63/69	% = 61.54 40/65
	Present	% = 8.70 6/69	% = 38.46 25/65

L. katipo and *L. atritus* catching-webs were usually positioned over open sand (Figure 3.24Figure 3.25). *L. katipo* retreats were predominantly located within 1-5 cm of open sand at the edge of small to medium sized plants and driftwood or flotsam, whereas *L. atritus* retreats were generally found within 1-10 cm of open sand in medium and large size plants and driftwood or flotsam (Figure 3.26Figure 3.27.

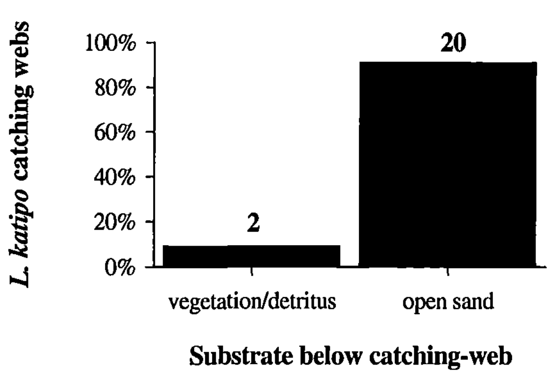

Figure 3.24 Substrate types below *L. katipo* catching webs (Chi^2 = 17.190, df = 1, p = 0.001)

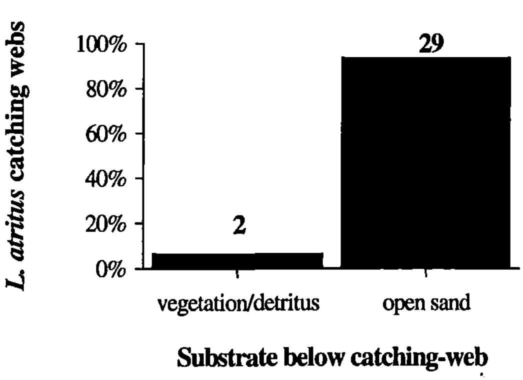

Figure 3.25 Substrate types below *L. atritus* catching-webs (Chi^2 = 22.533, df = 1, p = 0.001)

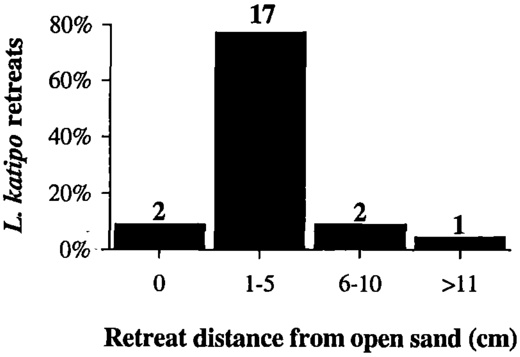

Figure 3.26 Distance from *L. katipo* retreats to open sand ($Chi^2 = 35.190$, df = 3, p = 0.001)

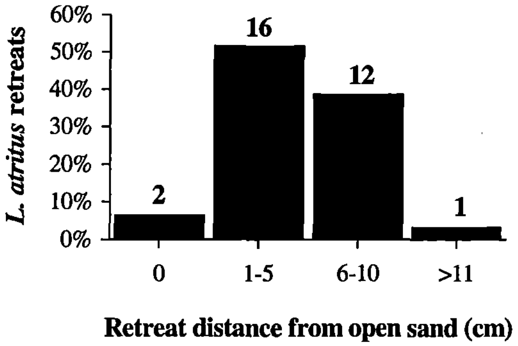

Figure 3.27 Distance from *L. atritus* retreats to open sand ($Chi^2 = 20.333$, df = 3, p = 0.001)

Discussion – Section Two

Stratified sampling revealed the model was useful for identifying dune regions at which *L. katipo* and *L. atritus* were likely to be present or absent. The model correctly predicted *L. katipo* presence and absence at 23% and 94% of points sampled, and predicted *L. atritus* presence and absence at 38% and 91% of points sampled (Table 3.4 & Table 3.5). These results indicate that the characteristics of *L .katipo* and *L. atritus* web sites identified in the model designations appear typical of *L. katipo* and *L. atritus* web sites around New Zealand, irrespective of regional variation in dune vegetation and dune geomorphology. As with transect surveys, however, the model predicted absence more accurately than presence. This was particularly so for *L. katipo* that was present at only 23% of sites sampled in optimal habitat during stratified sampling.

It is not clear why the model did not predict *L. katipo* and *L. atritus* presence more accurately, but it is possible that intra-specific competition prevents either species from filling a greater proportion of potential web sites in optimal habitat, as has been observed in other spider species (Morse and Fritz 1982; Nentwig 1987; Wise 1993; Shear 1994). In some dune systems inter-specific competition with *S. capensis* might also restrict *L. katipo* and *L. atritus* numbers, as contended by Hann (1990). That I rarely observed *S. capensis* inhabiting prostrate shrubs, dune grasses or pingao, but more frequently recorded this species from driftwood and flotsam, however, suggests that *L. katipo* and *L. atritus* have different habitat preferences from *S. capensis*. This assertion is consistent with Hann's (1990) finding that *S. capensis* was more common in small logs than *L. katipo*, but was less common than *L. katipo* in marram.

Invertebrate abundance may also influence patterns of *L. katipo* and *L. atritus* distribution as has been shown in other spider species (Wise 1975; Wise 1979; Wise 1993; Foelix 1996). The high proportion of *L. katipo* inhabiting driftwood in the littoral zone[6] at some beaches (pers. obs.), for example, may be related to the high insect abundance associated with this dune region (Duffey 1968). Similarly, the association between *L. atritus* and prostrate shrubs within dune meadows[7] (pers. obs.) might also be related to invertebrate abundance, as dune meadows are considered to contain high invertebrate abundance and diversity (Duffey 1968; Hodge 1999). Because *L. katipo* and *L. atritus* are apparently unable to build catching-webs at micro sites without suitable structural supports, however, these species are associated with patches of vegetation and driftwood or flotsam that may also provide favourable thermal conditions for many dune dwelling invertebrates (Ranwell 1972; Riechert and Gillespie 1986; Hodge 1999). Consequently, *L. katipo* and *L. atritus* might be associated with micro sites that are characterised by comparatively high invertebrate abundance. If this is the case, prey abundance may not influence *L. katipo* and *L. atritus* web site selection, as their preference for web sites in vegetation patches and driftwood or flotsam will ensure they establish webs at sites with

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[6] A band of driftwood and flotsam found along the high tide mark

[7] An area of fixed dune containing high plant diversity commonly situated toward the inland margin of dunes

sufficient prey. This assertion is supported by Lubin (1993) who found that the web site selection of *L. revivensis*, that also inhabits patchy vegetation in a xeric environment, did not appear to be associated with invertebrate abundance.

Alternatively, the model may not accurately reflect *L. katipo* and *L. atritus* web site preferences. For example, at *L. katipo* and *L. atritus* web sites located during stratified sampling, all catching-webs were built over open sand, and retreats were most frequently built within 10 cm of open sand at the edge of plants, pieces of driftwood or flotsam. These results suggest that the reason *L. katipo* or *L. atritus* are rarely found in dune grasses characterised by dense (67-100%) ground cover may be related to the absence of patches of open sand over which catching-webs are often constructed. Correspondingly, *L. katipo* and *L. atritus* presence in prostrate shrubs, which are commonly characterised by dense ground cover (pers. obs), may be associated with areas of open sand that are present underneath most prostrate shrubs. Thus, although transect survey results suggested that percent ground cover may be an important predictor of *L. katipo* or *L. atritus* presence, it is probable that *L. katipo* and *L. atritus* web sites may be associated with patches of open sand rather than percent ground cover *per se*.

Similarly, the association between northerly aspect and *L. katipo* and *L. atritus* web sites is unlikely to be related to aspect in itself, but may instead be related to temperature. Sites with northerly aspect are generally exposed to greater solar radiation than those with easterly, westerly or southerly aspect and, consequently, are likely to be characterised by higher daytime ground-level temperatures. Perhaps more importantly, however, greater exposure to solar radiation during the day may mean that northerly slopes radiate more heat at night when *L. katipo* and *L. atritus* are active. In turn, higher nocturnal ground level temperature could promote increased activity levels amongst *L. katipo* and *L. atritus* leading to increased prey capture, higher fecundity and lower over wintering mortality rate, which would explain why both species appear to favour sites with northerly aspect. Although results revealed that *L. katipo* and *L. atritus* web sites were most frequently associated with sites characterised by low standardised daytime temperature, temperature samples at web sites were taken underneath retreats, which are generally shaded from direct insolation (pers. obs.). Low standardised temperature records at web sites, therefore, reflect the daytime temperature of the retreat that may be positioned to protect *L. katipo* and *L. atritus* from extreme daytime temperatures when both species are generally inactive (Chapter two).

The relatively low proportion of *L. katipo* web sites located at points defined by characteristics frequently associated with *L. katipo* presence may be related to the timing of the stratified sampling, which was undertaken during winter when spider abundance is generally low (Nentwig 1987; Foelix 1996). Because *L. katipo* inhabits cooler regions of New Zealand, it is subjected to lower winter temperatures than *L. atritus*. Consequently, *L. katipo* abundance may suffer greater decline than *L. atritus* over winter months, because cooler temperatures can slow spiders' metabolic rate inhibiting locomotion needed to capture prey, escape predation and to maintain the catching-web and retreat

(Savory 1977; Nentwig 1987; Foelix 1996). This assertion is supported by stratified survey results that showed *L. atritus* was present at 48% of points sampled in optimal habitat during winter, whereas *L. katipo* was present at only 23% of points, despite being recorded at 49% of sites defined as optimal habitat in transect data, which were collected in the summer. Alternatively, the low proportion of *L. katipo* web sites found in dune regions defined as optimal habitat during stratified sampling may be related to habitat quality.

Coastal dune systems in the lower North Island and upper South Island of New Zealand have undergone greater modification than dune systems in the north of the North Island (Johnson 1992; Partridge 1992). As a result, few dune regions are defined by characteristics associated with *L. katipo* and *L. atritus* presence and these are often isolated by substantial (1-5 km) sections of coastline that are defined by characteristics associated with *L. katipo* and *L. atritus* absence (pers. obs.). Consequently, *L. katipo* numbers may be more likely to decline as a result of habitat fragmentation than *L. atritus*, which inhabits comparatively unmodified and extensive dune areas. This assertion is supported by results that revealed high *L. katipo* and *L. atritus* abundance was most frequently associated with relatively unmodified dune regions (Figures 22-24). Although transect survey results showed that *L. katipo* was present at 49% of sites sampled in optimal habitat, this result may have been skewed by data collected from the Kaitorete Spit where *L. katipo* abundance was very high (

Figure 3.20.).

Although no solid conclusions explaining *L. katipo* and *L. atritus* web site specificity can be drawn from the results, the implications of web site specificity among *L. katipo* and *L. atritus* are more obvious. Smith (1971) estimated that *L. katipo* density at South Brighton Beach was ≈1.1 spiders/m^2 in 1971. When the site was resurveyed in 1998, only one male and two female *L. katipo* (≈ 0.004 spiders/m^2) were found. Although the apparent decline in *L. katipo* abundance between the two surveys might be explained by differences in the methodology (Smith's stratified survey method may have produced a higher density estimate than that resulting from the stratified random method I used), I believe it is unlikely that methodological discrepancies could be solely responsible for such a marked difference in *L. katipo* abundance. Changes in plant species composition and dune structure, however, may be associated with the decline in *L. katipo* abundance at the site surveyed. When Smith surveyed the South Brighton Beach for *L. katipo* in 1971, the dunes at South Brighton had only recently been planted with marram (Smith 1971). Consequently, pingao remained at ≈ 8 % of sites sampled and, marram, which was predominantly sparse (distinct tussocks interspersed with open sand), was present at ≈ 66 % of sites sampled (Smith 1971). In contrast, when I surveyed the area in 1999 no pingao remained, and dense marram (tussocks indistinct and no sand visible) was the most common vegetation type (≈ 89 % of vegetation types surveyed).

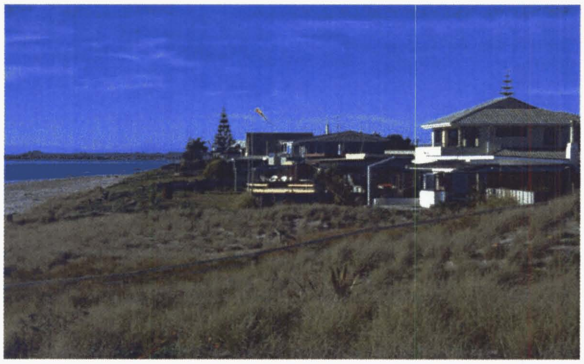

Plate 3.5. Housing development in the foredunes at Papamoa Beach

Plate 3.6. Driftwood stacked in piles ready for burning on Wanganui Beach

Plate 3.7. Rabbit browse at Opoutere Spit

These results, and additional anecdotal evidence documenting the decline of *L. katipo* and *L. atritus* in dune systems where exotic sand binding plants have been introduced to inhibit sand movement (Lyn Forster, 1999, pers. com.), suggest that once exotic plants become established in dune systems they may reduce the availability of optimal *L. katipo* and *L. atritus* habitat. This assertion, is further supported by the low number of *L. katipo* or *L. atritus* associated with modified dune systems, compared with higher numbers in dune systems characterised as relatively unmodified (Figures 22-24). Furthermore, unlike *L. hasselti, L. mactans*, *L. hesperus, L. geometricus* Koch 1841 and other *Latrodectus* spp. (Kaston 1970; Raven and Gallon 1987) that are frequently associated with human settlement, *L. katipo* and *L. atritus* have rarely been recorded from human dwellings, forestry or farmland. This implies that the extensive reclamation of dune systems for human development and agriculture may have further reduced the availability of optimal *L. katipo* and *L. atritus* habitat (Plate 3.5). So too, human activities, such as the use of off road vehicles in dune systems, the burning or collection of driftwood (Plate 3.6), and animal browsing by rabbits, hares, sheep, cattle and horses may additionally reduce the availability of optimal *L. katipo* and *L. atritus* habitat (Plate 3.7).

