

The bionomics of an invasive species *Sitona lepidus* during its establishment in New Zealand

P.J. Gerard^{1*}, S.L. Goldson², S. Hardwick², P.J. Addison^{1†}
and B.E. Willoughby^{1‡}

¹AgResearch, Ruakura Research Centre, Private Bag 3123, Hamilton 3240,
New Zealand; ²AgResearch, Private Bag 4749, Christchurch 8140,
New Zealand

Abstract

The egg, larval, pupal and adult abundance of the clover root weevil *Sitona lepidus* Gyllenhal (Coleoptera: Curculionidae) was monitored at three sites for the first ten years following the discovery of this exotic pest in the Waikato region of New Zealand. The species went through an initial boom and bust cycle at two sites, with populations reaching up to 1800 larvae m⁻². Thereafter, winter larval populations were relatively stable, ranging between 450–750 m⁻². Unlike in the Northern Hemisphere, *S. lepidus* was found to have two generations a year in the Waikato region of New Zealand. Pasture white clover content at the time of peak adult numbers was positively related to the subsequent peak larval populations for each generation. The factors contributing to the emergence of *S. lepidus* as one of the most important pasture pests in New Zealand are discussed.

Keywords: *Sitona lepidus*, white clover, invasive pest, boom and bust

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Introduction

New Zealand's primary industries are highly dependent on introduced plant and animal species. Through geographic isolation, this country has remained relatively free of pests and diseases; and, in combination with a favourable climate, such circumstances have created a valuable trade advantage. However, the species paucity in New Zealand's relatively simple production ecosystems continues to make them very susceptible to invasion. It has been found repeatedly that when a new species arrives, it will often exhibit explosive invasive characteristics (Barlow & Goldson, 2002).

A recent example is the clover root weevil (*Sitona lepidus* Gyllenhal (Coleoptera: Curculionidae)). This was first confirmed in 1996 in pastures at the Ruakura Research Centre dairy farm (37°46'S, 174°27'E) near Hamilton in the North Island, and retrospective examination of stored samples from the site indicated the species had been present at Ruakura since May 1994 (Barratt *et al.*, 1996). The species' size, cryptic colouring and behaviour, and close similarity in appearance to *Sitona discoideus* Gyllenhal, a species already present in New Zealand, all contributed to the lag in detection. Between February 1995 and April 1996, its distribution was assessed based on a broad survey of North Island pastures combined with retrospective inspections of stored samples from other surveys (Barker *et al.*, 1996). It was subsequently confirmed that eradication would be impossible; the weevil was distributed throughout the Waikato basin, coastal areas of the Bay of Plenty and in North Auckland (Willoughby & Addison, 1997). Thereafter, *S. lepidus* advanced through the North Island at approximately 10–70 km per year (Hardwick *et al.*, 2004). It was confirmed to be well established in Wairarapa at the

*Author for correspondence

Fax: 64 7 838 5073

E-mail: pip.gerard@agresearch.co.nz

†Current address: Nufarm NZ Ltd, PO Box 22407, Auckland 1640, New Zealand

‡Current address: 8 Bond St, Hamilton 3216, New Zealand

southern end of the North Island in 2005, in Nelson at the northern end of the South Island in 2006 and, following capture of a single adult in a semiochemical trap, extensive sampling showed low levels were present also around Christchurch in 2006 (Phillips *et al.*, 2007).

Researchers in Northern Ireland have deduced that the weevil has a significant role in reducing clover persistence (Mowat & Shakeel, 1988a; Leydlaw & Mowat, 1991). The latter observed that regular pesticide application to ryegrass (*Lolium perenne* L.)/white clover (*Trifolium repens* L.) sward infested by this pest more than trebled the white clover content in two years, compared to untreated pasture. Generally, in England, *S. lepidus* was not thought to pose a threat to established swards, although the destructive effects of the weevil in seedling establishment had long been widely recognised (e.g. Clements & Murray, 1993; Murray & Clements, 1995). The species does not appear to be a major problem elsewhere (Barker *et al.*, 1996).

