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The invasive Australian redback spider, *Latrodectus hasseltii* Thorell 1870 (Araneae: Theridiidae): current and potential distributions, and likely impacts

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Abstract Populations of the Australian redback spider, *Latrodectus hasseltii* Thorell 1870, were first recorded in New Zealand in the early 1980s and in Osaka, Japan in 1995. Reliable records suggest that naturalised populations of *L. hasseltii* in New Zealand are present only in Central Otago and New Plymouth. In Central Otago, *L. hasseltii* feeds on endangered invertebrates, such as *Prodontria modesta* (Broun 1909). *Latrodectus hasseltii* is also a hazard to the New Zealand endemic *L. katipo* through interbreeding and competitive displacement. CLIMEX^TM was used to model the potential global distribution of *L. hasseltii* based on current climate, and using ArcGIS® 9.2, areas of suitable climate in New Zealand were overlaid with favourable habitats to identify areas most suitable for *L. hasseltii* establishment. In addition, shelter that urban areas offer *L. hasseltii* were modelled in CLIMEX and incorporated into ArcGIS to produce maps indicating cities and built up areas where the species could establish. The presence of *L. hasseltii* in New Zealand and Japan, and its possible spread to other areas, is of human health significance, and the species may also impact on native biodiversity.

Keywords CLIMEX · GIS · Human health · Invasive species · Biodiversity threat

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Introduction

The spider genus *Latrodectus* Walckenaer 1805 (Araneae: Theridiidae) occurs in temperate and tropical zones throughout the world, with 30 currently recognised species (Platnick 2010). The Australian redback, *Latrodectus hasseltii* Thorell 1870, is found across much of Australia (Raven and Gallon 1987; Isbister and Gray 2003) except at the highest altitudes (Sutherland 2001) and in some parts of Tasmania (Hickman 1967). It has been suggested that *L. hasseltii* may not be endemic to Australia because it is most common in urban areas and had not been

recorded in Australia before 1870, when about 200 spider species had already been described (Raven and Gallon 1987). However, *L. hasseltii* was already known from South Australia in 1850 (Main 1993), which was only 14 years after European settlement there, suggesting they were present before Europeans arrived. *Latrodectus hasseltii* is listed as occurring in Southeast Asia (Platnick 2010), including New Guinea (Chrysanthus 1975), the Philippines (Cariaso 1967) and India (Patel 1973; Manju and Kumar 2001) and, more recently, has become established outdoors in New Zealand (Forster 1984; Forster and Forster 1999) and Japan (Ori et al. 1996; Nihei et al. 2004), as well as in greenhouses in Belgium (Blick et al. 2004). Other *Latrodectus* species have also established well outside their natural range: *L. hesperus* Chamberlin and Ivie 1935 (western black widow) from western North America has naturalised in Israel and Hawaii (Levy and Amitai 1983; Beatty et al. 2000); and *L. geometricus* C.L. Koch 1841 (brown widow), which is thought to originate from Africa (Levi 1959), has established in Australia, Japan, USA (Southeast, southern California, Hawaii), South America and Israel (Levi 1959, Levy and Amitai 1983, Raven 1992; Ono 1995, Brown et al. 2009, Vincent et al. 2009, Garb et al. 2004).

The first post-border records of *L. hasseltii* in New Zealand were in 1981–1982 when female spiders were independently discovered in three outdoor locations in Southland and Central Otago in the southern South Island (Forster 1982, 1984, 1985). It is unclear whether the spiders at the three locations were from single or multiple introductions (Forster 1984). No action was taken to eradicate *L. hasseltii*, apparently because it was neither seen as a pest of plants, nor as harmful to stock and wildlife (Forster 1985). It has since been reported to have become established around New Plymouth on the west coast of the North Island (McCutcheon 1992), but no details on locality or population size were given.

In Japan, *L. hasseltii* was first recorded in Osaka Prefecture in 1995 (Ori et al. 1996), and has since spread inland (Nihei et al. 2004). It is unknown if they resulted from a single or multiple introductions. Kobelt and Nentwig (2008) also reported *L. hasseltii* had been found in Denmark, but this was an error as the spiders were imported with cars from the USA and should have been recorded as a North American species, probably *L. mactans* (Fabricius 1775)

(southern black widow) or *L. hesperus* (N. Scharff, personal communication). Although *L. hasseltii* has been recorded from Southeast Asian localities (Cariaso 1967; Patel 1973; Chrysanthus 1975; Manju and Kumar 2001), it is unclear whether these records are of established populations, and could even be misidentifications of another *Latrodectus* species.

Some Australian spider species are likely to have dispersed naturally to New Zealand by ballooning on long, buoyant strands of silk (e.g. Vink and Sirvid 2000; Framenau and Vink 2001) and *L. hasseltii* exhibits behaviours associated with ballooning during early juvenile stages (Forster 1995), but it seems that natural long distance dispersal is rare in *L. hasseltii*. The genetic distance between *L. hasseltii* and the closely related *L. katipo* Powell 1870, a New Zealand endemic species, indicates that the two species have been isolated from each other for hundreds of thousands of years (Griffiths et al. 2005; Vink et al. 2008). *Latrodectus hasseltii* were not found in aerial samples of spiders collected over one month in an agricultural area in New South Wales (Greenstone et al. 1987). Also, Nihei et al. (2004) studied *L. hasseltii* dispersal in Japan and found that it does not spread by ballooning, but hitchhikes on vehicles or walks.

Latrodectus hasseltii probably invaded human-modified habitats in New Zealand, Japan and Europe via international trade. At the New Zealand border, quarantine authorities made over 136 recorded interceptions of *L. hasseltii* between February 1988 and July 2005 (MAF Biosecurity New Zealand, unpublished data). Between November 2002 and August 2005, eight interceptions were made in transitional facilities where uncleared imported goods are held, and a further 40 interceptions were made in imports that had cleared quarantine (MAF Biosecurity New Zealand, unpublished data; A.R. Flynn, personal communication). Redbacks have been most frequently intercepted with shipments of steel and in imported used and new vehicles (Biosecurity New Zealand 2007, MAF Biosecurity New Zealand, unpublished data), but have also been found in fresh produce such as grapes (Reed and Newland 2002) and in goods that are unpacked in warehouses then delivered to shops and homes (MAF Biosecurity New Zealand, unpublished data). Food deprivation studies showed that *L. hasseltii* can survive long periods of starvation if incarcerated in cargo, with some adults

surviving for more than 300 days without food (Forster and Kavale 1989). Moreover, a single gravid female can give rise to a viable population, since siblings can successfully interbreed (Forster 1984).

