Multi-trophic Effects of Predator Exclusion Fencing for the Robust Grasshopper (*Brachaspis robustus*): implications for invertebrate conservation

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Liam Richard McIver

School of Biological Sciences
University of Canterbury
Christchurch, New Zealand
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Contents

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Abstract

Evidence is mounting that the earth is entering a sixth mass extinction event. However, species conservation, essential to prevent further loss, is costly and some management actions may have unintended negative effects for the species they aim to protect. Mammalian predator exclusion is a key action implemented for many species. In New Zealand the scale of predator control is set to increase drastically as we progress towards Predator Free 2050 goals. However, the response of some taxa, such as invertebrates, to predator eradication even at a small scale is not well understood. To better use conservation resources and improve outcomes for threatened species, unintended detrimental effects of conservation must be identified and mitigated.

I examined the effect of a newly designed low predator exclusion fence on a population of the Nationally Endangered robust grasshopper (*Brachaspis robustus*). This flightless, large bodied insect is believed to be suppressed by mammalian predators, so I expected that exclusion of mammals would increase the grasshopper's abundance. However, I also hypothesised that predator exclusion and the fence structure itself could have unintended effects on other organisms and the environment with possible negative consequences for *B. robustus*. As such, as well as confirming predators had been excluded, I also monitored skink populations, microclimate, and vegetation change.

Robust grasshopper abundance within the fence did not differ from open sites in the first five months after exclusion fencing was installed, possibly because of a lag in response related to grasshopper lifecycle, or suppression by an apparent increase in bird abundance related to the exclusion fence itself. Following that, *B. robust* abundance was lower within the fence compared with open sites one year after fence installation, possibly because of

meso-predator release of native skinks, or potential fence mediated alterations to microclimate affecting *B. robustus* development. There was no evidence that lagomorph (rabbit, *Oryctolagus cuniculus*; and hare, *Lepus europaeus*) exclusion by the predator fence affected vegetation. However, this conclusion is limited by the timing of vegetation sampling so vegetation changes affecting *B. robustus* could not be ruled out. This negative response by *B. robustus* indicates that management in addition to mammal control may be required to conserve this species.

The observed response of *B. robustus* to increased skink abundance suggests that native meso-predator release has the potential to prevent or slow recovery of threatened invertebrates. These findings have implications for threatened invertebrates within areas subject to wide-scale mammal control, as expected with the approach of a Predator Free 2050. Overall, this result reinforces that a better understanding of the consequences of certain conservation methods on invertebrates is required so that effective and efficient management action can be undertaken to give the best outcome for threatened species.

Chapter 1 General Introduction

1.1 Global mass extinction

There is mounting evidence that the earth is entering a mass extinction event (Barnosky et al. 2011, Dirzo et al. 2014). Only five known events of the same magnitude have occurred in the 3.8 billion years life has been present on this planet (Raup 1986, Mojzsis et al. 1996). As humans push the planet further into the Anthropocene[1], it is likely negative pressures on the earth's biodiversity will only grow stronger (Butchart et al. 2010). Without significant efforts to reduce or counteract these pressures, near unprecedented rates of global biodiversity loss are likely (Pimm et al. 1995, Ehrlich and Pringle 2008, IPBES 2019).

1.2 Global conservation action

Conservation researchers and practitioners have been working for many years to prevent species extinctions by taking actions such as reducing threats (e.g. Elliott et al. 2001, Sybersma 2015, Taylor et al. 2019), enhancing or protecting habitat (e.g. Kelly et al. 2000, Gopal and Chauhan 2006, Goulson et al. 2008), translocating individuals (e.g. Player 1967, Sherley et al. 2010, Hammer et al. 2013) and captive breeding for reintroduction (e.g. Bruning 1983, Pearce-Kelly et al. 1998, Preston et al. 2007). Such actions are undertaken to maintain ecosystem services (Carpenter et al. 2009, Cardinale et al. 2012) as well as to preserve species because of their moral worth (Piccolo et al. 2018). Collectively, it is estimated that without conservation efforts to date, one fifth more vertebrate species would have been lost on top of those already known to have gone extinct (Hoffmann et al. 2010). This shows that conservation action works. However, there is still much to be done,

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[1] The proposed current geological epoch where the influence of humans on the planet now rivals the forces of nature (Steffen et al. 2007)

in part because there are known research and action biases in favour of large vertebrates over other taxa (Clark and May 2002, Seddon et al. 2005, Régnier et al. 2009). Comparatively neglected groups include invertebrates which make up the largest proportion of biodiversity on Earth (Stork et al. 2015).

1.3 Threats to New Zealand biodiversity

Protection of New Zealand biodiversity is vital for maintaining global biodiversity because of the country's high endemicity (Myers et al. 2000). Some of the key threats to New Zealand's endemic biodiversity include climate change (McGlone et al. 2010) and pollution of waterways (Collier 1993, Weeks et al. 2016). Habitat loss is also a significant threat (Kingsford et al. 2009). For example, even though 30% of New Zealand's land area is protected, some areas are not well represented (Logan 2001). In particular, New Zealand drylands, despite containing some of the country's most threatened species, have little protection (Cieraad et al. 2015), allowing for ongoing habitat loss (Weeks et al. 2013). Drylands also appear to have been subject to less biodiversity protection research than other New Zealand ecosystems like forests, although more recently the amount of published dryland research has increased (e.g. Norbury 2001, Walker et al. 2014a, b). Despite the severity of the above threats, arguably, the overwhelming threat to New Zealand biota is invasive species, heavily impacting drylands along with the rest of the country (Craig et al. 2000, Department of Conservation 2000).

1.4 New Zealand invaders

Significant terrestrial invaders in New Zealand are exotic mammals that were introduced during Māori settlement c. AD 1300, and European colonisation beginning in 1769 (Massaro et al. 2008). Over that time, 31 wild or feral exotic mammal species have become established in New Zealand (Parkes and Murphy 2003). The species that arguably pose the biggest risk to native fauna are the predators (Parkes and Murphy 2003): ship rats (*Rattus rattus*), Norway rats (*Rattus norvegicus*), common brushtail possums (*Trichosurus vulpecula*), cats (*Felis catus*), stoats (*Mustela erminea*), weasels (*Mustela nivalis*), ferrets (*Mustela furo*), mice (*Mus musculus*), and hedgehogs (*Erinaceus europaeus*). Additionally, more than 25,000 species of plant have been introduced to New Zealand, of which 2,200 are naturalised (Williams and Cameron 2006). At least 328 of these are considered ‘environmental weeds’, i.e. species that are controlled by the Department of Conservation, or would be if resources were sufficient (Howell 2008). These weeds can have a large effect on native biota, for example, wilding pines (made up of ten main conifer species such as *Pinus contorta*, *Pinus radiata*, and *Larix decidua*) have invaded New Zealand grasslands, including drylands, causing species replacement, reductions in invertebrate biodiversity, and the threat of local extinction for some species (Pawson et al. 2010).

1.5 Vulnerability to predation

Mammalian predators have such a large effect in New Zealand because it has been geographically isolated for the past 80 million years (Cooper and Millener 1993) meaning native biota evolved predator avoidance and defence mechanisms in the absence of terrestrial mammals (Tennyson 2010). Many species, across taxa, have traits that provide protection from avian and lizard predators, such as crypsis and a freeze response when threatened (Gibbs 2010), making them vulnerable to mammals that generally hunt using their olfactory ability (Hughes et al. 2010). This high susceptibility to mammalian predation, combined with frequent gigantism which is linked with low population density and slow reproduction in native species (Daugherty et al. 1993), has led to drastic population declines and extinctions (Innes et al. 2010).

The vulnerability of New Zealand’s well studied native birds to predators has been recognised for some time (Côté and Sutherland 1997, Seabrook-Davison 2010). More recently, attention has been drawn to the possible role of introduced mammals in the decline of other, lesser known taxa, including large native flightless insects (Cranston 2010). For example, translocation of several wētā species (Orthoptera: Anostostomatidae) to predator free offshore islands resulted in improved survival relative to mainland populations (Watts et al. 2008). Most research has focussed on mustelids, rodents, and cats because of the impact of those species on native birds, but hedgehogs may be a significant, less recognised, threat to native biota because of their impact on native invertebrates. For example, very large numbers of insects have been found in the stomachs of hedgehogs in the Waitaki Basin, including rare species such as the carabid beetle *Metaglymma aberrans* (Jones et al. 2005). One individual’s gut contained the legs of 283 *Hemiandrus* wētā, which is at least 47 wētā consumed in one night of foraging. Rodents also have a large impact on native invertebrates and there are now many examples of rodents supressing and causing local extinction of invertebrates in New Zealand (see St Clair 2011).

1.6 Predator Free 2050

To try to address the threat posed by invasive predatory mammals, the New Zealand government recently adopted a target of eradicating rats, possums, and stoats from New Zealand by 2050 (Bell 2016). This target represents a general shift to landscape scale predator control which so far has largely relied on improvements in aerial sowing of poison (Murphy et al. 2019) and has enabled eradication of mammals from offshore islands. The largest successful island eradication in New Zealand to date was undertaken on the 11,300 hectare Campbell Island (Towns and Broome 2003), although mammal eradications are in progress on larger islands such as Resolution Island, Fiordland (McMurtie et al. 2008). Eradication programs have begun across large areas of the mainland (e.g. Taranaki, Hawkes Bay, Wellington) but because aerial bait application is not possible in human inhabited areas, these will rely on other methods, like trapping and bait stations aided by natural and constructed barriers, and yet to be developed technologies (Russell et al. 2015).

1.7 Predator exclusion fencing

Globally, fencing is used for a variety of conservation applications (Hayward and Kerley 2009). Predator exclusion fencing is commonly used in New Zealand so that mammalian predators can be eradicated from an area (Innes et al. 2012). These fences are generally constructed from wire mesh fixed to 2 m tall posts to exclude jumping animals, with an overhanging top rail to exclude climbing animals (Boulton and Bowman 2006). Fences have received criticism because they are expensive to build and maintain, and it has been suggested that translocating species to predator free offshore islands is a better alternative (Scofield et al. 2011). This criticism has some basis, as predator fences are less cost effective than trapping protocols for areas over ~1 ha (Norbury et al. 2014). However, suitable habitat for many threatened species does not exist on predator free offshore islands, so fencing can allow for total removal of predators from mainland sites that is necessary to protect those species. Additionally, fences can allow for positive social outcomes like community education, as well as positive biodiversity outcomes (Innes et al. 2012). If Predator Free 2050 goals are met, the long term need for exclusion fencing may be reduced. However, predator exclusion fences are still urgently needed to prevent immediate biodiversity losses, and to assist in meeting Predator Free 2050 goals. These fences will also continue to be important for exclusion of species not targeted under Predator Free 2050, particularly hedgehogs and mice that have a large impact on endemic insect and lizard species (St Clair 2011, Jones et al. 2013).

1.8 Unintended effects of predator control

Although control or eradication of invasive species can be beneficial to multiple species, it can have unintended or unexpected outcomes for some native and invasive species (Pech and Maitland 2016). There is the known potential for direct effects of control on non-target organisms; i.e. through consumption of bait, secondary poisoning, trapping, or exclusion from an area. For example, kea *(Nestor notabilis*) deaths occur from consumption of 1080 (sodium fluoroacetate) poison (van Klink and Crowell 2015). Some other possibilities include targeted pest eradication indirectly affecting other species by altering the environment, or by causing changes to the interactions between species in ecosystems. For example, beetle abundance at Zealandia sanctuary (Karori, Wellington) decreased after predator exclusion, likely because of increased predation by birds or mice that were not eradicated (Watts et al. 2014). This is an example of ‘meso-predator release’, that is top predator removal resulting in increases to predators at lower trophic levels. Modelling shows this is a likely outcome in dryland New Zealand ecosystems if only a subset of predators is controlled (Ramsey and Norbury 2009), as planned under Predator Free 2050, and it is reasonable to assume that this may be the case in other ecosystems. To maximise the benefits and efficiency of predator control across threatened species, research effort needs to be concentrated on predicting, eliminating, or minimising detrimental effects, and monitoring to ensure that eradication or control is leading to the desired conservation outcomes (Pech and Maitland 2016).

1.9 Predation threat to *Brachaspis robustus,* a braided river grasshopper

The robust grasshopper (*Brachaspis robustus* Bigelow, Orthoptera: Acrididae) is an endemic species that is likely being supressed by mammalian predators. This Nationally Endangered[2] species is found only in the Mackenzie Basin, a dryland area in the South Island of New Zealand (White 1994). It is a generalist herbivore, flightless, visually cryptic, and naturally found in the rocky riverbeds and associated terraces of the Ohau, Pukaki, and Tekapo catchments (Bigelow 1967, White 1994). Only c. 6 populations remain; there is evidence suggesting these are threatened by many of the introduced predators mentioned previously (mice, rats, stoats, ferrets, hedgehogs, cats), however this is not unequivocal (Schori et al. 2019). Other threats to grasshopper populations potentially include weed invasion that removes the open gravel habitats of braided river beds that *B. robustus* prefer (Thorsen 2010), native predators that have a large effect because their predation pressure has been artificially increased, and non-mammalian introduced predators such as birds (White 1994). More recently, pathogens such as the fungus *Beauveria bassiana* have also become a concern (T. Murray, *pers. Comm.*).

1.10 Protection of *Brachaspis robustus*

As of 2018, no *B. robustus* populations had any form of physical protection, be that predator or weed control, despite the rarity of this species. Schori et al. (2019) investigated the effect of introduced predators on several endemic grasshoppers and found that supressing

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[2] *Brachaspis robustus* is classified as Nationally Endangered (Trewick et al. 2014) under the New Zealand Threat Classification System (Townsend et al. 2008)

predators to low numbers was not enough to improve *B. robustus* survival. It was suggested instead that total elimination of predators would be required to benefit *B. robustus*, but this could not be tested at the time. In November 2018 however, a 30 m wide x 200 m long low-height predator exclusion fence, designed with help from Zero Invasive Predators, was constructed providing a site to test this hypothesis.

The low-height predator exclusion fence was constructed as part of the Te Manahuna Aoraki (TMA) project, a large-scale conservation project aiming to restore the natural landscapes and threatened species of the upper Mackenzie Basin and Aoraki National Park over a total area of 310,000 hectares. It is a partnership of Te Rūnanga o Ngāi Tahu Iwi, Government departments, charitable foundations, local bodies, and landowners. Aside from predator exclusion fence construction, some key activities undertaken so far include weed control, a feasibility study of rabbit elimination, and expansion of mammal trapping networks along braided rivers (TMA 2019). The predator exclusion fence aims to exclude all introduced predators, except cats which could jump over it, from a *B. robustus* population at Patersons Terrace, near Tekapo. The grasshopper population at Patersons Terrace occurs on an unused gravel road installed during the construction of the Tekapo canal; grasshoppers either colonised the road naturally from the nearby Forks river or were transported to the site with gravel taken from the bed of the Tekapo River during canal and road construction in the 1970s (McKay et al. 1978). It may seem unusual to carry out conservation research at Patersons Terrace rather than at more natural sites, but all other natural populations are associated with braided rivers that flood periodically, precluding construction and maintenance of an exclusion fence in these areas.

The installation of this fence presented the opportunity to address several important questions including the effect of total mammal elimination on *B. robustus*, the efficacy of predator exclusion fencing to mitigate these threats, and the non-target impacts of fence construction in a dry grassland ecosystem. At the same time, this fence could secure a *B. robustus* population from threatening processes, rather than delaying potentially beneficial conservation action by gaining certainty about which threats are important first and then implementing a treatment afterward. This was the first field trial of this prototype exclusion fence in the Mackenzie Basin environment.

1.11 Aims and thesis structure

Specifically, the aims of my research were to:

1. Assess the efficacy of low-height predator exclusion fencing in terms of its ability to exclude mammalian predators and to withstand environmental conditions in the open drylands of the Mackenzie Basin. This aim is covered in Chapter 2.
2. Assess the unintended effects of predator exclusion and predator exclusion fencing, including the potential for meso-predator release, edge effects altering local microclimate, and changes to vegetation abundance and composition through herbivore exclusion. This aim is covered in Chapter 2.
3. Determine whether installation of the predator exclusion fence, results in a change to the abundance of robust grasshoppers. Chapter 3 covers this aim.

In Chapter 3 I also discuss how the processes investigated in Chapter 2 could be responsible for the patterns observed in grasshopper populations and make recommendations for their management in light of the results of this study. I discuss these aims and the findings of this research in a wider context in a fourth chapter.

This research was conducted from November 2018 to January 2020. I assessed the aims above by building on previous years of *B. robustus* monitoring at the same site (Schori 2020), which imposed some limitations on the methodology used. The results of this study could improve conservation outcomes for *B. robustus* by determining whether a population of this Nationally Endangered species has been secured from a threatening process. Lessons learned from this study could also inform conservation management of this species at other sites and potentially suggest appropriate action for other threatened invertebrate species. Low height predator exclusion fencing could also be more cost effective than regular predator exclusion fencing (Agnew and Nichols 2018). If this research shows that low-height exclusion fencing effectively excludes mammalian predators, then limited conservation funding could be spread further to protect more threatened species. Such low-cost predator exclusion technology could aid in meeting Predator Free 2050 goals.

Brachaspis robustus is listed as protected under Schedule 7 of the Wildlife Act 1953 so all monitoring and handling of B. robustus was carried out under DOC research permit DOCCM-6057237.