Soon after discovery, it became apparent that with the combination of a favourable environment and high fecundity, *S. lepidus* was inevitably going to become one of New Zealand's most damaging pests of white clover (Willoughby & Addison, 1997). Unlike the situation in much of Europe and North America, *S. lepidus* in the Waikato region of New Zealand exhibits two generations a year with adult populations peaking in early and late summer (Gerard *et al.*, 1999). Further, the adults can live for several months with the females laying up to several hundred eggs (Markkula, 1959). Neonate larvae mainly feed on clover (*Trifolium* spp.) root nodules; and, thereafter, as they mature, they move onto the roots and stolons (Gerard, 2001). Adults feed on the foliage of clovers (Murray & Clements, 1994). Dispersal by flight occurs during the summer and is facultative with the proportion of adults having flight or reproductive capability dependent on prevailing climatic conditions. A greater proportion of the female population is reproductive when there is abundant clover and summer rainfall or irrigation and less when there is drought (Addison *et al.*, 1998; Willoughby & Hardwick, 1999; Gerard & Arnold, 2002).

The discovery of *S. lepidus* early in the invasion phase provided a rare opportunity to study the dynamics of invasion and establishment. This paper summarises population behaviour at three sites during the first ten years of *S. lepidus* in the Waikato region.

Methods

Sites

All three Waikato sites were non-irrigated dairy pasture located on well-drained silt loam soils.

1. Ruakura (37°46'S, 174°27'E). This was a research farm site where population census data were being gathered for the Argentine stem weevil *Listronotus bonariensis* (Kuschel) and its parasitoid *Microctonus hyperodae* Loan (Barker & Addison, 2006), and where *S. lepidus* was first confirmed. The dairy pasture at this site was established in 1991 and consisted of a mixture of *Lolium multiflorum* Lam., *L. perenne* L. and *T. repens* L. The site was terminated in 2001 when the site required pasture renewal for other purposes.
2. Springdale (37°32'N, 175°33'E). From existing research on this privately-owned farm, it was known that *S. lepidus* was not recorded prior to 1996. However, it is likely that it

was present earlier at very low densities as at Ruakura. The site selected was in long term *L. perenne*/*T. repens* pasture (greater than ten years old) and sampling commenced in December 1996.

3. Otorohanga (38°12'N, 175°22'E). This privately-owned farm was offered as a study site prior to any record of *S. lepidus* in the district in 1997. The site comprised long-term *L. perenne*/*T. repens* pasture (greater than ten years old). Sampling commenced in August 1997 when *S. lepidus* was detected and terminated in February 2003.

Monitoring of *S. lepidus* field populations

At the Ruakura site, adult *L. bonariensis* populations were sampled at weekly intervals by taking 50 soil cores 75 mm diameter × 100 mm deep randomly throughout the site from mid-1991 onwards. The invertebrate fauna were, thereafter, removed using a wet-sieving and flotation technique reported by Barker & Addison (1989), sorted, the *L. bonariensis* counted and all weevil stages present pooled and preserved. This material, thus, allowed useful retrospective assessment of the presence of *S. lepidus* and its approximate population densities.

At the other sites, and Ruakura from August 1997 onwards, *S. lepidus* was sampled in a similar manner. Thirty soil cores (100 mm diameter × 100 mm deep) were taken randomly along an approximate 50 m transect, initially at three weekly intervals and, from early 2003 onwards, monthly. The transect started approximately 5 m away from paddock edge and while the same transect was not used each time, it generally crossed the middle of the paddock. The exception was when break-feeding of stock had commenced within the paddock, whereupon sampling was carried out on the ungrazed section of the site. The *S. lepidus* larvae, pupae, adults and eggs were extracted and counted from these cores using a modification of the above wet-sieving and flotation technique. The eggs were extracted by passing all remaining floating material through a 600 µm sieve, and the material retained on a 250 µm mesh sieve was searched for eggs. Egg counts were discontinued at the Ruakura site in 1998 and at the Otorohanga and Springdale sites in 2002 and early 2003, respectively, because there was insufficient resources to continue this labour-intensive assessment.

From December 2003, additional sampling for adults was carried out using a Vortis® suction insect sampler (Burkard Manufacturing Co. Ltd, Rickmansworth, Hertfordshire, UK). The machine was operated at five randomly chosen points within an area of approximately 2 m² for five seconds at full throttle to maximise collection of adults sheltering and clinging to material deep in the turf. The total catch was then pooled to constitute one sample. This was repeated across the site alongside the soil core transect to give a total of ten samples.