Habitat fragmentation and reduction resulting from dune modification could impede *L. katipo* and *L. atritus* dispersal (Chapter five), thereby reducing the probability that either species could recolonise dune regions from which they have been displaced. The displacement of *L. katipo* by *S. capensis* after perturbation as reported by Hann (1990) (Chapter two), therefore, may result from impeded recolonisation capacity rather than active displacement by *S. capensis*. *S. capensis* appears to be less habitat specific than *L. katipo* and is commonly found in a broad range of habitats that include wood and debris, human dwellings and occasionally, low growing vegetation (pers. obs.). Unlike *L. katipo* it is not restricted to the coast, but is associated with a wide range of habitats (Hann 1990). Consequently, although *S. capensis* may be displaced from localised areas within dune systems during perturbation, it may be more readily able to recolonise these areas from extensive reservoir populations inland. In contrast, if *L. katipo* is displaced during perturbation, the probability of recolonisation is comparatively low, because neighbouring populations of *L. katipo* are also likely to been affected by the perturbation and, as mentioned above, in many case areas of dense dune vegetation may impede dispersal.

Although *L. katipo* and *L. atritus* persist in modified dune systems, they are frequently found in small aggregated populations at the back of the foredune, where large deposits of wind-blown sand inhibit the formation of dense ground cover. In these dune areas, *L. katipo* and *L. atritus* are buried by wind-blown sand during storms (pers. obs). Consequently, *L. katipo* and *L. atritus* are unlikely to be able persist indefinitely in highly modified dune systems, such as those found at Pegasus Bay, Canterbury (Figure 3.21).

It is not clear whether sub-adult female or male *L. katipo* and *L. atritus* are also affected by dune modification but, since their webs appear to be associated with dune regions similar to those selected by adult females, it is probable that habitat modification may also reduce the abundance of potential sub-adult female or male web sites.

Conclusions

Transect surveys revealed that adult female *L. katipo* and *L. atritus* web sites were associated with tightly defined structural and microclimatic conditions, indicating that both species appear to have strict web site preferences. These did not appear to vary markedly between species or location, suggesting that *L. katipo* and *L. atritus* have similar web site preferences and that these are not affected by regional variation in dune geomorphology or climate. Variation between web site preferences, however, did occur between plant and flotsam types. Consequently, variable ranges that were most frequently associated with *L. katipo* and *L. atritus* web sites, such as northerly, were not reliable predictors of *L. katipo* and *L. atritus* presence in all habitat types.

A model was constructed that accurately predicted *L. katipo* or *L. atritus* absence (> 90% of points sampled) irrespective of habitat type, but less accurately predicted *L. katipo* or *L. atritus* presence (33 –38% of points sampled) (Section two). It was argued that the model may have been less accurate at predicting presence either because intra-specific competition prevents *L. katipo* or *L. atritus* from filling a greater proportion of potential web sites in optimal habitat or that the model did not accurately define web sites. The latter was supported by stratified survey results that indicated that almost all *L. katipo* and *L. atritus* catching-webs were constructed over open sand, indicating that web sites may be associated with patches of open sand rather than ground cover *per se*. Moreover, it was also suggested that the association between northerly aspect and *L. katipo* and *L. atritus* web sites might be related to temperature rather than aspect.

Although a solid hypothesis explaining *L. katipo* and *L. atritus* web site specificity can not be drawn from the results, the implications of web site specificity in *L. katipo* and *L. atritus* were more apparent. The web site requirements of *L. katipo* and *L. atritus* do not appear to be met by dense exotic dune grasses that have been introduced to stabilise New Zealand's dune systems. Furthermore, that *L. katipo* and *L. atritus* have rarely been recorded in habitats other than dune systems suggests that dunes modified by agriculture, forestry or urban development may also fail to meet the habitat requirements of *L. katipo* or *L. atritus.* In turn, dune modification or truncation resulting from urban and agricultural development or forestry may have led to the reduction and fragmentation of *L. katipo* and *L. atritus* habitat, impeding dispersal. Consequently, these species' capacity to recolonise vacated dune regions may have decreased.

The apparent displacement of *L. katipo* by *S. capensis* discussed by Hann (1990), therefore, may be a symptom of dune modification rather than the causal agent of *L. katipo* decline. *S. capensis* inhabits a wider range of habitats than *L. katipo* and, consequently, may be more readily able to recolonise dune regions after perturbation than *L. katipo*. As a result, *S. capensis* may displace *L. katipo* in some modified dune systems as observed by Hann (1990). The results presented in this chapter, however, indicate that the modification of New Zealand's dune systems, which is likely to result in the fragmentation and reduction of *L. katipo* and *L. atritus* habitat, is a probable principal agent of the decline in *L. katipo* abundance and may also be related to an apparent decrease in *L. atritus* numbers.

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Chapter Four
Structural and microclimatic context of *L. katipo* and *L. atritus* web sites

Introduction

Web-building spiders appear to have specific micro-habitat requirements (Savory 1977; Shear 1986; Nentwig 1987; Foelix 1996). At a fundamental level, the structural requirements of spider webs dictate where they may or may not be built (Schaefer 1978; Uetz *et al.* 1978; Shear 1986; Nentwig 1987; Foelix 1996; Carrel 2001), but micro-climate and prey abundance are also believed to be determinants of suitable web sites (Uetz *et al.*1978; Morse and Fritz 1982; Riechert and Gillespie 1986; Hodge 1987). Because of their small body mass and large surface area, spiders are particularly vulnerable to hypothermia, hyperthermia and dehydration, which can all impair motor function and result in loss of mobility (Foelix 1982; Riechert and Gillespie 1986). As prey capture, predator avoidance, web maintenance and construction depend on mobility, it is critical that spiders inhabit microsites with suitable climatic conditions and a regular supply of prey, the primary source of water and nutrients (Savory 1977; Nentwig 1987; Foelix 1996).

Stratified surveys (Chapter three) revealed that *L. katipo* and *L. atritus* catching-webs are almost always constructed over open sand. Spiders inhabiting dune grasses, for example, constructed catching-webs in open spaces between grass tufts, whereas those inhabiting prostrate shrubs built catching-webs on the underside of the plant overhanging open sand. That *L. katipo* or *L. atritus* were not found in dune regions where dense marram or other plants, such as kikuyu or buffalo grass, excluded interplant gaps, suggests that patches of open sand may be a structural requirement of *L. katipo* or *L. atritus* catching-webs. Moreover, the strong association between *L. katipo* or *L. atritus* web sites and dune regions characterised by northerly, easterly or westerly aspect suggests that factors associated with aspect, such as temperature, may also influence *L. katipo* and *L. atritus* web site selection.

In this chapter, I examine the effect of marram density on *L. katipo* and *L. atritus* web construction, prey capture and weight. I also investigate whether the preference exhibited by *L. katipo* and *L. atritus* for sites with northerly, easterly or westerly aspect is related to temperature and light.

Methodology

Equipment and apparatus

Eight microcosms were created in round plastic containers (20 cm radius, 20 cm deep) with beach sand and live marram grass. In each container, a conical sand mound was created. The perimeter of the mound was positioned 5 cm below the container rim to prevent spiders and prey escaping, while the centre of the mound was raised 5 cm above the container rim. Sparse vegetation was simulated in four containers by planting four tufts (5-8 cm in diameter) of marram interspersed with areas of open sand (Plate 4.1). Marram tufts were planted in the remaining four containers with no inter-plant spaces > 2 cm to simulate dense vegetation (Plate 4.2). In all containers, a gap of ≈ 8 cm was maintained between plants and the edge of the container to help prevent the escape of spiders. The possibility of escape was further reduced by pruning and tying marram grass tufts so that no tillers overhung the container rim and by placing each container within a larger container filled with water creating a 2 cm moat around each microcosm.

Plate 4.1. Sparse marram microcosm

Plate 4.2. Dense marram microcosm

All microcosms were numbered and initially placed in a controlled temperature room that followed the outdoor ambient air temperature. Due to health and safety concerns related to keeping poisonous spiders in proximity to people, however, the experiment was relocated to a shed that was covered in white shade cloth allowing natural light penetration and limited air movement. Relocation did not appear to change the spiders' activity patterns or web building behaviour.

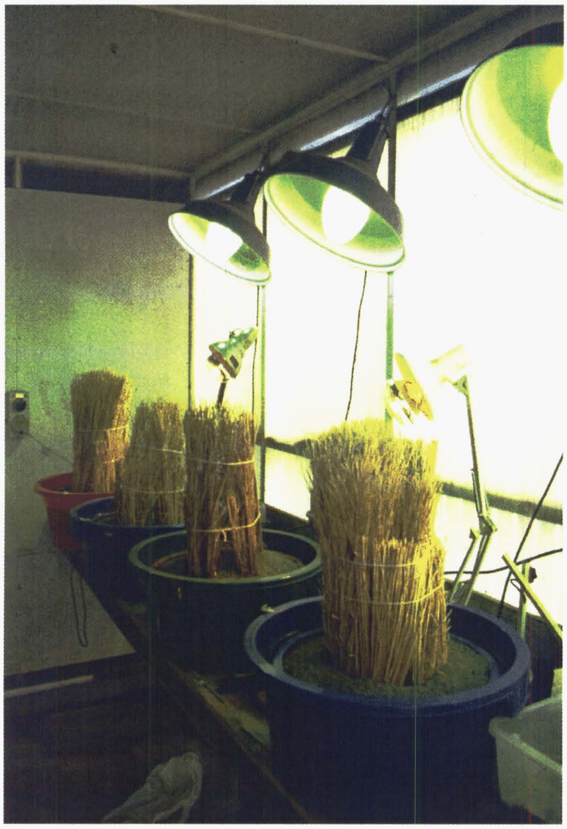

Plate 4.3. Habitat structure experiment apparatus

Illumination and heat were provided to one side of each microcosm with six 400 W and four 200 W heat lamps (Plate 4.3). A timing switch controlled all lights so that they were on for 16 hours and off for 8 hours simulating summer daylight hours. Simulated nighttime occurred during the actual hours of darkness, because the shade cloth allowed light to enter the shed. For the same reason, all lights were positioned on the northern side so that the shaded sides of microcosms did not receive additional light. During simulated daylight, a coarse temperature and light gradient (low = shaded 14°C - 19°C, medium = exposed to oblique light 18°C – 27°C, high = direct light 26°C – 38°C) was present on all microcosms (Plate 4.3).

Experimental protocol

The *L. katipo* and *L. atritus* individuals used in this experiment were all adult females reared in the laboratory. Adult females were chosen because they are less likely to relocate web sites than male or sub-adult female *L. katipo* and *L. atritus* (Lubin 1993; Forster and Forster 1999). Furthermore, because of the large energy requirements associated with egg production and eggsac construction, and the microclimatic conditions required for spiderling development, web site preferences among adult female *L. katipo* and *L. atritus* may be more tightly defined than web site preferences by males or sub-adult females. A focus on adult female *L. katipo* and *L. atritus*, therefore, was considered more likely to provide information on the fundamental micro-habitat requirements of *L. katipo* and *L. atritus*.

Randomly selected laboratory reared adult female *L. katipo* were introduced, one to the centre of each of the eight microcosms. After 48 hours, to allow all introduced spiders to acclimatise, one randomly selected laboratory reared *Tenebrio molitor* (Coleoptera: Tenebrionidae) was introduced to the edge of each microcosm. *T. molitor* was used as prey because it were easily reared in the laboratory and because there was little weight variation (+/- 0.025g, n = 20) between individuals. Furthermore, *L. katipo* and *L. atritus* are able to catch *T. molitor* using the same method they use to capture prey species caught in the field and are able to persist on a diet comprising solely *T. molitor* (pers. obs.). After 48 hours, all unsnared *T. molitor* were removed and another randomly selected laboratory-reared *T. molitor* was introduced to each microcosm in its place. This feeding regime continued until the cessation of the experiment, which ran for two weeks, excluding the 48 hour acclimatisation period. At the end of each replicate, all webs were inspected and notes made on the number of prey items snared, the position of the web and retreat and the catching-web size (small = < 6 cm^2, medium = 6

$cm^2 - 10\ cm^2$ Large = $>10\ cm^2$).

Before their introduction, two of the *L. katipo* introduced to sparse microcosms and two of the *L. katipo* introduced to dense microcosms were weighed. These individuals were reweighed at the end of the experiment when they were removed from microcosms. The remaining spiders were not weighed to control for any disturbance associated with weighing.

The experiment was replicated six times with *L. katipo* and *L. atritus.* Before the commencement of the each replicate, all webbing and prey exoskeletons from the previous replicate were removed.

Several attempts were made to restrict spider web-building to the area within the grass clumps by painting the area from the base of the sand mound to the container rim with Teflon© paint and by raising the sand mound so that it was flush with the rim, but both these attempts failed. Teflon© paint failed to stop spiders attaching silk thread to the container's edge and raising the sand mound, though partially successful in restricting web building, resulted in several spiders and prey drowning. Consequently, both attempts were abandoned and no further attempts were made to stop spiders constructing webs between the grass clumps and the container rim. It should be recognised, therefore, that all spiders in this experiment were not restricted to building webs within the grass clumps, but were able to utilise the space between grass clumps and the container's edge.

Analysis

Data were analysed using χ^2 tests to determine whether the structure and position of catching-webs, the number of prey items caught or spiders' weight differed significantly ($p = <0.05$) between dense and sparse microcosms.

