Spatial associations between invasive tree lupin and populations of two katipo spiders at Kaitorete Spit, New Zealand

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Abstract: Spatial associations between the invasive tree lupin (Lupinus arboreus), the New Zealand endemic widow spider Latrodectus katipo (katipo), and the introduced South African spider Steatoda capensis (false katipo) were examined within the nationally significant Kaitorete Spit dune system in Canterbury, New Zealand. These dunes are considered to be a stronghold for L. katipo, but with the decline in preferred vegetation for capture-web attachment as a result of tree lupin invasion, a decline in the spider's population was expected. On other New Zealand dune systems a decline in L. katipo abundance has corresponded with an increase in the abundance of the introduced S. capensis. Spider population data collected over a 6-year period and vegetation data collected in 2008 and 2009 were used to examine the spatial associations at Kaitorete Spit. The abundance of S. capensis was not significantly related to the abundance of L. katipo. The ratio of S. capensis to L. katipo declined annually over the 6 years. The 2008 and 2009 vegetation surveys found that S. capensis was not located in areas where tree lupin was present. Latrodectus katipo was found in areas with up to 40% tree lupin cover. The abundance of L. katipo recorded in areas dominated by tree lupin was not significantly different from the abundances recorded in association with native plant cover. The presence of L. arboreus at Kaitorete Spit is not considered to be a direct threat to the population of L. katipo; Kaitorete Spit is still a stronghold.

Keywords: dune system; ecological niche; habitat; Latrodectus katipo; Lupinus arboreus; Steatoda capensis

Introduction

The introduction of invasive alien species into an ecosystem often changes its character, including its species richness and evenness (Huston & Smith 1987; Rejmánek 2000; Ehrenfeld 2003; Simberloff 2005). Such effects can be seen after the introduction of a disease organism, an invertebrate pest or a vertebrate herbivore. Introduced species can, however, also impact on native species at the same trophic level, in essentially the same niche. For example, in American tallgrass prairie the invasive Sorghum halepense (Johnson grass) can displace the native dominant grass Schizachyrium scoparium (little bluestem), with effects on the whole plant community (Rout et al. 2013). In Melbourne, Australia, the Argentine ant (Linepithema humile) competitively displaces native ant species and alters the richness of invertebrate species found in native coastal scrub (Rowles & O’Dowd 2009). The ant achieves dominance, through exploitative and aggressive behaviour, along with the creation of super colonies (Rowles & O’Dowd 2009). The success of non-native species in a foreign ecosystem is often attributed to a higher intrinsic competitive ability displayed by the non-native species (Rowles & O’Dowd 2009; Vonshak et al. 2010), but an alternative explanation is the absence of its natural pests (Torchin et al. 2001; DeWalt et al. 2004), increasing its vigour and population size. Invasion by an alien plant species can also affect species at other trophic levels. For example, Severns (2008) observed that in western USA invasion of native prairie by the alien grass Arrenatherum elatius (tall oat grass) decreased the fitness of populations of the insect Icaricia icarioides fenderi (Fender’s blue butterfly).

As well as the reduction of intrinsic conservation values that occurs when alien species alter ecosystem functions, species richness, or species behaviour, there is often a social effect: something valued by people has been lost (McPherson et al. 1997; Turner et al. 2003). Species conservation and ecological restoration therefore attempt to mitigate current or past negative impacts of alien species (Owen 1998; Timmins 2004). Implementing any form of conservation or restoration management for this purpose requires an understanding of the functioning of the original ecosystem at the particular site, of the degree it is affected by the invading species, and by what mechanism (Thiele et al. 2010). Such information could identify novel and more effective management strategies. However, in some situations ecosystem functions may continue, little affected by alien invasion (Mascano et al. 2012), and on the other hand if functions are altered the effects of the invader may persist for some time after it is removed (Corbin & D’Antonio 2012).

Here we investigate the spatial associations of native and non-native species on a New Zealand sand dune system to determine site-specific information and in light of the results address whether a novel management strategy for a rare spider is evident or even required.