Pasture clover

Pasture clover was estimated in a similar manner as described by Lodge *et al.* (2003). At each *S. lepidus* population sampling occasion, visual assessments were made of ten randomly placed 64 × 40 cm quadrat along a diagonal transect across the paddock. Two experienced persons each estimated the percentage bare ground, clover, grass and

broadleaf weed cover independently and an average was obtained. Pasture herbage cuts, at approximately 2 cm above ground level, were taken from within representative quadrats and dissected into grass, clover and weed components as follows: Ruakura, September 1997–June 2001; Springdale, December 1996–February 2003; Otorohanga, August 1997–February 2003. The means from the dissections were used to calibrate visual estimates to obtain an overall estimate for each date.

Data analyses

As the population data were skewed rather than normally distributed, the data for each sampling date were normalised using log transformation. The estimated means and standard errors were back-transformed for presentation. Standard errors and confidence intervals could not be calculated for *S. lepidus* population estimates based on retrospective counts from pooled weevil fauna preserved at each collection date during the 1995–1997 *L. bonariensis* census collections at the Ruakura site.

Results

Patterns of *S. lepidus* establishment and population trends

After the discovery of adult *S. lepidus* at the Ruakura site in March 1996, retrospective inspection of preserved soil weevil fauna showed no larvae or pupae present until small peaks in February 1996 (fig. 1b, c). The adults reached a summer peak in February 1997 of 135 m^{-2} with a smaller second autumn generation peak of 90 m^{-2} in late April (fig. 1d). There was considerable overlap between these peaks but the second peak immediately followed a pupation peak in late February (fig. 1c) and coincided with the presence of teneral adults in the samples. Oviposition by the combined population led to a very high (and destructive) winter larval population that peaked at 1291 m^{-2} in September 1997 (fig. 1b). This resulted in a spring pupal density of 138 m^{-2} in late October (fig. 1c), which in turn produced a summer adult population of 110 m^{-2} in late January 1998 (fig. 1d).

While there were similar spring adult emergence patterns in the subsequent seasons, this did not necessarily apply to the autumnal generations. Beyond the 1996–1997 season, the autumn pupal generation was consistently lower than the spring generation (fig. 1c) with resultant small adult generations (fig. 1d). The corresponding winter larval populations collapsed to 200 m^{-2} in late August 1998 and $<35\text{ m}^{-2}$ in May 1999 (fig. 1b). There was a late recovery to 215 larvae m^{-2} in September 1999. This grew to 737 m^{-2} in early September 2000 and almost 477 m^{-2} by May 2001 (fig. 1b).

At the Springdale site, *S. lepidus* adult and immature stage populations showed a similar 'boom and bust' pattern during 1996–1999 (fig. 2a–d), again with a very large 1997 winter (late May) larval population that peaked at 1805 m^{-2} , fell in 1998 to a maximum of 207 m^{-2} , then recovered in 1999 to over 400 m^{-2} . The egg data shows relatively few eggs were present during most of 1998 and 1999 compared to winter 1997 and 2000 onwards (fig. 2a). As at the Ruakura site, the *S. lepidus* population recovered in late 1999, and the 1999/2000 summer larval generation was of similar size to that in 1996/1997. However, although the 2000 winter larval