Results

Plate 4.4. This extensive catching-web constructed in a sparse microcosm is typical of those built by *L. katipo* and *L. atritus* in the field

L. katipo and *L. atritus* catching-web construction was not confined to the marram tufts as expected. Consequently, *L. katipo* and *L. atritus* inhabiting dense microcosms were able to construct catching-webs over open sand between marram tufts and the container wall (Plate 4.4). Though most catching-webs and retreats established by *L. katipo* and *L. atritus* under experimental conditions appeared similar to those observed in the field (Plate 4.4), one *L. katipo* and two *L. atritus* built retreats and partial catching-webs at the top of marram tufts. As this web-building behaviour has not been observed in wild populations, possibly because of wind-related grass movement, these individuals were considered to misrepresent web-building behaviour in the field and were excluded from analysis. One *L. katipo* and one *L. atritus* that escaped from microcosms (both were subsequently recovered), and three *L. katipo* and five *L. atritus* that constructed eggsacs during the experiment were also excluded from analysis.

Most catching-webs constructed by *L. katipo* and *L. atritus* were built around the periphery of microcosms in the gap between marram tufts and the container rim, but more extensive catching-webs spanning peripheral gaps and central interplant spaces were constructed in sparse microcosms. Because spiders inhabiting dense microcosms did not build catching-webs within dense marram tufts, web construction was confined to the peripheral gaps (Figure 4.1 &Figure 4.2). Consequently, catching-webs constructed by the inhabitants of dense microcosms were frequently smaller than those constructed by spiders inhabiting sparse microcosms (Figure 4.3 & Figure 4.4). Retreats were built in the base of marram tufts usually <5 cm from the catching-web. Although there was a significant difference ($p < 0.05$) between the number of tenebrionids snared by *L. katipo* inhabiting dense and sparse microcosms (Figure 4.5 &Figure 4.6), no significant difference was observed in the number of prey items caught by *L. atritus.* A strong relationship between catching-web size and the number of prey snared by *L. katipo* and *L. atritus* (Figure 4.7 & Figure 4.8) was revealed, but no significant difference was found in weight gained or lost by *L. katipo* or *L. atritus* during exposure to experimental conditions in the dense and sparse microcosms (Figure 4.9 & Figure 4.10). Most *L. katipo* and *L. atritus* favoured warmer sectors within the microcosms close to the heat and light sources (Figure 4.11 &Figure 4.12). There were no significant differences between those spiders weighed during the experiment and those in the control for any of the variables measured.

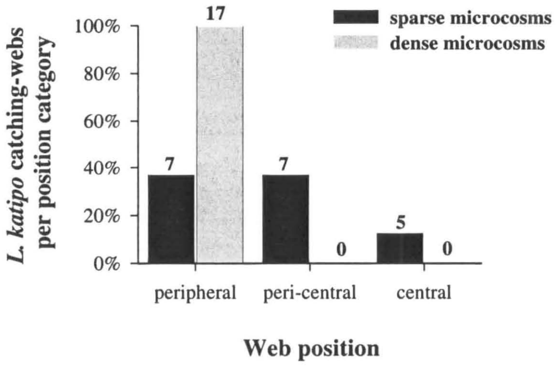

Figure 4.1. Location of *L. katipo* catching-webs in sparse and dense microcosms (Chi^2 = 15.150, df = 2, p = 0.001)

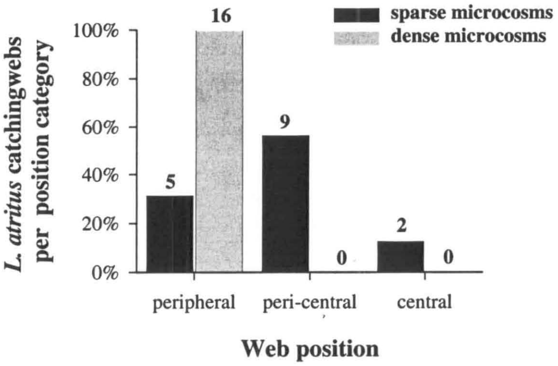

Figure 4.2. Location of *L. atritus* catching–webs in sparse and dense microcosms(Chi^2 = 11.889, df = 2, p = 0.003)

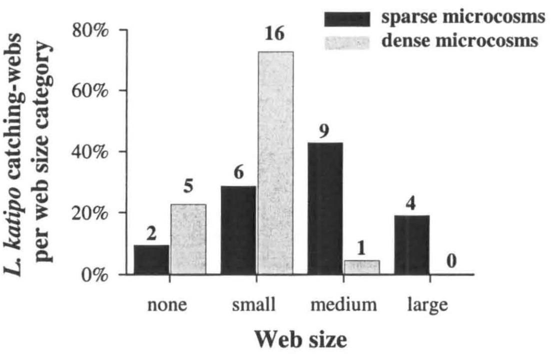

Figure 4.3. Percentage of *L. katipo* catching–webs constructed/size category(Chi^2 = 15.250, df = 3, p = 0.002)

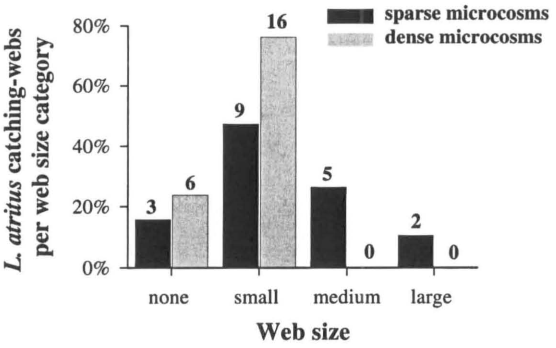

Figure 4.4. Percentage of *L. atritus* catching–webs constructed/size category(Chi^2 = 9.083, df = 3, p = 0.028)

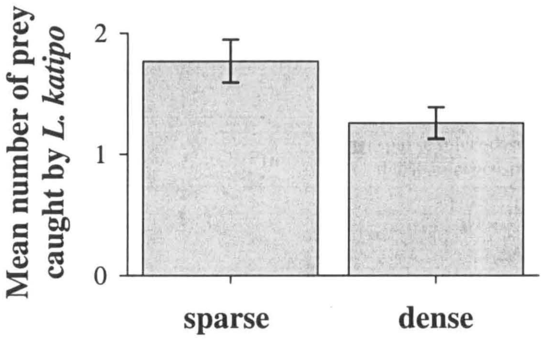

Figure 4.5. Mean number of prey items snared by *L. katipo* inhabiting dense and sparse microcosms (t = 2.539, p = 0.020, df = 20). Standard error from the mean is indicated by a bar

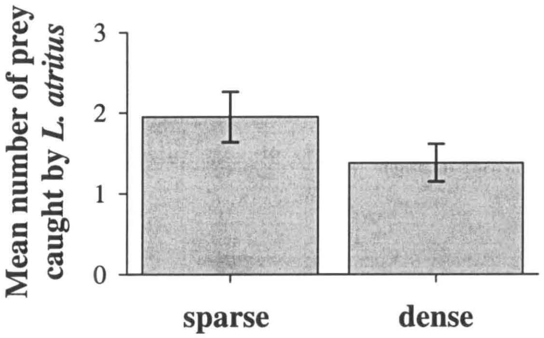

Figure 4.6. Mean number of prey items snared by *L. atritus* inhabiting dense and sparse microcosms (t = 2.041, p = 0.056, df = 18). Standard error from the mean is indicated by a bar

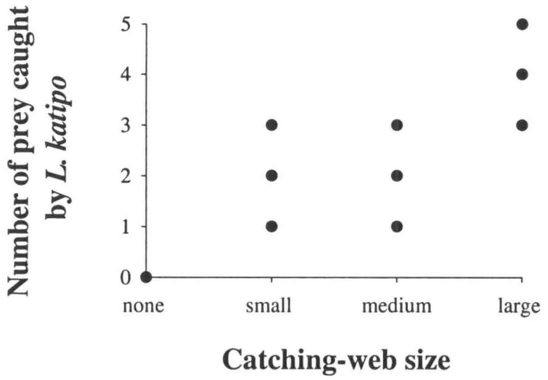

Figure 4.7. The relationship between *L. katipo* catching-web size and the number of prey caught ($R_s = 0.822$, N = 43, p =0.001)

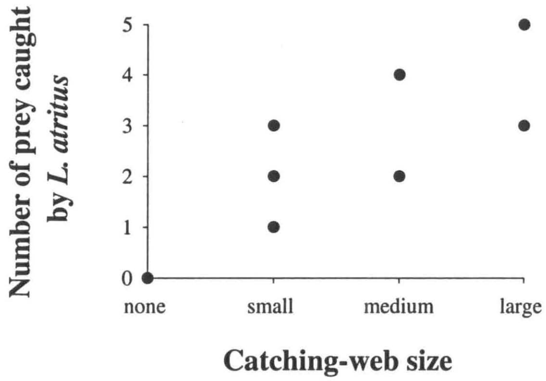

Figure 4.8. The relationship between *L. atritus* catching-web size and the number of prey caught ($R_s = 0.708$, N = 41, p = <0.001)

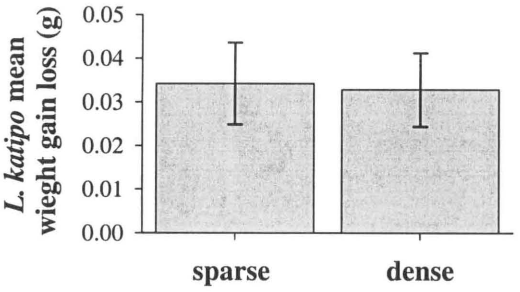

Figure 4.9 Mean weight gained or lost by *L. katipo* in inhabiting sparse and dense microsms (t = 0.208, p = 0.840, df = 9).

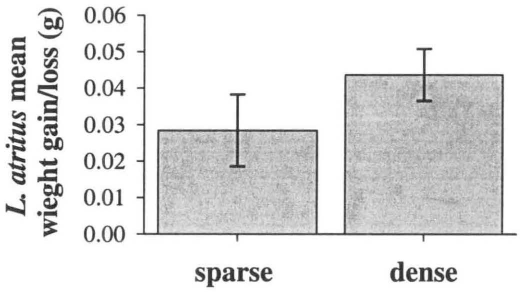

Figure 4.10 Mean weight gained or lost by *L.atritus* in inhabiting sparse and dense microsms (t = -0.867, p = 0.411, df = 8).

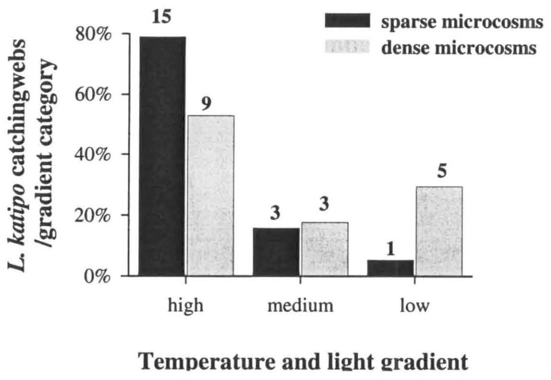

Figure 4.11. Location of *L. katipo* catching-webs on a temperature and light gradient.(low = shaded 14°C - 19°C, medium = exposed to oblique light 18°C – 27°C, high = direct light 26°C – 38°C) (Chi^2 = 4.068, df = 2, p = 0.131)

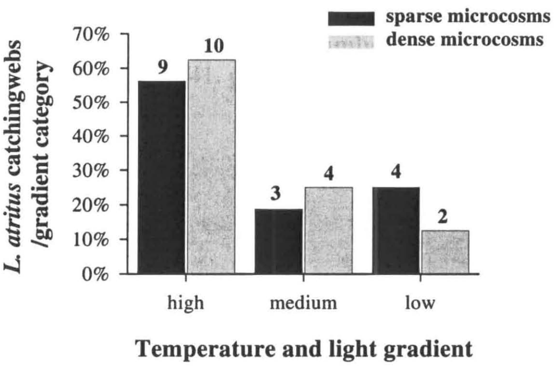

Figure 4.12. Location of *L. atritus* catching-webs on a temperature and light gradient. (low = shaded 14°C - 19°C, medium = exposed to oblique light 18°C – 27°C, high = direct light 26°C – 38°C) (Chi^2 = 0.778, df = 2, p = 0.678)

Discussion

The results supported the hypothesis that *L. katipo* and *L. atritus* select web sites in dune regions where patches of open sand are present. No catching-webs were constructed within dense marram tufts, whereas spiders inhabiting sparse microcosms were able to construct catching-webs throughout interplant spaces at the centre of microcosms. Although *L. katipo* and *L. atritus* inhabiting both dense and sparse microcosms were able to construct catching-webs between marram tufts and the inside wall of microcosms, these webs were also constructed over open sand.

The reasons catching-webs were not established in dense marram tufts may be linked to the web design and prey catching method employed by *L. katipo* (pers. obs.) and *L. atritus* (Court 1971; pers. obs.). *L. katipo* and *L. atritus* catching-webs comprise a lattice platform that spans gaps of 15-30 cm between vegetation, wood and other materials (pers. obs.). From this platform, usually positioned ≈ 5–10 cm above the ground (pers. obs.), a number of catching threads are attached to the substrate. Within a few centimeters of the base of each catching line is a series of sticky globules, to which prey, primarily ground dwelling beetles, adhere (Forster and Forster 1999). Struggling prey send vibrations up the catching line, alerting the resident spider. Once located, prey is trussed in a mass of sticky thread and bitten, often a number of times. Prey is subsequently hauled up into the main body of the web and later consumed.

Although *L. katipo* and *L. atritus* may be able to modify their catching-webs to suit different structural supports (Court 1971), it seems unlikely that there would be sufficient space in dense marram grass to construct the lattice platform component of the catching-web. Furthermore, catching lines could become entangled with marram tillers muting vibrations of struggling prey and grass tillers could make prey trussing difficult. That *L. katipo* and *L. atritus* frequently inhabit dense prostrate shrubs (Chapter three), however, suggests that habitat density precludes catching-web construction only in some plants. This may be related to plant structure. Marram, as with other dune grasses such as spinfex, buffalo grass and kikuyu grow vertical tillers from rhizomes buried underneath the sand (Crowe and Parkkali 1995). Consequently, when these dune grasses reach high densities, the dune surface is almost entirely fragmented by grass tillers. In contrast, prostrate shrubs, such as *C. acerosa* and *M. complexa,* grow from a central stem and sprawl over the sand. Underneath these plants, the dune surface is largely unfragmented (pers. obs.) and appears to provide optimal *L. katipo* and *L. atritus* habitat (Plate 4.5) (Chapter three).