Native katipo

Latrodectus katipo Powell, 1871 (Theridiidae) (henceforth referred to as katipo) is a widow spider endemic to New Zealand’s coastal dune systems (Patrick 2002). The katipo spider was recently classified as an ‘at risk’ species with the rank of ‘declining’ (Sirvid et al. 2012) in view of the reduction in its spatial range over the past 30 years (Hann 1990; Ward 1998; Patrick 2002). Early work established that the katipo was present on most dune systems on New Zealand’s western coasts between Greymouth and Waitara, and sporadically further north, as well as irregularly on the east coast of both islands with its southern limit at Karitane (Fig. 1; McCutcheon
A survey of 90 dune systems across New Zealand, which included all of the locations identified by McCutcheon (1976), was undertaken at the turn of this century to re-evaluate the spider’s distribution (Patrick 2002). Almost 30 years after McCutcheon’s (1976) description of the spider’s distribution, Patrick (2002) found populations remained on only 26 of those 90 dune systems.

Three explanations have been offered for the observed reduction in the katipo’s range: habitat reduction, habitat specialisation, and competition (Griffiths 2001; Patrick 2002; Costall & Death 2009). Firstly, the katipo is a species restricted to the coast, and the modification of coastal dune systems for residential development, forestry, farmland and recreational activities (Hilton et al. 2000; Costall & Death 2009) has reduced the area of active dunes in New Zealand from 129 402 ha to 38 949 ha (Hilton 2006). The effects of this loss are exacerbated by the specialisation of katipo to north-facing dune slopes, and largely to areas with sparsely-distributed *Ficinia spiralis* (Cyperaceae), *Carmichaelia* spp. (Fabaceae), *Muehlenbeckia complexa* (Polygonaceae), and in more northerly areas *Spinifex sericeus* (Poaceae) (Griffiths 2001; Patrick 2002; Costall & Death 2009). It has been suggested that these plant species provide a suitable structure for attaching the spider’s untidy capture webs (Patrick 2002). Driftwood is also an important component of the spider’s habitat, especially when situated within a short distance (< 10 m) from vegetation (Costall & Death 2009). The introduction of *Ammophila arenaria* (marram grass, Poaceae) for dune stabilisation (and subsequent conversion to forest) has resulted in the invasive spread of this sand-binding plant species across the majority of New Zealand’s dune systems (Johnson 1992; Partridge 1992). Densely covering marram grass seems less favourable than native plant species and driftwood for the attachment of katipo capture webs (Smith 1971; Costall & Death 2009). Lastly, the South African spider *Steatoda capensis* Hann, 1990 (‘false katipo’; henceforth referred to as steatoda) has been reported to have similar habitat requirements to katipo (Hann 1990; Costall & Death 2009), and may compete with the native katipo. This is supported by observed declines in katipo abundance that corresponded with increases in steatoda abundance, particularly in the lower North Island (Hann 1990; Patrick 2002; Costall & Death 2009). Although direct competition between these two spiders has not been demonstrated, there is strong evidence suggesting that steatoda is opportunistic and will quickly establish itself when katipo numbers decline (Hann 1990).

**A stronghold for katipo**

Patrick (2002) identified 19 dune systems as strongholds for the endemic katipo spider due to the limited presence or influence of the three factors noted above. One of these is Kaitorete Spit, a dune system of national significance (Johnson 1992) situated on the southern side of Banks Peninsula, separating Lake Ellesmere (Te Waihora) from the Pacific Ocean (Fig. 1). The recorded abundance of katipo at Kaitorete Spit is attributed to the extensive cover of the native sand-binding sedge *Ficinia spiralis* (Burrows 1969; Johnson 1992; Griffiths 2001; Patrick 2002; Lettink & Patrick 2006), the lack of development on the spit, and the scarcity of marram grass.

Although the Kaitorete Spit dune system is identified as suitable for katipo (Patrick 2002), the population may be indirectly threatened by the spread across the central dunes of a non-native nitrogen fixer, *Lupinus arboreus* (Fabaceae; tree lupin). Where tree lupin is established, a change in native plant cover has been observed. The primary concern here is a decline in the native sedge *Ficinia spiralis*, potentially reducing habitat suitable for katipo (Hetherington 2012). If katipo numbers decline, steatoda abundance may increase (Hann 1990). Alternatively, due to its similar habitat requirements, the introduced steatoda may also decline with increasing tree lupin cover and declining native plant cover.