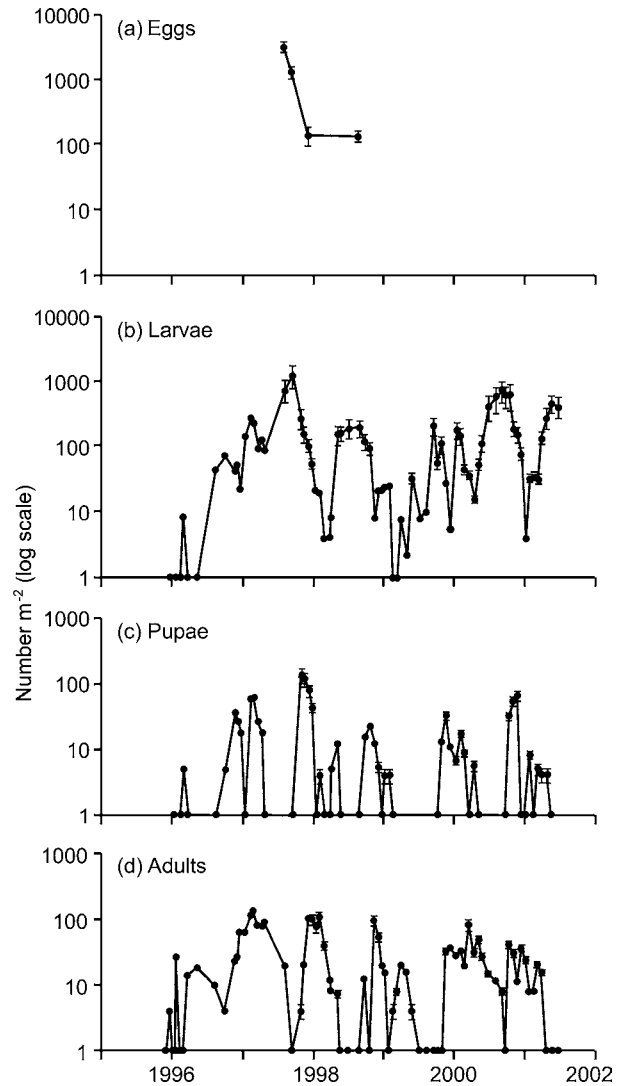


Fig. 1. *S. lepidus* populations ($\pm 95\%$ CI) at Ruakura from December 1995 to June 2001: (a) eggs m^{-2} ; (b) larvae m^{-2} ; (c) pupae m^{-2} ; and (d) adults m^{-2} .

generation almost reached 1000 m^{-2} , subsequent larval populations over the next five years were generally stable, peaking between $450\text{--}650\text{ m}^{-2}$ in late winter/early spring.

The seasonal pattern of the *S. lepidus* developmental stages at the Otorohanga site were similar to those of the other sites (fig. 3). As sampling commenced at this site when the weevil was first observed in the district, initial populations were low in comparison. However, while larval (figs 1b and 2b) and pupal (figs 1c and 2c) abundance declined markedly at the other two sites in 1998/1999 in the winter, abundance increased at Otorohanga. Larval populations appeared to continue upwards although they never exceeded 600 m^{-2} over the five years of observation (fig. 3c). Notable also were steady winter increases in larval abundance into spring, indicating on-going recruitment until the abrupt reductions coinciding with the onset of pupation in October/November each year.

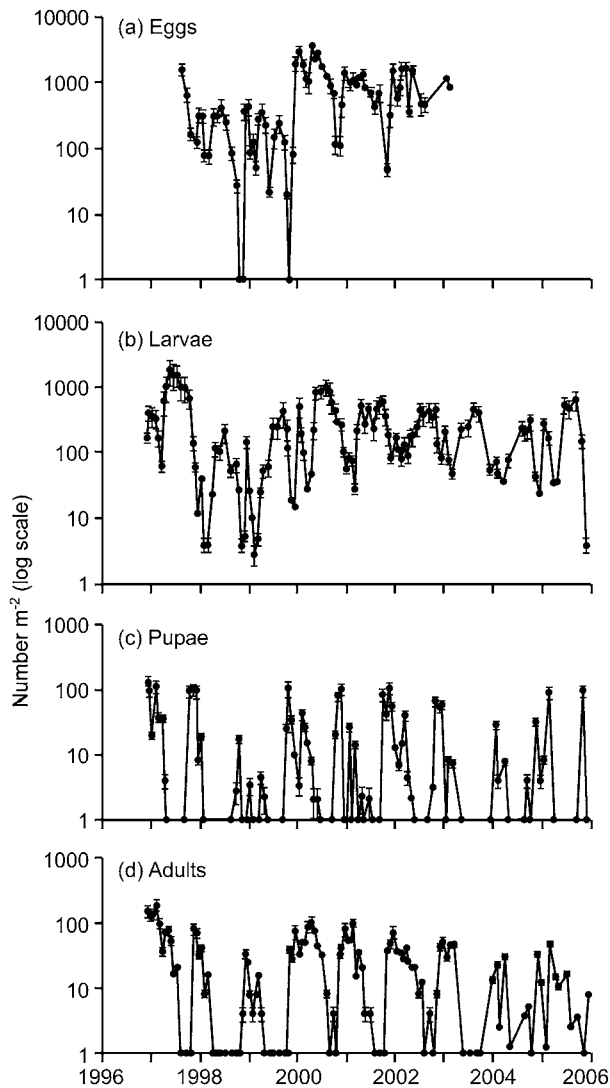


Fig. 2. *S. lepidus* populations ($\pm 95\%$ CI) at Springdale from December 1996 to December 2005: (a) eggs m^{-2} ; (b) larvae m^{-2} ; (c) pupae m^{-2} and (d) adults m^{-2} .