Chapter 2 Exploring the range of effects of a new design predator exclusion fence for robust grasshoppers

2.1 Introduction

2.1.1 Unintended effects of conservation

Without concerted effort to minimize human impact on the environment and conserve threatened species, rates of global biodiversity loss unprecedented in recent geological time are imminent (IPBES 2019). Invasive species are a significant driver of biodiversity loss (IPBES 2019). Invasive species are controlled (Mack et al. 2000), but the global funding available for conservation falls short of what is required to halt species extinctions (McCarthy et al. 2012). Conservation action, including invasive species control (Caut et al. 2009, Pech and Maitland 2016), can sometimes cause feedbacks in biological systems and human behaviour which can make the action do less good than intended, or even cause harm to threatened species (Polasky 2006). Biologically mediated unintended effects of invasive species control can be a direct result of control actions (van Klink and Crowell 2015) or can be a result of the trophic relationships between invasive and native species (Gangoso et al. 2006). To increase the efficacy of conservation spending, negative unintended effects of conservation actions must be identified and mitigated. The conservation action that is the focus of this study is predator exclusion fencing.

2.1.2 Reducing the cost of conservation: Predator exclusion fencing

Globally, fencing is used for a variety of conservation applications (Hayward and Kerley 2009). In New Zealand, predator exclusion fencing is commonly used to protect native biodiversity by allowing for eradication of invasive mammalian predators within (Innes et al. 2012). Fences have been criticised because they are expensive to build and maintain

(Scofield et al. 2011), costing between $200 and $400 dollars per metre depending on terrain (Campbell-Hunt 2008, Bell 2014). Critics suggest that protection of species by translocation to predator free offshore islands is a better alternative, however islands do not meet the habitat requirements of all species. Additionally, although sustained trapping is more cost effective than fencing for areas over ~1 hectare, trapping may not be beneficial for species that are very sensitive to mammalian predators because it suppresses rather than eradicates mammals (Norbury et al. 2014). Exclusion fencing may also assist in meeting Predator Free 2050; the New Zealand Government target of eradicating a suite of mammalian predators by 2050 (Bell 2016). Fencing will continue to be important for exclusion of species not targeted under Predator Free 2050, particularly hedgehogs and mice that have a large impact on endemic insect and lizard species (St Clair 2011, Jones et al. 2013).

The necessity of predator exclusion fencing combined with its high cost has led to attempts to alter fence design. One approach is to lower fence height (normally 2 m). A 1.1 m fence has been trialled as a 4 m by 4 m enclosure pen to determine minimum height to prevent predator escape (Agnew and Nichols 2018). It prevented escape for at least 95 percent of all rats, stoats, and possums trialled. Those animals that successfully escaped did so by exploiting the 90° angle at the corners of the fence; an artefact caused by the cap being on the inside of the fence for the purpose of the experiment, and the small size of the enclosure. In a real field application of this fence design, these exploitable corners would not exist. This suggests that a 1.1 m low-height predator exclusion fence would effectively exclude all introduced mammalian predators in New Zealand, except for feral cats (*Felis catus*) which can jump higher than this.

2.1.3 Field trial of low predator exclusion fence

A 1.2 m successor of the Agnew and Nichols (2018) trial low-height predator exclusion fence was constructed at Patersons Terrace in the Mackenzie Basin in November 2018, to protect a population of the Nationally Endangered (Trewick et al. 2014) robust grasshopper (*Brachaspis robustus*). As well as assessing the impact of predator exclusion fencing on a *B. robustus* population (see Chapter 3), I assessed the efficacy of the low-height fence in terms of predator exclusion, the strength of this fence design in exposed conditions, and three possible negative consequences of predator exclusion fencing; meso-predator release, edge effects, and vegetation release from grazing.

2.1.4 Meso-predator release

Meso-predator release occurs when the decline of a top predator results in increased abundance, or altered behaviour, of predators at a lower trophic level (meso-predators) (Prugh et al. 2009). Increased abundance of meso-predators can cause sustained or increased predation on lower trophic level species when it might be expected that predation would lessen due to the suppression of the target predator. Evidence for this comes from a range of ecosystems globally (e.g. Crooks and Soulé 1999, Choquenot and Ruscoe 2000, Schmidt and Ostfeld 2003, Báez et al. 2006, Ritchie and Johnson 2009).

In New Zealand, studies of meso-predator release focus on removal of introduced mammalian predators of birds and lizards releasing another introduced mammal, such as rats (e.g. Rayner et al. 2007, Norbury et al. 2013). However, investigation of invertebrate responses to mammalian predator removal where meso-predator release could occur is less common (but see Norbury et al. 2013, Watts et al. 2014, Watts et al. 2017). Two native skink species present at Patersons Terrace, *Oligosoma maccanni* and *Oligosoma polychroma*, could experience meso-predator release. They primarily consume arthropods (Hare et al. 2016), so an increase in their abundance could reduce robust grasshopper survival. If rats or mice remained in the predator exclusion fence and other species were excluded, they could also be released from predation and increase in abundance.

2.1.5 Edge effects

Edge effects are ecological changes that occur at habitat edges (Ries et al. 2004). They are widely studied (Ries and Sisk 2004) and occur at a range of scales (Cadenasso et al. 2003). Proximity to an edge can negatively affect some species by altering environmental conditions and species interactions (Haddad et al. 2015). Study of edge effects for conservation focuses on the effect of habitat loss and fragmentation; factors that increase the prevalence of edge effects, as small habitat patches have a large proportion of their area at an edge (Harper et al. 2005). However, construction of barriers for control of invasive species could also cause edge effects (Hayward and Kerley 2009). For example, barriers can modify species behaviour (van Dyk and Slotow 2003) and could impact the environment by altering wind dynamics and providing shade.

In New Zealand, there has been little study of the edge effects caused by predator exclusion fencing. This lack of understanding could have negative consequences for species conservation, particularly where the area being fenced is small, as is the case for the fence trial at Patersons Terrace.

2.1.6 Plant community release from herbivory

Another consequence of conservation with possible unintended effects is a change to plant communities caused by herbivore control. Plant community structure is controlled by abiotic factors, such as climate and resource availability, and biotic factors, such as competition, herbivory and mutualism (Lavorel and Garnier 2002). Of those factors, herbivory is pervasive, as it can reduce plant biomass and abundance, change community composition (Jia et al. 2018), and can be implicated in both maintenance and reduction of plant diversity (Parker et al. 2006, Borer et al. 2014). In New Zealand, invasive herbivore control has allowed native vegetation recovery in some ecosystems, but has been detrimental for some plant species, particularly where introduced plants are present (Coomes et al. 2006). Plant community alterations caused by invasive herbivores can have flow-on effects for other species (Côté et al. 2004) by changing the physical structure of habitat (Fuller 2001), which then affects microclimate, including temperature, soil moisture, and wind exposure (Wilson and Agnew 1992, Busing and Pauley 1994), and succession (Smale et al. 1995). As such, invasive herbivore control must be monitored to ensure that positive outcomes for targeted species are occurring. At Patersons Terrace, herbivores were expected to be excluded by the predator fencing despite not being a target species, potentially resulting in changes to vegetation.

I hypothesised that at Patersons Terrace; 1) predator exclusion fencing would exclude all mammalian predators, except feral cats as per the earlier experimental trial (Agnew and Nichols 2018), and exclude rabbits and hares, 2) fencing would cause a significant edge effect that altered microclimate, 3) a degree of meso-predator release would occur if the target mammalian predators were excluded, and 4) herbivore exclusion would allow for increased vegetation biomass, and changes to plant community relative composition favouring stronger competitors previously suppressed by grazing.

2.2 Methods

2.2.1 Site description

This study was conducted on an unused gravel road at Patersons Terrace, located along the eastern edge of the Tekapo Triangle Conservation Area in the intermontane Mackenzie Basin of New Zealand's South Island (Figure 2.1 A). The Mackenzie Basin is a dryland area. It has warm summers, cool winters, and low rainfall (typically <500 mm annually) with little variation across seasons (Appendix 1, Macara 2016). Mean wind speeds are low (10 to 20 km h^{-1}), however a strong westerly föhn wind often arises in the afternoon, with gusts exceeding 120 km h^{-1} (Appendix 1); of importance in the Tekapo Triangle where the terrain is flat with little shelter.

The gravel road is bordered by semi-modified grassland mainly composed of fescue tussock, introduced pasture grasses, hawkweed (*Pilosella* and *Hieracium sp.*), and other herbs (Department of Conservation 2004). The road substrate is mostly small stones < 64 mm in diameter with minimal soil. Plant species on the road are sparse and of short stature. They include *Hieracium pilosella*, the mat forming daisy *Raoulia australis*, and grasses such as *Poa annua*.

Three 100 m long transects were established along the road at Patersons Terrace (Figure 2.1 B) in November 2015 for *B. robustus* population monitoring (Schori 2020). A predator exclusion fence was constructed around one of these transects in November 2018 (Appendix 2) so that grasshopper abundance within could be compared to counts from previous years as well as counts from the two road sites that remained unprotected. The fence was constructed at the central site, henceforth the fenced site (F) while the remaining two sites were left open, henceforth open south (O_s) and open north (O_n) (Figure 2.1 B).

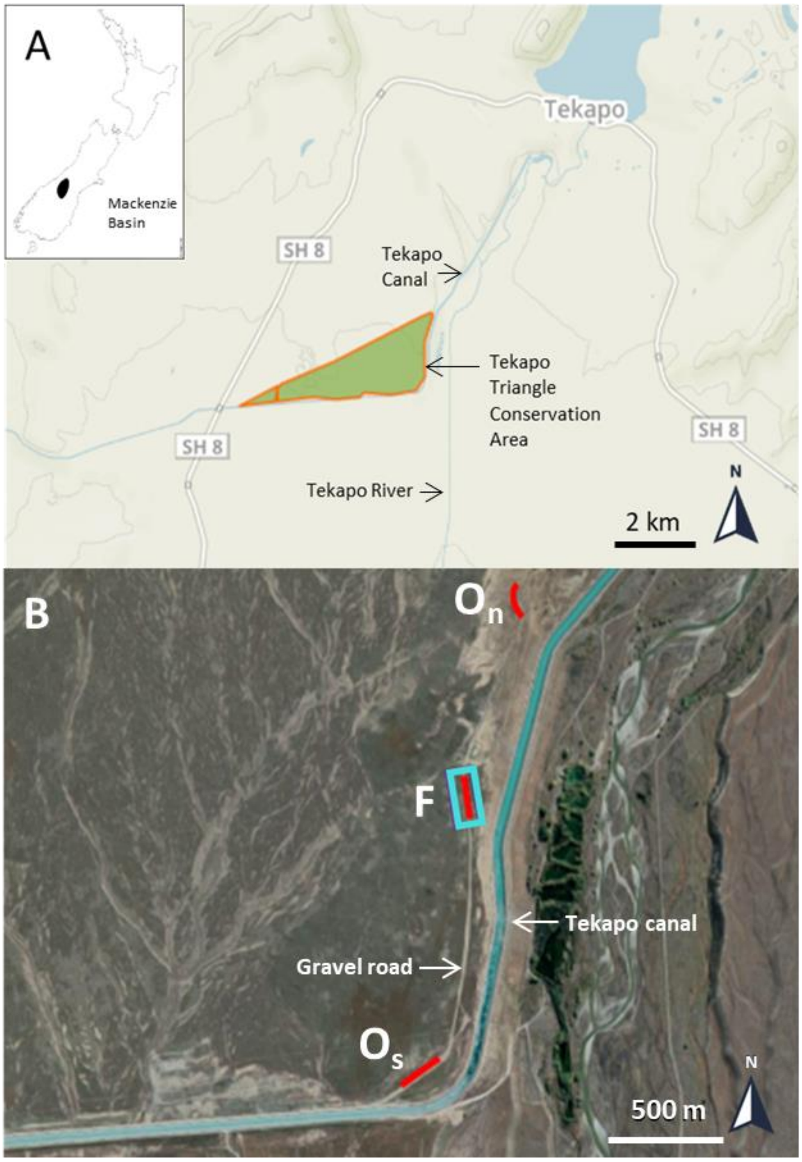

Figure 2.1 (A) The Tekapo Triangle Conservation Area (source- Protected Planet https://bit.ly/37IbvDG), and (B) the approximate location of the grasshopper monitoring transects (red) at the three sampling sites on the gravel road at Patersons Terrace (O_s=open south, F=fenced, O_n=open north). The footprint of the predator exclusion fence is shown in teal (source- google maps).

2.2.2 Study design

I sampled within one predator exclusion fence and compared this to two open sites which did not allow for true spatial replication. This limitation is often problematic for studies of applied conservation (Radford et al. 2018); at Patersons Terrace, greater replication was not possible because of the high cost of exclusion fencing and the scarcity of *B. robustus* habitat. The ability to make statistical comparisons to inform management was considered more valuable than being paralyzed by a lack of true replication, so pseudo-replicates were used, and inferences adjusted accordingly. In addition, a Before-After-Control-Impact (BACI) study design was used to make tests more robust (Christie et al. 2019). However, the timing of fence construction prevented before sampling of vegetation and skinks, so sampling was conducted soon after construction was completed. Results are interpreted with this in mind.

2.2.3 Predators: Tracking tunnels

I used 23 100 mm x 100 mm x 500 mm Black Trakka^{TM} tunnels (Gotcha Traps Ltd) to evaluate mammal relative abundance, following Gillies and Williams (2013). I installed ten tunnels at each open site and three at F, because of the small area within the fence. All tunnels were spaced 50 m apart in the middle of the gravel road and secured with a wire hold down and rocks. Rats and mustelids can be neophobic (Barnett 1958, King et al. 2009), so I left tunnels for one month before I set out Black Trakka^{TM} pre-inked cards (Gotcha Traps Ltd) baited with peanut butter. Peanut butter was removed after three nights and tracked cards replaced before baiting with rabbit meat for an additional three nights. This ensured hedgehogs, rats and mustelids were all targeted while minimising interference between these species. This was repeated four times at site O_s and F (three at site O_n) between December 2018 and February 2019, and once each at all sites in November and December 2019, giving 370, 111, and 250 tracking nights for sites O_s, F, and O_n, respectively (number of nights x number tracking cards).

Footprints were visually identified using Ratz (1997) and independently checked by Department of Conservation (DOC) staff. Large insect prints were identified using Carpenter et al. (2016). I calculated the percentage of tunnels tracked at each location for hedgehogs, mustelids, rats, mice, cats, skinks and insects. Mammals were not recorded inside the predator exclusion fence, so analysis was not undertaken.

2.2.4 Predators: Trapping

Inside the exclusion fence, DOC staff set and monitored three DOC 150 and three DOC 250 traps baited with rabbit meat, and eighteen peanut butter baited Victor® mouse traps. Two-tier mouse trap boxes were used, with the trap on the top tier, to minimise skink capture. Nine of the mouse traps were placed in the vegetation on either side of the gravel road at 20 m intervals, 5 m from the fence line. Traps were set out in early November 2018 and left to 'settle in'. They were checked every day for the first five days in December 2018 and then every two weeks for the duration of the study.

2.2.5 Predators: Trail cameras

Four Acorn LTL 5210 trail cameras were installed at site F ~50 cm above the ground. Two were positioned 1.5 m from the fence to cover the external east and west fence lines. The other two were positioned at opposite ends of the road inside the fence to capture any mammal activity on *B. robustus* habitat. Cameras captured a burst of three photos when motion was detected, and then disabled for ten seconds; reducing triggers by the same animal. Cameras were active from February to March, and from July to December 2019 day and night (using infrared light). In November 2019 I moved the two cameras on the road to the vegetated verges inside the exclusion fence to cover the internal east and west fence lines.

I visually assessed all images and recorded animal identity, and time and date of each animal visit for images from February and March 2019. Two images of the same species were only considered separate sightings if separated by > 5 minutes. Due to time constraints I archived all images collected after March 2019 and only reviewed those captured inside the fence to confirm mammal absence.

2.2.6 Meso-predators: Artificial retreats

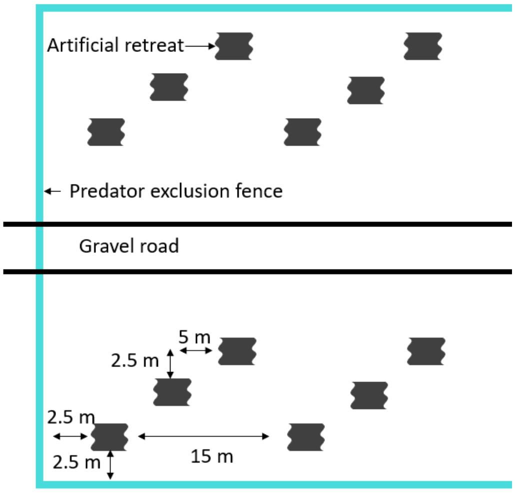

Figure 2.2 Layout of artificial retreats at each site at Patersons Terrace. Diagram not to scale.

I used 289 (~ 30 cm x 45 cm) Onduline (distributed by Composite, Christchurch NZ) artificial retreats (ARs) to monitor lizard numbers within the vegetated habitat adjacent to the gravel road, following Lettink (2012). In November 2018 I installed the ARs in six lines, three each side of the gravel road (Figure 2.2) at sites F and O_s (156 covers each) and left them to 'settle in' for one month. Vegetation at site O_n is sparse because of historic removal of top soil (Department of Conservation 2004). As such, I assumed skink numbers there would not be representative of most locations at Patersons Terrace, therefore O_n was not assessed.

Artificial retreats were checked under the same appropriate conditions on all occasions as in Hoare et al. (2009). Checks involved lifting the AR, noting presence or absence of lizards and visually identifying the species. I assessed both sites in January, February, and November 2019. In December 2019 DOC staff assessed the lizard population under ARs at both sites by catching each lizard and recording their species, classifying them as adult or juvenile based on snout to vent length, and determining whether females were gravid following DOC best practice methods described in Lettink (2012).

Analysis (unless otherwise stated this was performed in R v 3.6.1) involved comparing skink abundance inside and outside the fence using a repeated measure generalized linear mixed effects model (lme4 package version 1.1-21) treating each AR as a replicate. I used a binomial distribution because only one skink was ever found under any one retreat. I assessed significance of the two-way interaction between the fixed effects time period

(Season 1: January and February; versus Season 2: November and December 2019), and fence treatment (fenced versus open) while accounting for a random effect (the unique number of each skink retreat) using a likelihood ratio test.