**Tree lupin in New Zealand**

Tree lupin can now be found across the coastal zone, and inland, around New Zealand. This observed distribution of tree lupin is unexpected given its extensive dieback across New Zealand in the late 1980s, attributed to the smut fungus *Colletotrichum gleosporoides* (Molloy et al. 1991; Dick 1994). Sixty percent of the tree lupin plants across the South Island and approximately 95% in the North Island were killed by this fungus (Dick 1994). At that time (1984–1990), Molloy et al. (1991) surveyed a large stand of tree lupin at the western end of Kaitorete Spit, documenting the effect of the fungus. The stand of tree lupin surveyed is likely to have been present since the late 1970s (Hetherington 2012). Molloy et al. (1991) noted that by 1990 the fungus had ‘left the area originally occupied by healthy tree lupin as a virtual sand desert littered with decaying stems’ (p. 352) and concluded that at Kaitorete Spit tree lupin was unlikely to return to its pre-fungal extent. A ground survey of the Kaitorete dune system in December 2002 identified 19 dune systems as strongholds for the endemic katipo spider due to the limited presence or influence of the three factors noted above. One of these is Kaitorete Spit, a dune system of national significance (Johnson 1992) situated on the southern side of Banks Peninsula, separating Lake Ellesmere (Te Waihora) from the Pacific Ocean (Fig. 1). The recorded abundance of katipo at Kaitorete Spit is attributed to the extensive cover of the native sand-binding sedge *Ficinia spiralis* (Burrows 1969; Johnson 1992; Griffiths 2001; Patrick 2002; Lettink & Patrick 2006), the lack of development on the spit, and the scarcity of marram grass.

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Study area
Kaitorete Spit is in fact a barrier beach, of c. 7000 years in age (Armon 1973; Soons 1998; Hart & Bryan 2008) with a younger, globally-rare, area of mixed sand and gravel dune system, 1000 years old (Burrows 1969; Soons 1998). The dunes are known for their extensive cover of *F. spiralis* and a number of locally endemic plant and animal species (Johnson 1992; Davis 2002).

Data collection
Katipo and steatoda abundance
Data on spider abundance were obtained from Department of Conservation annual surveys (in January–March from 2004 to 2009) of 10 transects (1 m wide and 50 m long) that began at the edge of the front dune vegetation and were spaced at 2-km intervals along Kaitorete Spit. Each transect was divided into five 1 × 10 m sections and searched thoroughly to ensure all spiders were counted (A. Spencer, DOC, pers. comm.).

Katipo and steatoda habitat
Spider habitat was surveyed in 2008 and 2009, covering the areas in which the Department of Conservation abundance surveys were undertaken. Each transect was extended to 5-m width to include the surrounding vegetation, which is likely to be part of the spider’s habitat. The 10 transects (5 × 50 m) were each divided into five 5 × 10 m sections for survey. Visual estimates of vegetation, total bare ground and driftwood were made and assigned one of the following cover classes: <5%, 6–10%, 11–20%, 21–30%, 31–40%, 41–50%, 51–60%, 61–70%, 71–80%, 81–90% and 91–100%. Three of the 10 transects fell within the area of dense tree lupin cover, as mapped by Hilton et al. (2006). One of those transects was within an area sprayed in late 2008 with the herbicide clopyralid (Versatill™) by the Department of Conservation in an attempt to control tree lupin spread. Spider habitat was surveyed in 2008 and 2009. The first habitat survey was undertaken in April 2008 before the herbicide was applied, and the second in July 2009, 8 months after the herbicide was applied.

Data analyses
Statistical analysis was undertaken using R (version 2.15.2; R Development Core Team 2012). Statistical significance was assumed at *P* < 0.05 for all statistical tests.

Katipo and steatoda association
The association between katipo and steatoda abundance was examined using the Spearman rank correlation, due to non-normality. The association between spider types – male (M), female (F) and juvenile (J) katipo and the steatoda – blocked by year (2004–2009) was examined with the Friedman test to determine if the abundance of spiders was proportional between spider type and over the 5-year period. The variability in abundance of each spider type (M, F, J and steatoda) recorded annually from 2004 to 2009 was examined using a Kruskal–Wallis test. The general trends in abundance, for each spider type, were determined using a generalised linear model with Poisson errors and a log-link function. The spiders’ distributions along the 50-m transects were analysed using a Kruskal–Wallis test of the total counts of katipo and steatoda across all 10 transects.

The proportions of steatoda and katipo (F, M and J) recorded in 2008 and 2009 across the 10 transects were examined using a chi-square test. Following Costall & Death (2009), a Monte Carlo estimate of exact significance was calculated, as spider frequencies of less than five were expected within the chi-square table.