Pasture clover

Clover cover between September 1997 and June 2001 at the Ruakura site, where *S. lepidus* was well established, averaged $9.6 \pm 1.1\%$. It was generally found to peak at *ca.* 20% in summer (January–February) and reached a low of *ca.* 5% in late winter/early spring (July/August) (fig. 4a).

At the Springdale site (fig. 4b), monitoring commenced in 1997, which coincided with maximum clover and *S. lepidus* larval abundance; thereafter, the clover cover declined rapidly and remained at $<10\%$ until late 1998, when it recovered to *ca.* 20% and remained at such a level from May 1999–May 2000. In June–October 2000, clover content declined to *ca.* 7%, coinciding with a resurgence in larval numbers at this time (fig. 4b). Subsequently, clover levels were generally between 10% and 20% in 2001 and 2002 and eventually reached 20–30% in 2003. Monitoring ceased in 2004, and the farmer commenced application of low levels of

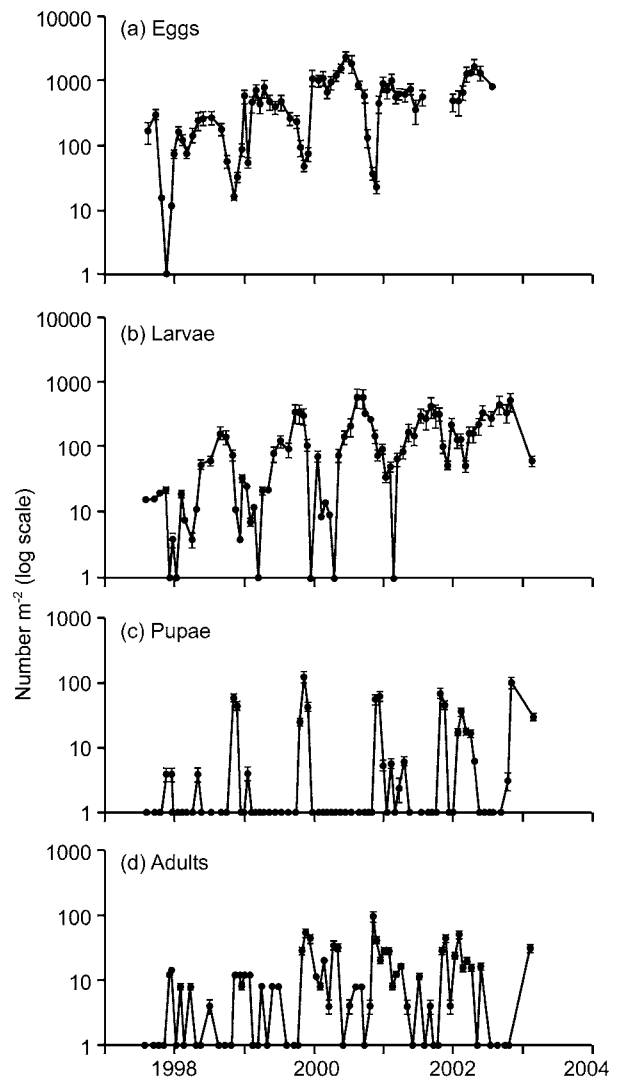


Fig. 3. *S. lepidus* populations ($\pm 95\%$ CI) at Otorohanga from August 1997 to February 2003: (a) eggs m^{-2} ; (b) larvae m^{-2} ; (c) pupae m^{-2} and (d) adults m^{-2} .

urea. The level used ($30 \text{ kg N ha}^{-1} \text{ annum}^{-1}$) was likely to enhance rather than depress clover performance in the presence of *S. lepidus* (Eerens & Hardwick, 2003).