Latrodectus hasseltii populations can survive surprisingly cold temperatures (Ori et al. 1996; Kamimura et al. 1999; Matsuse et al. 1999; Nihei et al. 2004). Representatives of all *L. hasseltii* developmental stages survived a Japanese winter when temperatures fell to -3°C (Kamimura et al. 1999), and the species also withstands sub-zero temperatures in New Zealand (Forster 1982) where spiderlings assume a state of quiescence if appropriately low temperatures prevail (Forster 1995). Laboratory studies found that 50% of adults survived 30 min at -10.5°C (Matsuse et al. 1999). In addition, studies on another theridiid, *Parasteatoda* [previously *Achaearanea*] *tepidariorum* (C.L. Koch 1841), have shown that freeze tolerance in spiders can be facilitated by the consumption of freeze tolerant prey (Tanaka 2001). Although low winter temperatures do not seem to limit redback survival, warm summer temperatures are needed for successful breeding (Forster 1982). It takes 2–3 months of temperatures ranging from 15 to 25°C for redback spiders to breed and their offspring to reach maturity (Forster 1985), and laboratory experiments found 25°C to be optimal for their development (Downes 1987).

The survival of *L. hasseltii* in relatively cool climates could be facilitated by its tendency to build webs in anthropic environments (Matsuse et al. 1999) that provide some shelter from extreme temperatures. Such environments probably also satisfy the species' requirement for low relative humidity (Forster 1984). In Japan, the preferred habitats of *L. hasseltii* are closely associated with humans, such as buildings, cemeteries and parking lots, and its spread has been limited to housing complexes in urban habitats, rather than in surrounding agricultural land or nearby areas of native vegetation (Nihei et al. 2004). Forster (1984) suggested that the reliance of *L. hasseltii* on arid habitats, adequate summer temperatures for breeding, and appropriate conditions for overwintering would mean that much of New Zealand would be unsuitable for this species. However, research in Japan (Matsuse et al. 1999; Nihei et al. 2004) has indicated that urban areas may provide redbacks with the shelter they require to expand their range into climate zones that would be intolerable in less

modified environments. The ability of *L. hasseltii* to withstand temperatures from below 0°C (Forster 1982; Kamimura et al. 1999) to 40°C (Forster 1995) suggests that shelter from extreme temperatures may not be the principle benefit of human modified environments and, rather, shelter from rain and high soil moisture may be more important.

Latrodectus hasseltii is a venomous spider and is clearly a human health concern since, in Australia, it bites hundreds of people each year (Sutherland 1983). However, it also has potential for significant ecological impacts. Invasive spider species can harm endemic species through competitive displacement (Nyffeler et al. 1986; Hann 1990; Bednarski et al. 2010) and invasive arthropod predators can impact on native communities (Snyder and Evans 2006). As a generalist predator, *L. hasseltii* is likely to eat any appropriately sized insect or arthropod that is caught in its web. Ground-dwelling beetles and *Porcellio scaber* Latreille 1804 (Isopoda: Porcellionidae) are very common in the diet of *L. hasseltii* in Australia (McKeown 1952).

In this study, published and unpublished records, and our own observations, are used to clarify the current distribution of *L. hasseltii* in New Zealand. We evaluate its potential distribution in New Zealand, Japan and worldwide, initially using climate matching software. This approach has previously been used to model the potential distributions of many plants and invertebrates (e.g., Samways et al. 1999; Kriticos et al. 2003; Wharton and Kriticos 2004; Sutherst and Maywald 2005; Stephens et al. 2007; Poutsma et al. 2008; Sutherst and Bourne 2009). Although climate match ignores other restrictions to geographic distributions such as habitat availability, competition, predation, parasitism, dispersal and population genetics (Hulme 2003; Samways 2003; Sutherst et al. 2007a), species distribution boundaries are often significantly associated with aspects of climate (Parmesan 2006; Sexton et al. 2009), and climate match remains one of the most reliable predictors of establishment success for diverse taxa (Hayes and Barry 2008; Bomford et al. 2009). We refine our climate-based predictions with spatial data on habitat availability, but do not model other possible constraints to *L. hasseltii*'s potential distribution. This is partly due to insufficient data, but also because several potentially important biotic constraints are probably not strongly applicable to

this generalist predator, which has few natural enemies (Downes 1984; Austin 1985; Bouček 1988) and no known pathogens. Clear evidence that *L. hasseltii* can be transported in association with humans also indicates dispersal will not strongly limit its distribution, and successful sib-mating (Forster 1984) will limit the impact of some Allee effects on founding populations. We use our models to explore how the geographic range of *L. hasseltii* could respond to the shelter provided by human modified environments, and evaluate its potential to negatively impact humans and native biodiversity.

Methods

Latrodectus hasseltii populations are considered to be established in New Zealand (Reed and Newland 2002; Garb et al. 2004; Platnick 2010), but their locations and status are unknown. To clarify the distribution of *L. hasseltii* in New Zealand, we obtained reliable records that had been based on expert identification of specimens using criteria outlined in Vink et al. (2008). This was achieved by a thorough search of the published literature, consultation with other arachnologists, examination of arthropod collections and records from the following organisations: MAF Biosecurity New Zealand (MAFBNZ), New Zealand Arthropod Collection (NZAC), Museum of New Zealand Te Papa Tongarewa (MONZ), Auckland Museum (AMNZ) and Otago Museum (OMNZ).

As a preliminary evaluation of the impact of *L. hasseltii* on native invertebrates, we collected the contents of two redback webs collected near Alexandra (45°15.3′S, 169°24.2′E) and identified prey to species where possible.

The software package CLIMEX™ for Windows version 3 (Sutherst et al. 2007b) was used to develop a model of climatic suitability for *L. hasseltii*. CLIMEX is based on the observation that climate is an important factor in the distribution of plants and poikilothermic animals (Andrewartha and Birch 1984; Woodward 1987). CLIMEX uses an annual growth index to express the potential for population growth during favourable climatic conditions, and four stress indices (cold, wet, hot and dry) to estimate the probability that a population can survive unfavourable conditions. The parameters used in the

CLIMEX model for *L. hasseltii* are shown in Table 1, and the role and meaning of these parameters are fully described in Sutherst and Maywald (1985) and Sutherst et al. (2007b). The growth and stress indices were calculated weekly, and combined into an overall annual index of climatic suitability, the ecoclimatic index (EI), a value from 0 to 100. An EI of 0 indicates that the species will not survive. Generally, EI values between 1 and 9 are marginal for the species, between 10 and 19 are suitable and over 19 is favourable (e.g., Sutherst and Maywald 2005; Stephens et al. 2007).

Parameter values describing the climatic tolerance of *L. hasseltii* were initially based on the semiarid template that is included with CLIMEX (Sutherst et al. 2007b). Temperate parameter values were inferred from information on *L. hasseltii* biology (Table 1). The lower temperature threshold (DV0) was based on a temperature threshold for *L. hasseltii* eggsac development (14.7°C) calculated using the values in Downes (1987). By regressing the rate of development (1/days to develop) against temperature, the threshold temperature for development is the x intercept (−constant/slope) (Campbell et al. 1974). The upper temperature threshold (DV3) was set at 40°C as this appears to be close to the highest temperature that *L. hasseltii* can tolerate for prolonged periods (Forster 1995). This initial CLIMEX model was then run using the "compare location" function with the database of meteorological climate station data in CLIMEX; the moisture parameter values were then modified so that EI values were ≥1 at all climate station locations where *L. hasseltii* is known to occur in Australia (throughout), Japan (Osaka) and New Zealand (Alexandra and New Plymouth). Southeast Asian localities (Cariaso 1967; Patel 1973; Chrysanthus 1975; Manju and Kumar 2001) were not included in setting the parameter values as precise locality information was unavailable and specimen identifications were sometimes questionable. Belgian locations were not included as *L. hasseltii* has only been reported from greenhouses there (Blick et al. 2004).