Plate 4.5. Large *C. acerosa* in which five adult *L. atritus* web sites were located (denoted by white arrows)

The value of an effective catching-web was emphasised by the difference in the numbers of prey caught by inhabitants of sparse and dense microcosms during the experiment. *L. katipo* inhabiting sparse microcosms snared significantly more *T. molitor* than those inhabiting dense microcosms (Figure 4.1). Similarly, *L. atritus* inhabiting sparse microcosms also caught more prey than those inhabiting dense microcosms (Figure 4.2). Strong rank correlations between web size and the number of prey caught (Figure 4.7 & Figure 4.8) suggest web size (Figure 4.3 & Figure 4.4) was principally responsible for differences in the number of prey captured, although differences in vegetation cover may also have contributed. Dense microcosms may have offered more refugia for *T. molitor* than sparse microcosms and consequently, may have reduced the probability that prey would have encountered catching-webs. Furthermore, higher levels of disturbance associated with the removal of uncaught prey items from dense microcosms may have had a negative effect on prey capture in dense microcosms, although care was taken to avoid interfering with webbing.

Despite differences in the number of prey caught by inhabitants of sparse and dense microcosms, no differences in the weight gained or lost by inhabitants of sparse and dense microcosms were observed. This may be related to *L. katipo* and *L. atritus* physiology. *L. katipo* and *L. atritus* both gain weight very quickly and may double in weight within 24 hours after eating one or two *T. molitor* (pers. obs.). As *L. katipo* and *L. atritus* approach weights of 0.25 – 0.30 g, weight gain slows dramatically as spiders appear to become satiated, although prey continues to be caught and stored in the web (pers. obs.). Weight loss, in contrast, is very slow. It may take a month under laboratory conditions for *L. katipo* or *L. atritus* to lose the weight gained over a couple of days (pers. obs.). These factors suggest that had spiders been exposed to experimental conditions for a longer time with less frequent prey introductions, weight differences would have become more pronounced and may have resulted in changed activity levels. Prey are spiders' primary source of water and nutrients (Foelix 1996). If body fluids are excessively depleted, due to lack of prey, spiders can lose mobility and become lethargic (Nentwig 1987). If this occurs, catching-web maintenance and construction can be undermined, further inhibiting the capture of prey. Furthermore, if *L. katipo* or *L. atritus* are unable to snare sufficient prey, reproductive success may also be undermined.

Spiders' activity levels have been linked to temperature (Foelix 1982; Shear 1986; Nentwig 1987).

Maintaining the appropriate body temperature, therefore, is necessary to capture prey, avoid predators and for catching-web and retreat maintenance or construction (Nentwig 1987; Foelix 1996). Moreover, embryonic and spiderling development depends on particular microclimatic conditions (Forster and Forster 1999) (Chapter two).

Most *L. katipo* and *L. atritus* in this experiment exhibited a preference for web sites located in microcosm sectors associated with high temperature and light levels (Figure 4.11 & Figure 4.12). This finding supports the results of field surveys that found most *L. katipo* and *L. atritus* web sites were characterised by northerly, easterly or westerly aspect where they would presumably receive maximum exposure to solar radiation. These results suggest that *L. katipo* and *L. atritus* may use light or heat cues to locate suitable web sites, although the use of light cues is less probable as these species are seldom active during the day (Forster and Forster 1999). By building catching-webs and retreats at sites exposed to high levels of solar radiation or, in the case of this experiment, heat lamps, *L. katipo* and *L. atritus* may be able to maintain their body temperature at levels that would promote activity necessary for prey capture, predator avoidance and catching-web and retreat maintenance or construction. As both species are active at night, however, it is likely that the *L. katipo* and *L. atritus* benefit most from heat radiating from sand exposed to solar radiation during the day.

It is uncertain whether the web site selection, web building or prey catching behaviour exhibited by *L. katipo* and *L. atritus* individuals included in this experiment is representative of *L. katipo* and *L. atritus* in the field. For example, the rate of prey flow past the catching-web, the absence of wind or rain or artificial light may have influenced *L. katipo* and *L. katipo* web site selection, web building or prey catching behaviour. Consequently, the results of this experiment might not represent the behaviour of either species under field conditions. Despite these reservations, however, the web site selection, catching-web and retreat formation, and the behaviour of *L. katipo* and *L. atritus* under experimental conditions reflected observations I have made in the field. Furthermore, the results of this experiment concur with the results of transect and stratified surveys. It is probable, therefore, that the results of this experiment do reflect the behaviour of *L. katipo* and *L. atritus* in the field, but further field based experiments would be needed to attain a greater level of certainty.

Conclusions

Results indicated that *L. katipo* and *L. atritus* web sites are constructed within a particular structural and microclimatic context that appears to be related to the presence open sand and exposure to solar radiation. It was argued that *L. katipo* and *L. atritus* catching-webs must be positioned over open sand to function effectively, as the prey catching method used by both species employs a number of catching lines that are attached to the substrate from a hammock-like platform positioned close to the ground. Where dense dune grasses have eliminated interplant gaps, *L. katipo* and *L. atritus* appear unable to build the hammock-like component of the catching-web and the catching lines may be ineffective because vegetation may interfere with spiders' ability to 'listen' to the web. Moreover, prey wrapping may be difficult in confined surroundings. Because the majority of *L. katipo* and *L. atritus* included in the experiment favoured web sites at the 'sunny' side of microcosms, it was inferred that *L. katipo* and *L. atritus* web site selection may be linked to certain heat or light cues. These cues may help spiders locate web sites in dune regions that are characterised by microclimatic conditions required for embryonic and spiderling development or that promote activity levels necessary for prey capture, predator avoidance, web maintenance and construction.

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Chapter Five
L. katipo and *L. atritus* dispersal and its ecological implications

Introduction

Little is known about the dispersal mechanisms employed by *L. katipo* or *L. atritus*. Consequently, it is uncertain how far these species are likely to disperse or how readily they might colonise suitable but uninhabited dune systems.

Current *L. katipo* and *L. atritus* distributions span numerous geographical barriers including headlands, large rivers, estuaries and areas of open sea (Forster and Forster 1999)(Chapter three). If *L. katipo* and *L. atritus* have crossed these barriers, as their distribution implies, both species must have the capacity to disperse over distances of up to 25 km.

Records pertaining to the dispersal of *Latrodectus* spp. are scarce, but research on other spider species provides clues about how *L. katipo* and *L. atritus* might disperse. Spiderlings from many species, for example, climb to high points on logs, stones, or vegetation from which they release a silk thread from their spinnerets. Thermal currents rising from the ground then lift the spiderlings into fast moving airstreams on which they are subsequently dispersed (Greenstone 1982; Decae 1987; Greenstone *et al.*1987; Bishop 1990; Crawford *et al.*1995; Crawford 1996). Although it is difficult to estimate exactly how far spiders could travel using this dispersal mechanism, known as 'ballooning', they have been recorded landing on ships >300 km from land (Gertsch 1979), indicating they are capable of travelling large distances under optimal conditions. This could explain why *L. katipo* and *L. atritus* distributions span geographic barriers and may explain genetic similarities between the endemic Australian and New Zealand widow spider fauna (Chapter six).

Because 'ballooning' is weight dependent, it is principally used by spiderlings, usually shortly after emerging from the eggsac (Decae 1987; Greenstone *et al.*1987; Bishop 1990). Although sub-adults and adults of some species retain the ability to balloon, Greenstone et al. (1987) asserted that spiders whose weight exceeds 30 mg are unlikely to disperse in this way. Thus, although adult male *L. katipo* and *L. atritus,* which may weigh < 30 mg, could retain the ability to balloon, adult female *L. katipo* and *L. atritus*, which may weigh > 300 mg, are unlikely to balloon.

Despite being unlikely 'ballooners', adult females of both species do relocate web sites. Out of 10 covered pitfall traps (≈10 cm diameter) placed <30 cm from adult female *L. katipo* web sites, one was inhabited by an adult female *L. katipo* within a week (pers. obs.). Similarly, out of 20 covered pitfall traps placed placed <30 cm from adult female *L. atritus* web sites, five were inhabited by adult female *L. atritus* within five days (pers. obs.). In each case, the pitfall traps appeared to have been colonised by the neighbouring adult female, since examination of the closest web site revealed that it had been vacated. It is unclear how the adult females travelled from their original web sites to the pitfall traps, but I have observed adult female *L. katipo* and *L. atritus* walking across the sand at night, which has also been observed in *L. mactans* (Forster 1995). This method of dispersal, however, would permit only localised movement and, therefore, does not explain why *L. katipo* and *L. atritus* distributions span geographic barriers.

In contrast, 'hitchhiking' is a means by which spiders are known to disperse over large distances (Forster 1984). As the term suggests, 'hitchhiking' is where a spider or eggsac is carried from one place to another by an external force. Spiders regularly hitchhike from one country to another on imported and exported goods, such as used tyres, cars, wood, and food products (Forster 1973; Forster 1984; Decae 1987). In the absence of human trade, they may also hitch rides on pieces of driftwood or flotsam washed off beaches and river margins (Foelix 1982). Though the chances of survival at sea are probably quite low, over millions of years it is possible that a gravid female or eggsac will survive long enough at sea to journey from one place to another. As *L. katipo* and *L. atritus* often inhabit driftwood or flotsam just above the mean high tide mark, they, or their pre-emergent offspring within an eggsac, are perhaps more likely to succeed in 'hitchhiking' from one location to another by sea than most other spider species (Plate 5.1).

In this chapter, I examine the dispersal mechanisms employed by *L. katipo* and *L. atritus* spiderlings within 24 hours of emerging from the eggsac and examine the potential for water-borne dispersal of adult female *L. katipo* and *L. atritus* and their eggsacs. Adult male dispersal was not examined, because complications in rearing adult male *L. katipo* and *L. atritus* in the laboratory and the difficulty locating them in the field meant experiments involving adult male *L. katipo* or *L. atritus* were impractical. Furthermore, since adult males are unable to establish new colonies of *L. katipo* or *L. atritus* their dispersal is unlikely to greatly influence patterns of distribution.

Plate 5.1. Driftwood and flotsam awash at high tide during a storm

Methods

Dispersal mechanisms employed by *L. katipo* and *L. atritus* spiderlings were examined under different observation conditions; *L. atritus* was investigated in the laboratory, whereas *L. katipo* was examined in the field. Differing observation conditions were necessary, because I was unable to conduct field based observations on *L. atritus* in the South Island where the release of this species could lead to the genetic contamination of endemic *L. katipo* populations (Chapter three).

Spiderling dispersal – *L. atritus*

Eggsacs were removed from the webs of laboratory-reared adult female *L. atritus* and were examined over a bright light to determine the degree of spiderling development. Eggsacs that were semi-transparent and contained visibly active spiderlings were selected for the ballooning experiments, because these characteristics indicate that spiderlings are due to emerge. Eggsacs that were opaque, or in which spiderlings did not appear to be active, were returned to the webs from which they were taken (Plate 2.8).

Ballooning behaviour was assayed using an apparatus (Plate 5.2) adapted from Greenstone (1982). A galvanised metal tray (500 mm x 700 mm x 70 mm) was filled with ≈ 0.01m^3 of beach sand. Twenty tillers of marram grass were inserted into the sand forming a grass tuft ≈ 250 mm from the base to the top. A warm (25-30°C) airstream ≈ 0.5-1m/s, generated by an electric fan blowing air over a electric element, was directed upward across the marram tuft at an angle of 25° from horizontal simulating thermal currents that rise from sand heated by solar radiation. A 250 W incandescent bulb placed 500 mm above the marram tuft provided heat and illumination.

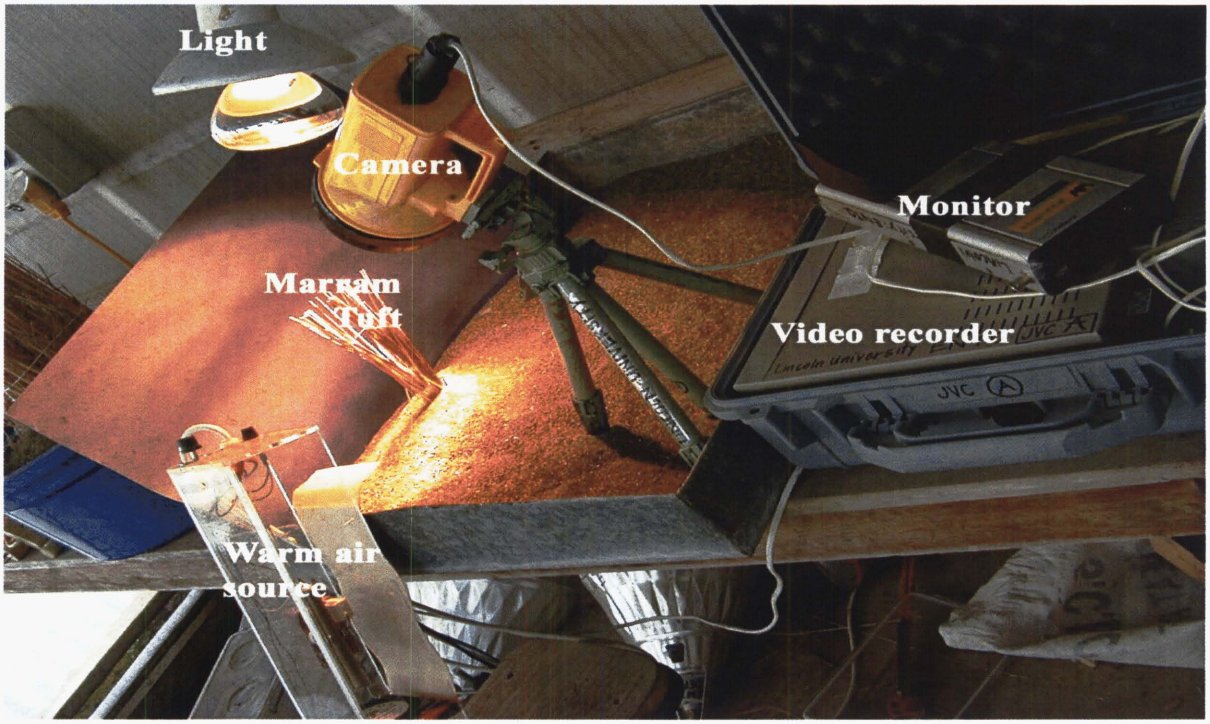

Plate 5.2. Apparatus used to examine the dispersal mechanisms employed by *L. atritus* spiderlings

A single eggsac was randomly selected from those chosen for the experiment and a small hole (3–5 mm) was made in the eggsac wall with tweezers to allow the spiderlings to escape. The eggsac was then placed at the base of the marram tuft and videoed using a timelapse video recorder and micro camera. After 24 hours any spiderlings remaining on the marram tuft or in the eggsac were counted and removed from the tuft along with the eggsac and any webbing. The experiment was repeated five times. Video footage was later analysed to determine how spiderlings dispersed.