Habitat preference
The katipo and steatoda habitat preference was determined through a cluster analysis of vegetation cover data in each section, using a flexible sorting strategy (β = 0.25), and the proportional-difference distance measure (PD; Sneath & Sokal 1973), with computer software Gollwog (version 2011, J.B. Wilson). The dendrogram was truncated at the level of four habitat clusters. Habitat preferences displayed by katipo and steatoda were compared using a Kruskal–Wallis test. The abundance of katipo recorded in the transect sprayed with...
herbicide was compared between 2008 and 2009 using a paired *t*-test.

**Results**

**Katipo and steatoda association**

The abundance of steatoda recorded between 2004 and 2009 on the Kaitorete Spit dune system was not related to the abundance of katipo (*r* = +0.007, *P* = 0.969). The maximum number of katipo recorded was 32 spiders per transect in 2009, with significant differences in the median counts, from 6.5 to 14 per transect, over the survey period (*H* = 17.3, *P* < 0.001, Fig. 3). The maximum abundance of steatoda per transect was recorded in 2004, nine spiders, although this was not significantly greater than any other year (*H* = 1.1, *P* = 0.956). No linear trend in steatoda abundance was evident over the duration of this study (*P* = 0.202). Between 2004 and 2006, the median number of steatoda per transect was 1.0 (ranges are shown in Fig. 3); this declined to a median of 0.0 steatoda per transect in 2007, from which it did not recover. The ratio of steatoda to katipo spiders declined on an annual basis, from 1:4.1 in 2004 to 1:20.6 in 2009 (Table 1). There was a significant difference in the abundances recorded for each spider type (F, M, J and steatoda), blocked by year (*χ*² = 15.2, *P* = 0.002). Specifically, the numbers of female katipo recorded across the duration of this study differed significantly (*H* = 17.07, *P* = 0.004), medians ranging between 2.5 and 8.5 female spiders per transect (Fig. 3).

![Figure 3](image-url)

**Figure 3.** Median, maximum and minimum number of spiders per transect (*N* = 10) of (a) katipo (*Latrodectus katipo*) and (b) steatoda (*Steatoda capensis*) recorded each survey year. Abundance of female (c), male (d) and juvenile (e) katipo per transect are given to show the composition of the katipo population.
Table 1. Ratios of total steatoda (*Steatoda capensis*) counts to total katipo (*Latrodectus katipo*) counts per annum, showing the gradual decline in steatoda to katipo over the 5-year period, and ratios of total male to female katipo counts (M:F).

<table>
<thead>
<tr>
<th>Year</th>
<th>steatoda:katipo</th>
<th>M:F katipo</th>
</tr>
</thead>
<tbody>
<tr>
<td>2004</td>
<td>1:4.1</td>
<td>1:5.2</td>
</tr>
<tr>
<td>2005</td>
<td>1:7.2</td>
<td>1:1.6</td>
</tr>
<tr>
<td>2006</td>
<td>1:7.8</td>
<td>1:3.6</td>
</tr>
<tr>
<td>2007</td>
<td>1:5.2</td>
<td>1:4.6</td>
</tr>
<tr>
<td>2008</td>
<td>1:11.6</td>
<td>1:4.5</td>
</tr>
<tr>
<td>2009</td>
<td>1:20.6</td>
<td>1:1.8</td>
</tr>
</tbody>
</table>

Katipo per transect (Fig. 3). The median number of male katipo recorded between 2004 and 2009 showed less variability, ranging between 0.0 and 2.5 spiders per transect (*H* = 10.5, *P* = 0.061; Fig. 3). The abundances of female and male katipo did not exhibit a linear trend over the duration of this research (*P* > 0.05; Fig. 4).

A median of 18.0 katipo per transect (range 3–27) was recorded in 2008 (Fig. 3). Tree lupin was recorded in three of the 10 transects in 2008, and no steatoda were recorded on these transects. Tree lupin was restricted to one of the four habitat clusters identified from the cluster analysis (Fig. 5). Four habitat clusters were identified from the vegetation cover recorded in 2008 and 2009 (Fig. 5), but there was no significant difference in katipo abundance among the four clusters (*H* = 4.3, *P* = 0.229). The median number of steatoda recorded per 5 × 10 m section, for each habitat cluster, was 0.0 and did not differ between habitat types (*H* = 5.4, *P* = 0.146) (ranges are presented in Table 2).