The parameter values used for *L. hasseltii* derived from biology and climatic data associated with their known distribution (Table 1) are hereafter referred to as the "natural CLIMEX model". Ecoclimatic index (EI) values for the natural CLIMEX model for different New Zealand locations were calculated using the "compare location" function in CLIMEX. Interpolated climate data for each of 11,491 locations

Table 1 CLIMEX parameter values used for *L. hasseltii* derived from biology and climatic data associated with their known distribution

Index	Parameter	Values[a]
Temperature	DV0 = Lower threshold[b]	15°C
	DV1 = Lower optimum temperature[b]	22°C
	DV2 = Upper optimum temperature[b]	37°C
	DV3 = Upper threshold[c]	40°C
Moisture	SM0 = Lower soil moisture threshold	0.01
	SM1 = Lower optimum soil moisture	0.1
	SM2 = Upper optimum soil moisture[d]	0.5
	SM3 = Upper soil moisture threshold[d]	1.35
Cold stress	TTCS = Temperature threshold	0°C
	THCS = Stress accumulation rate	0.005 week^{-1}
Heat stress	TTHS = Temperature threshold[c]	40°C
	THHS = Stress accumulation rate	0.005 week^{-1}
Dry stress	SMDS = Soil moisture dry stress threshold	0.01
	HDS = Stress accumulation rate	0.005 week^{-1}
Wet stress[e]	SMWS = Wet stress threshold	1.35
	HWS = Wet stress rate	0.01 week^{-1}

The role and meaning of these parameters are described in Sutherst et al. (2007b) and Sutherst and Maywald (1985)

[a] Values without units are dimensionless proportions

[b] Parameter values inferred from Downes (1987)

[c] Parameter value inferred from Forster (1995)

[d] Parameters set to 2 to simulate the effect of shelter in urban environments

[e] Wet stress inactivated to simulate the effect of shelter in urban environments

that cover all of New Zealand in a 0.05° latitude/longitude grid, based on measurements for the period 1960–2004 (Tait et al. 2006), were applied in the *L. hasseltii* climate model. In separate analyses, the climate normals dataset of points spaced on a 0.5° latitude/longitude grid for Australia, Japan and the world, available in CLIMEX and based on measurements for the period 1961–1990 (Sutherst et al. 2007b), were also applied.

Latrodectus hasseltii is often found associated with human dwellings (Forster 1985; Kavale 1986) that would offer shelter from unfavourable climatic conditions, such as rainfall. Therefore, we developed a second CLIMEX model, hereafter referred to as the "urban CLIMEX model", by removing wet stress and modifying the moisture index to simulate the effect that shelter provided by urban areas could have on climatic suitability for *L. hasseltii*. We modified the moisture index by excluding the wet stress and setting the upper optimum soil moisture and upper soil moisture threshold parameters to 2, which removed

the effect that high rainfall would have. However, this approach is unlikely to allow for locations where urban areas do not provide shelter from very high humidity, which can be fatal to *L. hasseltii* (Forster 1984). Minimum rainfall requirements were retained in the urban CLIMEX model because anecdotal evidence suggested that redback numbers in Canberra decreased during the recent drought there (A.D. Blest, personal communication). Since *L. hasseltii* does not require any moisture other than what it obtains from its prey (Forster 1984), its decline was likely due to drought-induced reductions in prey populations. The urban CLIMEX model was applied to the datasets for New Zealand, Japan, Australia and the world, and estimated EI values were recorded.

The New Zealand EI values and their corresponding geographical coordinates from the natural and urban CLIMEX models were imported to ArcGIS® Version 9.2 (Environmental Systems Research Institute, Redlands, California) and natural neighbour interpolation was used to produce a continuous range

of EI values between those calculated for locations on the 0.05° latitude/longitude grid. Our observations (Table 2) indicated that *L. hasseltii* had persisted for over two decades at a relatively cool New Zealand location, Alexandra, with an EI value of 9 so we assigned this as the minimum threshold for the species' persistence. This corresponded well with the minimum of 10 that has typically been applied in other studies (e.g., Sutherst and Maywald 2005; Stephens et al. 2007). EI values of 0–0.99 were arbitrarily classified as unsuitable, 1–8.99 as 'marginal', 9–19.99 as 'suitable', and values ≥20 as 'favourable'.

Potential habitats for *L. hasseltii* in New Zealand were chosen based on observations in Australia and Japan of its frequent occurrence in urban areas (Raven and Gallon 1987; Nihei et al. 2004). In addition, previous publications (Forster 1984, 1995; Waterworth 2009) and our own observations of *L. hasseltii* in New Zealand (Table 2) indicated its persistence for many years in three further habitats: vineyards, low producing grassland and mixed exotic shrubland. The spatial distributions of these four habitats in New Zealand were mapped using the New Zealand Land Class Database 2 (LCDB2; Ministry for the Environment 2004) in ARCGIS Version 9.2. The LCDB2 is a thematic classification of 43 land cover and land use classes covering New Zealand that was released in ESRI shapefile format in July 2004, and used Landsat 7 ETM + satellite imagery acquired over the summer of 2001/02 (Ministry for the Environment 2004).

The EI values for New Zealand from the natural CLIMEX model were overlaid with the distribution map for vineyards (LCDB2 classification 31), low producing grassland (LCDB2 classification 41) and mixed exotic shrubland (LCDB2 classification 56) to produce a map showing locations with both suitable habitat and suitable climate (EI ≥ 9) for *L. hasseltii*. Similarly, the EI values generated by the urban CLIMEX model were overlaid with the distribution map for 'built up areas' (LCDB2 classification 1) to produce a map showing New Zealand urban areas with suitable climate (EI ≥ 9) for *L. hasseltii*. These two maps were combined to produce a composite.

The world EI values and their corresponding geographical coordinates from the natural and urban CLIMEX models were imported to ArcGIS Version 9.2 and interpolated using natural neighbour interpolation to produce a continuous range of EI values between those calculated for locations on the 0.5° latitude/longitude grid. The two layers of interpolated EI values were then overlaid, in separate analyses, with a layer of the world's major cities to produce maps showing the cities predicted by each CLIMEX model to have unsuitable, marginal, suitable or favourable climates for *L. hasseltii*.

Results

We compiled reliable records of redback spiders that had evaded New Zealand import quarantine controls and were then transported into the New Zealand environment (i.e. post-border detections); these are listed in Table 2 and shown in Fig. 3c. From 1981 to February 2009, there were 54 records at 37 locations throughout New Zealand. Twenty of the records were from seven port cities or their urban satellites (Whangarei, Auckland, Tauranga, Gisborne, New Plymouth, Wellington and Invercargill) including four from around New Plymouth. There were a further 20 records from Central Otago.