The commencement of Otorohanga site clover cover monitoring (fig. 4c) coincided with the first observations of *S. lepidus* on-farm, and the data demonstrated most clearly the then anecdotal reports of the impact the invasion of *S. lepidus* had on Waikato pasture clover levels (Eerens *et al.*, 1998). Whereas in the first instance, clover cover was generally $>30\%$ and only once dropping $<20\%$ in the first year of monitoring, from mid-1999 onwards, mean cover remained at a low of around 9% (fig. 4c).

The influence of clover cover on larval abundance

Regression analysis of the largest data set (Springdale site) demonstrated that the percent clover cover at one month after the time of peak adults (about the time of peak

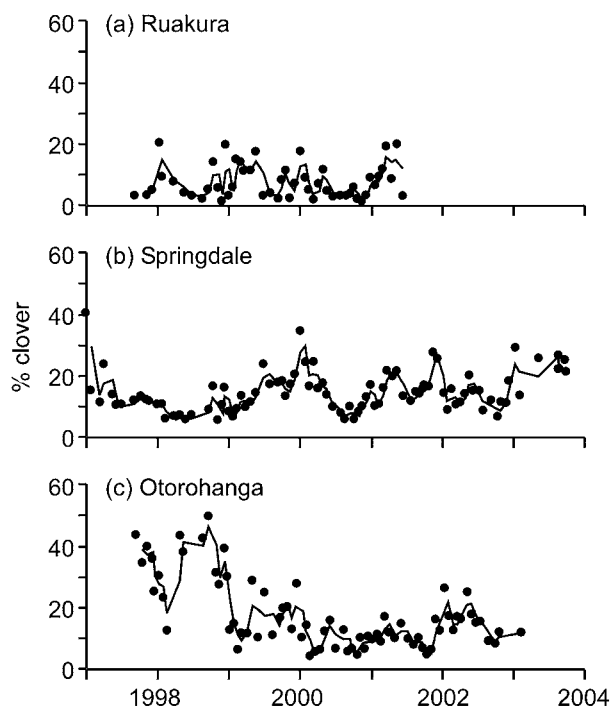


Fig. 4. White clover content in pastures at three Waikato sites 1997–2004. Solid lines show moving average for each site.

larval establishment) populations significantly influenced ($P < 0.05$) the subsequent peak larval populations. This was particularly so in the winter months (fig. 5).

Relationship between rainfall and *S. lepidus*

Analysis of the data collected across all sites and seasons showed no apparent direct relationship between monthly or seasonal rainfall and/or temperature and *S. lepidus* egg, larval or adult populations (results not presented). While Addison *et al.* (1998) had shown that the percentage of reproductive females in the Ruakura and Springdale 1997 and 1998 summer populations did vary in apparent accord with rainfall, there was no evidence that climate had a direct effect on the ratios of eggs to adults present or larvae to eggs present in this data set.

Discussion

Ecologically, New Zealand's productive pastures are unique, consisting almost entirely of introduced perennial grasses, white clover and a low level of adventive weeds. The seed was introduced without the biodiversity of the native grasslands from which they originated. Thus, these ecosystems are exceptionally species-poor in that entire families of northern hemisphere plants, vertebrates and invertebrates are absent. Such ecosystems are also very vulnerable to invasive plant herbivores that feed on the dominant species. Examples of New Zealand's pastoral agricultural experience dealing with exotic invasive insect species, including *Listronotus bonariensis* and *S. discoideus*, are outlined by Barlow & Goldson (2002). It can be conjectured

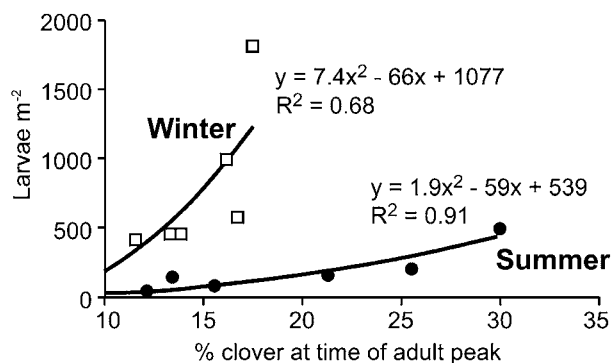


Fig. 5. Relationship between clover present one month after peak spring and autumn *S. lepidus* adult populations and subsequent peak larval populations at the Springdale site.

that this is partly because of a lack of co-evolved natural enemies responsive to rapid increases in pest abundance. Exacerbating this is the continuous presence of an abundant food source, both at the paddock and landscape scale. Finally, within this ecosystem there is little or no competition between related species for resources and niches (e.g. Goldson *et al.*, 1997), thereby further increasing susceptibility to invasion.