Spiderling dispersal – *L. katipo*

Five study-sites were selected at ≈ 20 km intervals between Kaitorete Spit and Leithfield Beach on the Canterbury Coast. Study-sites were spaced at ≈ 20 km intervals to provide a representative sample of the range of habitat types found within this region. This included relatively unmodified pingao-dominated dunes at Kaitorete Spit and a range of modified dunes dominated by marram from South Brighton to Leithfield Beach. At each study site, the first adult female *L. katipo* web site containing eggs sacs with spiderlings due to emerge was selected. A small hole was made in one eggsac wall with tweezers and a time-lapse video and micro-camera were set up to record spiderling behaviour over a 24 hour period. Because of time constraints and the availability of cameras and time-lapse video recorders, web sites were videoed over three weeks in February in varied weather conditions. Video footage was later analysed and notes on spiderling behaviour made.

Water-borne dispersal

Eight pieces of driftwood (10 – 20 cm long) on which adult female *L. katipo* were resident and eight similar pieces of driftwood containing only *L. katipo* eggsacs were collected from Kaitorete Spit. Four of the pieces of driftwood with resident adult female *L. katipo* were selected randomly and introduced to an empty Perspex™ container (600 mm x 600 mm x 600 mm), while the remaining four were introduced to an identical container half filled with sea water. All pieces of driftwood were positioned so that the spiders were on the upper surface.

Similarly, four randomly selected pieces of driftwood containing eggsacs were introduced to an empty Perspex™ container (600 mm x 600 mm x 600 mm), while the remaining four were introduced to a container half-filled with seawater as above. All pieces of driftwood in the treatments were watered with ¼ l of seawater once every 24 hours to simulate gentle wave action. The experiment was conducted over a two-week period in the laboratory under fluorescent lighting at a temperature of 20°C.

All pieces of driftwood on which spiders were present were examined once every 24 hours to determine whether the resident spiders were alive. The pieces of driftwood containing eggsacs in the treatment were removed from the seawater container after two weeks and were placed in a dry perspex container where they were observed over six weeks to determine whether any spiders emerged from the eggsac.

The experiment was repeated substituting laboratory reared *L. atritus* for *L. katipo.*

Results

Spiderling dispersal

Video footage of *L. atritus* spiderlings revealed that, after emerging from the eggsac, most spiderlings moved to the high points on the marram tuft where they aggregated in clusters. Subsequently, many spiderlings raised their abdomens and released a silk thread into the warm air stream (Plate 5.3). Many spiderlings then ballooned away from the marram tillers (Plate 5.4), however, the silk thread released by some of these spiderlings, apparently attempting to balloon, adhered to neighbouring apparatus and walls creating a bridge. Instead of resuming attempts to balloon spiderlings traversed the silk thread 'bridging' gaps (>50 cm) between the marram tillers and neighbouring objects. Once established, these 'bridging lines' were used by other spiderlings. It was not determined whether spiderlings reattempted ballooning after crossing 'bridging lines' as they were out of camera range, but personal observations during the experiment did not reveal any evidence to suggest that spiderlings did reinitiate ballooning. A small number of spiderlings failed to disperse at all and remained at the base of the marram grass tuft for 24 hours before they were removed before the commencement of the next experiment (Table 5.1)

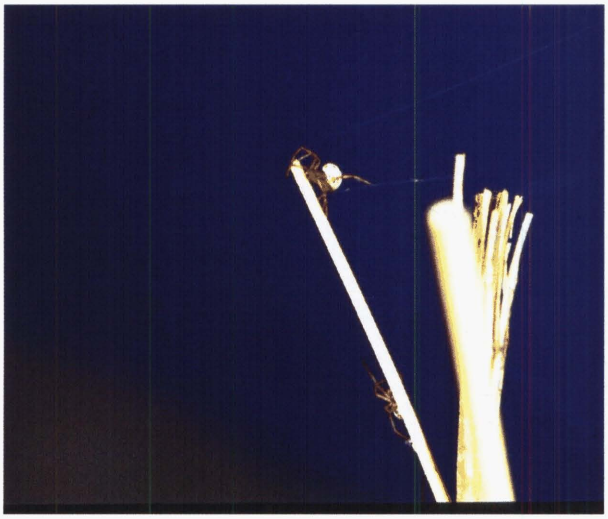

Plate 5.3. A *L. atritus* spiderling releasing silk thread into warm airstream

Plate 5.4. A *L. atritus* spiderling ballooning away from a marram tuft

Due to problems with film exposure and wind in the field (two cameras were blown over) filming and video analysis of *L. katipo* spiderling dispersal was difficult. Consequently, field based spiderling dispersal observations were less clear than laboratory based experiments and should, therefore, be interpreted with caution. Despite filming difficulties, however, some video footage clearly showed *L. katipo* spiders ballooning from the tops of marram and pingao, whereas other footage showed spiderlings dispersing on 'bridging lines' to neighbouring grasses and bushes. As with *L. atritus* spiderlings, a few *L. katipo* spiderlings remained at the base of the grass tufts (Table 5.1).

In the field-based experiments 'ballooning' appeared to take place on calm sunny days. This was determined by the amount of grass movement and the shadow intensity at the time spiderlings were observed 'ballooning'. In contrast, more 'bridging' appeared to occur during periods of increased grass movement. Some *L. katipo* and *L. atritus* spiderlings may have used other dispersal mechanisms such as crawling, but these were not observed (Table 5.1).

Table 5.1 Dispersal behaviours of *L. atritus* and *L. katipo* spiderlings revealed by video footage

Spider species	Total number of observed spiderlings	% observed ballooning	% observed bridging	% observed using other dispersal mechanisms	% remaining on marram tuft or in eggsac after 24 hours
L. katipo	36	28	61	0	11
L.atritus	157	50	43	0	7

All percentages were rounded to the nearest whole number

Water-borne dispersal of adult females and eggsacs

Water-borne dispersal experiments revealed that a small number of adult female *L. katipo* and *L. atritus* were able to survive on waterlogged driftwood subject to a saltwater regime (Table 5.2). One *L. katipo* survived 14 days subjected to the saltwater regime and continued to live for six months in a terrarium in the laboratory, where it is supplied with *T. molitor* every four days. Most adult females, however, died within the first 2 days. No spiderlings of either species emerged from eggsacs subject to the salt water regime in the six-week incubation period following the experiment, but spiderlings from both species emerged from some eggsacs in the control (Table 5.3).

Table 5.2. Survival of adult female *L. katipo* and *L. atritus* on waterlogged driftwood showered with ¼ litre of salt water/24 hours

Spider species	Treatment /Control	N	Maximum days survived	Minimum days survived	Mean days survived	Standard error
L. katipo	Treatment	4	>14	≤1	5.75	3.09
	Control	4	>14	14	14	0
L. atritus	Treatment	4	8-9	≤1	3.25	1.93
	Control	4	>14	14	14	0

Table 5.3. Number of emergent spiderlings from *L. katipo* and *L. atritus* eggsacs showered with ¼ litre of salt water/24 hours vs control

Spider species	Treatment /Control	N	N° of eggsacs from which spiderlings emerged	Mean number of emergent spiderlings	Standard error
L. katipo	Treatment	4	0	0	0
	Control	4	2	30.5	17.9
L. atritus	Treatment	4	0	0	0
	Control	4	3	21	8.01

Discussion

With the exception of a small number of spiderlings that remained near the eggsac at the base of marram tufts, most *L. katipo* and *L. atritus* spiderlings were observed dispersing by 'ballooning' or 'bridging' (Table 5.1). Other dispersal mechanisms, such as crawling across the ground may also have been employed by spiderlings, but these were not observed in video footage, as the micro-cameras were focused on the top of marram tillers. Although there were differences between the percentages of *L. katipo* and *L. atritus* spiderlings dispersing by 'ballooning' or 'bridging' (Table 5.1), these may be attributed to differences in the methods used. Bishop (1990) found that variation in wind speed and direction was associated with lower numbers of 'ballooning' spiders, whereas studies by Richter (1970) revealed that the optimum wind speed for 'ballooning' in several Lycosidae species was 1.0 m/s. Laboratory conditions, therefore, may have promoted increased 'ballooning' among *L. atritus* spiderlings because the strength and direction of the warm airstream generated in the laboratory was consistent and the wind speed (0.5-1.0 m/s) optimal for 'ballooning'. In contrast, because there were large fluctuations in wind speed and direction in the field (pers. obs.), optimal 'ballooning' conditions may have occurred less frequently reducing the number of *L. katipo* spiderlings 'ballooning'.

Results from water-borne dispersal experiments suggest that some adult female *L. katipo* and *L. atritus* can tolerate direct exposure to salt water and may persist in a waterlogged environment for one to two weeks (Table 5.2). This indicates that adult female *L. katipo* and *L. atritus* may have the capacity to disperse on ocean currents attached to driftwood. In contrast, spider embryos housed within eggsacs appeared unable to tolerate the conditions created in the treatment (Table 5.3).

Ballooning behaviour in *L. katipo* and *L. atritus* spiderlings and evidence of water-borne dispersal in adult females could explain how both species' distributions have come to span geographical barriers such as estuaries, headlands and small areas of open sea (≈ 20 km). These dispersal mechanisms may also explain how *L. katipo* and *L. atritus* arrived in New Zealand, if they were not present before the fragmentation of Gondwana, as argued by Forster (1995) (Chapter three). Ballooning spider species are known to travel large distances (up to 300 km) (Decae 1987; Greenstone *et al.*1987; Crawford *et al.*1995) and there is evidence to suggest that water-borne spiders may also have the capacity to travel large distances (Foelix 1982).

As *L katipo* and *L. atritus* inhabit a linear environment, ballooning is likely to be an expensive dispersal strategy (Forster and Forster 1999). Spiders are not thought to be able to control the direction in which they balloon (Riechert and Gillespie 1986), consequently many *L. katipo* and *L. atritus* spiderlings are likely to be blown out to sea or inland where they would probably perish if they were unable to re-initiate ballooning (Riechert and Gillespie 1986). Despite the high probable failure rate, however, the large number of spiderlings (≈ 60-100 in each of 1-3 eggsacs) (Forster and Kingsford 1983) produced annually by each adult female increases the probability that over time conspecific male and female spiderlings will balloon to dune regions un-inhabited by other *L. katipo* or *L. atritus.* Moreover, because spiderling dispersal is weather related (Bishop 1990), suitable climatic conditions are likely to trigger mass ballooning events. These would further increase the probability that *L. katipo* and *L. atritus* might colonise uninhabited dune systems. These colonists would be likely to provide an important ecological buffer for *L. katipo* and *L. atritus,* as they extend the distribution of *L. katipo* and *L. atritus* beyond geographical barriers that could otherwise confine their distribution. Consequently, 'ballooning' is likely to increase both species resistance to stochastic events, such as storms or fires and could promote gene flow between populations, reducing the probability that populations of *L. katipo* or *L. atritus* might become genetic isolated (Mayr 1970).

In contrast with the high risks associated with 'ballooning', spiderlings dispersing by 'bridging' probably face lower risks, as they are likely to remain in a dune region characterised by suitable habitat, thus increasing the chances of locating a suitable web-site. Although some 'bridging' spiderlings may reattempt 'ballooning' (Riechert and Gillespie 1986), juvenile and sub-adult *L. katipo* and *L. atritus* are frequently aggregated within a small radius of an adult female web (pers. obs.), indicating that a number of spiderlings dispersing by 'bridging' may become established within small distances of their origin. If this is the case, mating opportunities are likely to be frequent because of the aggregated nature of the population. Competition for suitable web sites and prey, however, is likely to be high, as is the probability that the entire aggregated population could be wiped out by a single stochastic event.

It is uncertain whether 'ballooning' and 'bridging' are outcomes of two distinct behaviours or whether they result from the same silk releasing behaviour undertaken in varying climatic conditions. Observations, however, revealed no obvious distinction in the behaviour of 'ballooning' or 'bridging' spiderlings prior to dispersal, suggesting that 'ballooning' and 'bridging' do result from the same silk releasing behaviour undertaken in different climatic conditions. On calm hot days convection currents rising from the sand might readily enable spiderlings to 'balloon' as they release silk thread from the tops of dune grasses or bushes. In contrast, on windy cold days silk releasing behaviour may result in released silk thread adhering to neighbouring dune vegetation, driftwood or flotsam promoting 'bridging'. Because conditions in the field are seldom stable (pers. obs.), it may be inferred that most *L. katipo* and *L. atritus* spiderlings will disperse by 'bridging' rather than 'ballooning'. This assertion may explain why *L. katipo* and *L. atritus* have retained the capacity to 'balloon' despite inhabiting a linear environment that seems likely to select against 'ballooning'.