Two webs collected from near Alexandra on 28 December 2007 and 4 January 2008 contained 18 and 34 arthropod carcasses, respectively. The 18 arthropods from the first web consisted of nine woodlice (presumably *Porcellio scaber*), four *Mimopeus* sp. (Coleoptera: Tenebrionidae), as well as five *Prodontria modesta* (Broun 1909) (Coleoptera: Scarabaeidae), which is a species of conservation significance (Vink et al. 2003; Barratt 2007; Hitchmough et al. 2007). The 34 arthropods from the second web consisted of 20 *Mimopeus* sp., 13 *Costelytra zealandica* (White 1844) (Coleoptera: Scarabaeidae) and one *P. modesta*. Specimens of *P. modesta* were indentified using Emerson and Barratt (1997) and were confirmed by B.I.P. Barratt (personal communication).

The Australian distribution of *L. hasseltii* estimated by the natural CLIMEX model (Fig. 1a) conformed to the species' known distribution with unsuitable or marginal EI values around the Great Divide and western Tasmania and optimal EI values (≥30) in most other parts of the country. The potential distribution of *L. hasseltii* in Japan estimated by the natural CLIMEX model is shown in Fig. 2a. The areas with the highest EI values (maximum 2) for *L. hasseltii* were around Osaka,

**Table 2** Post-border detections of *L. hasseltii* localities not directly linked to any recent import

Location[a]	Life stages	Date	Source
Whangarei, ND	Adult female	January 1992	MAFBNZ
Maungaturoto, ND	Adult female	March 1990	MAFBNZ
Waiheke Island, AK	Adult female	October 2002	MAFBNZ
Auckland, AK	Adult female	July 1984	OMNZ
Howick, AK	Adult female	December 1985	OMNZ
Mount Wellington, AK	Adult female	December 1999	MAFBNZ
Papatoetoe, AK	Adult female	February 1989	MAFBNZ
Hunua, AK	Adult female	January 2007	MAFBNZ
Drury, AK	Adult female	1980s	Forster (1985)
Pukekohe, AK	Adult female	August 1991	MAFBNZ
Waikawau Bay, CL	2 Adult females	May 1999	MAFBNZ
Coromandel, CL	Adult female	May 1999	MAFBNZ
Thames, CL	Adult female (reared)	March 1989	MAFBNZ
Cambridge, WO	Adult female	June 2005	MAFBNZ
Papamoa, BP	Juvenile female	February 2007	MAFBNZ
Reporoa, BP	Subadult female	March 2005	MAFBNZ
Gisborne, GB	Adult female	February 1998	MAFBNZ
Gisborne, GB	Juvenile female	February 2005	MAFBNZ (specimen at MONZ)
Lake Taupo, TO	Adult female	March 1989	MAFBNZ
Waitara, TK	Juvenile female	May 2006	MAFBNZ
Bell Block, TK	Adult female	2002?	MONZ
New Plymouth, TK	2 Adult females, 2 juveniles	March 1991	MONZ
Taranaki, TK	Adult female	February 2005	MAFBNZ
Wellington?, WN	2 Adult females	June 1983	OMNZ
Seatoun, WN	Juvenile female	October 2008	MAFBNZ
Patriarch Station, MB	Juvenile female	March 2007	MONZ
Greymouth, BR	Not reported	1980s	Forster (1985)
Culverden, NC	Not reported	1980s	Forster (1985)
Twizel, MK	Adult female	1981	Forster (1985)
Glendu Bay, OL	Adult female with eggsac	February 2009	C.J. Vink
Near Wanaka, OL	Population	1981	Forster (1995)
Near Wanaka, OL	Population	1983	Forster (1995)
Near Wanaka, OL	Population	1990	Forster (1995)
Near Wanaka, OL	Adult female	March 1982	Forster (1984)
Wanaka, OL	Adult female with 4 eggsacs	January 1993	OMNZ
Near Bannockburn, CO	Adult female	March 1999	OMNZ
Bannockburn Inlet, CO	Adult female	January 2009	C.G. Wilson
Near Bannockburn, CO	Juvenile female	May 2007	R.H. Kleinpaste
Bannockburn, CO	2 Adult females	January 2008	C.B. Phillips
Central Otago, CO	Adult female	December 2002	MAFBNZ
Galloway, CO	Adult female	June 1999	OMNZ
Alexandra, CO	Adult female	April 1987	MAFBNZ
Alexandra, CO	Subadult female	August 1999	OMNZ
Alexandra, CO	Adult female	October 1999	OMNZ
Alexandra, CO	Juvenile female	March 2005	MAFBNZ

Table 2 continued

Location[a]	Life stages	Date	Source
Alexandra, CO	Adult female	December 2005	MAFBNZ
Alexandra, CO	Adult male	December 2007	C.B. Phillips
Alexandra, CO	3 Adult females, 1 juvenile female	January 2008	C.B. Phillips
Alexandra, CO	Adult female with eggsac	February 2009	C.J. Vink
Te Anau, OL	Adult female	1981	Forster (1985)
Te Anau, OL	Adult female	1982	Forster (1985)
Invercargill, SL	Adult female	October 2003	MAFBNZ
Invercargill, SL	Juvenile female	July 2007	MAFBNZ
Bluff, SL	Juvenile female	October 2007	MAFBNZ

Localities are listed geographically, north–south

[a] The two-letter area codes follow Crosby et al. (1998); *ND* Northland, *AK* Auckland, *CL* Coromandel, *WO* Waikato, *BP* Bay of Plenty, *GB* Gisborne, *TO* Taupo, *TK* Taranaki, *WN* Wellington, *MB* Marlborough, *BR* Buller, *NC* North Canterbury, *MK* Mackenzie, *OL* Otago Lakes, *CO* Central Otago, *SL* Southland
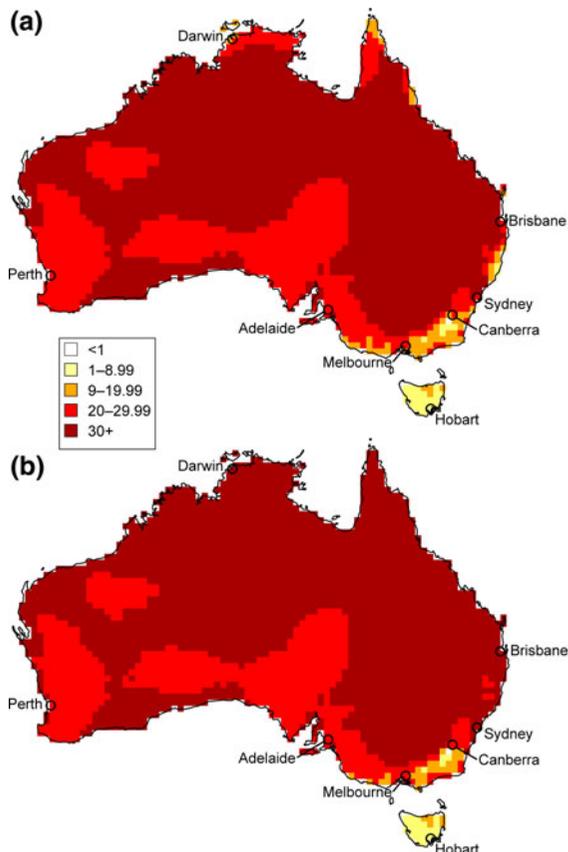
Fig. 1 The climate suitability (EI) for *L. hasseltii* in Australia **a** based on the natural CLIMEX model, **b** based on the urban CLIMEX model; <1 unsuitable, 1–8.99 marginal, 9–19.99 suitable, 20–29.99 favourable, 30 + optimal. *Open circles* are the locations of major cities