Sitona lepidus feeds only on *Trifolium* spp. with a strong preference for white clover (Murray & Clements, 1994; Crush *et al.*, 2008). In keeping with the trends observed with invasive populations of *S. discoideus* in lucerne (Goldson *et al.*, 1986), *S. lepidus* larval survival has been found to increase linearly with increasing availability of root nodules, which provide food and protection for the vulnerable first instar larvae (Gerard, 2001). In both cases, no other invertebrates preferentially utilised the host plant nodule niche, allowing the invading *Sitona* spp. to establish with minimal competition. This study confirmed previous research showing that the abundance of *S. lepidus* larvae is correlated positively to available clover (Gerard *et al.*, 2007) but also indicates that there are seasonal differences with fewer larvae establishing in summer compared to winter irrespective to clover level (fig. 5). There was no apparent direct evidence of rainfall influencing the proportion of eggs developing to subsequent larval populations. Several factors could contribute to lower larval establishment in summer than in winter. These include the proportion of adults capable of reproduction (Addison *et al.*, 1998; Willoughby & Hardwick, 1999), desiccation of egg and first instars (Eerens & Hardwick, 2003), abundance of generalist predators and reduced replacement of nodules when clovers are stressed by soil moisture deficits and heat.

Populations of *S. lepidus* elsewhere in the world have been found to be modest relative to those at the sites reported in this paper. In their survey throughout England, Murray & Clements (1995) at most found mean densities of 16 m^{-2} *S. lepidus* adults. Similarly, in Ireland, Mowat & Clawson's (1996) data indicated peak larval densities of $c.30\text{ m}^{-2}$ and, in England, Murray & Clements (1995) found that combined *S. lepidus*, *S. hispidulus* and *S. lineatus* larval populations peaked at 34–90 larvae m^{-2} .

The Waikato populations of *S. lepidus* were strikingly higher, especially in the initial 'boom' phase, as exemplified by the 1290 larvae m^{-2} observed in this study in September

1997 and the 1400 larvae m^{-2} found by Willoughby & Addison (1997). However, other factors aside from lack of competition for an abundant food resource also contributed to the ongoing abundance.

Prior to the introduction of *Microctonus aethiopoidea* from Ireland in 2006 as a biocontrol agent (Gerard *et al.*, 2006), the New Zealand pasture environment had no natural co-evolved defences against *S. lepidus*. Intensive white clover breeding in New Zealand for improved agronomic performance commenced in the 1920s; but, while there was selection for rust resistance and stem nematodes (Caradus *et al.*, 1996), there was no selection for resistance or tolerance to root herbivores. It is likely that some plant defence or tolerance attributes, present in original genotypes from European and Mediterranean countries where *Sitona* spp. are endemic, have been lost, resulting in the high vulnerability of New Zealand white clover cultivars to *S. lepidus* compared to some other clover species (Gerard *et al.*, 2005; Crush *et al.*, 2007). In addition, while generalist predators and pathogens cause some mortality (Willoughby *et al.*, 1998), there has been no evidence of any density-dependent interactions, presumably because of the presence and abundance of alternative hosts.

A further factor contributing to population abundance is the ability to have two generations a year and year round development in the Waikato region of New Zealand. *Sitona lepidus* is Palaearctic in origin and the number of generations a year is dependent on temperature. In the Northern hemisphere, it is regarded as univoltine, with adults emerging in spring (Levesque & Levesque, 1994) or late summer (Culik & Weaver, 1994; Mowat & Clawson, 1996) and two peaks of adult activity in autumn and spring. However, the pattern of larval, pupal and adult abundance in figs 1–3 provides clear evidence of two generations a year in northern New Zealand. The data shows eggs were abundant at all times except in spring when the majority have hatched and adults were at lowest densities. Generally, egg numbers rose then fell through the winter, with a corresponding increase in larval numbers, most clearly evident at the Otorohanga site (fig. 3). This indicates that winter temperatures in the Waikato were above developmental thresholds. This continual development allows this species to rapidly increase in abundance when conditions are favourable and clover abundant.