2.2.7 Fence integrity and microclimate

Periodically the exclusion fence was visually inspected for damage. Wind direction and wind speed were recorded on the gravel road ~ 5 m outside the fence to avoid any sheltering effects (HOBO S-WSET-B Wind Speed & Direction Smart Sensor Set). Data were recorded every minute from November 2018 to April 2019. Wind speed and direction were plotted.

Microclimate was assessed inside and immediately outside the exclusion fence using two weather stations (HOBO Micro Station Logger V5 - Onset Computer Corporation). Ground surface, and soil temperature 3 cm below the surface (HOBO 12-bit temperature smart sensors), and air temperature and relative humidity (HOBO 12-bit temperature/relative humidity smart sensor in a solar radiation shield) were recorded. Smoothed conditional means from the daily maximum, minimum, and average, of each variable were plotted using the *loess* method, to allow for visual comparison of site conditions. Statistical analysis was not performed because there was only one weather station in each location.

Ground surface temperature on the gravel road (road trial) and vegetated edges (vegetation trial) was monitored inside the fence and in an area directly outside using HOBO Pendant® Temperature/Light 8K Data Loggers. For the road trial I set out thirty loggers but four were defective, giving a total of 26 loggers; ten inside the fence, seven to the north, and nine to the south. In each area I fixed loggers to the road surface in two evenly spaced lines running parallel to the grasshopper monitoring transect, on either side of the road centre (Figure 2.3). Loggers recorded temperature every ten minutes over 18 days in January 2019.

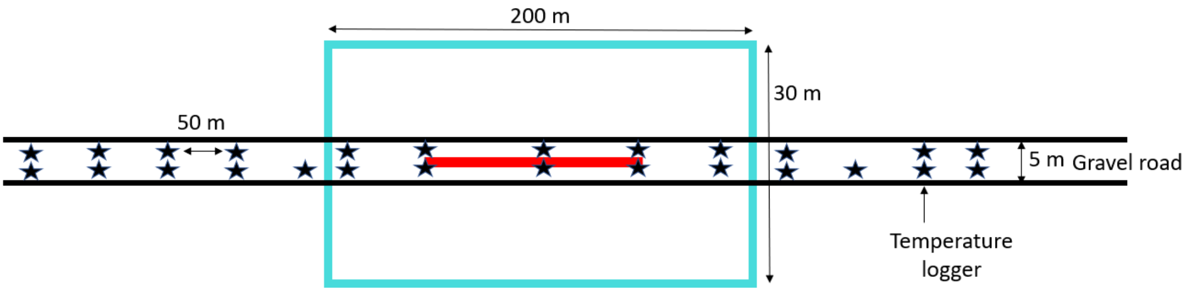

Figure 2.3 Layout of the road temperature trial at Patersons Terrace. Temperature loggers (stars) are positioned on the road surface inside and immediately outside the predator exclusion fence (teal) centred around the grasshopper monitoring transect (red).

For the vegetation trial I used twenty-four loggers; eight inside the fence, eight to the north, and eight south of the fence. At each location I fixed four loggers to the ground, one at 7.5 m and the other 12.5 m from the centre of the gravel road (Figure 2.4). Logger location was selected to minimise differences in vegetation and aspect between the inside and outside of the exclusion fence to assess the direct effect of the fence on temperature. Temperature was recorded every ten-minutes for 22 consecutive days in February and March 2019.

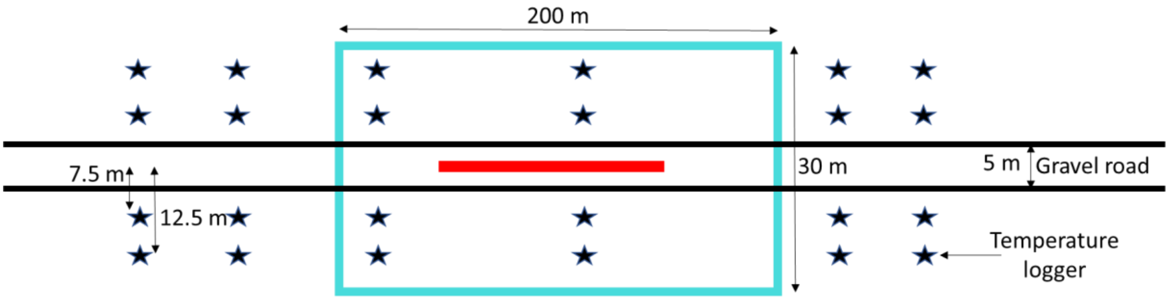

Figure 2.4 Layout of the vegetation temperature trial at Patersons Terrace. Temperature loggers (stars) are positioned inside and immediately outside the predator exclusion fence (teal) centred around the grasshopper monitoring transect (red).

The mean daily temperature minimum, mean, maximum, and range per logger over the whole time period, were used for analysis. After visually assessing the normality of data using quantile-quantile plots, I generated a general linear model for each temperature variable to explain the effect of location (inside, north, or south of the fence) and tested significance using ANOVA. *P* values were subject to Bonferroni correction to account for the non-independence of the 4 temperature variables so alpha was 0.0125.

2.2.8 Vegetation

I used a modified Scott height-frequency method (Rose 2012), to monitor vegetation because it captures changes in vegetation height; a factor that could affect native lizard and grasshopper behaviour. I established four 50 m transects at each of sites O_s and F running parallel to the gravel road; two on the road and two in the vegetated verges to either side. Site O_n was not assessed because it had sparse vegetation likely resulting from historic top-soil removal (Department of Conservation 2004). Paired transects at O_s and F were positioned randomly within the bounds of the habitat that was to be sampled, but at least 100 m apart.

The plant species present within a 4.47 x 4.47 cm area in 5 cm height interval was recorded every 50 cm along each transect, giving a series of stacked 100 cm^3 sampling cubes. Grass and lichen species were recorded collectively under the categories “grass” and “lichen”. Vegetation at both sites was assessed in mid-February 2019, (four months after the fence around site F was completed) and again in January 2020.

I calculated the frequency of sampling cubes in which each plant species was present per transect, and pooled these into five-meter sections, henceforth treated as replicates, similar to Rose (2012). This gave 20 replicates per site per habitat type. These data were analysed using repeated measure generalised linear mixed effects models (lme4 package version 1.1-21) for 1) the gravel road, and 2) the vegetated verges. First, the frequency of each species was treated as the response variable, modelled with a Poisson distribution, to give an indication of vegetation biomass at each site. This likely inflates biomass, as it relies on presence/absence within a volume but indicates coarse changes. Vegetation group, fence treatment (site O_s versus F), and time period (February 2019 versus January 2020) were fixed factors, and the unique identifier of each replicate was a random factor. Significance of interactions and some main effects were tested using a likelihood ratio test. Uncommon species were excluded to avoid model singular fit, leaving grass, *H. pilosella* (hawk weed), *Rumex acetosella* (red sorrel), and lichen on the road, and *Achillea millefolium* (yarrow), grass, *H. pilosella*, and *R. acetosella* on the vegetated verges. Second, relative vegetation composition (i.e. the frequency of each vegetation group as a percentage of the total vegetation frequency) was assessed using the above statistical tests but with a binomial distribution. However, only interactions with vegetation group as a covariate were tested because removing vegetation identity with this data structure does not provide a meaningful result. Significant interactions for vegetation frequency and relative composition were assessed using pairwise contrasts between estimated marginal means of each level of a factor using the emmeans function (emmeans package version 1.4.3.01).

2.3 Results

2.3.1 Predators: Tracking tunnels

Mammals were not detected inside the fence over the study period (Figure 2.5). Rats were not detected at any site, and cats, skinks and mice were detected at very low levels at open sites. Mustelids were only detected in January and February 2019 at relatively low rates but were present consistently at both open sites. The only organisms with tracking rates greater than 5 percent per night were large insects (overwhelmingly wētā) and hedgehogs. Large insect tracking rate varied between months with no indication of an association with the exclusion fence. Hedgehogs always tracked at high rates (up to 32% per night) at both open sites.

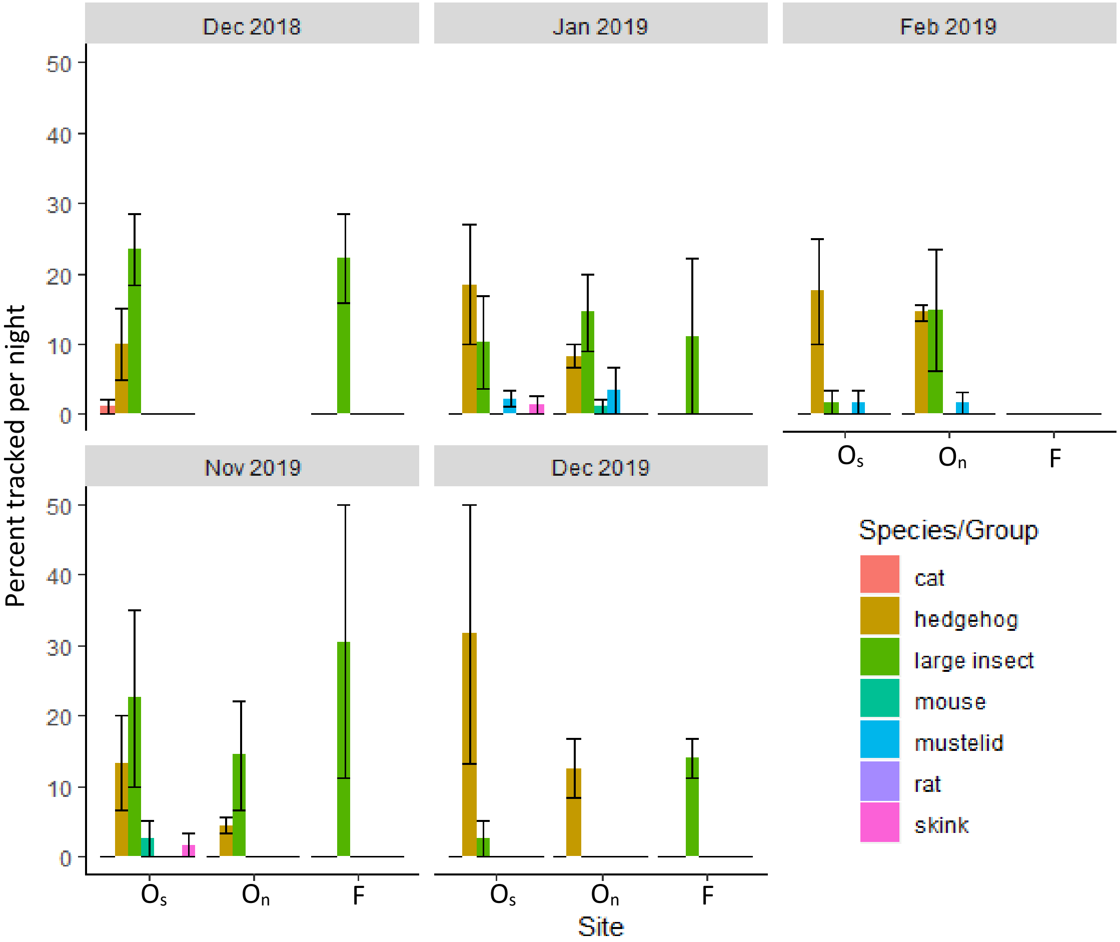

Figure 2.5 Mean and standard error of the percent tracking rate of tunnels per night over five months at Patersons Terrace. F = fenced site, O = open sites. Data were not collected at site O_n in December 2018.

2.3.2 Predators: Trapping

No mice were caught over the study period inside the fence. Some traps were falsely triggered, likely because of high wind. DOC 150 and DOC 250 traps inside the fence did not catch any mammals.

2.3.3 Predators: Trail cameras

Mammals were not recorded inside the fence. In February and March 2019, cameras located outside the fence captured 86 mammal visits (Table 2.1). Ninety percent were lagomorphs (e.g. Figure 2.6 A), and the remaining ten percent were predatory mammals (mostly cats e.g. Figure 2.6 B). Forty-six bird visits were recorded outside the fence, and two (a pair of Australian magpies, *Gymnorhina tibicen*, Fig 2.6 C) were recorded within the fence. Sixty-seven percent of visits outside the fence were Australian magpies and the remainder were groups of up to 6 starlings (*Sturnus vulgaris*). Most birds were perching on the predator exclusion fence (e.g. Figure 2.6 D).

Table 2.1 Number of separate animal sightings (i.e. groups of images separated in time by >5 mins) at site F in February and March 2019. Lagomorphs include rabbits (*Oryctolagus cuniculus*), and hares (*Lepus europaeus*).

Group	Outside predator exclusion fence (n=2 cameras)	Inside predator exclusion fence (n=2 cameras)
Lagomorph	77	0
Cat	7	0
Ferret	1	0
Hedgehog	1	0
Australian magpie	31	2
Starling	15	0

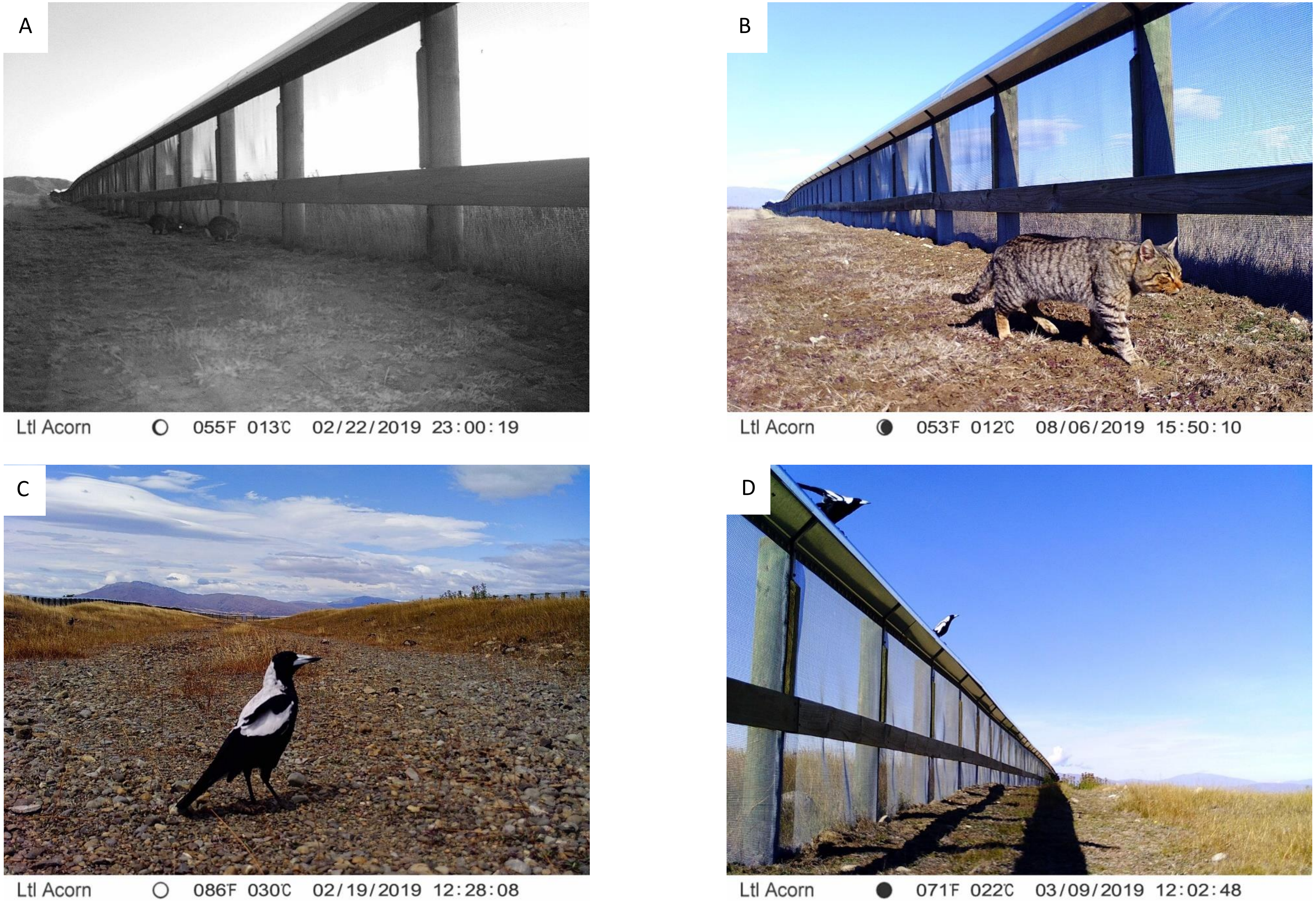

Figure 2.6. Examples of animals recorded by trail cameras at Patersons Terrace in and around a new design predator exclusion fence. Date (mm/dd/yyyy), time (24 hour), and temperature (Fahrenheit and Celsius) are displayed below each image. A) Two rabbits outside the fence. B) A cat outside the fence. C) Two Australian magpies on the road surface inside the fence. D) Two Australian magpies perched on the fence cap.

2.3.4 Meso-predators: Artificial retreats

Oligosoma maccanni and *O. polychroma*, were the only lizard species recorded under ARs. I could not always distinguish species, so only the total number of skinks is reported. At site O_s skink numbers were stable across all sampling periods, three in January and February, eight in November and four in December. Site F had similar numbers to site O_s in January and February (seven and three), but numbers were significantly higher in November and December (33 and 28) (Figure 2.7, time by site interaction: Likelihood ratio statistic = 6.306, p=0.012). In December 2019, 57% of the 28 skinks caught at site F were adults, all female, 75% were gravid; all four skinks caught at O_s were sub-adults.