where it already occurs (Nihei et al. 2004), and around Tokyo. The model also predicted favourable EI values (≥ 20) in locations (not shown) where it has been reported in India (Patel 1973; Manju and Kumar 2001), the Philippines (Cariaso 1967) and New Guinea (Chrysanthus 1975).

The New Zealand natural CLIMEX model suggested that the only area with a favourable climate for *L. hasseltii* (EI = 20) was around Napier (Fig. 3a). However, suitable EI values (≥ 9) were predicted for areas throughout New Zealand (Fig. 3a). Locations with suitable EI values where *L. hasseltii* has previously been detected included Auckland, Gisborne and Twizel (Table 2, Fig. 3). EI values from each locality where *L. hasseltii* is established are as follows: near Wanaka, 10.8; Bannockburn, 12.9 and 14 (two sites); Alexandra, 9; New Plymouth, 2. The New Zealand areas classified as suitable or favourable became greatly reduced once habitat availability was considered (Fig. 3c).

Due to wet stress, the natural CLIMEX model predicted marginal suitability in Osaka (EI = 2) and New Plymouth (EI = 2), which was inconsistent with the species' persistence there, particularly at Osaka where the redback population has reached high densities (Matsuse et al. 1999; Nihei et al. 2003; Nihei et al. 2004). This discrepancy was addressed by the urban CLIMEX model, in which parameter values relating to wet stress were relaxed and no upper limit to the tolerance of *L. hasseltii* to rainfall was imposed.
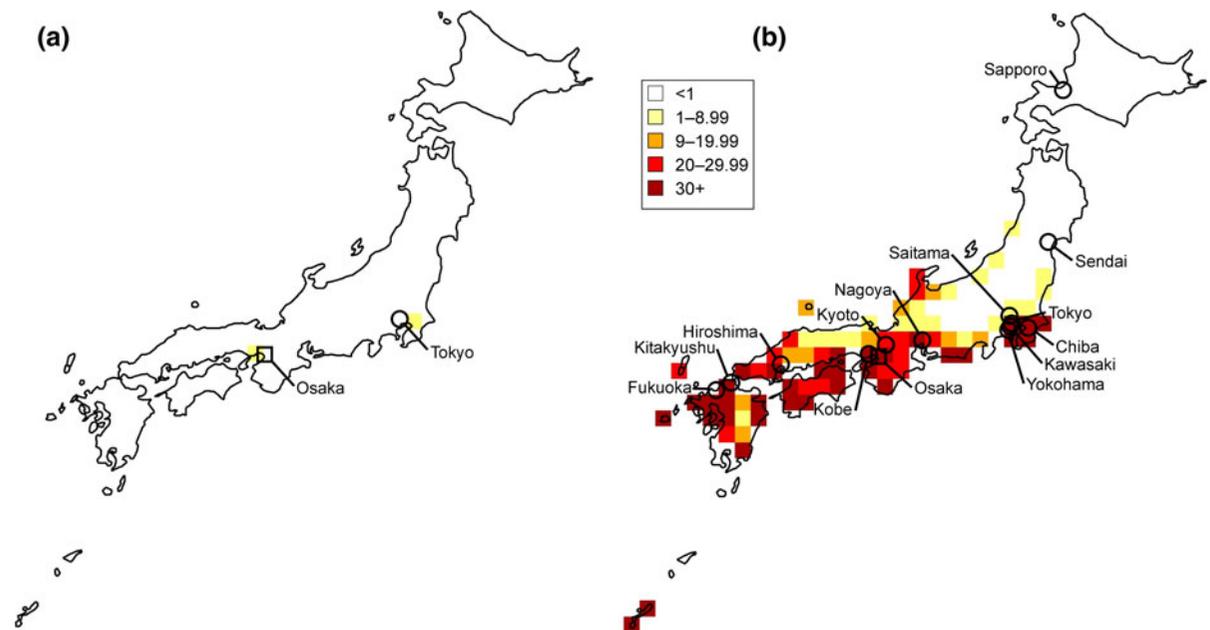
Fig. 2 The climate suitability (EI) for *L. hasseltii* in Japan **a** based on the natural CLIMEX model, **b** based on the urban CLIMEX model;<1 unsuitable, 1–8.99 marginal, 9–19.99 suitable, 20–29.99 favourable, 30 + optimal; open square is Osaka where an *L. hasseltii* population has established, *open circles* are the other 13 major Japanese cities

The results from the urban CLIMEX model are shown for Australia (Fig. 1b), Japan (Fig. 2b) and New Zealand (Fig. 3b). The closer similarity between the natural and urban CLIMEX predictions for Australia (Fig. 1a vs. Fig. 1b), than between those for Japan (Fig. 2a vs.Fig. 2b) and New Zealand (Fig. 3a vs. Fig. 3b), is explained by Australia's much drier climate (Bureau of Meteorology 2003) where rainfall has a lesser influence on the distribution of *L. hasseltii*. Under the urban CLIMEX model, the EI values for New Plymouth and Osaka increased from 2 to 13 and 42, respectively. This model also estimated that 12 of Japan's 14 largest cities have EI values of over 34 (Fig. 2b), while suitable EI values (≥9) were predicted for all of New Zealand's main urban areas except Dunedin and Invercargill (Fig. 3c).

The urban CLIMEX model predicted a greater number of worldwide cities would be suitable for redbacks (Fig. 4b) than the natural CLIMEX model (Fig. 4a). The difference between the two models was evident mainly in tropical regions (Fig. 4a vs. Fig. 4b) where rainfall would be too high for redbacks to persist without the shelter afforded by urban environments. The difference between the two models was also evident in temperate countries with

relatively high rainfall, including some cities in Belgium (Fig. 4a) where redbacks have been reported in greenhouses (Blick et al. 2004); Brussels, Antwerp and Gent all went from marginal to suitable.