The relatively long-term nature of this study enabled demonstration of the impacts of unregulated *S. lepidus* populations on pasture in northern New Zealand. In particular, fig. 4c shows how the proportion of clover tracked downwards to a lower point of equilibrium (ca. 10%) after the arrival of *S. lepidus* in 1997 at the Otorohanga site. However, multiple interacting factors influence pasture clover levels and a 1998 farmer survey showed that, where fertiliser and grazing management restricted stolon exposure in summer and competition from grasses, clover persistence was not necessarily compromised (Gerard *et al.*, 2004). The agronomic impact of the *S. lepidus* populations can be appreciated better when some of these factors are eliminated. A pot trial by Mowat & Shakeel (1988b) demonstrated that one larva per plant is sufficient to cause a significant reduction in clover production. Likewise, Murray & Clements (1998) showed that modest English populations of *Sitona* spp. larvae were able to detach up to 30% of clover root material. In a New Zealand pot trial *S. lepidus* larval feeding reduced white clover dry matter production by 20%

and shoot to root ratios by 50% (Eerens & Hardwick, 2003). Such reports of damage potential have been well supported by small plot trial data from New Zealand. Gerard *et al.* (2007) applied different rates of *S. lepidus* eggs into two-year-old pasture and found mean winter densities of 333 larvae m^{-2} reduced white clover yield by 35% annually, with greatest losses in spring. These levels of larvae were reached most years after the 'boom and bust' phase at the three sites (figs 1–3) and were typical of populations on North Island dairy farms at the time. Modelling estimated that similar *S. lepidus* infestation levels would result in a 16% reduction in profits for a typical Waikato farm unless nitrogen fertiliser was applied to lift pasture production (White & Gerard, 2006). This impact is well in excess of what is observed in Europe and demonstrates the risk exotic invasive species pose to New Zealand agriculture.

In conclusion, the success of *S. lepidus* as an invasive species in New Zealand is due to the combination of environmental and biological factors similar to those shared by other invasive species elsewhere in the world. The new habitat provided favourable abiotic conditions, a continuum of plentiful food resources and contained few natural enemies or competitors. While *S. lepidus* reproduces sexually, the combination of adult longevity, mobility and propensity to mate multiple times (Gerard, personal observation) would help to diminish Allee effects associated with low-density establishing populations (Liebhold & Tobin, 2008). The species has considerable plasticity: the life cycle duration is flexible, enabling it to succeed over a wide climatic range; and the proportion of the population in a reproductive or dispersal physiological state during summer varies with environmental conditions (Gerard & Arnold, 2002). Each female can produce hundreds of eggs in her lifetime, and the species has excellent flight capability. In their initial work, Willoughby & Addison (1997) found an annual rate of dispersal of about 35 km.

The release of a specialist natural enemy, the Irish strain of *Microctonus aethiopoidea* (Hymenoptera: Braconidae), as biocontrol agent for *S. lepidus* in 2006 (Gerard *et al.*, 2006) may modify the pattern of invasion currently taking place in the South Island. Initial modelling suggests that, although the speed of invasion of *S. lepidus* in the presence of *M. aethiopoidea* is unlikely to be different to that observed in the North Island, the size of *S. lepidus* population at any given site is unlikely to reach the levels observed at North Island sites during the initial 'invasion phase' (Kean *et al.*, 2009). With the new natural enemy sharing the same environmental advantages as *S. lepidus*, and having the ability to multiply rapidly by asexual reproduction, it too appears to be a successful invasive species. Following rapid establishment and initial apparent efficacy of the biocontrol agent in reducing adult numbers (Gerard *et al.*, 2008), there is likely to be a shift in *S. lepidus* population dynamics. With the Irish *M. aethiopoidea* well established in the North Island and being introduced into newly-detected South Island *S. lepidus* populations, the New Zealand pastoral industry is hopeful that *S. lepidus* will cease to be of economic importance.

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