Water-borne dispersal of adult female *L. katipo* and *L. atritus*, if it takes place, has distinct advantages over 'ballooning' and 'bridging'. If washed out to sea along the New Zealand coast on driftwood or flotsam, strong coastal currents could quickly transport adult females of either species long distances (Garner 1955). If a water-borne adult female survived the journey and was washed ashore again, there is a strong possibility that it would make landfall in an area in which it could survive, as most of New Zealand's coastline is characterised by sandy beaches backed by dune systems (Johnson 1992; Partridge 1992). Thus, while more risky than 'bridging', water-borne dispersal may be more likely to target areas of suitable habitat than ‘ballooning’. Furthermore, because of the large number of spiderlings produced by adult female *L. katipo* and *L. atritus* (Forster and Kingsford 1983)(Chapter three), water-borne dispersal of gravid females of either species could result in the introduction of many individuals to suitable but uninhabited dune regions. Consequently, mating opportunities would be frequent and competition for web sites might be expected to be lower than in the case of ‘bridging’ spiderlings who not only have to compete with their siblings, but with offspring of neighbouring conspecific adults.

Although the dispersal mechanisms discussed in this chapter have weaknesses when considered independently, in combination they are more robust. ‘Ballooning’ and water-borne dispersal provide means by which *L. katipo* and *L. atritus* could colonise previously uninhabited but suitable dune systems or re-colonise dune systems from which either species has been displaced. In contrast, ‘bridging’ spiders are likely to maintain stable populations from which long distance dispersal can occur. Increasing dune modification and fragmentation (Chapter three), however, may reduce the probability that ballooning or water-borne *L. katipo* and *L. atritus* could reach suitable dune systems and may increase the chances that aggregated populations could be displaced by stochastic events.

Conclusions

L. katipo and *L. atritus* possess behavioural and physiological attributes that could promote dispersal over large distances. This may explain why geographical barriers such as headlands, estuaries and areas of open sea do not appear to restrict their distribution. Furthermore, the propensity for long distance dispersal in *L. katipo* and *L. atritus* may explain how *L. katipo* and *L. atritus* arrived in New Zealand. This is supported by evidence that the New Zealand widow spider fauna is genetically very similar to *L. hasselti* (Chapter six), but differs from Forster's hypothesis that *L. katipo* and *L. atritus* were present in New Zealand before the fragmentation of Gondwana (Forster 1995).

While both 'ballooning' and water-borne dispersal probably have a high failure rate, because these dispersal mechanisms are likely to enable *L. katipo* and *L. atritus* to become distributed beyond geographical barriers, both species resistance to stochastic events, such as large storms or fire may be increased. Dune modification and fragmentation, however, may reduce the probability that *L. katipo* or *L. atritus* could successfully colonise previously uninhabited but suitable dune regions or re-colonise dune systems from which they have been displaced.

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Chapter Six
Gene flow

Introduction

L. katipo and *L. atritus* spiderlings are able to disperse by ballooning and adult female *L. katipo* and *L. atritus* may be able to survive up to three weeks on driftwood at sea under optimal conditions (Chapter five). These findings indicate that both species are probably good dispersers and, as their distribution implies, are not likely to be restricted by geographical barriers such as headlands, estuaries and small areas of open sea (<25 km). Observations of captive *L. hasselti* spiderlings have revealed behaviour characteristic of ballooning (Forster 1984), implying that *L. hasselti* may also have the capacity to disperse over geographical barriers. If this is the case, under optimal conditions, some *L. hasselti* spiderlings may have crossed the Tasman Sea to New Zealand. The strong westerly air-stream running between Australia and New Zealand has enabled a number of Australasian birds and bats to colonise New Zealand from Australia, and many invertebrates routinely arrive in New Zealand from Australia each year (Jardine and McKenzie 1972; Stevens *et al.*1988; Hoare 2000; Trewick 2000). Moreover, there is growing speculation that the westerly air-stream may have influenced the New Zealand spider fauna (Vink and Sirvid 2000).

L. katipo, *L. atritus* and *L. hasselti* are morphologically and physiologically similar, which has resulted in much debate regarding the taxonomic designation of these species (Chapter two) (Levi 1959; Forster and Kingsford 1983). Although *L. katipo*, *L. atritus* and *L. hasselti* are currently designated as distinct species, mating experiments undertaken by Forster (1992) revealed that *L. katipo* and *L. hasselti* could interbreed successfully, producing viable F1 hybrids. This suggests that inter-specific gene flow could occur between *L. katipo* and *L. hasselti*, and may indicate that New Zealand's separation from Gondwana has not halted all gene flow between the Australian and New Zealand endemic widow fauna, as postulated by Forster (Chapter two). Alternatively, selection may not have favoured a change in mating behaviour or genitalia.

In this chapter, I examine intra-specific genetic relationships within the ND1 gene region between selected *L. katipo* and *L. atritus* populations in order to assess whether they are genetically isolated. I also examine inter-specific genetic relationships between *L. katipo*, *L. atritus, L. hasselti* and *L. mactans* to assess whether the genetic evidence supports current taxonomic species designations. The ND1 gene region was chosen because it is fast evolving and has been successfully used to examine genetic differences between arthropod species and populations (Pashley and Ke 1992; Hedin 1997a; Hedin 1997b; Pruser and Mossakowski 1998). I did not examine the morphology of any specimens because morphological similarities between *Latrodectus* spp. have previously confounded the taxonomy of this genus (Levi 1959; Forster and Forster 1999; pers. com.)(Chapter two).

Methods

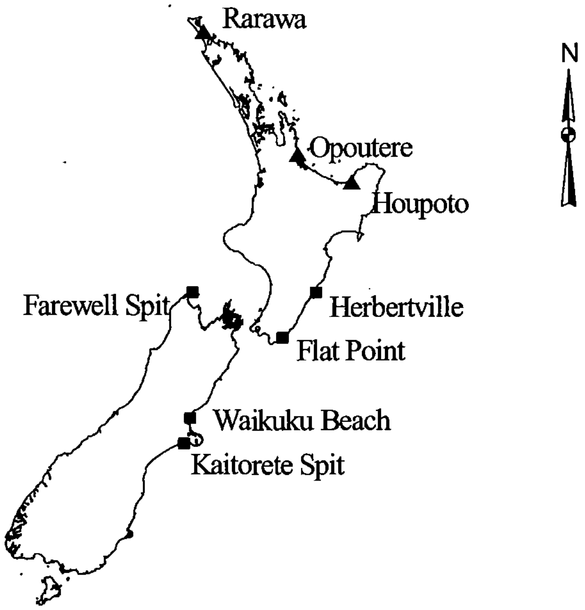

Figure 6.1. Sites where *L. katipo* (■) and *L. atritus* (▲) samples were collected for molecular analysis

Adult female *L. katipo* and *L. atritus* were collected from eight sites around New Zealand (Figure 6.1.) and were stored in 100% EtOH at –80° C to maintain high quality DNA. Voucher specimens are stored at Ecology and Entomology, Research Collection, Lincoln University, New Zealand. Sites at which samples were collected were selected throughout the distributions of both species to fully examine intra-specific genetic variation. Distances between collection sites varied so that the effect of geographic separation on intra-specific genetic relationships could be assessed. *L. katipo* was collected from Kaitorete Spit and Waikuku Beach, Canterbury, from Farewell Spit, Golden Bay, and from Flatpoint and Herbertville on the east coast of the lower North Island (Figure 6.1). *L. atritus* were collected from Houpoto, Rarawa and Opoutere in the upper North Island (Figure 6.1), whereas *L. hasselti* was collected from Western Australia and Brisbane, Queensland. A *L. mactans* intercepted by MAF (Ministry of Agriculture and Fisheries) on table grapes from California, USA was used as an out-group. The entire front leg and hind leg from one side of each sample were removed and washed in sterile deionised, distilled water to remove excess OH. Genomic DNA was extracted from samples using a proteinase-K digestion and high salt precipitation method (White *et al.*1990). DNA was suspended in 1:20 TE (10mM Tris, 1mM EDTA, ph 8.0).

The mitochondrial ND1 (NADH dehydrogenase subunit 1) gene region was amplified from diluted genomics in 25 µl PCR reactions using the primers N1-J-12261 and TL1-N-12718 (Hedin 1997a). Each 25 µl reaction contained 2.5 µl of buffer (10x), 2.5 µl dNTPs (2.5 µM), 2 µl of $MgCl_2$ (25 µM), 1µl of each primer (10pmol), 0.25 µl *Taq* DNA polymerase (Roche), 14.75 µl of water and 1µl diluted genomic DNA. Amplification took place in a GeneAmp® 2400 Thermocycler and included an initial denaturation of 4 min. at 94° followed by 40 cycles of 40 s at 94° C, 40 s at 45° C, 40 s at 72° C and a final extension of 5 min. at 72° C. The resulting PCR product was purified by precipitation with 50 µl of isoproponol and 25 µl NH_4Ac (2.5M) to remove excess salts and primers. Purified dsDNA samples were washed in 70% EtOH and suspended in 6 µl of sterile deionised, distilled water. All dsDNA samples were subsequently sent to the Waikato DNA Sequencing Facility where they were sequenced in both directions.

DNA sequences were aligned against a complementary-strand sequence in DNAMAN (version 4.02), and checked against hard copy chromatograms by eye. Corrections were made where necessary. A multiple alignment of all sequences was compiled in CLUSTALX (Higgins and Sharp 1998) and imported into PAUP*4.0b4a (Swofford 2000) for analysis.

Data were analysed as unordered characters using parsimony with the branch and bound option selected. Bootstrap values (Felsenstein 1985) for monophyletic groups were calculated from 1000 replicates using the heuristic search option in PAUP*4.0b4a. Model test version 3.06 (Posada and Crandall 1998) was used to select the maximum likelihood parameters and the HKY+Γ model (Hasegawa *et al.* 1985) used to estimate the maximum likelihood tree. Branches were collapsed creating polytomies if the branch length was ≤ 1e-08. Bootstrap values for the maximum likelihood tree were calculated using a fast heuristic search (1000 replicates).

Results

The nucleotide composition was C depauperate (29% A, 22% C, 10% G, 39% T) which is atypical for arthropods (Simon *et al.* 1994), but was similar to that of Nesticidae (Hedin 1997b), a sister family of Theridiidae.

Parsimony analysis yielded 16 equally parsimonious trees, 97 steps long with a consistency index, excluding uninformative characters, of 0.875 and a retention index of 0.889 (Figure 6.2). Of the 427 characters included, 91 were variable of which 10 were parsimony informative. Maximum likelihood analysis yielded 45 trees with a score of 909.738. The consensus likelihood tree was congruent with the consensus of the 16 most parsimonious trees, but was not identical. Parsimony analysis placed specimens from Opoutere, Waikuku, Fairwell Spit and Houpoto in a monophyletic group, whereas maximum likelihood analysis placed specimens from Opoutere and Waikuku in a clade within this group. This branch had <50 % bootstrap support.

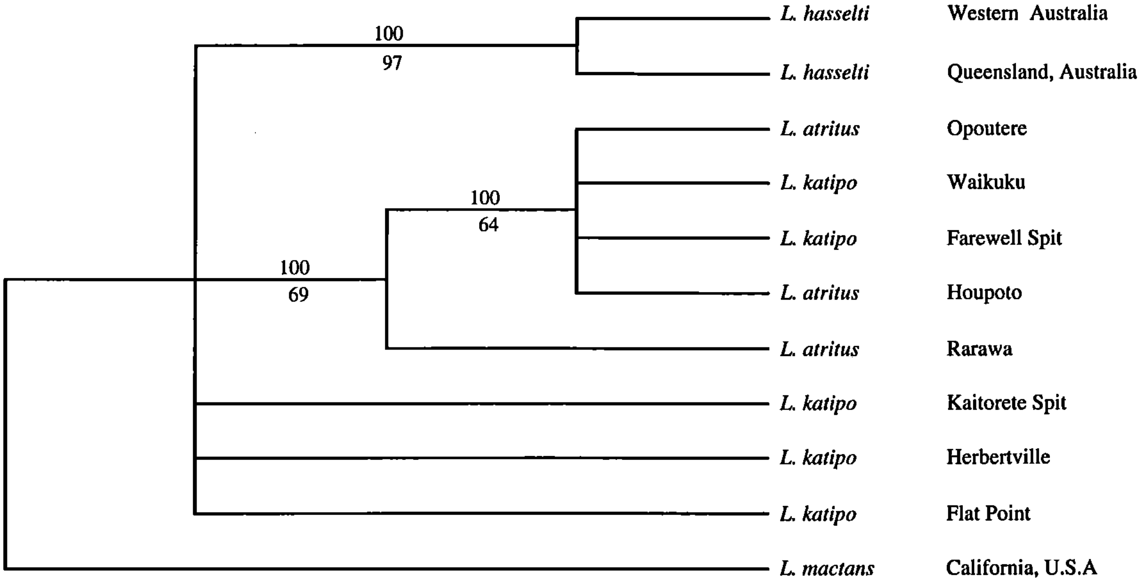

Figure 6.2.Consensus of the 16 most parsimonious trees with consensus values displayed above branches and bootstrap values (>50 %) displayed below branches

The largest inter-specific pairwise distance between *L. katipo*, *L. atritus* and *L. hasselti* was 2.2 %, whereas the smallest pairwise distance between the Australasian specimens and *L. mactans* was 24.0 % (Table 6.1). In contrast, the largest intraspecific pairwise distance between *L. katipo* specimens was 1.2 %, which was greater than the largest pairwise distance between *L. atritus* specimens 0.7 %, *L. hasselti* specimens 0.0%, or between *L. katipo* and *L. atritus* 0.9 % (Table 6.1).