**Tree lupin eradication**

Aerial application of the herbicide clopyralid in late 2008 resulted in the sections of one transect (43°50′04.561″ S, 172°33′07.990″ E) being reclassified in 2009 from habitat cluster ‘tree lupin’ to one of the two *F. spiralis* habitat clusters. The abundance of katipo on this transect increased from a median of two per section (range 0–13, *n* = 5) in 2008 to a median of four per section (range 1–12) in 2009, but this increase was not significant (*t* = 1.5, *P* = 0.149).
The percentages of katipo (F, M and J) and steatoda recorded in 2009, when the vegetation was surveyed after the herbicide application, varied significantly between the 10 transects ($\chi^2 = 64.6$, d.f. = 27, $P = 0.004$; Fig. 6). Male katipo and steatoda were absent from the area of dense tree lupin (Transects 4 and 5; Fig. 6). Male katipo were, however, recorded along the transect that had been sprayed with herbicide the previous year (Transect 6; Fig. 6). In 2009, steatoda were recorded within the area of scattered tree lupin at the western and eastern ends of the dense shrub cover, but no tree lupin was recorded within these transects (a similar pattern was observed in 2008). Female and juvenile katipo were found in all but one of the transects sampled (Transect 9; Fig. 6); this transect contained sections with limited and dominant *F. spiralis*.

**Discussion**

**Katipo and steatoda association**

We found no evidence of an association between the abundance of katipo and the abundance of steatoda on the Kaitorete Spit dune system, based on data from 2004 to 2009. A decline in katipo abundance at Kaitorete Spit was recorded in 2007, dropping to a median of 6.5 spiders per transect; at this time...
steatoda also declined (Fig. 3). Over the following two years katipo abundance increased, while the steatoda remained at a median 0.0 per transect (Fig. 3). The negative association between katipo and steatoda described by Hann (1990) and other authors (Patrick 2002; Costall & Death 2009) is not evident at Kaitorete Spit in these six years. Hann (1990) described a decline in katipo abundance and increase in steatoda abundance over a 2 year period following storm disturbance to a Motueka dune system that flattened the marram grass and killed off stands of tree lupin.

The declining ratio of steatoda to katipo, observed annually in this dataset, is suggested here to be driven by either that (1) the population of steatoda may be too small to respond and take the available habitat when katipo abundance declines or (2) Kaitorete Spit may be the extreme limit of the introduced steatoda’s range. The cooler southern climate may be affecting the reproductive output of the spider, thus limiting the population size, whereas the warmer temperatures of the North Island and northern South Island are more suitable for reproduction to occur (Hann 1990).

Steatoda were, however, recorded in greater abundance in the first 10 m of the transects, on the south-facing side of the front dune where they would be exposed to cool southerly winds. Katipo were also found on the south-facing side of the front dune, but equally so across the length of the transect (Fig. 4), which included dune lows and north-facing slopes. This limited dataset could be indicating a degree of niche partitioning or the displacement of steatoda.

The ratios of male to female katipo recorded at Kaitorete Spit over the 6-year period fall within the bounds of ratios recorded at South Brighton Beach, 1:1.5 (Smith 1971), and along the Manawatu–Wanganui coastline, 1:5.16 (Costall & Death 2009), but the ratio of one male to 11.6 female katipo recorded at Himatangi Beach (west of Palmerston North; Costall & Death 2010) shows extreme gender imbalance compared with the Kaitorete population. The greater abundance of female katipo to male katipo has been attributed to differences in lifespan: the male katipo lives for only a few weeks past its final moult, while the female lives for approximately 2 years beyond the final moult (Griffiths 2001).

Tree lupin and katipo

Infiltration invasion of tree lupin across the Kaitorete Spit dune system is resulting in a decline in native vegetation cover (Hetherington 2012). It was hypothesised that the decline in native vegetation, specifically the decline in *F. spiralis*, would lead to a decline in katipo abundance. Three transects intersected the area of dense tree lupin cover, with a median of 1.5 katipo per section grouped into the tree lupin habitat cluster (Table 2), but this was not significantly different from the three cluster groups dominated by native vegetation cover (Table 2). Within the ‘tree lupin’ habitat cluster there were two distinct subclusters, differing in the cover of tree lupin (Fig. 5). One subcluster contained 5 × 10 m sections with 31–60% cover of tree lupin, the remaining cover being of adventive species, such as *Hypochaeris radicata* (Asteraceae), *Lagurus ovatus* (Poaceae), plus the native *Calystegia soldanella* (Convolvulaceae). The second subcluster contained sections with 21–40% tree lupin cover, with a further 11–40% of the section covered by the native *F. spiralis*. The first subcluster, dominated by tree lupin, recorded a median 0.0 katipo per section (range 0–10). The second subcluster, where tree lupin and *F. spiralis* cover were both <40%, recorded a median 2.5 katipo per section (range 0–13). The native vegetation habitat cluster, with limited cover of *F. spiralis* (<30%), recorded a median 2 katipo per section (Table 2). This suggests that the *F. spiralis* cluster and the second tree lupin subcluster provide the spiders with enough native plant material and enough space between the plants for the capture webs to be hung. *Ficinia spiralis* also provides a suitable structure for the funnel-shaped nests that are spun tightly at the base of the capture web (Smith 1971; Griffiths 2001). Based on this dataset, there is evidence of an association between the density of tree lupin and the abundance of katipo.