Discussion

In New Zealand, previous records (Forster 1982, 1984, 1985, 1995; Forster and Forster 1999) and our own observations have confirmed *L. hasseltii* is established in Alexandra, Bannockburn and near Wanaka. Although only four records from around New Plymouth have been backed up by voucher specimens, reliable reports (McCutcheon 1992; M. Langford, personal communication) indicate it is also established there. Other New Zealand records (Table 2) were of single specimens and subsequent searches by biosecurity agents recovered no further spiders. These were probably individuals that had been accidentally imported to New Zealand, or perhaps their first generation offspring, which subsequently failed to found persistent populations. This is supported by observations in Australia and Japan where established populations of *L. hasseltii* are

Fig. 3 The climate suitability (EI) for *L. hasseltii* in New Zealand **a** based on the natural CLIMEX model, **b** based on the urban CLIMEX model, **c** based on overlap of suitable habitats (built up areas, vineyards, low producing grassland and mixed exotic shrubland) with suitable EI values; <1 unsuitable, 1–8.99 marginal, 9–19.99 suitable, 20 + favourable. *Open squares* are localities where *L. hasseltii* populations have established, *open circles* are localities where *L. hasseltii* have been found (see Table 2)
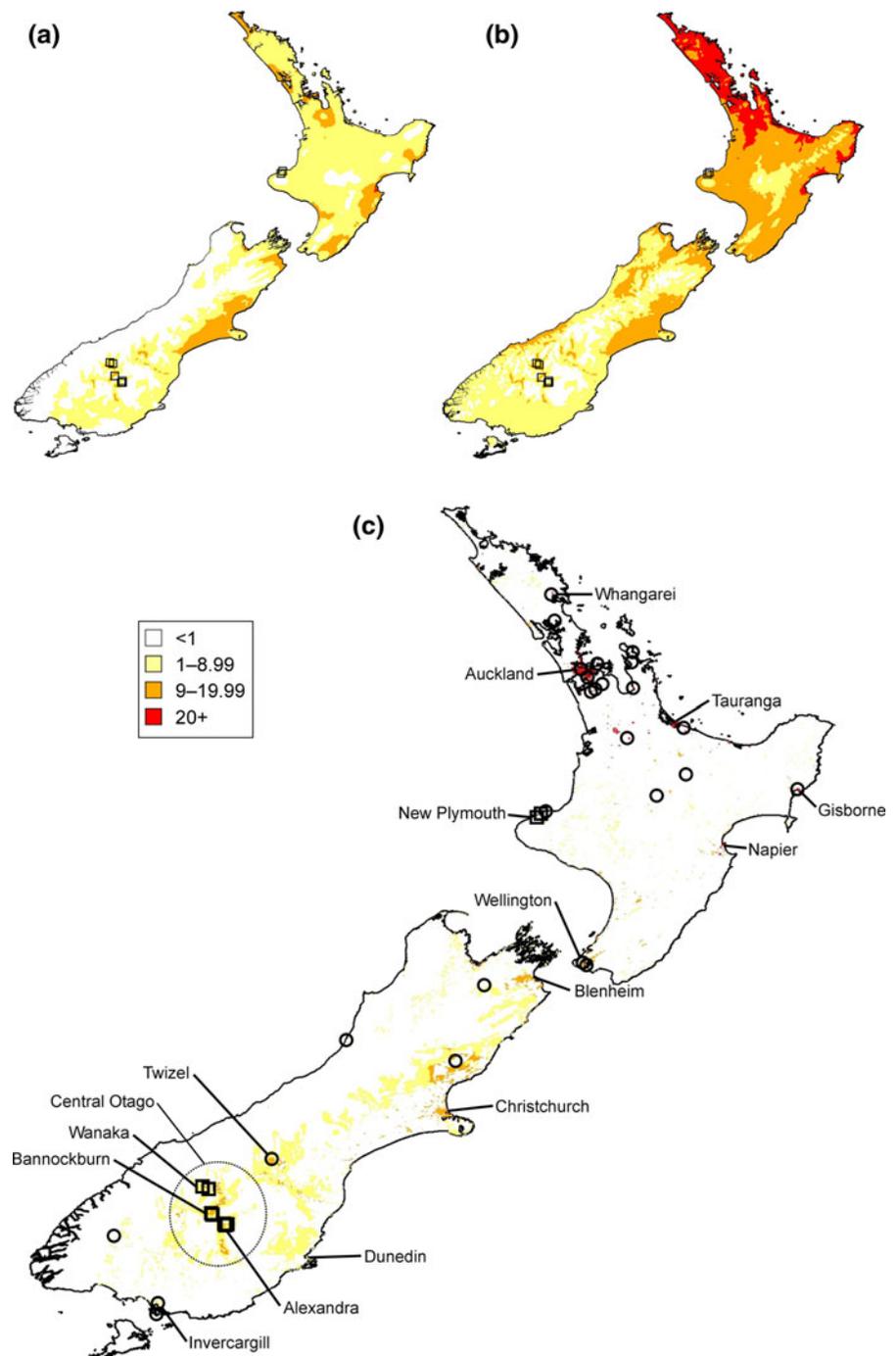
generally manifest as dense groupings of spiders (R.J. Raven, personal communication); a phenomenon we also observed near Alexandra. Numerous anecdotal reports of *L. hasseltii* in other New Zealand areas have not been backed up by specimens and have

tended to dissipate with time, so we have discounted them as evidence of establishment. It is possible for non-experts to mistake introduced species in the sister genus *Steatoda*, which also occur in urban habitats, for *Latrodectus* species.
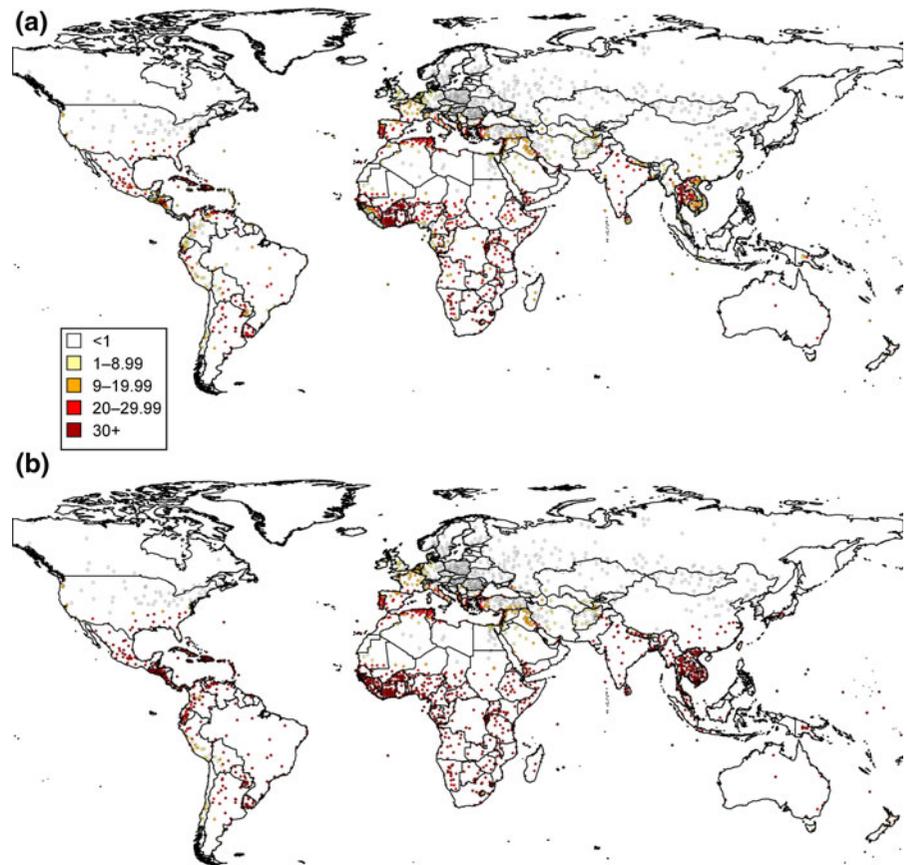
Our prediction of the potential distribution of
L. hasseltii, based on CLIMEX and GIS data, shares
limitations with predictions developed using many
other approaches to species distribution modelling;
this includes reliance on haphazardly collected
occurrence data (Elith et al. 2006), use of current
distribution data that may not span all of the species'
environmental tolerances (Elith and Leathwick 2009;
Sutherst and Maywald 2005), an absence of poten-
tially important model parameters other than those
pertaining to climate and habitat availability (Hulme
2003; Samways 2003; Sutherst et al. 2007a), and
difficulties with validation (Elith and Leathwick
2009; Sutherst and Bourne 2009). Nonetheless,
CLIMEX predictions have proven accurate in other
studies (Sutherst et al. 2007a; Sutherst and Bourne
2009) and ours, further refined with data on habitat
availability, have clearly illustrated that our hypoth-
eses (urban habitats enable *L. hassletii* to escape
its natural climatic limitations and thereby create
high potential for it to significantly increase its