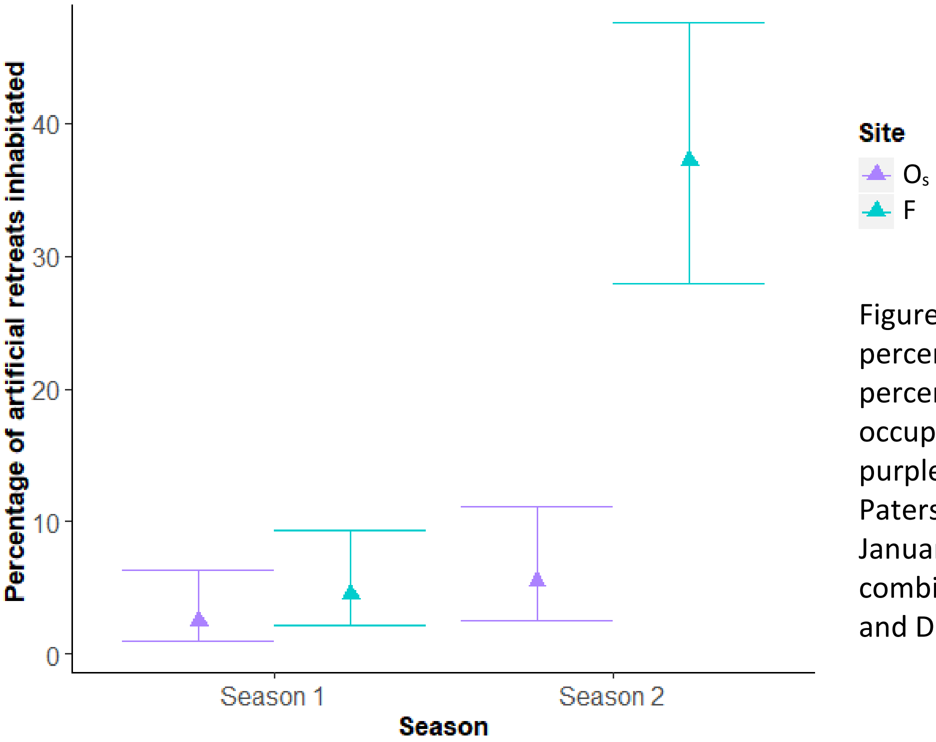

Figure 2.7 Model fits and ninety-five percent confidence intervals of the percentage of artificial retreats occupied at an open site (O_s, purple), and a fenced site (F, teal) at Patersons Terrace. Season one = January and February 2019 data combined, season two = November and December 2019 data combined.

2.3.5 Fence integrity and microclimate

Between December 2018 and April 2019, maximum wind speed was 65km h^{-1}, a 'fresh gale' on the Beaufort wind force scale, and maximum gust speed was 82 km h^{-1}. Winds from the SW were most common, (16% of time), followed by wind from the NE, (12% of time, Figure 2.8). The strongest wind came from the NE and was between 30 and 45 km h^{-1} over 4% of the time period. No damage to the predator exclusion fence was observed.

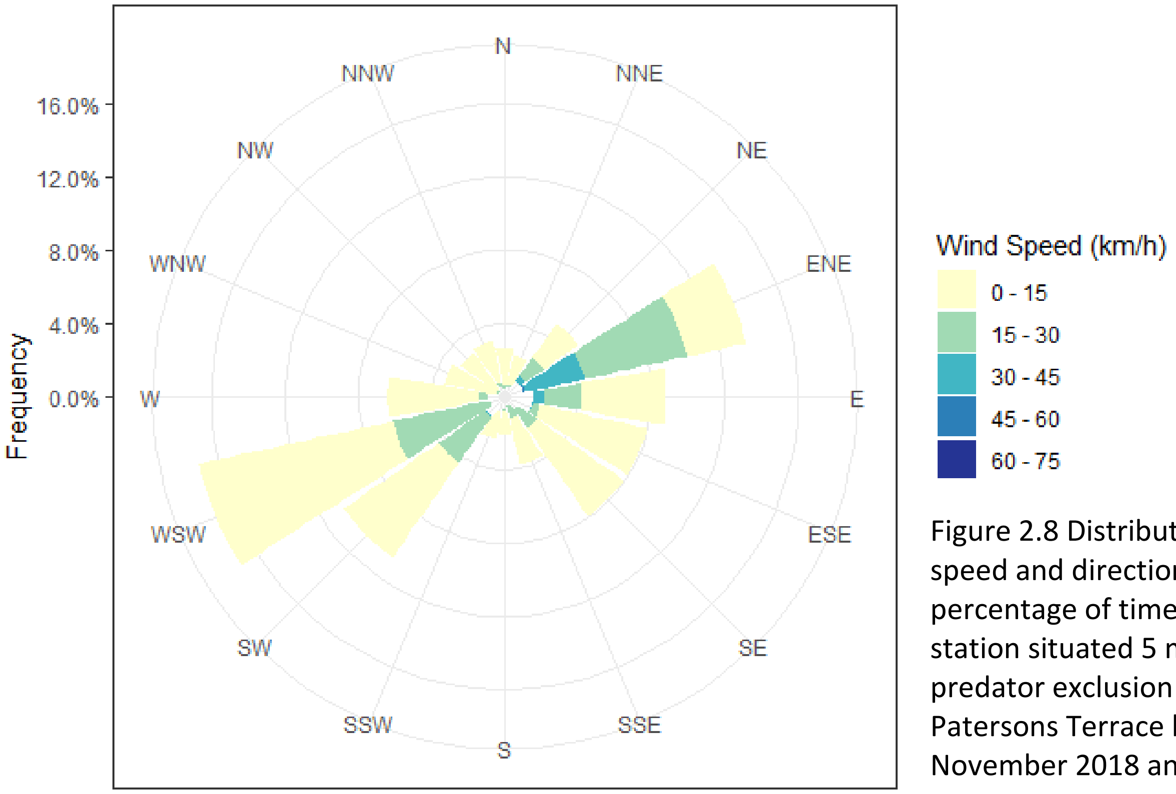

Figure 2.8 Distribution of wind speed and direction as a percentage of time at a weather station situated 5 m outside the predator exclusion fence at Patersons Terrace between November 2018 and April 2019.

There were minor differences in air temperature (Figure 2.9 A), soil temperature (Figure 2.9 C) and relative humidity (Figure 2.10) inside versus outside the predator exclusion fence, particularly for maximum values. There were larger differences in minimum, average, and maximum ground surface temperatures from March to May (Figure 2.10 B). Ground surface temperatures were up to 10 °C colder within the fence over this period.

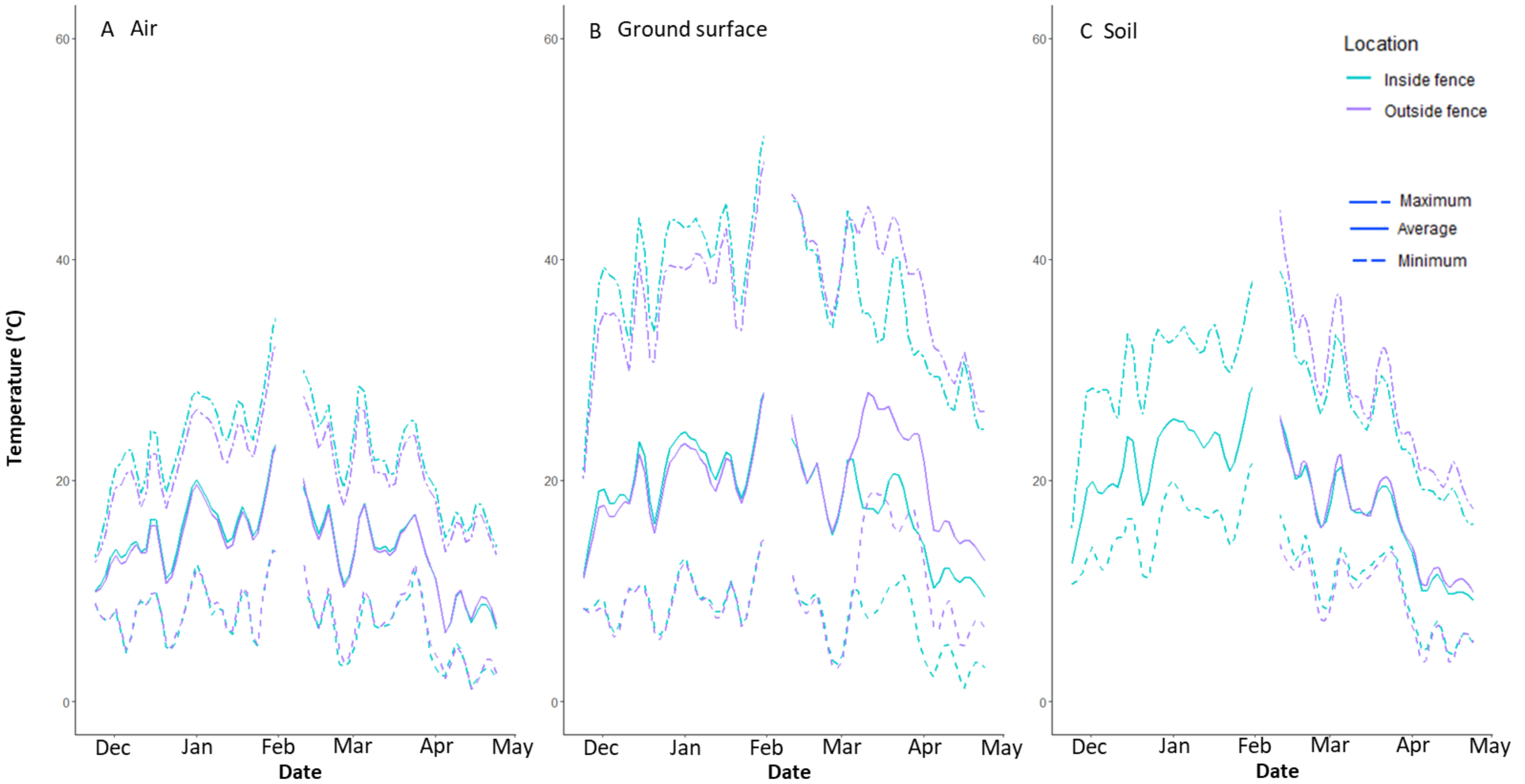

Figure 2.9 Smoothed conditional means of the daily maximum, average, and minimum air (A), ground surface (B), and soil (C) temperature inside and outside the predator exclusion fence at Paterson’s Terrace between December 2018 and April 2019. Note that accurate soil temperature data were not recorded outside the predator exclusion fence before February 2019.

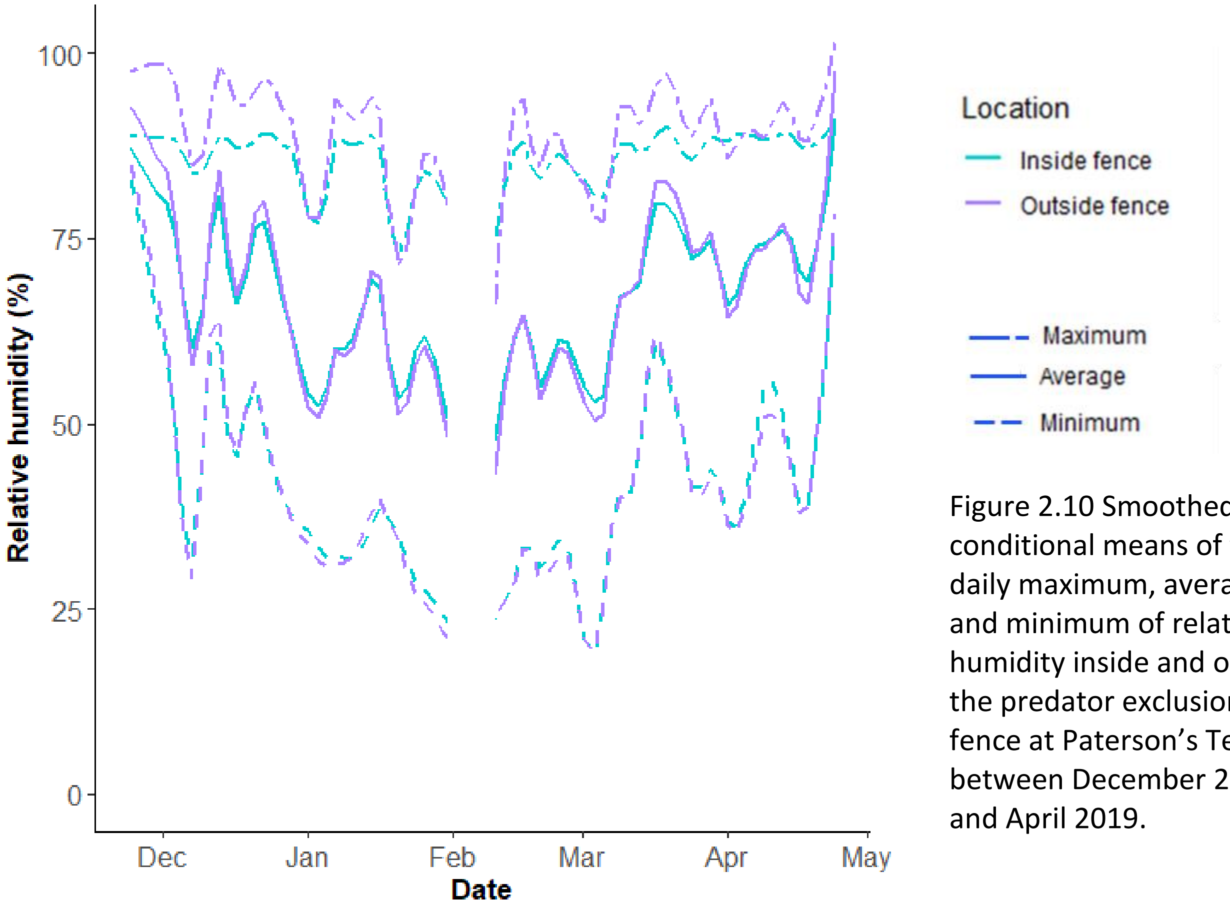

Figure 2.10 Smoothed conditional means of the daily maximum, average, and minimum of relative humidity inside and outside the predator exclusion fence at Paterson’s Terrace between December 2018 and April 2019.

Mean daily temperature minimum, average, maximum, and range inside the predator exclusion fence did not differ from those outside the fence on the road or in the vegetation (Figure 2.11). This suggests that ground temperature on the gravel road and in the surrounding vegetation was not significantly affected by the fence over the summer. Maximum temperature and range varied much more in the vegetation at all locations compared to the road.

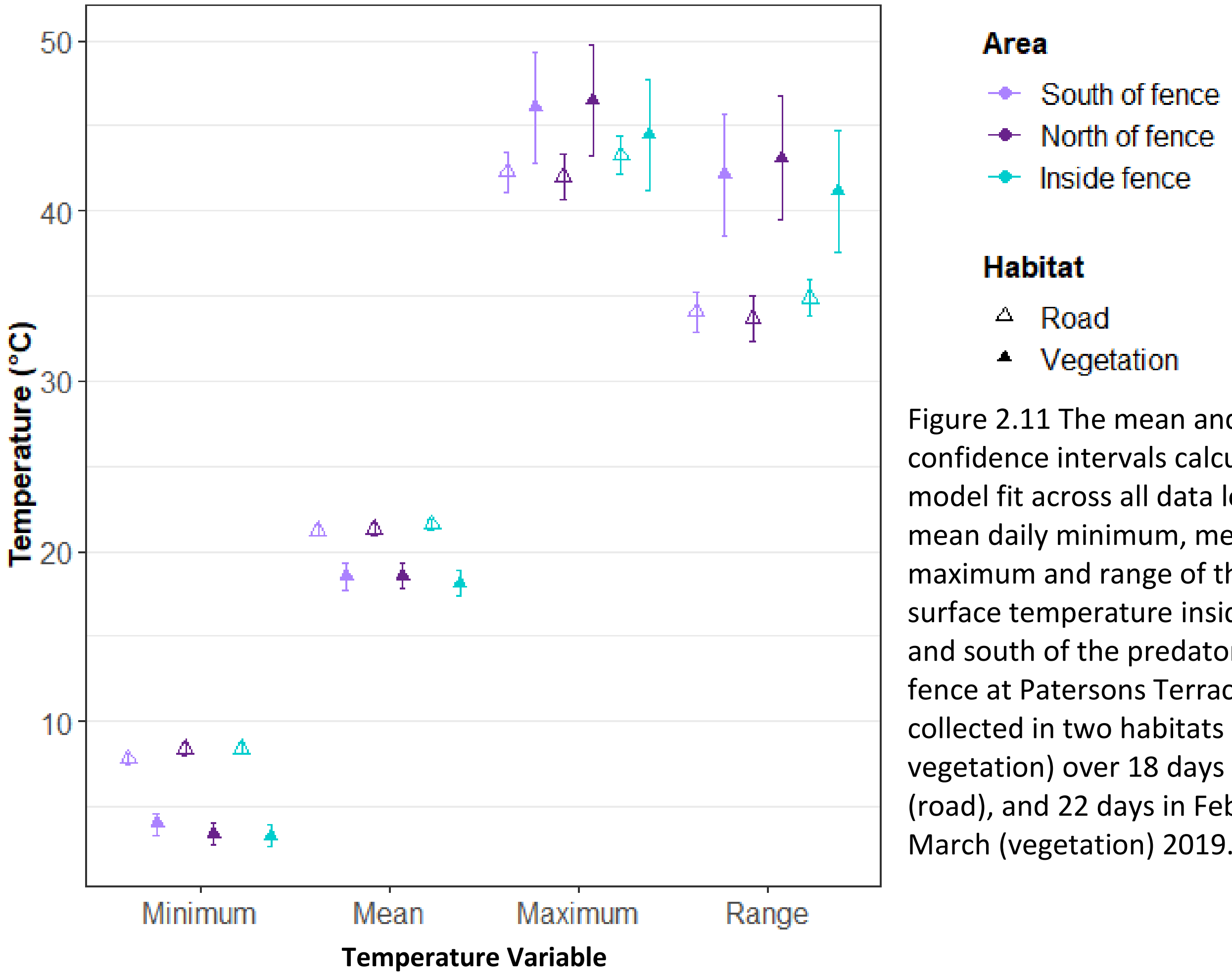

Figure 2.11 The mean and 95% confidence intervals calculated from model fit across all data loggers of the mean daily minimum, mean, maximum and range of the ground surface temperature inside, north, and south of the predator exclusion fence at Patersons Terrace. Data were collected in two habitats (road and vegetation) over 18 days in January (road), and 22 days in February and March (vegetation) 2019.