Table 6.1. Pairwise distances between ND1 sequences of *Latrodectus* spiders using the HKY + Γ model parameters

		1	2	3	4	5	6	7	8	9	10
L. hasselti	(Western Australia)	-									
L. hasselti	(Queensland, Aus.)	0.00000	-								
L. atritus	(Houpoto)	0.01667	0.01667	-							
L. atritus	(Opoutere)	0.01911	0.01911	0.00235	-						
L. atritus	(Rarawa)	0.01667	0.01667	0.00471	0.00709	-					
L. katipo	(Kaitorete)	0.01425	0.01425	0.00709	0.00948	0.00709	-				
L. katipo	(Waikuku)	0.02156	0.02156	0.00471	0.00235	0.00948	0.01188	-			
L. katipo	(Farewell Spit)	0.01911	0.01911	0.00235	0.00471	0.00709	0.00948	0.00948	-		
L. katipo	(Flat Point)	0.01425	0.01425	0.00709	0.00948	0.00709	0.00000	0.01188	0.00948	-	
L. katipo	(Herbertville)	0.01425	0.01425	0.00709	0.00948	0.00709	0.00000	0.01188	0.00948	0.00000	-
L. mactans	(California, USA)	0.24645	0.24645	0.24692	0.25059	0.25068	0.23960	0.25066	0.24699	0.23960	0.23960

Discussion

Although too few genetic samples were collected to gain a definitive view on intra-specific gene flow between L. katipo or L. atritus populations, an indication of how much intra-specific gene flow is likely to occur may be inferred from the results. The maximum intra-specific pairwise distance among L. katipo and L. atritus populations was 1.2 %, which was smaller than most of the pairwise distances found between *Nesticus* sampled from the same population that varied between 1.1 % and 15.6 % within the ND1 gene region (Hedin 1997b). Low intra-specific pairwise distances among *L. katipo* and *L. atritus* populations, therefore, indicate that these populations are not genetically isolated, and suggest that *L. katipo* and *L. atritus* are able to disperse across geographic barriers, such as sections of coastline with no dunes or open sea as postulated in Chapter five.

Inter-specific gene flow may also occur between *L. katipo* and *L. atritus* populations, since the maximum pairwise distance between these species was 0.9 % and parsimony analysis revealed that these taxa were paraphyletic. These results suggest that the current taxonomic designation of *L. katipo* and *L. atritus* as distinct species may be questionable. Although mating experiments conducted by Forster (1999) (Chapter two) and marked differences between *L. katipo* and *L. atritus* colouration and distribution offer support for the current taxonomic designation of these species, supporting evidence may be misleading. That *L. katipo* and *L. atritus* have not been observed mating does not preclude the possibility that these species may interbreed. Moreover, if colour variation between the species were related to an environmental variable, such as temperature, differences in morphology and distribution may be explained.

Although parsimony analysis provided strong support for a clade of *L. hasselti* as distinct from *L. katipo* and *L. atritus*, a low maximum pairwise distance of 2.2 % between the Australian species and the New Zealand widow fauna suggests that some gene flow may occur, or have occurred until recently between these *Latrodectus* populations. If the New Zealand widow fauna had been genetically isolated from *L. hasselti* since the fragmentation of Gondwana, greater pairwise distances would be expected. This assertion is supported by the comparatively large minimum pairwise distance of 24.0 % that separates the Australasian specimens from *L. mactans* (California, USA). It is probable, therefore, that if *L. katipo* and *L. atritus* were present when New Zealand split from Gondwana as postulated by Forster (1984), they have not evolved in isolation (Chapter two). Rather, limited gene flow between *L. hasselti* and the New Zealand widow fauna has linked Australian and New Zealand *Latrodectus* populations, slowing genetic divergence (Nichols 2001). This assertion would explain why pairwise distances between *L. hasselti* and the New Zealand widow fauna are low. Greater intra-specific variation found among populations of *L. katipo* or *L. atritus* than between the Australian specimens might be attributed to allopatric speciation resulting from the introduction of low numbers of *Latrodectus* to New Zealand. Alternatively, genetic divergence might have resulted from periods of glaciation or rising sea levels that could have restricted gene flow between *L. katipo* or *L. atritus* populations in New Zealand, but are unlikely to have affected *L. hasselti* (Stevens 1985;

Stevens *et al.*1988; Nichols 2001; Trewick 2001). Moreover, Main (1992) and Raven (1992) suggested that *L. hasselti* may have only recently been introduced to eastern Australia from South Australia, which would explain the lack of genetic variation between the *L. hasselti* specimens.

Alternatively, *L. katipo* and/or *L. atritus* may have arrived in New Zealand more recently. This assertion is supported by growing evidence that the New Zealand spider fauna has been, and continues to be influenced, by the arrival of spiders from Australia (Vink and Sirvid 2000). The genetic diversity observed among the New Zealand widow spider fauna may have occurred as a result of one or several bottlenecks after they arrived, or as a consequence of multiple colonisation events. Given that suitable *L. katipo* and *L. atritus* habitat has probably been present in New Zealand for a long time (Stevens *et al.*1988) and that the genetic evidence indicates *L. hasselti* is a good disperser; it seems likely that *L. katipo* and *L. katipo* are not recent arrivals to New Zealand. In the absence of datable fossil records, however, it is unlikely that the time *L. katipo* and *L. atritus* arrived in New Zealand will be precisely known. The possibility that inter-specific geneflow has occurred or may still occur between *L. hasselti* and the New Zealand widow fauna would confound molecular dating techniques.

Although the ND1 gene region has previously been used to examine intra-specific variation between arthropod populations (Hedin 1997a; Hedin 1997b), this gene region did not evolve fast enough to provide the definition required to examine intra-specific gene flow among populations of *L. katipo* and *L. atritus*. Moreover, the low number of samples examined in this project also made it difficult to gain a definitive view of intra-specific gene flow. This problem might be overcome if sequence data from fast evolving nuclear gene regions or other fast evolving mitochodrial gene regions, such as parts of CO1, were used (Lunt *et al.*1996) and more samples were examined.

Conclusions

Low intra-specific pairwise distances among *L. katipo* and *L. atritus* populations suggest that gene flow has recently occurred and may still occur between the populations sampled. This result implies that both species were, and may still be, able to disperse over geographic barriers such as open sea, estuaries and headlands as postulated in chapter five. Low inter-specific pairwise differences between *L. katipo* and *L. atritus* suggest that gene flow may also have recently occurred or still occur between the two New Zealand *Latrodectus* spp., raising questions about the validity of the current taxonomic distinction between *L. katipo* and *L. atritus*.

Although parsimony analysis offered strong support for a clade of *L. hasselti* as distinct from the New Zealand *Latrodectus* spp., low pairwise distances between *L. hasselti* and the New Zealand widow fauna indicate either: that if *L. katipo* and *L. atritus* were present in New Zealand before the fragmentation of Gondwana, gene flow has recently occurred between the Australian and New Zealand *Latrodectus* spp. reducing genetic divergence, or that *L. katipo* and *L. atritus* have recently arrived in New Zealand. Greater intra-specific genetic diversity observed in the New Zealand widow species the between *L. hasselti* populations might be explained either: by allopatric speciation resulting from genetic bottlenecks, genetic isolation resulting from rising sea levels or glaciation or by multiple colonisation events. Comparatively low genetic diversity among *L. hasselti* might also be explained by the recent spread of this species to Western Australia from South Australia.

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Chapter Seven
General conclusions

This thesis set out to develop a greater understanding of *L. katipo* and *L. atritus* web site preferences, dispersal and species status in order provide information that could be used to conserve these species. This aim was expressed in the following objectives.

1. To identify micro-habitat characteristics that are associated *L. katipo* and *L. atritus* web sites and to develop a model/s that defines both species web sites
2. To determine how micro-habitat structure and aspect influence *L. katipo* and *L. atritus* web structure, web site preferences and prey capture
3. To determine how *L. katipo* and *L. atritus* disperse
4. To examine intra-specific and inter-specific genetic relationships between *L. katipo*, *L. atritus* and the *L. hasselti* in order to infer likely levels of gene flow between and within the species

Addressing the above objectives has meant this thesis has focused on the distribution of *L. katipo* and *L. atritus* at different spatial levels. At the smallest spatial scale, the thesis examined ***L. katipo* and *L. atritus* micro-habitat characteristics** in terms of the immediate biotic and abiotic context of the web, whereas, the **dispersal mechanisms employed by *L. katipo* and *L. atritus*** were investigated to better understand these species' distributions at a regional and national scale. Examination of the **intra and inter-specific differences between *L. katipo, L. atritus* and *L. hasselti* in the ND1 gene region** provided further information about the national distributions of *L. katipo* and *L. atritus*, but also addressed questions relating to the international distribution of these species arising from uncertainty surrounding *Latrodectus* taxonomy.

L. katipo and *L. atritus* micro-habitat characteristics

Surveys of the biotic and the abiotic context of *L. katipo* and *L. atritus* webs suggest that both species have similar habitat requirements and that these are defined by northerly, easterly or westerly aspect ($<60^\circ$ or $>300^\circ$), 34-66 % ground cover, the absence of detritus, sloping ground and low standardised ground-level temperature. There were inter-specific differences between the habitat types in which *L. katipo* and *L. atritus* web sites were located, their distance and relative elevation from the high tide mark, but these differences may be explained by regional variation in habitat availability and dune geomorphology. Web site characteristics did not appear to vary markedly between locations. This suggests that *L. katipo* and *L. atritus* web site preferences are not affected by regional variation in dune geomorphology or climate. Variation in web site characteristics, however, did occur between different plant types and driftwood or flotsam. Consequently, variable ranges that were most frequently associated with *L. katipo* and *L. atritus* web sites, such as northerly, easterly or westerly aspect, were not reliable predictors of *L. katipo* and *L. atritus* presence in all plant types and driftwood or flotsam.

Using habitat classification trees, a model was constructed that was useful for predicting *L. katipo* and *L. atritus* presence and absence irrespective of habitat type. The model accurately predicted *L. katipo* or *L. atritus* absence at > 90% of points sampled, but less accurately predicted *L. katipo* or *L. atritus* presence at 38 - 40% of points sampled. It was argued, that the model may have been less accurate at predicting presence; either because intra-specific competition prevents *L. katipo* or *L. atritus* from filling a greater proportion of potential web sites in optimal habitat, or that the model did not accurately define web sites. The latter was supported by stratified survey results that revealed almost all *L. katipo* and *L. atritus* catching-webs were constructed over open sand. This result suggests that web sites may be associated with patches of open sand rather than ground cover *per se*. Moreover, it was also suggested that the association found between northerly, easterly or westerly aspect and *L. katipo* and *L. atritus* web sites might be related to temperature rather than aspect.

The apparent preference by *L. katipo* and *L. atritus* for dune regions defined by patches of open sand and northerly easterly or westerly aspect was examined under experimental conditions in the laboratory (Chapter four). Experimental results suggested that the construction of *L. katipo* and *L. atritus* catching-webs appeared to be inhibited by the absence of interplant gaps, and that web sites appeared to be positioned so as to receive greater exposure to solar radition. It was argued that *L. katipo* and *L. atritus* catching-webs must be positioned over open sand so as to function effectively, as the prey catching method used by both species employs a number of catching lines that are attached to the substrate from a hammock like platform positioned in proximity to the ground. Where dense dune grasses have eliminated interplant gaps, *L. katipo* and *L. atritus* are unlikely to be able to build the hammock-like part of the catching-web. Futhermore, the catching lines may be ineffective as vegetation may interfere with spiders' ability to 'listen' to the web and prey wrapping may be impeded by confined surroundings. Results also showed that the majority of *L. katipo* and *L. atritus* included in the experiment favoured web sites at the 'sunny' side of microcosms. It was asserted, therefore, that *L. katipo* and *L. atritus* web site selection is likely to be linked to heat cues. These cues may help spiders locate web sites in dune regions that are characterised by microclimatic conditions necessary for embryonic and spiderling development and that promote activity levels required for prey capture, predator avoidance, web maintenance and construction.

Collectively, the results of transect and stratified surveys (Chapter three) and the micro-habitat prefernce experiment (Chapter four) suggest that *L. katipo* and *L. atritus* web sites are characterised by specific structural and microclimatic conditions. These, it was argued, appear to be absent in dune regions where exotic plants such as marram, kikuyu or buffalo grass have reached densities that exclude interplant gaps. Moreover, the absence of *L. katipo* and *L. atritus* records from dune regions modified by urban development or forestry and agriculture, imply that the habitat requirements of *L. katipo* and *L. atritus* are not met by the above types of land use. Consequently, *L. katipo* and *L. atritus* may be displaced in dunes extensively modified through the introduction of exotic plant species and urban or rural development.

Because a large proportion of New Zealand's dune systems have now been modified by exotic vegetation and rural or urban development (Brian Patrick 2001, pers. com.; Trevor Partridge 2001, pers. com.; pers. obs.), *L. katipo* and *L. atritus* habitat has become fragmented and has decreased in abundance. These factors may impede *L. katipo* and *L. atritus* dispersal, inhibiting both species' capacity to recolonise dune regions from which they have been displaced due to perturbation. Furthermore, the above factors may also reduce the gene flow between populations, resulting in inbreeding. It follows, therefore, that dune modification is a likely principal agent of the decline in *L. katipo* numbers and may be implicated in the reported decline in *L. atritus* numbers. Although the apparent displacement of *L. katipo* by *S. capensis* (Hann 1990) (Chapter two) may result in a decline in *L. katipo* numbers in some dune systems, the scale (nationwide) and timing (within the last 50 years) of dune modification in New Zealand (Brian Patrick 2001, pers. com.; Trevor Partridge 2001, pers. com.) suggests that it is a more likely principal agent of the decline than *S. capensis,* which I have not recorded from many dune systems in which *L. katipo* and *L. atritus* have apparently decreased in numbers.

Dispersal mechanisms employed by *L. katipo* and *L. atritus*

The dispersal mechanisms employed by *L. katipo* and *L. atritus* were investigated (Chapter five) to determine how readily either species is likely to be able to recolonise dune regions from which they have been displaced. The results of these investigations showed the *L. katipo* and *L. atritus* juveniles disperse by 'bridging' and 'ballooning' and that adult females of both species were able to withstand periods of up to nine days floating on driftwood that was showered with salt water once daily (Chapter five). These results indicate that both *L. katipo* and *L. atritus* possess behavioural and physiological attributes that could promote dispersal over large distances. This may explain why geographical barriers such as headlands, estuaries and areas of open sea do not appear to restrict their distribution, and may explain how *L. katipo* and *L. atritus* arrived in New Zealand.