international distribution) are robust, and worthy both
of further scientific scrutiny and precautionary action
by biosecurity authorities.

The presence of *L. hasseltii* in Japan, Belgium and
New Zealand, combined with our modelling, dem-
onstrates there is potential for redbacks to establish
throughout much of the world. Its capacity to disperse
in association with international trade is evidenced by
interception records from quarantine inspections of
cargo (Reed and Newland 2002, Biosecurity New
Zealand 2007, MAF Biosecurity New Zealand,
unpublished data). It is possible that the global
distribution of *L. hasseltii* is greater than records
suggest because small founder populations can be
difficult to detect. Female redbacks build webs in
inconspicuous localities and remain in the web, while
males are unlikely to be noticed because they are
relatively short-lived, considerably smaller (body
length of 3–4 mm) and less conspicuous than
females. In New Zealand, all post-border detections
were of females or immature females, and only one

male has been recorded, which we found during a specific search for males. In Osaka, *L. hasseltii* was not recorded until large numbers were found in late 1995 and it is likely to have gone unnoticed for some years before then (Ori et al. 1996). It is also possible that many incursions of *L. hasseltii* go undetected and perish before they are noticed.

Qualitatively, current records of established redback populations exhibit little correspondence with our estimates of climatic suitability and habitat availability. For example, although numerous cities appear to be suitable or favourable for redback establishment (Fig. 4), so far only Osaka has been invaded. Furthermore, in New Zealand where redbacks might have been expected to first establish in a relatively warm urban area with a major port (e.g. Auckland), they were instead first found in barely suitable localities without major ports (i.e. Wanaka, Bannockburn, Alexandra and New Plymouth). Indeed, post-border detections of redbacks in New Zealand to date have shown little association with major ports, and the number of detections per year does not appear to be increasing with time (Table 2) despite the increasing volume of imports from Australia and Japan (Statistics New Zealand 2009). The apparently capricious nature of redback establishments is reinforced by its presence in greenhouses in Belgium (Blick et al. 2004), where the urban CLIMEX model predicts suitable climates in some cities. The initial spread of redbacks from Australia to Japan and New Zealand can perhaps be rationalised by these countries' relative proximity and their strong trading relationships, but there are few other readily explained patterns in the redback records. This could be the outcome of numerous factors including stochasticity in the probability of establishment, regional and temporal variations in search effort and reporting, variable quarantine management regimes at different locations, and insufficient understanding about redback invasion pathways and establishment processes. Nevertheless, we suggest that new records of redback establishments are likely to increasingly conform to our hypothesis as the sample size increases. We therefore argue that our models currently offer the only rational means both of ranking the locations that are vulnerable to redback introductions, and of allocating resources for minimising the species' spread between and within countries.

The urban CLIMEX model indicated that most New Zealand urban areas are suitable or favourable for further redback establishments, which may occur either by dispersal within New Zealand from Central Otago and New Plymouth, or through further accidental introductions from overseas. The Auckland metropolitan area (including Howick, Mount Wellington and Papatoetoe; Table 2) appears to be particularly vulnerable because there have already been multiple detections in that area (Table 2, Fig. 3), and it is the point of arrival of 39% of all New Zealand's import cargo, 18% of which comes from Australia (Statistics New Zealand 2009). Whangarei, Tauranga, Gisborne and Napier (Fig. 3c) are other North Island port cities also favourable for *L. hasseltii* establishment. Gisborne and Napier also have potentially suitable non-urban habitats near them, mainly vineyards. There are no favourable areas in the South Island, but the built up area of Blenheim is surrounded by numerous vineyards (Fig. 3c), which together coincide with suitable climate for *L. hasseltii*. The urban area of Christchurch is also suitable and is adjacent to a busy port.

The CLIMEX predictions for *L. hasseltii* were based on climate data for the period 1960–2004 for New Zealand, and 1961–1990 for the rest of the world. However, if climate change continues as predicted, then eastern areas in New Zealand will become warmer and drier (Hennessy et al. 2007), as will many other worldwide localities (Parry et al. 2007), which will likely increase their climatic suitability for *L. hasseltii*.

Conservation impacts of *L. hasseltii* establishment

Although we did not investigate the suitability of non-urban habitats for countries other than New Zealand, it is likely that areas suited to *L. hasseltii* exist in other countries. Like other invasive arthropod predators (Snyder and Evans 2006), *L. hasseltii* could impact on native arthropod communities as it invades non-urban habitats both in New Zealand and elsewhere. The webs we examined from near Alexandra contained the beetle *P. modesta*, which is already restricted to a small area around Alexandra (Vink et al. 2003; Barratt 2007; Hitchmough et al. 2007), and our results suggest it is under further pressure from *L. hasseltii*. Similarly, we found many specimens of *Mimopeus* sp. in the webs, and 14 *Mimopeus*

spp. are listed as "range restricted" by the Department of Conservation (Hitchmough et al. 2007). About 63% of the prey of *L. hasseltii* found near Wanaka were *Odontria* spp. (Forster and Forster 1999), which are closely related to *Prodontria* (Emerson and Wallis 1995) and share similar habitats. Another species likely to be predated by *L. hasseltii*, therefore, is the "nationally endangered" Cromwell chafer beetle, *Prodontria lewisii* Broun 1904 (Barratt 2007; Hitchmough et al. 2007); redbacks have been seen in a nature reserve established especially for this beetle at Cromwell (B·I.P. Barratt personal communication), although none was found during a search of the reserve by CBP in January 2008.