2.3.6 Vegetation

In both 2019, four months after fence construction, and 2020, over one year after fence construction, a total of nineteen distinct plant groups were recorded at Patersons Terrace (Appendix 3). The non-significant site by species by year, and site by year interactions suggest that lagomorph removal at site F did not affect vegetation frequency or relative composition (Table 2.2). However, the two sites did differ for other unknown reasons. In both years (i.e. regardless of time since fence construction and lagomorph removal) *Hieracium pilosella* and grass were more frequent on the gravel road and vegetated verges at site F compared to O_s (Figure 2.12 A; mean comparisons in Appendix 4), while *R. acetosella* was less frequent. Additionally, the frequency of grass, *H. pilosella*, and *R. acetosella* increased while lichen frequency decreased on the gravel road between 2019 and

2020 at both the fenced and open site (Figure 2.12 B). Total vegetation frequency increased in the vegetated verges at both sites between 2019 and 2020 (Figure 2.12 C).

Table 2.2 The model likelihood ratio statistic (LRT) and significance value (*p*) for the effect of each predictive variable or interaction on vegetation frequency and relative composition on the gravel road and in the vegetated verges. Site by year interactions were not tested for relative composition because the species identity is necessary to do so.

	Road				Vegetated Verges			
	Frequency		Relative composition		Frequency		Relative composition	
Predictive variable/ interaction	LRT	*p*	LRT	*p*	LRT	*p*	LRT	*p*
site:species:year	3.164	0.367	3.184	0.364	0.116	0.99	0.125	0.989
site:species	99.821	<0.001	124.84	<0.001	85.12	<0.001	104.931	<0.001
site:year	2.393	0.122	-	-	1.498	0.221	-	-
species:year	19.416	<0.001	23.236	<0.001	0.447	0.93	0.697	0.8738
site	-	-	-	-	-	-	-	-
year	-	-	-	-	6.127	0.013	-	-
species	-	-	-	-	-	-	-	-

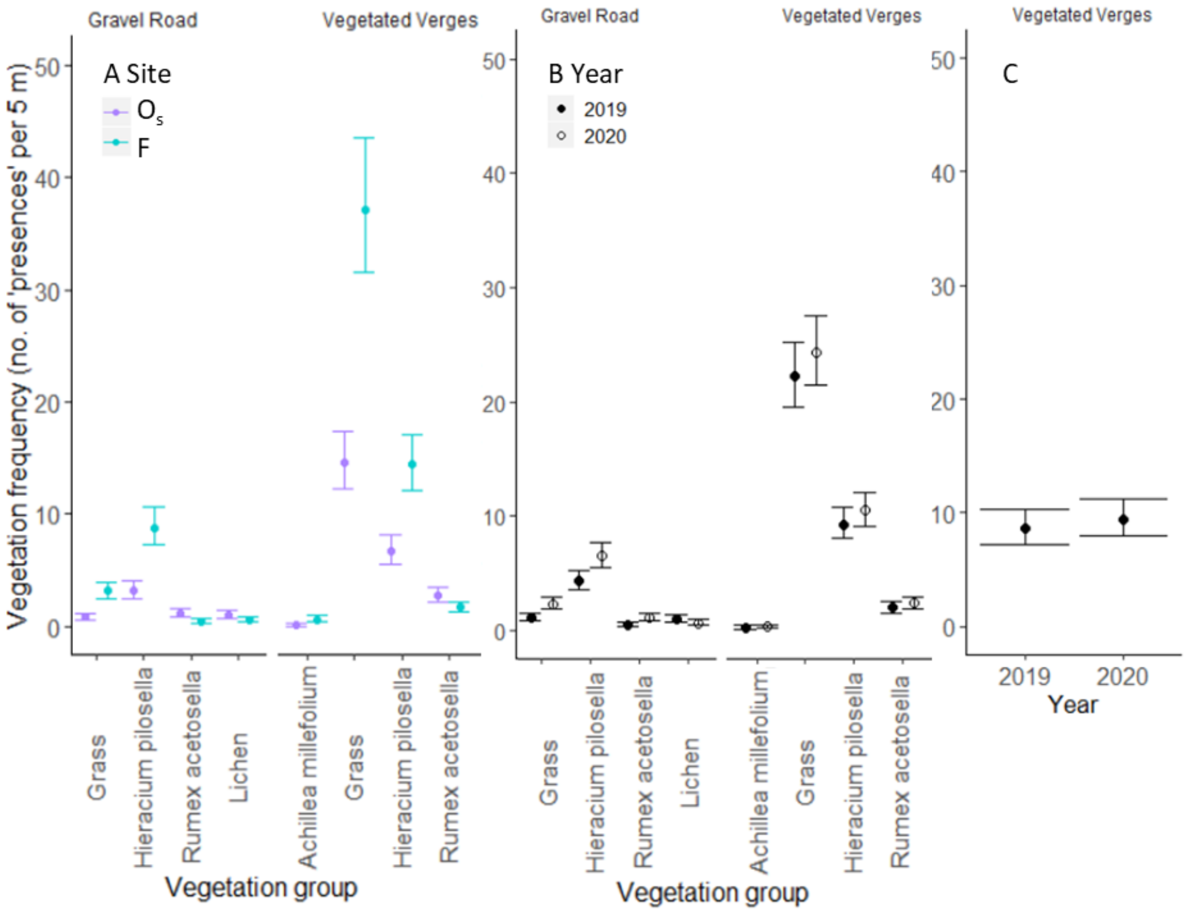

Figure 2.12 Model fits and 95 percent confidence intervals of (A) frequency of each species/group at the Open (O_s, purple), and Fenced (F, teal) sites in both years combined, (B) each species in 2019 (dot), and 2020 (open circle) at both sites combined, and (C) vegetation frequency regardless of species or site in each year. A and B show frequencies from both the gravel road and the vegetated verges, while C only shows frequencies from the vegetated verges.

Vegetation relative composition also differed between sites (Table 2.2), driven on the gravel road by site F having a higher proportion of grass and *H. pilosella*, and a lower proportion of *R. acetosella* and lichen than site O_s (Figure 2.13 A). On the vegetated verges, grass and *H. pilosella* also made up a higher proportion of the vegetation at site F than at site O_s (Figure 2.13 A). The relative composition of vegetation on the gravel road changed between years (Table 2.2) driven by a reduction in lichen composition in 2020 from 2019 (Figure 2.13 B).

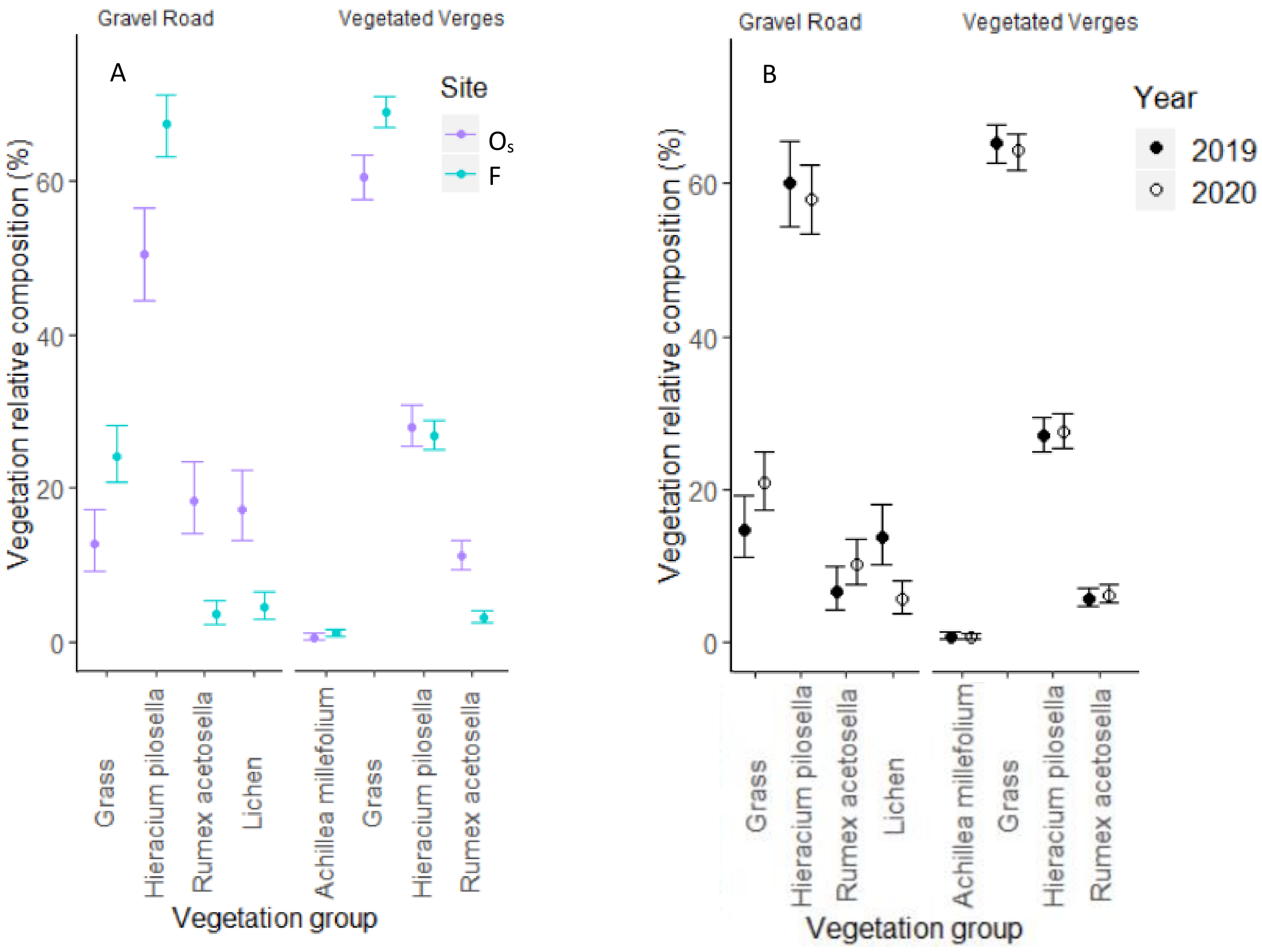

Figure 2.13 Model fits and 95 percent confidence intervals of vegetation relative composition of each species at the Open (O_s) vs Fenced (F) site in both years combined (A), and each species in 2019 (circle), and 2020 (open circle) at both sites combined (B).

2.4 Discussion

Invasive species pose a serious threat to biodiversity (IPBES 2019); however, their control can be expensive (Scofield et al. 2011) and can cause unintended effects for species that are the target of conservation action (Caut et al. 2009, Pech and Maitland 2016). These issues are pertinent in New Zealand, where invasive species are an overwhelming conservation problem (Craig et al. 2000) but best practice methods for invasive control to benefit threatened invertebrates have not been developed. I tested whether the first field trial of low-height predator exclusion fencing effectively excluded the targeted mammalian predators. I also tested for unintended effects of predator exclusion fencing, including meso-predator release, changes to microclimate, and changes to vegetation biomass and composition. Each of these factors could be detrimental for survival of robust grasshoppers, the target of this conservation intervention.

2.4.1 Effect of low-height predator exclusion fencing on mammals

Based on my tracking tunnel, trapping and trail camera results, the predator exclusion fence installed at Patersons Terrace to protect *B. robustus* successfully excluded hedgehogs, mustelids, and lagomorphs. This partially supports my hypothesis that this fence design can exclude mammalian predators (except cats) and lagomorphs, in a real field application. Mammals were not detected using any monitoring method inside the predator exclusion fence, but no monitoring method is perfect. Where multiple detection methods are used, these imperfections can be quantified by calculating the probability of a monitoring device detecting a mammal that is present (henceforth detection probability).

I could not calculate detection probability at Patersons Terrace because mammals were not detected inside the fence; the only location with different types of detection device.

However, at a nearby South Island braided river, three tracking tunnels had a detection probability that would record 90 percent of cats, ferrets, stoats, hedgehogs, and mice in 80 nights or less (Pickerell et al. 2014). In contrast, I only used tracking tunnels for 37 nights within the fence, but they were at a higher density than Pickerell et al. (2014), which would increase detection probability. DOC 250 traps also have detection probabilities sufficient to give a 90 percent chance of detecting any mammal that was present in the monitoring period at Patersons Terrace (Pickerell et al. 2014). Published trail camera and mouse trap detection probabilities from New Zealand non-forested environments are not available. However, trail cameras are at least as effective as tracking tunnels for detecting hedgehogs, rats, and mice (Anton et al. 2018), and modelling from other environments indicates the mouse trap density and monitoring period at Patersons Terrace were sufficient to detect mice with greater than 90% accuracy (Russell et al. 2017). Additionally, two searches of the exclosure with thermal imaging equipment only found one mammal (a rabbit, see 2.4.2). Given several methods were used to detect mammals, each with a high chance of success, I am confident that any mammal inside the fence at Patersons Terrace would have been detected, and the site is predator-free.

Despite the fence’s success, its ability to exclude all target mammals in the field was not robustly tested in this trial. Outside the fence, mice were only tracked at low rates, and rats not at all. This indicates that rodents are rare in the area and may have been absent within the fence by chance, rather than because they were unable to cross it, although for rats this is unlikely because previous small-scale testing indicated that they cannot cross the fence (Agnew and Nichols 2018). Rodents will likely stay at low densities at Patersons Terrace because mast seeding *Chionocloa* species that allow for population booms are not present (Department of Conservation 2004, Wilson and Lee 2010). As such, to rigorously test whether this fence design can exclude rodents in the field, it should be tested in forest or *Chionochloa* grassland where rodents are abundant.

2.4.2 Thermal imaging efficacy

Trail cameras inside the fence did not detect lagomorphs. However, prior to camera installation, the fence was searched on two separate nights by a DOC contractor using thermal imaging equipment after discovery of rabbit sign. The only mammal detected was a rabbit (subsequently shot) on the second search night. The rabbit was probably trapped during fence construction because there was no sign of an entry point. It likely avoided detection in the first search because it was in a burrow, highlighting the difficulty of detecting some mammals that have taken refuge, even in a small area. This is consistent with the knowledge that dense structures can prevent animal detection with infrared technology (Boonstra et al. 1994). For example, rabbit detection with thermal imaging equipment on Macquarie Island was more accurate than spot counts, but rabbits under the ground could not be detected (Terauds et al. 2014).

2.4.3 Effect of low-height fencing on cats

Cats were not detected inside the predator exclusion fence even though they can jump higher than 1.2m, and at least one cat was repeatedly recorded by trail cameras directly outside the fence. This contradicts my expectation that cats would cross low-height predator exclusion fencing. However, cats generally select habitat based on the abundance of rabbits, their main prey (Recio et al. 2014) and rabbits were eliminated within the fenced area. Therefore, it is likely that cats chose not to enter the fenced area. As such, low height fencing should only be used where cat exclusion is not necessary or where there is no incentive for cats to enter an area.

2.4.4 Low-height fencing cost

As outlined above, low height predator exclusion fencing at Patersons Terrace was effective, but construction cost NZ $ 131,983.20. At 460 m in length that is $286.92 per metre, within the $200 - $400 range of 'normal' predator exclusion fences (Campbell-Hunt 2008, Bell 2014). However, as the first field application of this fence design, costs will likely decrease as a result of lessons learned during construction. Several other low-height fence designs are being trialled in the Mackenzie Basin to assess whether sufficient strength for this exposed environment can be achieved at a reduced cost (TMA 2019).

Monitoring and maintenance are essential to ensure exclusion fencing remains effective, resulting in an ongoing cost. For example, the chance of mammal entry within 24 hours of damage to traditional exclusion fencing can be as high as 85 to 99% (Connolly et al. 2009). However, this research is from lowland podocarp-broadleaf forest surrounded by farmland, which will have both higher rates of physical damage due to tree-fall and flooding, and higher densities of some mammals than Patersons Terrace (Brockie 1975, King et al. 1996, Innes 2005b, King and Murphy 2005). The exclusion fence at Paterson's Terrace withstood strong wind and snowfall with no signs of damage, possibly indicating low ongoing maintenance and monitoring costs. However, accumulated snow may reduce the effective height of the predator exclusion fence against small mammals. This would necessitate a search of the fenced area for mammals at the end of winter or after unseasonal snowfall to coincide with *B. robustus* emergence from their winter refugia and the loss of protection that provides.

2.4.5 Meso-predator release: Native skinks

The exclusion of mammals at Patersons Terrace may have led to meso-predator release. Meso-predator release occurs when the decline of a top predator results in increased abundance of predators at a lower trophic level (meso-predators) (Prugh et al. 2009). Rats and mice were not detected within the fence, so meso-predator release could not be tested for these species. The increased number of artificial retreats inhabited by skinks within the fence compared with an open area at Patersons Terrace one year after fence completion supports my hypothesis of skink release with mammalian predator removal. However, one aspect of my results does question this hypothesis.