Tree lupin and steatoda

It was expected from the literature (e.g. Hann 1990) that tree lupin invasion at Kaitorete Spit would lead to a decrease in katipo abundance, and perhaps as a result an increase in the abundance of steatoda. Alternatively, due to the strong similarities in the spiders’ habitat preferences (Hann 1990), a decline in both katipo and steatoda abundance corresponding to an increase in tree lupin density could be a more likely result. The Kaitorete data suggest that steatoda is more dependent on native vegetation than katipo, as not one steatoda was found, in 2008 or 2009, in any section where tree lupin was recorded.

Tree lupin eradication

The aerial application of clopyralid to an area densely covered by tree lupin resulted in death and deterioration of the plant’s above-ground biomass in less than a year. The abundance of juvenile and male katipo recorded along the transect that intersected the spray area increased after herbicide application. The sections of the transect that received the herbicide spray were grouped before the spraying into the ‘tree lupin’ cluster, but after spraying into one of the two *F. spiralis* habitat clusters. As the tree lupin broke down after herbicide application, *F. spiralis* responded favourably reaching a cover that ranged between 11% and 50% of the sections in 2009.

Conclusion

There is little evidence here of a negative association between tree lupin cover and katipo abundance. In the survey, there was no significant difference in katipo abundance between habitat/vegetation types, though the trend was for the greatest katipo abundance to be in areas with a combination of *F. spiralis* cover with tree lupin cover of less than 40%. The eradication of tree lupin through herbicide application did not result in a significant increase in katipo by the following year, though male katipo had returned to the area and the median number of katipo per section increased twofold. Steatoda has the potential to displace katipo (Costall & Death 2009), but there was no indication of a negative association between these two species at Kaitorete Spit. Moreover, steatoda was found to avoid areas where tree lupin was present: another potential benefit from tree lupin. Non-native invaders are often assumed to have only negative effects on conservation values, not least in New Zealand (Howell 2012). Positive benefits have, however, been reported worldwide (e.g. Bartomeus et al. 2008; Wolkovich et al. 2009; Mattingly et al. 2012), or essentially no change in ecosystem function (Mascaro et al. 2012). Tree lupin has in fact been identified as an important host species for several species of thrips in New Zealand (He et al. 2009).

The lack of firm evidence for a negative impact of tree lupin on katipo, and its classification as only ‘at risk’, not
‘threatened’, suggest that the allocation of conservation resources to complete removal of tree lupin in order to benefit katipo is not warranted at this time. However, the condition of the whole ecosystem at Kaitorete Spit, a nationally significant dune system and one where katipo has been recorded in great abundance, is being threatened by the establishment of tree lupin (Hetherington 2012). Tree lupin densely covers a 7-km stretch of the dune system (Hilton et al. 2006) and the present study, be it short term, indicates that dense tree lupin is not favourable habitat for katipo. Without management, the Kaitorete dunes could be dominated by tree lupin in a relatively short period. The results presented here imply a potential and novel management strategy of containment but not eradication of tree lupin cover, creating a mosaic of 20–40% tree lupin and 10–40% F. spiralis. Such a strategy would, according to our current knowledge, provide suitable habitat for the katipo but not for the steamdota. It would also be practically viable; it is unlikely that tree lupin could be completely eliminated in the short term, or perhaps ever, given the economic constraints on repeatedly spraying such a large area, given the persistent seed pool of the species, and given the likelihood of spontaneous reinvasion. Maintaining a mixed native-species / tree-lupin state is a practical compromise that will preserve much of the cultural and ecological value of the dune system and give scientists and managers the opportunity to monitor faunal response and to adjust management accordingly—the ‘research by management’ (Innes et al. 1999) and ‘adaptive management’ (Keith et al. 2011) approaches.

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