The natural CLIMEX model of world cities (Fig. 4) suggests *L. hasseltii* has potential to establish in many localities where other *Latrodectus* spp. are already found (Levi 1959; Garb et al. 2004), and competitive displacement of indigenous *Latrodectus* spp. by *L. hasseltii* could occur, as it has in other spiders (Nyffeler et al. 1986; Hann 1990; Bednarski et al. 2010). *Latrodectus geometricus* has been accidentally introduced to southern California where it is thought to be displacing *L. hesperus* (Vincent et al. 2009), and in New Zealand there is potential for *L. hasseltii* to displace *L. katipo*, a closely related endemic species (Garb et al. 2004; Griffiths et al. 2005; Vink et al. 2008) that is now classified as in "serious decline" due to human activities (Patrick 2002; Hitchmough et al. 2007). To date, *L. hasseltii* has not been recorded from sand dunes where *L. katipo* occurs, and its potential to invade this habitat remains uncertain. However, another exotic theridiid *Steatoda capensis* Hann 1990 is now common in New Zealand sand dunes and its superior ability to re-colonize disturbed habitats may be contributing to the decline of *L. katipo* (Hann 1990).

Invasive species can bring about a form of extinction by hybridization (Rhymer and Simberloff 2003). This is a further threat to *L. katipo* as laboratory studies have shown that *L. hasseltii* males can mate with *L. katipo* females, although *L. katipo* males are rejected by *L. hasseltii* females (Kavale 1986; Forster 1992, 1995). Genetic evidence of interbreeding between the two species has been found at a site near Gisborne (Vink et al. 2008) where post-border detections of *L. hasseltii* have been recorded (Table 2) and where our models suggest

suitable habitat and climate are coincident (Fig. 3c). It is, therefore, possible that an unreported population of *L. hasseltii* exists in the Gisborne area.

In addition, accidental introductions of egg parasitoids of *L. hasseltii* via host eggsacs represent hazards to native *Latrodectus* spp. and their close relatives, some of which will be naïve to parasitism. In New Zealand there are no known parasitoids of the endemic *L. katipo*, but in Australia, egg parasitoids of *L. hasseltii* include *Eurytoma arachnophaga* (Girault 1925) and *E. latrodecti* (Fullaway 1953) (Hymenoptera: Eurytomidae), and an undescribed *Paraphylax* sp. (Hymenoptera: Ichneumonidae) (Austin 1985; Bouček 1988). *Eurytoma latrodecti* was originally described from Hawaii (Fullaway 1953) and has also been found in Florida (Brambila and Evans 2001), but the origin of this species is uncertain and there are related species in Africa and Australia (Fullaway 1953; Bouček 1988; Lotfalizadeh et al. 2007). Eggsacs of *L. hasseltii* have been accidentally transported into New Zealand in imported vehicles (Biosecurity New Zealand 2007).

Latrodectus hasseltii also has potential to impact vertebrates in its invaded range because it captures and kills lizards in Australia (McKeown 1952; Raven 1990; Orange 2007). In New Zealand, there is both suitable climate and habitats for *L. hasseltii* in several parts of Central Otago where redbacks could predate endangered skinks, as both animals inhabit similar habitats there. No predation of lizards has been observed in artificial shelters shared with *L. katipo* in New Zealand (Lettink and Patrick 2006), but *L. katipo* is smaller, less aggressive and has a weaker web than *L. hasseltii* (Forster 1985), so is less likely to capture and kill a lizard.

Human health impacts of *L. hasseltii* establishment

Our models and previous observations of *L. hasseltii* in populated places (Forster 1985; Kavale 1986; Matsuse et al. 1999; Nihei et al. 2004) indicate that *L. hasseltii* has potential to establish in numerous cities throughout the world where they would likely be encountered by humans. In Australia, *L. hasseltii* bites are the most common cause of potentially serious envenomation of humans (Mead and Jelinek 1993; Sutherland 1983, 2001; Isbister and Gray 2003). There were at least 13 recorded deaths in

Australia prior to the late 1950s (Sutherland 2001), but since the development of an antivenom in 1956 there have been no further fatalities (Sutherland 1983; Mead and Jelinek 1993).

Female *L. hasseltii* are of greatest concern, since the sexes are strongly dimorphic and the smaller males are usually incapable of biting through human skin (Sutherland 1983). Although two cases of bites by a male and a subadult male have been reported, the effects were not as serious as those of bites by females (Isbister and Gray 2003). Hybrid males of *L. hasseltii* and *L. katipo* can be as large as females (Kavale 1986), which, coupled with the tendency of males to wander in search of females, could increase the frequency and severity of male bites in New Zealand.

In Osaka, the number of bites increased in proportion with the density of spiders (Nihei et al. 2003) and this may also occur as *L. hasseltii* invades urban areas elsewhere. In New Zealand, redbacks are already a health and safety concern in some vineyards around Bannockburn (Waterworth 2009). Increased contact between *L. hasseltii* and humans in urban areas could also have significant social and cultural impacts. Arachnophobia is one of the most widespread forms of specific phobia; sufferers experience intense fear of spiders and develop strong spider avoidance behaviours (Paquette et al. 2003). New Zealand is relatively free of venomous organisms (Slaughter et al. 2009) and most of its citizens are unaccustomed to dealing with them, particularly at home or work. Public education could be useful for minimising the number of bites, but might also increase anxiety. This is already an issue with widespread myths surrounding the danger to human health associated with white-tail spiders (*Lampona* spp.) in New Zealand (Derraik et al. 2008).

Conclusions and recommendations

The presence of *L. hasseltii* in New Zealand and Japan, and the climatic suitability of numerous other countries are of public health concern, since the species has the potential to become established in a number of areas where it would likely be found in close association with human dwellings. If *L. hasseltii* were to establish in major urban areas, sufficient stocks of antivenom would need to be maintained in hospitals and the public be educated of the dangers. In addition, *L. hasseltii* could have negative impacts on native arthropod communities as a predator or by displacement of other species. So far, populations of redbacks have only been recorded in parts of New Zealand (Central Otago and New Plymouth), Japan (Osaka) and in greenhouses in Belgium. In New Zealand, a delimiting survey, especially targeting areas where suitable climates and habitats overlap (Fig. 3c), would be a valuable tool to identify the actual distribution of *L. hasseltii*. Assuming that the current distribution of *L. hasseltii* is indeed somewhat limited, eradication of geographically limited population(s) may be viable. However, because redbacks are found in the vicinity of endangered invertebrates, new species-specific methods would need to be developed, which could also be applicable to border quarantine.

Surveillance should be undertaken at major ports near suitable urban areas (Figs. 2b, 3c, 4) and where cargo from Australia is unloaded (e.g., McNeill et al. 2009). If climate change continues as predicted, many other urban areas and suitable habitats around the world will become more suitable for *L. hasseltii*.

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