Skinks produce their offspring in spring-summer, and it takes at least two years for *O. polychroma*, and *O. maccanni* to reach adulthood (Cree and Hare 2016). As such, the number of adult skinks inside the fence in November and December 2019 could not have been recruited from the population that was present in January and February 2019. One possible explanation is that immigration rates have increased; potentially because the absence of mammalian predators means that skinks that do enter the fenced area are more likely to persist. Alternatively, skinks may be less likely to leave because predators are not present. While not tested at Patersons Terrace, skinks are able to pass through a similar fence at a Central Otago site (Wilson et al. 2017), so such increased immigration is possible.

Another possibility is that the true number of skinks at both sites was equal in late 2019, but their use of artificial retreats was altered inside the fence. The presence of predators outside the fence could have reduced retreat occupancy by skinks (Downes and Shine 1998, Robert and Thompson 2007, O'Donnell and Hoare 2012). However, there was no evidence of predators inhabiting artificial retreats at Patersons Terrace, so this is unlikely to have significantly affected skink occupancy of retreats. Tall vegetation may also increase skink numbers under retreats, possibly because it makes the thermal properties of retreats more attractive (Chavel et al. 2012). This is also unlikely because skink abundance did not relate to vegetation changes, but some effect of vegetation height cannot be entirely ruled out because of the limitations of vegetation sampling (section 2.4.9).

Because skinks were monitored at different times of year in initial and follow up monitoring, a site-specific seasonal fluctuation in skink abundance cannot yet be ruled out. However, it is overall most likely that immigration followed by reduced mortality in the absence of mammalian predators is largely responsible for increased adult skink numbers within the fence at Patersons Terrace, suggesting this may be meso-predator release.

Evidence for release of skinks at Patersons Terrace is consistent with skink response to predator control in other New Zealand locations. For example, decreased hedgehog density resulted in increased juvenile *O. maccanni* abundance at an Otago site (Jones et al. 2013). As another example, populations of Otago skinks (*O. otagense*) and grand skinks (*O. grande*) grew after mammalian predator control or near elimination (Reardon et al. 2012). My result is also consistent with global examples, such as predator control releasing several small lizard species from predation in Australian semi-arid shrubland (Olsson et al. 2005). This places skink release from predation at Patersons Terrace in line with, and reinforces, the global observations of frequent meso-predator release when top predators are removed (Prugh et al. 2009). Meso-predator release has negatively affected other insects (e.g. Pacala and Roughgarden 1984, Schoener and Spiller 1987), although these examples involve other invertebrates being released from predation. This suggests *B. robustus* within the fence at

Patersons Terrace may be negatively affected by increased skink abundance and that skink management should be considered (discussed further in Chapter 3).

2.4.6 Predator fencing edge effects: Microclimate

An edge effect refers to the ecological changes that occur at the edges of a patch of habitat; these are widely studied phenomena (Ries et al. 2004) that occur at a range of scales (Cadenasso et al. 2003). Proximity to an edge can negatively affect some species by altering conditions and species interactions (Haddad et al. 2015). I monitored to determine whether low-height predator exclusion fencing can alter microclimate because this could affect the *B. robustus* population the fence was constructed to protect.

The observed large difference in autumn ground surface temperature between the inside and outside of the exclusion fence provides some support for my hypothesis that microclimate would be altered within the Patersons Terrace fence. However, without multiple fences (prohibited by their cost) or before fence data, the effect of the fence cannot be separated from the effect of terrain which differs slightly inside and immediately outside the fence. If the difference in autumn ground surface temperature is truly an effect of the exclusion fence, which is possible given potential shading effects, then the fence itself may have affected *B. robustus* survival (more detail in Chapter 3). This is because *B. robustus* are ectothermic and regulate their temperature by basking. Ground surface temperature will therefore affect their metabolism, development rate (Zuo et al. 2012), behaviour, and vulnerability to pathogens (Inglis et al. 1996).

As for ground surface temperature, changes to relative humidity, and air and soil temperature could affect *B. robustus* survival. For example, relative humidity differences could alter grasshopper susceptibility to fungi (Marcandr 1987), like *Beauveria bassiana* that appears to cause mortality in *B. robustus* (T. Murray *Pers Comm*), or soil temperature differences could affect development of *B. robustus* eggs while they overwinter underground (Mason 1971). However, the differences in these temperature variables were so small that even if they were caused by the fence, which is unlikely given the possible effects of terrain, they were probably not biologically significant.

There appears to be no published research on the effects of predator fencing on microclimate, possibly because existing fences have been constructed primarily for birds that are not as strongly affected by microclimate. If patterns like that observed at Patersons Terrace occur elsewhere, then the impact for insects could be significant where sites are small. Generally, however, existing fences encompass such large areas that most of the environment within is unlikely to be affected by the fence directly. For animals, any such effect will likely be limited to ectotherms as ambient temperature affects their metabolic rate, but plants could show a large response to altered light or temperature, which would have flow on effects for other organisms (see section 2.4.8).

2.4.7 Predator fencing edge effects: Bird behaviour

Edge effects can be difficult to predict (Ries and Sisk 2004), and edge effects at Patersons Terrace proved to be no exception. The high number of birds observed perched on the fence suggests that the fence affected bird behaviour and increased the number of birds in the area, or the time they spent there. This effect is consistent with the response seen in other birds, such as hooded crows (*Corvus corone cornix*) in Sweden that show a preference for man-made structures (Wallander et al. 2006). However, bird abundance was not monitored at the Patersons Terrace open sites because this response was not predicted, so it is unclear how strong the ‘attraction’ effect of the fence was. In addition, this attraction is possibly being weakened by a wire fence ~20 m away from the exclusion fence, which may also be attractive to birds. While *B. robustus* are cryptic, protecting them to some extent from the avian predators with which they evolved, this apparent increased bird abundance could reduce population survival because other pressures mean those populations are already small (more detail in Chapter 3).

2.4.8 Vegetation response to lagomorph removal

Herbivores can affect plant biomass and community composition (Jia et al. 2018) and alter the course of succession (Walker et al. 2009, Perry et al. 2015, Bellingham et al. 2016). However, based on two monitoring occasions separated by a year, I found no support for my hypothesis that grazer exclusion would alter vegetation biomass or relative composition on the gravel road or in the vegetated verges after herbivore exclusion, although there are several limitations to this conclusion (see 2.4.9). I also found that the fenced site had more vegetation, and a higher proportion of grass than the open site, which could be because of differences in microtopography, fertility, or soil depth affecting the outcome of competition (Wilson and Tilman 1993, Casper and Jackson 1997, Liu et al. 2020).

It is possible herbivore removal did not alter vegetation because of the harsh Mackenzie Basin environment. This would be consistent with the response of vegetation in the nearby Lake Tekapo Scientific Reserve after sheep removal and rabbit suppression (Walker et al. 2015). While biomass increased over an eighteen-year period and vegetation became more grass dominated at some sites, cold winters, short summers, high seasonal moisture stress, and relatively low soil fertility limited biomass production (Walker et al. 2015). Further examples of a delayed response to grazer removal include Norwegian alpine tundra vegetation, which had not responded to herbivore removal after two years (Sørensen et al.

2018), and rainfall limiting vegetation response to herbivore exclusion in an arid Mongolian steppe (Wesche et al. 2010). As such, it is plausible that changes at Patersons Terrace could take more than one year, although both examples come from more extreme environments. In contrast, reduced rabbit abundance, caused by Rabbit Haemorrhagic Disease (RHD), was associated with greater vegetation biomass just one year after RHD was introduced to a semi-arid New Zealand grassland similar to Patersons Terrace (Norbury et al. 2002). Norbury et al. (2002) used the vegetation dry weight to calculate biomass, which is more sensitive than the method I used at Patersons Terrace and could explain why a rapid response was detectable in their study.

While vegetation has not yet responded to lagomorph exclusion at Patersons Terrace, based on Norbury et al. (2002) and Walker et al. (2015) it is highly likely that increased biomass and a shift to grass dominance will occur in future. This may negatively affect *B. robustus*. On the gravel road, increased biomass could reduce *B. robustus* survival by removing the open gravel habitats they prefer (Thorsen 2010). This could be through vegetation impeding grasshopper ability to escape from predators or reducing ground surface temperatures that limit basking opportunities. Increased vegetation on the road would likely also speed soil development (Mardhiah et al. 2014), causing positive feedbacks that would increase the rate of succession (Prach et al. 1993) and therefore the magnitude of impacts for *B. robustus*. Increased vegetation biomass along the road verges could shade the road and reduce grasshopper basking opportunities, or could support larger skink or other predator populations by increasing food and refuge availability (Norbury 2001). While there was little evidence altered skink abundance at Patersons Terrace was driven by vegetation changes, increased vegetation would decrease basking opportunities for skinks on the road verges (Chavel et al. 2012), forcing them onto the gravel road and increasing the chance of them encountering and consuming grasshoppers. If such negative effects do occur with vegetation release, it would mean that the presence of lagomorphs currently indirectly benefits *B. robustus* survival by limiting vegetation growth. This would be consistent with the effect of black-tailed prairie dogs (*Cynomys ludovicianus*) in Colorado, USA. They reduce tall vegetation near their colonies which appears to increase Acridid grasshopper abundance (Kenney et al. 2016). If future increases in vegetation affect *B. robustus*, it would add to the numerous global examples of herbivores indirectly affecting other species. A well-known example is the trophic cascade at Yellowstone National Park where wolf (*Canis lupus*) reintroduction reduced herbivory by decreasing elk (*Cervus elaphus*) abundance in some areas, allowing for increased growth of some plant species which was in turn associated with increased beaver (*Caster canadensis*) and bison (*Bison bison*) numbers (Ripple and Beschta 2012). Given the potential for a future response of vegetation to lagomorph exclusion and probable impacts for *B. robustus*, vegetation management, especially on the gravel road, may be necessary in future. Management may also be required regardless of the effect of lagomorph exclusion because, unlike a braided river, periodic floods that would remove vegetation do not occur at Patersons Terrace.

2.4.9 Vegetation monitoring limitations

There were several limitations of vegetation sampling at Patersons Terrace. Sampling covered a narrow footprint and likely missed rare species (Rose 2012), possibly explaining why few species were found compared to recordings of at least 74 vascular plant species at sites nearby (Walker et al. 2015). Although, knowledge of all species present was deemed of little importance for *B. robustus*, a generalist herbivore. A narrow sampling footprint could also limit detection of changes in plant cover without a related change in height. For example, *H. pilosella* is a prostrate rosette forming herb that could affect the availability of basking habitat for *B. robustus* by covering the gravel surface. *Hieracium pilosella* is capable of vegetative reproduction, so could have rapidly responded to lagomorph exclusion without being detected because the change would have been in cover not height. Furthermore, difficulty precisely aligning the sampling tape in both sampling periods could have increased statistical variability, limiting the ability to detect changes in vegetation over time. There was also a four-month delay between fence construction and initial vegetation sampling, which coincided with spring. A rapid vegetation response in spring could explain why vegetation differed between sites in both time periods, although this could not be separated from potential site effects. Such a rapid initial vegetation response may have limited the size of any detected changes between sampling periods to below the threshold for statistical significance. Finally, this method relies on presence/absence within a volume, meaning it is less sensitive to small changes. Aerial imagery was captured shortly after fence installation and follow-up imagery could allow more accurate assessment of vegetation biomass changes, particularly for species like *H. pilosella* where increased cover would be expected.

2.4.10 Conclusions

My research at Patersons Terrace demonstrated that low-height predator exclusion fencing is effective in the field, at least for hedgehogs and mustelids, and can withstand harsh environmental conditions without damage. This technology could be used in further predator control projects, but monitoring will be required to ensure that rats and mice are excluded. As yet, it is unclear whether low-height predator exclusion fencing significantly reduces costs therefore allowing conservation funding to be spread further, but it is no more expensive than current predator exclusion fencing. My research also suggests that vegetation response to herbivore exclusion may take more than one year in harsh dryland environments, however, future aerial imaging analysis will provide more certainty. If increased vegetation biomass and changes to relative composition do negatively affect *B. robustus* survival, then management to reduce vegetation biomass on the gravel road is recommended. The unintended effects of invasive species control that occurred at Patersons Terrace (meso-predator release, apparent altered bird behaviour and microclimate, and likely future vegetation changes) reinforce that monitoring of the impact of invasive species control must be broader than just measuring the response of target species. As 2050 draws closer and efforts to eradicate particular mammalian predators from New Zealand are increased, the scale and potential for unintended consequences of control will increase. Without careful planning, such large-scale invasive species control could do significant damage. This highlights the importance of research, such as that carried out at Patersons Terrace, where the unintended consequences of management that could affect threatened species populations are assessed alongside the implementation of control action. As for my research, this can inform adaptive management, ultimately benefiting threatened species by mitigating negative effects.

Chapter 3 Response of a robust grasshopper (*Brachaspis robustus*) population to a new predator exclusion fence

3.1 Introduction

3.1.1 Fencing for conservation

Fencing is used to protect biodiversity worldwide by separating threatened species from a threatening process (Hayward and Kerley 2009). There are many examples of fencing resulting in positive outcomes for biodiversity (e.g. Finlayson et al. 2008, Hewett Ragheb et al. 2019, Bruns et al. 2020) but, as with any conservation action, fencing could also have no benefit or a negative effect on biodiversity (e.g. van Dyk and Slotow 2003, Wallander et al. 2006, Newmark 2008).

In New Zealand, fencing is commonly used to exclude introduced mammalian predators (Innes et al. 2012). These fences have been criticised for being expensive and rarely achieving their goals (Scofield et al. 2011), although this claim is disputed (Innes et al. 2012). Specifically, predator exclusion fencing is well suited to protect organisms that are extremely sensitive to mammalian predators, and is more cost effective than trapping for small areas over a long time period (Norbury et al. 2014). Furthermore, work to reduce the cost of fencing is ongoing, and less expensive low-height fencing has been trialled on a small scale with some success (Agnew and Nichols 2018).

So far predator exclusion fencing has primarily been established for bird conservation and more commonly around forest fragments than in other environments (Burns et al. 2012). Only ~5% of New Zealand's threatened or at-risk terrestrial animal species are birds (Statistics New Zealand 2019). In contrast, invertebrates make up ~88% of that group (Statistics New Zealand 2019). The high cost of fencing interventions may to some extent explain this apparent focus on birds, promoting trade-offs and causing the management of certain species to be prioritised over others (Wilson et al. 2009). Other contributing factors may include difficulty assessing the outcome of management for some species (Chadès et al. 2008), or potentially limited public interest in their conservation (Davies et al. 2018). Exclusion fencing does benefit some non-avian taxa, including invertebrates (e.g. Watts et al. 2011), but its effect on many species remains to be tested. Low-height predator exclusion fencing is expected to be less expensive than long term trapping (Norbury et al. 2014) or traditional predator exclusion fencing (Agnew and Nichols 2018). These reduced financial limitations support construction and testing of fencing to protect a wider range of non-avian taxa, including invertebrates. If successful, this would allow a conservation method developed primarily for birds to be adapted for the creation of best practice management strategies for lesser known, non-avian, threatened species. Here I tested whether low-height predator exclusion fencing could protect a threatened invertebrate found only in the Mackenzie Basin, the Nationally Endangered (Trewick et al. 2014) braided river-dwelling robust grasshopper (*Brachaspis robustus*).

3.1.2 Causes of robust grasshopper decline

Possible causes of *B. robustus* decline include native and introduced predators, habitat degradation due to weed invasion, and hydroelectric development, however, none of these have been investigated fully (White 1994, Schori et al. 2019). More recently, pathogens such as the fungus *Beauveria bassiana* have also become a concern (T. Murray, *pers. comm.*). The few studies of *B. robustus* (White 1994, Trewick 2001, Thorsen 2010, Schori et al. 2019) contribute to the uncertainty.

The most likely driver of decline is predation by introduced mammalian predators including ship rats (*Rattus rattus*), Norway rats (*Rattus norvegicus*), cats (*Felis catus*), stoats (*Mustela erminea*), weasels (*Mustela nivalis*), ferrets (*Mustela furo*), mice (*Mus musculus*), and hedgehogs (*Erinaceus europaeus*) (Schori et al. 2019). *Brachaspis robustus* has characteristics that make it vulnerable to predatory mammals (Chapter 1 section 5), including crypsis as its primary means of predator avoidance (Bigelow 1967). Insects, including other orthoptera, make up a large proportion of mammalian predator diets in the Mackenzie Basin (Murphy et al. 2004, Jones et al. 2005, Dowding et al. 2015). While analysis of mammal gut contents on Mackenzie Basin braided rivers (*B. robustus* habitat) has not found *B. robustus* body parts (Murphy et al. 2004), the rarity of the species would now make it unlikely that they would be encountered. Schori et al. (2019) assessed whether reduced predatory mammal abundance led to increases in *B. robustus* abundance. They found evidence for a positive effect of mammal reduction on another Mackenzie Basin grasshopper species (*Sigaus minutus,* Status At Risk: Declining), but could not attribute changes in *B. robustus* survival to changes in mammal density. Pressures suppressing *B. robustus* populations to low levels must be identified to secure the species against extinction. This is why Schori et al. (2019) recommend that total predator exclusion, which is more intensive than the predator control they assessed, is required to conclusively test the theory that mammalian predators are suppressing *B. robustus* abundance.

3.1.3 Hypotheses

A low-height predator exclusion fence (Chapter 2) constructed around an area of *B. robustus* habitat on a gravel road at Patersons Terrace allowed the Schori et al. (2019) recommendation to be tested. Robust grasshoppers have been monitored for several years at three sites along the gravel road habitat, including the section now fenced. This allowed a rigorous test of the effect of mammal exclusion by comparing *B. robustus* abundance inside and outside the exclusion fence and comparing population counts with previous years in the same location prior to fence construction; a Before-After-Control-Impact (BACI) study design. I hypothesised that successful mammal exclusion (Chapter 2) would result in an increase in grasshopper population density within the fenced area when compared to adjacent unfenced sites accounting for any pre-existing site effects through the BACI study design.