The propensity for long distance dispersal indicates that *L. katipo* and *L. atritus* are likely to have the capacity to disperse beyond their current distributions suggesting that these species' distributions should have a larger overlap if temperature alone determined the extent of their distributions as postulated by Forster (1999) (Chapter three). All recent observations (Forster and Forster 1999; Patrick, in press, 2001; pers obs), however, indicate that the overlap between *L. katipo* and *L. atritus* occurs within ≈ 100 km, with little variation in temperature range between the northern and southern limits (McKenzie 1995). This implies that other factors, such as inter-specific competition, might restrict the northern extent of *L. katipo* distribution or the southern extent of *L. atritus* distribution. Alternatively, interbreeding between *L. katipo* and *L. atritus,* if it occurs, may blur the extent to which these species' distributions overlap. For example, if all black (red dorsal stripe absent) *L. katipo* morphs always result from *L. katipo* and *L. atritus* matings, the northern extent of *L. katipo* distribution might appear further south than it is.

Intra and inter-specific differences between *L. katipo, L. atritus* and *L. hasselti* in the ND1 gene region

Through analysis of ND1 sequence data, the intra and inter-specific genetic relationships between *L. katipo, L. atritus* and *L. hasselti* were examined (Chapter six) to determine whether the inferences drawn from the dispersal investigation were probable and to examine the species status of *L. katipo, L. atritus* and *L. hasselti.* Results revealed low pairwise distances among *L. katipo* and *L. atritus* populations. This suggests that intra-specific gene flow has recently occurred between the sampled populations, implying that both species were recently able to disperse over geographic barriers such as open sea, estuaries and headlands, as asserted above. Moreover, low pairwise differences were observed between *L. katipo* and *L. atritus* suggesting that gene flow may also have recently occurred between the two New Zealand *Latrodectus* spp.. This result was emphasised by parsimony analysis that placed *L. katipo* and *L. atritus* in a monophyletic group, raising questions about the validity of the current taxonomic distinction between these species.

Parsimony analysis offered strong bootstrap support for a clade of *L. hasselti* as distinct from the New Zealand *Latrodectus* spp.. Low pairwise distances between *L. hasselti* and the New Zealand widow fauna indicate that gene flow is likely to occur, or have recently occurred, between the Australian and New Zealand *Latrodectus* spp.. Consequently, Forster's (1995) hypothesis that *L. katipo* and *L. atritus* have evolved in isolation since the break up of Gondwana is improbable. Rather, gene flow between *L. hasselti* and the New Zealand widow fauna has slowed genetic divergence between these species or *L. katipo* and *L. atritus* have recently arrived in New Zealand.

Although genetic evidence indicates that gene flow is likely to have occurred between *L. katipo* and *L. atritus* populations in the recent past, current levels of gene flow were not determined. If *L. katipo* and *L. atritus* dispersal is impeded by the fragmentation and reduction of dune systems as asserted above, however, gene flow between *L. katipo* and *L. atritus* populations might be expected to decrease. This would be likely to lead to increased genetic variation between *L. katipo* and *L. atritus* populations and, consequently could induce speciation.

Research contribution

Before the current study, little was known about the ecology of *L. katipo* and the ecology of *L. atritus* had not been explored (Smith 1971; Hann 1990; Forster and Forster 1999). Furthermore, New Zealand's native dune communities have rarely been subject to scientific investigation, and have been largely ignored by the Department of Conservation, the agency primarily responsible for funding conservation research in New Zealand. The current study, therefore, not only provides important information about New Zealand's endemic *Latrodectus* spp. (above), but adds to the body of knowledge pertaining to New Zealand's native dune communities that are valuable because they include a large number of endemic species (Lands & Survey Dept 1984; Partridge 1992). Moreover, as few studies have focused on the web site preferences and web site selection of other *Latrodectus* spp. (Kaston 1970; Lubin 1993; Carrel 2001), the current study may also provide valuable insight into the web site preferences and web site selection of other *Latrodectus* spp., of importance due to their toxicity to humans.

Latrodectus spp. appear to exhibit similar behavioral traits, web site preferences, retreat and catching-web architecture, and are commonly associated with hot dry micro-climates (Kaston 1970; Smith 1971; Raven and Gallon 1987; Hann 1990; Lubin 1993; Forster and Forster 1999; Carrel 2001). In natural environments, they frequently inhabit patchy low growing vegetation, fallen wood or spaces under rocks, and are often associated with areas characterised by sandy or stony substrates (Kaston 1970; Smith 1971; Raven and Gallon 1987; Hann 1990; Lubin 1993; Forster and Forster 1999; Carrel 2001). Like *L. katipo* and *L. atritus*, other widow spiders display a high degree of web site specificity (Lubin 1993; Carrel 2001). Consequently, results from the current study that suggest *L. katipo* and *L. atritus* website specificity is strongly related to the structural requirements of the catching and retreat may also apply to other widow spp.. This assertion is supported by research conducted by Lubin (1993), which suggested juvenile *L. revivensis* might relocate to larger shrubs as they mature because greater space between branches of larger shrubs is necessary to accommodate the larger web size of adult spiders. Similarly, Carrel (2001), indicated that the structural requirements of the retreat and catching-web appeared to influence the distribution of *L. bishopi* Kaston 1938, which was restricted to two plant species *Serenoa repens* Bartram and *Sabal etonia* Swingle. In addition to web and retreat architecture, the current study found that *L. katipo* and *L. atritus* web site specificity might also be related to a particular temperature range. In the field, most *L. katipo* and *L. atritus* were associated with sites characterised by northerly, easterly or westerly aspect, where they would presumably receive greater exposure to solar radiation. In the laboratory, they favoured the warmer end of a temperature gradient. It was argued that the association between *L. katipo* and *L. atritus* and aspect, therefore, might be related to higher night-time ground-level temperature at sites with northerly, easterly, westerly aspect (Chapter four). That *L. hasselti* also favours sunny web sites and is absent from shady gardens indicates that preference for a particular temperature range might also be related to web site specificity in other *Latrodectus* spp.. This assertion is further supported by a study conducted on *L. revivensis* that showed this species' distribution also appears to be governed by temperature. In the cool season, for example, 47.8 % of all *L. revivensis* web sites were located within a 20 m wide strip of vegetation located at the edge of a wadi, whereas in the hot season 71.3 % of all web sites were located in the this area. Furthermore, Lubin (1990) argued that a likely benefit of web relocation in *L. revivensis* is improved thermal conditions at the web site. Lubin (1990) found no evidence to suggest *L. revivensis* web relocation was related to increased prey availability.

In addition to web site preferences and web site selection, this thesis also identified dispersal mechanisms employed by New Zealand's endemic *Latrodectus* spp. and examined the intra and inter-specific genetic pairwise differences in the ND1 gene region within and between *L. katipo, L. atritus* and *L. hasselti*. *L. katipo* and *L. atritus* were found to be good dispersers, as evidenced by low intra and inter-specific pairwise differences between and among *L. katipo, L. atritus* and *L. hasselti* populations that indicate gene flow has probably occurred recently between and within these species. This evidence suggests that these species are likely to be able to disperse over large distances such as the Tasman Sea and Cook Strait, which separates New Zealand's North and South Islands. Moreover, it implies that other *Latrodectus* spp. may also be able to disperse over large distances, which could explain the cosmopolitan distribution of this genus.

Because of the similarities between many *Latrodectus* spp., it might be inferred that, like *L. katipo* and *L. atritus,* the ecology of other widow spiders will be affected by anthropogenic change to the structure and extent of the ecosystems in which they live. If anthropogenic change reduces the availability of micro habitats favoured by a particular *Latrodectus* spp. and, consequently, results in the geographic isolation of patches of suitable habitat, as has occurred in New Zealand, it is likely that the species will decline in abundance and become fragmented in its distribution. In other cases, however, anthropogenic change may lead to an increase in abundance of micro-habitats preferred as web sites, as has occurred in *L. hasselti L. hesperus, L. geometricus* Koch 1841 and *L. mactans* that inhabit human dwellings. These species, as might be expected, have apparently increased in number (Raven and Gallon 1987; Main 1992; Forster 1995). Moreover, because they are associated with human dwellings they have been readily distributed as a result of international trade, and have colonised many countries to which they are not native. *L. hasselti,* for example has successfully colonised New Zealand, Japan and the Philippines, whereas *L. geometricus* has established a localised distribution in Australia (Raven and Gallon 1987). *L. hesperus, L. geometricus* and *L. mactans* are regularly intercepted in food and produce imported by New Zealand and Australia (Raven and Gallon 1987), indicating that in time these species are also likely to become established in both countries, as suitable web sites in human dwellings are likely to be abundant. If *L. hasselti, L. hesperus, L. geometricus* or *L. mactans* spiderlings are able to balloon, as suggested by Raven and Gallon (1987) and Kaston (1970) and supported by observed ballooning in *L. katipo* and *L. atritus* spiderlings, it is probable that these species' distributions will expand rapidly where they become established. Moreover, similarities in the genital morphology of *Latrodectus* spp. (Levi 1958; Levi 1959) may enable the interbreeding between colonising widow spiders and endemics if their mating behaviour and ecology are compatible, as has been observed in *L. katipo* and *L. hasselti* (Forster and Forster 1999) and was implied by molecular results (Chapter six).

Recommendations for future research

In hindsight, transect and stratified sampling would be complemented by future research examining *L. katipo* or *L. atritus* abundance and distribution over a larger temporal scale (e.g. five years) so as to mitigate temporal confounding and to quantify the speed and scale of *L. katipo* and *L. atritus* decline. Habitat preference tests combined with data collected on *L. katipo* and *L. atritus* fecundity in different habitat types might be used to characterise optimal *L. katipo* and *L. atritus* habitat. This will enable conservation managers to direct conservation efforts to areas where they will have most effect. Further research should also be carried out to identify potential predators, competitors and parasites and to investigate their ecology, as research in this field might reveal agents of decline that were not been identified in this thesis and previous studies.

Although the habitat structure and micro-climate experiment (Chapter four) addressed the questions it set out to answer, the experiment would be improved if larger microcosms were used so that the gap between marram tillers and the container edge was sufficient to inhibit the construction of catching-webs. This improvement would be likely to increase the distinction between catching-web size and prey capture in sparse and dense microcosms. Furthermore, if *L. kaitpo* and *L. atritus* were subjected to experimental conditions for a longer time, such as four weeks, differences in the weight gained or lost by spiders inhabiting sparse and dense microcosms would be more likely to be significant. Moreover, the experiment would also benefit from additional field based replicates that could be used to determine whether the web site selection, web building or prey catching behaviour of *L. katipo* and *L. atritus* in the laboratory is representative of either species in the field.

The 'ballooning' experiment and field observations (Chapter five) conducted on *L. katipo* and *L. atritus* spiderlings provided useful information on the dispersal of post-emergent spiderlings, but would be complemented by future studies focusing on the conditions associated with 'ballooning' or 'bridging'. For example, wind, temperature, light levels and humidity could be sampled using data loggers in conjunction with video footage. This information would help to identify the types of conditions that trigger 'ballooning' or 'bridging' and may provide insight into the colonisation capacity of 'ballooning' spiderlings. Moreover, advancements in tracking devices may soon allow the tracking of 'ballooning' spiderlings, which could provide valuable information on the distances that 'ballooning' spiderlings travel, whether they re-initiate 'ballooning', and the numbers of spiderlings that fail to disperse to suitable habitat.

Although molecular analysis provided useful information on the intra and inter-specific relationships between *L. katipo, L. atritus,* and *L. hasselti*, too few samples were collected and the ND1 gene region did not evolve fast enough to gain a definitive view on the intra and inter-specific gene flow between and among *L. katipo, L. atritus* and *L. hasselti* populations. Future molecular analysis, therefore, might examine more samples from each species and could use fast evolving nuclear gene regions or other fast evolving mitochodrial gene regions, such as parts of CO1 (Lunt *et al.*1996). Information from molecular analysis that adopted the above recommendations would be more likely to provide definitive view of the levels of gene flow between and among the three Australasian species, and may address questions raised about the current taxonomy of these species. To obtain a clear picture of the relationships between the Australasian *Latrodectus* species, however, morphological and karyological data will also be required.

Mating experiments could also be conducted to determine whether *L. katipo* and *L. atritus* can interbreed. This would help to understand the genetic relationship between these species and might help explain the species' distributions. A better understanding of the species' distributions may also be gained by examining the highest temperature at which *L. katipo* embryos and spiderlings can develop.

Recommendations for agencies charged with the management of New Zealand's dune systems

Currently no strategy is in place for the conservation of *L. katipo* or *L. atritus*. If the Department of Conservation and Regional and City Councils are to conserve either of these species, something they are obliged to do under the Resource Management Act 1991 and the Agenda 21 agreement 1992, the following recommendations should be adopted where possible.

- That the model presented in the thesis is used to identify dune regions likely to provide optimal habitat for *L. katipo* and *L. atritus*
- That dune systems in which *L. katipo* and *L. atritus* are abundant are protected from dune modification and from human activities such as off road vehicle use or driftwood collection
- That dune systems dominated by native dune vegetation are protected from urban and rural development, and that the introduction of exotic plant species such as marram, iceplant, kikuyu or buffalo grass and other exotic plants be discouraged
- That invasive introduced plant species such as marram, iceplant, kikuyu or buffalo grass are eradicated from dune systems that are currently dominated by native vegetation
- That *L. katipo* and *L. atritus* are monitored in modified and relatively unmodified dune systems throughout their distributions to determine the rate at which their numbers are declining and to determine whether there is a difference in the rate of decline between modified and relatively unmodified dune systems
- That surveys are undertaken on other dune fauna to determine whether they are also effected by the modification and truncation of New Zealand's dune systems
- That further molecular investigations are undertaken to determine whether the current taxonomy of *L. katipo, L. atritus* and *L. hasselti* is accurate

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