3.1.4 Challenges to assessing robust grasshopper response

There were several challenges to assessing *B. robustus* response to predator removal. In general, testing conservation interventions in a rigorous experimental framework is challenging because the low numbers and small spatial distribution of rare and threatened species limits replication and controls (Radford et al. 2018). This was true for my research at Patersons Terrace where only one predator exclusion fence could be built because of the high construction cost, so spatial replication was not possible. However, two control sites were used. I further minimised the effect of low replication by using a BACI study design, which is more robust than Control-Impact or Before-After designs (Christie et al. 2019). Another difficulty is that accurate estimates of population size, which are necessary to assess the outcomes of conservation management (Sutherland et al. 2004), can be challenging to determine where species are rare or difficult to detect (Thompson 2004). Robust grasshoppers fall into both these categories (White 1994), so I used two different monitoring methods to increase the likelihood of accurately assessing grasshopper populations (see 3.2). I also recognised and tested for indirect effects of the fence (see Chapter 2).

3.2 Methods

I assessed the *B. robustus* numbers at three sites, one fenced (F), and two open (Open south, O_s; Open north, O_n) along a gravel road, described in Chapter 2, at Patersons Terrace near Tekapo, South Island, New Zealand. Straight-line distance transect counts had previously been carried out at the same three sites since November 2015 (Schori 2020). I continued these transect counts following the same method (detail below) after fence construction. I also trialled Capture-Mark-Recapture (CMR) monitoring to estimate survival and total population size, a method not fully tested for this species but one used successfully for *Sigaus minutus*, in very similar habitat (Schlump 2018). Robust grasshoppers are not active, or take shelter under low and very high temperatures or in heavy rain, which affects their detectability (Thorsen 2010). As such, all monitoring was conducted in fine conditions when the temperature at ground level was > 14 °C (Kestrel 3500 Pocket Weather Metre- GeoSystems New Zealand LTD), limiting monitoring to spring and summer. Ambient environmental conditions were also recorded to account for changing detectability, including air and ground surface temperature, relative humidity, barometric pressure, trend in barometric pressure, mean and maximum wind speed over thirty second, perceived wind strength, and cloud cover. These were not recorded on every occasion so could not be included in analysis (see 3.2.1). However, the availability of grasshopper refugia, therefore the effect of temperature on their detectability, may be reduced at Patersons Terrace where there are only small spaces between well compacted gravel particles, compared with large spaces between cobbles in their natural braided river habitat. Additionally, all sampling on the same day was carried out in a short period of time, at different times of day in each month, and each day the order in which transects were monitored was varied, further minimising any consistent detection bias that could be caused by temperature.

3.2.1 Straight-line distance transect counts

I counted *B. robustus* on three transects on six days in each month from November 2018, immediately after predator exclusion fence construction, to March 2019, and in November and December 2019. This method, established by Schori (2020), involved slowly walking a 100 m long by 1 m wide (100 m^2) transect searching for grasshoppers. Between each step, the lifted foot was waved in front before stepping down to provoke a jump response from grasshoppers, allowing visual detection of grasshoppers. Grasshoppers detected were captured by hand, and sex, body (top of head to end of abdomen) and femur length, and the distance along the transect were recorded. Grasshoppers were classified as nymphs or adults based on femur length (adult male femur ≥ 9 mm, adult female femur ≥16 mm). I then released the grasshopper behind me, to avoid catching the same individual twice and continued along the transect. For individuals <8 mm long I recorded location only to avoid injuring individuals through handling.

To allow for statistical comparison between sites in the unavoidable absence of fence replication, I split each 100 m transect into 20 m sections, henceforth a unit, and treated each unit in each sampling session as a 'replicate'. This level of pseudo replication was selected because lower replication, such as averaging across sampling sessions, caused the statistical model's fit to be singular because of a high proportion of zero values, preventing meaningful statistical interpretation. The same statistical issue was encountered when analysing adult counts alone. To overcome this, final instar nymphs (estimated to be females with a femur ≥ 14 mm, and males with a femur ≥ 8 mm) were included with 'adults' in these months. Reported juvenile results include individuals with femurs < 9 mm for males and < 16 mm for females. Although these size classes appear to overlap, individuals were not double counted because the effect of the exclusion fence on adult abundance in November and December, was assessed separately to juvenile abundance in January, February and March. Such analysis was selected because adults begin to die off at the end of December and nymphs (laid the previous season) begin to hatch in January; it would be erroneous to test for changes in the abundance of either age class in a time period when they are not consistently present. Using repeated measure generalized linear mixed effects models (R v 3.6.1, lme4 package version 1.1-21) I modelled the effect of month (November and December), predator exclusion (fence and no fence), and time (before, first year after fence construction, and second year after fence construction) on adult grasshoppers counts while including a repeated measure random effect (unit by site). I did the same for juveniles, but the levels of month were January, February, and March, and the levels of time were ‘before’ and ‘after’ fence construction. Significance of covariate interactions was tested using a likelihood ratio test. Significant interactions were assessed by contrasting estimated marginal means (emmeans package version 1.4.3.01). All before counts (2015, 2016, 2017, and early 2018) were undertaken by Schori (2020) using the same methodology. The difference in observer error was not investigated, but the BACI design ensures this would not impact the ability to detect an effect of the exclusion fence provided each observer was consistent between sites. Grasshopper sex could not be included as a factor for adults or juveniles because this caused model fit to be singular, preventing meaningful analysis. Environmental data were not recorded on only a few monitoring occasions because of a technical issue. Limiting analysis to those occasions where environmental data were recorded caused singular model fit. As such, for the monitoring occasions where environmental data were recorded, I plotted the relationship between ground surface temperature and total grasshopper count at each transect (Appendix 5).

3.2.2 Capture-Mark-Recapture

Capture-Mark-Recapture (CMR) trials were undertaken in two 40 m x 5 m areas, henceforth referred to as plots, at opposite ends of each grasshopper monitoring transect on the gravel road at Patersons Terrace, giving 6 plots in total, two at each site. In each case, I walked across the width of the road 40 times at one-metre intervals to cover the entire plot. Femur and body length were measured, and sex determined for all adult *B. robustus*. Each individual was uniquely marked with a non-toxic paint marker (Edding 780) using the 1-2-4-7 marking system (Buchweitz and Walter 1992). Each plot was left undisturbed for at least three hours, then searched again. Marked individuals were recorded, and any unmarked individuals were counted and measured (as above), but not marked before release. Recapture was repeated on three subsequent days and the whole capture-mark-recapture process was repeated five times between December 2018 and February 2019.

I fit a Jolly-Seber model using program Mark v 9.0 (White and Burnham 1999), for each week of CMR data, to minimise the effect of loss of marks from moulting. Model convergence could not be reached because of the low number of individuals marked. Following this, I fit the same model for data from all weeks, but the number of marked individuals was still not sufficient for model convergence. In lieu of this, the minimum number of grasshoppers was calculated at each plot by taking the sum of the unique marked individuals at each plot and the maximum number of unmarked individuals recorded in any one sampling session. I combined the minimum number at both plots within a site to give a minimum number of adult grasshoppers per 400 m^2 at each site.

3.2.3 Site ground surface temperature monitoring

To evaluate the possibility that ambient temperature differed between the three sampling sites, which could obscure any effect of the predator exclusion fence, I monitored ground surface temperature at each site using 24 HOBO Pendant® Temperature/Light Data Loggers (8 per site). At each site I fixed these to the surface of the road in two lines running parallel to the grasshopper monitoring transect. The two lines were evenly spaced across the width of the road and loggers in the same line were spaced at 50 m intervals (Figure 3.1). Loggers recorded temperature every 10 minutes over sixteen consecutive days in February 2019.

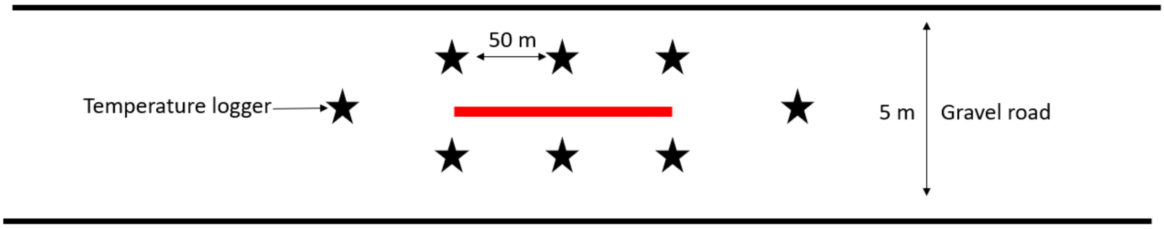

Figure 3.1 Distribution of pendant temperature monitors in relation to the grasshopper monitoring transect (red) at each site at Patersons Terrace. Diagram not to scale.

Daily temperature minimum, mean, maximum, and range were averaged for each logger over the 16 days for analysis. Data were normally distributed based on quantile-quantile plots, so a general linear model was fitted for each temperature variable with the three sites (O_s, O_n, and F) as predictors. *P* values were subject to Bonferroni correction to account for the non-independence of temperature minimum, mean, maximum, and range, so alpha was 0.0125.

3.3 Results

3.3.1 Straight-line distance transect counts

As expected, juvenile grasshopper densities were higher and more variable than adult densities (Figure 3.2). The maximum number of juvenile grasshoppers recorded in any 20 m unit was five, and the maximum number on a 100 m transect was eight. In both a unit and a transect, the maximum numbers of adult females and males were three and two, respectively. Zero counts were common in all months, particularly for adult females, reinforcing the rarity of this species.

For adult *B. robustus*, there was a significant predator exclusion by time interaction (Table 3.1). Pairwise contrasts in estimated marginal means for this interaction showed that grasshopper abundance did not differ significantly between the fenced and open sites before or immediately after fencing was installed (emmeans: before *p*= 0.80, year one *p*= 0.16, Figure 3.3 A). However, in the second year after fencing was installed *B. robustus* density was significantly lower at the fenced site compared to open sites (emmeans: *p* =0.03, Figure 3.3 A). The effect of month on adult and juvenile grasshopper abundance varied with time relative to fence construction (Table 3.1), possibly because emergence time and development rates differ each year based on variable weather conditions. The relative abundances of juvenile robust grasshoppers at the fenced and open sites did not change after installation of the predator exclusion fence (Figure 3.3 B, Table 3.1).

Table 3.1 The model likelihood ratio statistic (LRT) and significance value (*p*) for the effect of each predictive variable or their interactions on robust grasshopper density in each 20 m^2 sampling unit in each session. The levels of predator exclusion were Open and Fenced. For adults, levels of month were November and December, and levels of time were before (2015-2017), year one (2018), and year two (2019). The predator exclusion main effect was not tested for adults because of the significant predator exclusion by time interaction. For juveniles, levels of month were January, February and March, and levels of time were before (2016-2018), and after (2019).

	Adult		Juvenile	
Predictive variable	LRT	*p*	LRT	*p*
month: predator exclusion: time	2.67	0.26	2.48	0.29
month: time	17.53	<0.001	23.28	<0.001
month: predator exclusion	<0.001	1.00	2.25	0.32
predator exclusion: time	7.84	0.02	1.70	0.19
predator exclusion	-	-	0.91	0.34

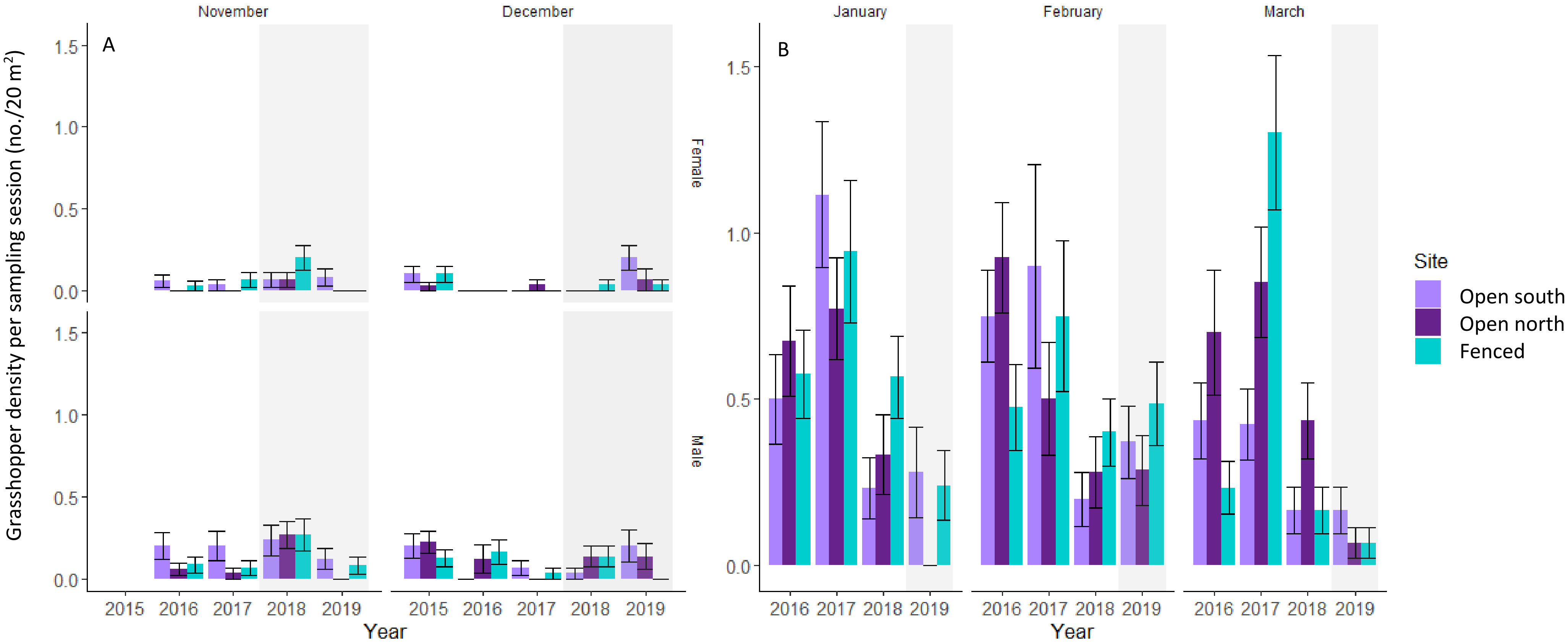

Figure 3.2 Mean (± standard error) of *B. robustus* density per 20 m^2 sampling unit in each session (month and year) for adult and near adult males and females (A), and for juveniles (B) at three Patersons Terrace sites. The grey shading indicates when the predator exclusion fence was present at the Fenced site.

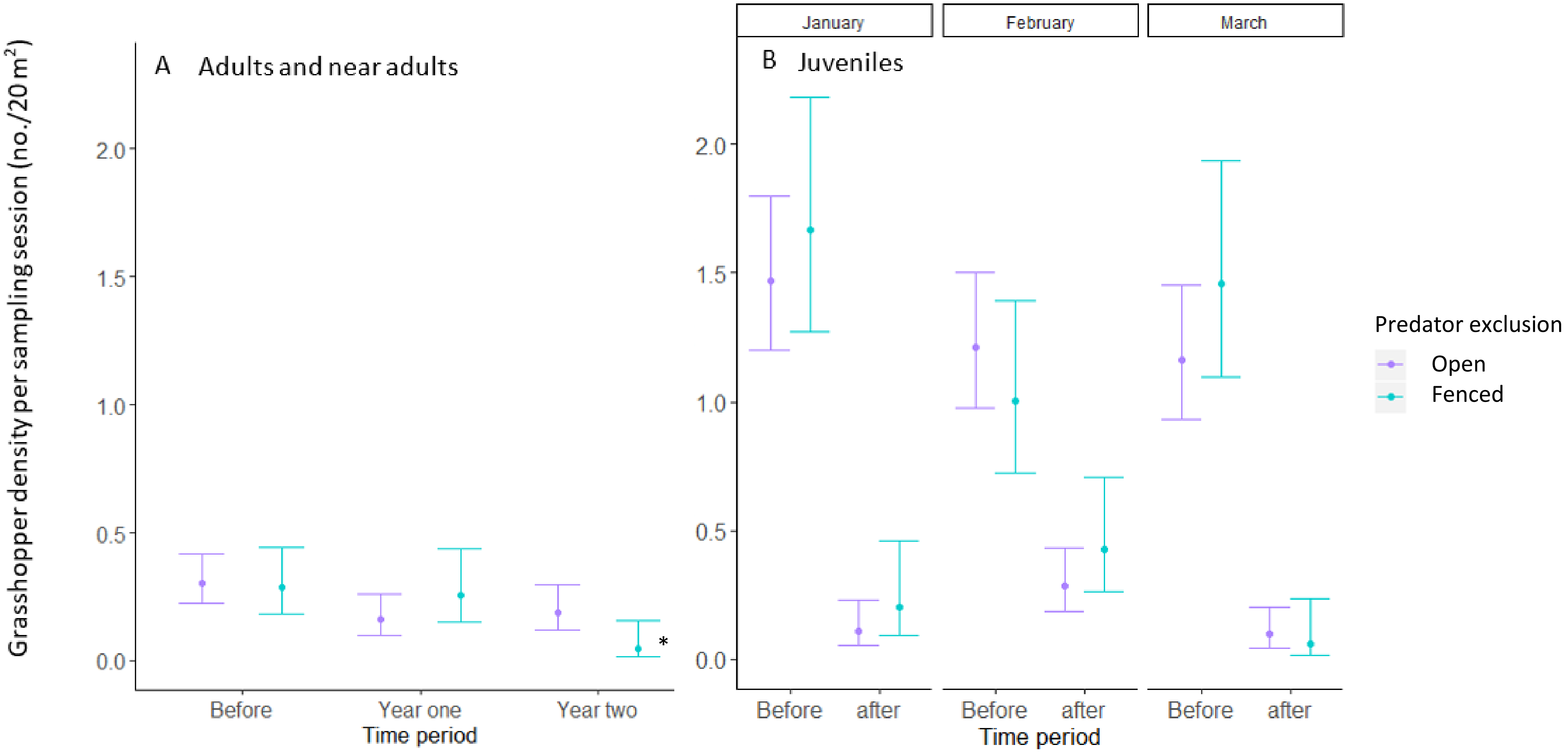

Figure 3.3 Model fits and 95% confidence intervals for robust grasshopper density in each 20 m^2 sampling unit in each session for adults and near adults (A) and juveniles (B) at Patersons Terrace. These values are displayed for open (two sites) and fenced sites (one site). Adult densities from November and December are combined and plotted before predator exclusion fence construction (Before, 2015-2017), in the first year it was present (year one, 2018), and in the second year it was present (year two, 2019). Juvenile densities are shown separately for January, February, and March before predator exclusion fence construction (Before, 2016-18), and in the first year after its construction (after, 2019). * indicates a significant difference between estimated marginal

3.3.2 Capture-Mark-Recapture

Thirty-five adult *B. robustus* were marked over all six 200 m^2 plots in the five weeks of CMR sampling (Table 3.2). Five of the marked individuals moved between plots within the same site. I did not find any evidence for movement of marked individuals between sites. The southern Open site had the highest recapture rate (100%), but this was based on only two adult females (Table 3.2). A larger number of individuals were marked at the fenced and northern Open site than at the southern Open site, but recapture rates were much higher within the fence (94%) compared with the northern Open site (35%).

A minimum of eleven adult males were present within the fence in December 2018 (Figure 3.4), the largest number of adult males recorded in any single week of monitoring. Following this, numbers generally declined at all sites, and the northern Open site reported the highest minimum numbers of grasshoppers in each sampling period. The northern Open site also had the highest number of adult females, four, in the fifth week of CMR. Minimum grasshopper abundance was not consistently higher within the fence after predators were excluded.

Table 3.2 The combined total number of adult robust grasshoppers marked, and proportion recaptured, in all five weeks of CMR monitoring (mid-December to mid-February) at open and fenced sites at Patersons Terrace.

Site	Sex	# of individuals marked	# of recaptures	% recaptured
Open south	Female	2	2	100
	Male	0	0	-
	Total	2	2	100
Open north	Female	3	1	33
	Male	14	5	36
	Total	17	6	35
Fenced	Female	3	2	67
	Male	13	13	100
	Total	16	15	94

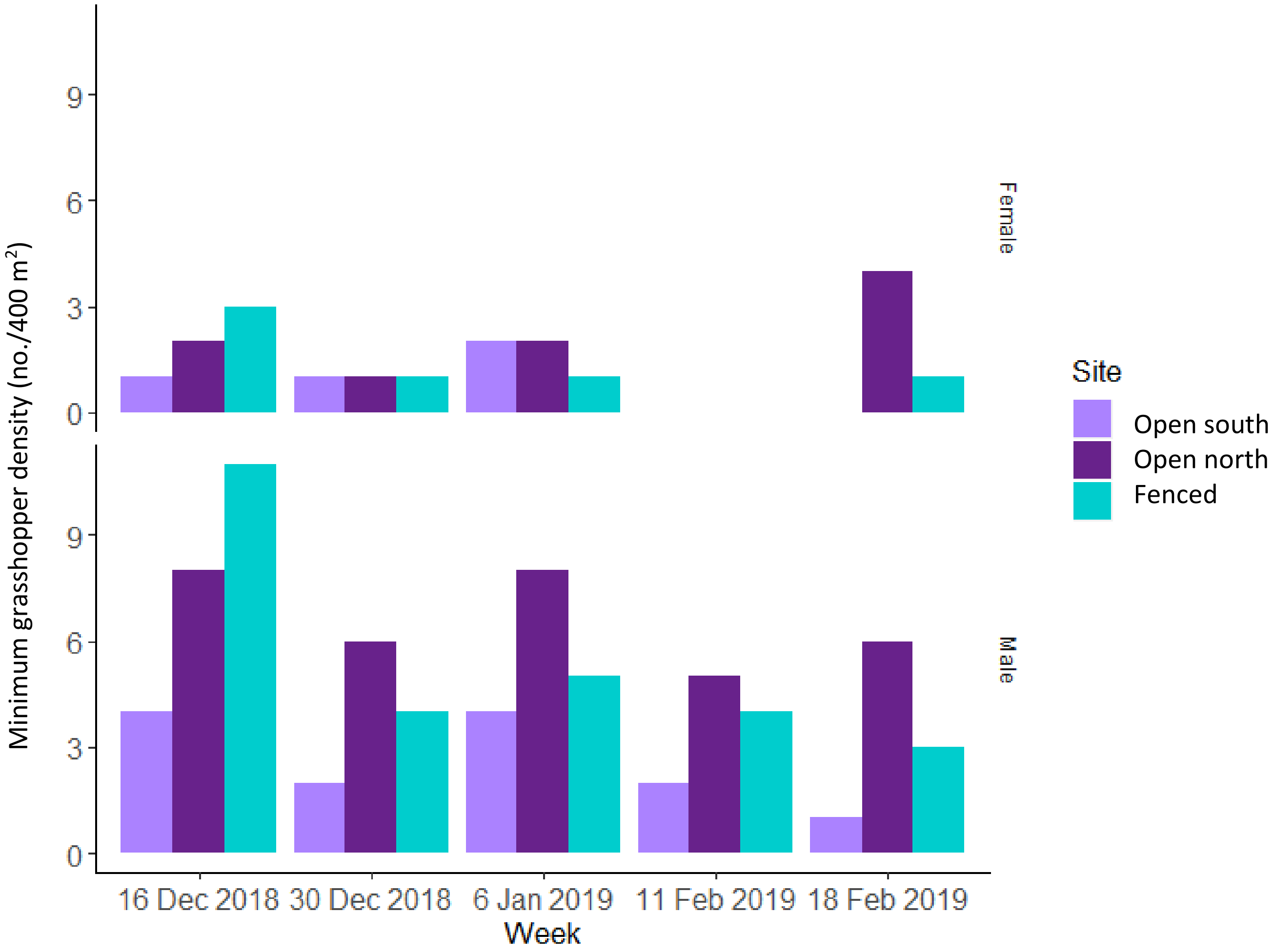

Figure 3.4 The minimum density (no. per 400 m^2) of adult male and female grasshoppers at two open and one fenced site in each week that Capture-Mark-Recapture took place at Patersons Terrace.

3.3.3 Site ground surface temperature monitoring

Daily temperature maximum and range varied more at all sites compared to minimum and mean values (Figure 3.5). There was no significant difference between sites in the daily temperature mean ($F_{2,21} = 0.408$, $p=0.67$), maximum ($F_{2,21} =0.966$, $p=0.397$), and range ($F_{2,21} = 2.188$, $p=0.137$) (Figure 3.5), but minimum temperature did differ between sites ($F_{2,21} =10.41$, $p<0.001$). Mean daily minimum temperature at O_s was 0.7 °C lower than F (Tukey test: $p=0.011$), and the mean daily minimum temperature at O_s was 1.0 °C lower than O_n

(Tukey test: $p<0.001$) over the sampling period. High temperatures were recorded on the gravel road, the maximum was 47.3 °C.

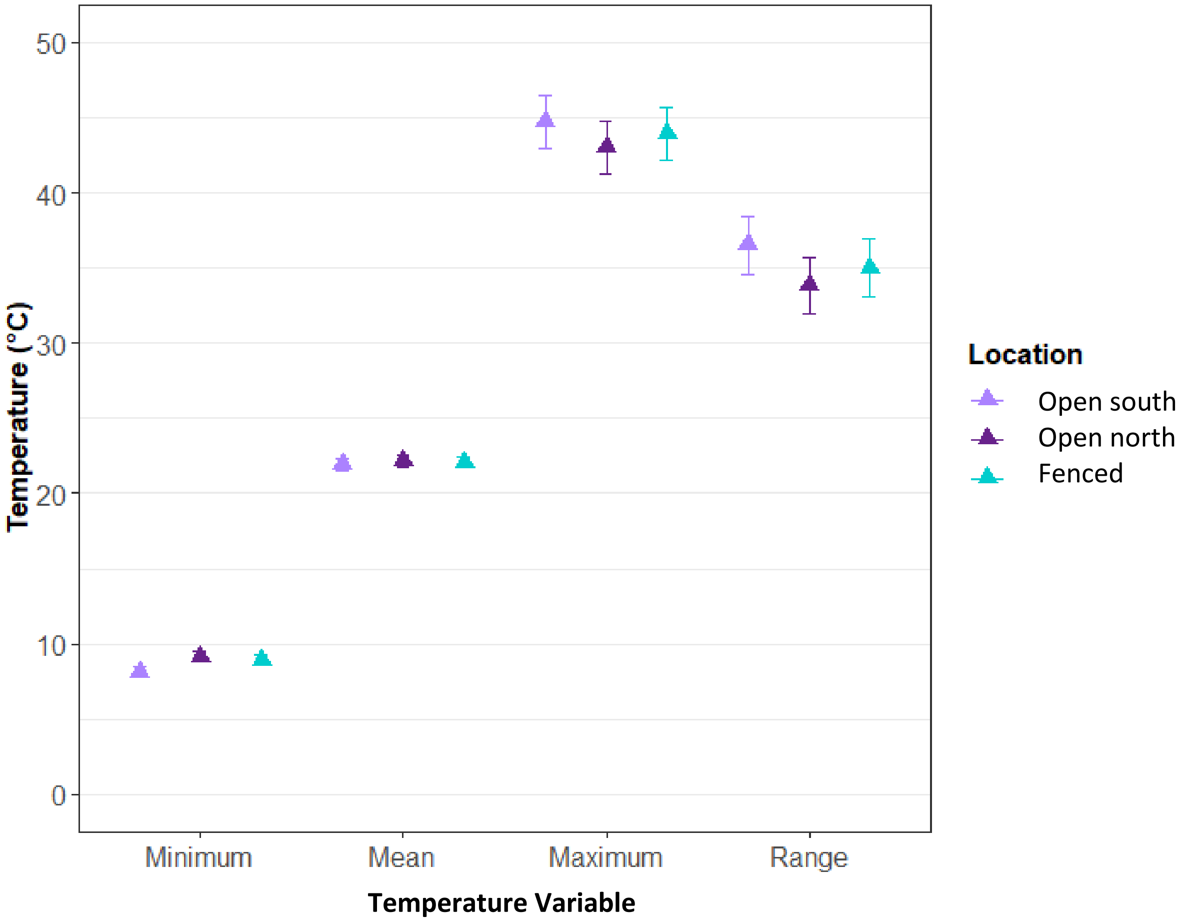

Figure 3.5 The model fits and 95% confidence intervals across all data loggers of the mean daily minimum, mean, maximum and range of the ground surface temperature at open, and fenced sites at Patersons Terrace over 16 days in February 2019.

3.4 Discussion

3.4.1 Predator exclusion fencing effect on robust grasshopper abundance

Conservation action is often limited by the availability of funding (McCarthy et al. 2012) so increasing the impact and efficiency of management actions could allow for better outcomes for more threatened species. I assessed the implementation of low-height predator exclusion fencing, a modification of a pre-existing technology, on a population of Nationally Endangered robust grasshoppers that live on a gravel road set in a grassland environment. If successful in improving outcomes for *B. robustus*, the use of low-height exclusion fencing for total predator exclusion could be less expensive than regular-height predator exclusion fencing (Agnew and Nichols 2018) or long term trapping to control predators (Norbury et al. 2014). Effective but less expensive predator exclusion fencing could enable its wider use, allowing for further development of best practice methods to better protect other threatened invertebrates that are generally not the priority of current exclusion fencing applications.

My hypothesis that *B. robustus* abundance would increase after predator exclusion fence installation was not supported. Grasshopper abundance did not respond positively to mammal exclusion in the first year and decreased in the second year after installation. CMR showed an increase in recapture rate at the fenced site over an unfenced site, possibly indicating higher survival. However, this could be solely an effect of the fence limiting large grasshopper mobility, so cannot be considered support for my hypothesis. My results suggest that, at Patersons Terrace, the relationship between predatory mammals and robust grasshoppers is more complex than that hypothesised by Schori et al. (2019). Robust grasshopper abundance not increasing immediately in response to predatory mammal exclusion could be explained by the apparent increase in abundance of avian predators, grasshopper mobility, temperature, and the potential for lags in the response of insect populations to mammal removal. Increased skink abundance and fence or vegetation effects on microclimate, alone or in addition to the previous factors, possibly explain why *B. robustus* abundance declined in the second year after predator exclusion. These unintended effects of the exclusion fence and other factors are discussed below and are presented in Figure 3.6 in relation to the timing of *B. robustus* response to aid interpretation of this section.

3.4.1.1 Avian predators

The predator exclusion fence at Patersons Terrace appeared to be attracting birds (Chapter 2). The common birds I observed, Australian magpies (*Gymnorhina tibicen*) and common starlings (*Sturnus vulgaris*), eat insects and other invertebrates (Angus 2013 [updated 2017], Flux 2013 [updated 2017]), and would likely consume *B. robustus*. This may have contributed to the lack of adult and juvenile *B. robustus* response to predator exclusion in the first year after fence construction. Birds limiting grasshopper abundance would be consistent with bird effects on other grasshopper species. For example, in Arizona, USA, bird presence can limit the abundance of several grasshopper species in grassland (Bock et al. 1992). However, at Patersons Terrace trail cameras on the gravel road itself recorded few birds and, given *B. robustus* crypsis likely evolved against bird predation, the presence of birds does not necessarily indicate increased predation pressure. Given the rarity of *B. robustus*, management of these bird species at the exclusion fence could be undertaken to rule out any possible ongoing detrimental effects.

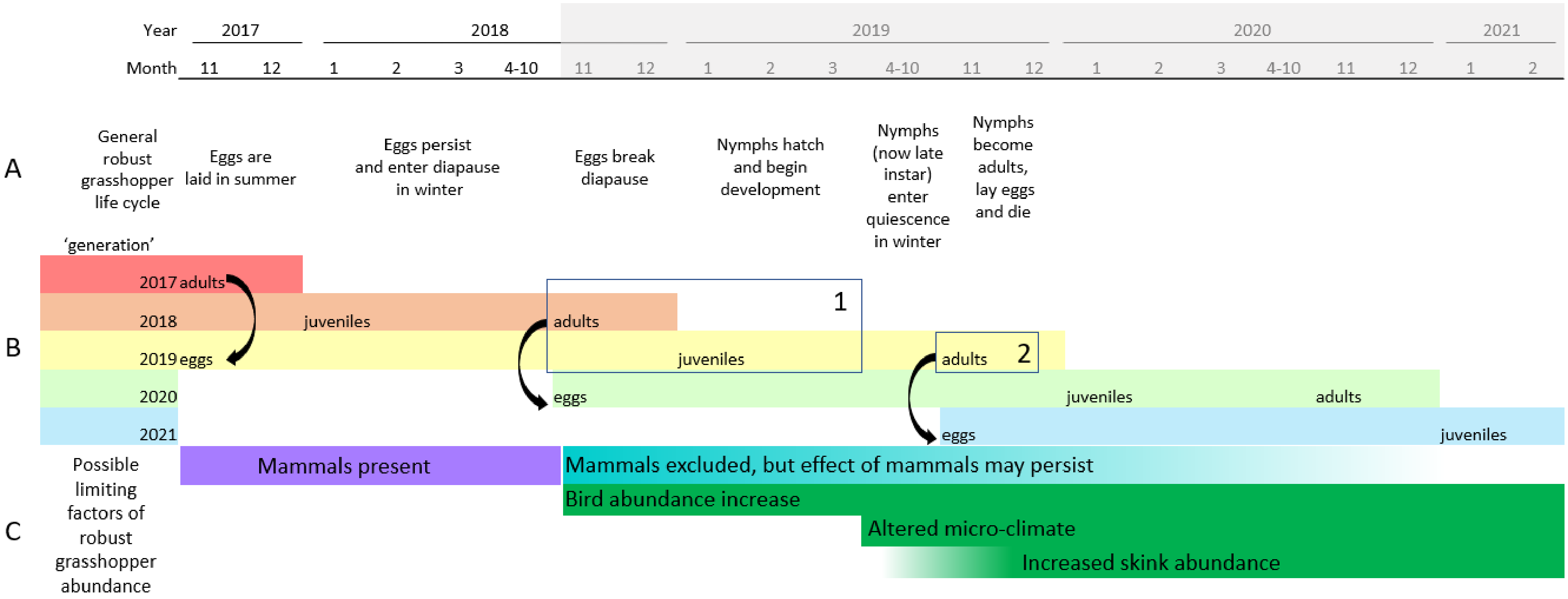

Figure 3.6 Diagram showing (A) a hypothesised general robust grasshopper life cycle, (B) the generations of robust grasshoppers assessed in this study at Patersons Terrace, and (C) the possible factors limiting *B. robustus* abundance in relation to the installation of the predator exclusion fence (grey shading). Boxes indicate (1) the 'year one' period where *B. robustus* abundance did not change in relation to predator exclusion, and (2) the 'year two' period where adult *B. robustus* abundance declined within the predator exclusion fence in comparison with unfenced sites. The '2021' juvenile generation will be the first to hatch where the entire generation before them has been free from mammalian predators.

3.4.1.2 Grasshopper mobility and temperature

Two factors may have confounded my ability to detect a *B. robustus* response to predator exclusion; grasshopper mobility, and temperature. I found differences in recapture rate between the fenced and northern open site which could indicate higher survival at the fenced site or could be because the exclusion fence was reducing mobility of large grasshoppers, while there were no restrictions for open populations. This is supported by a spike in adult abundance at the northern open site in late summer (Figure 3.4), in contrast to an expected decline that late in the season, and by the knowledge that adult female *B. robustus* have a home range of 300 m^2 or more (Schori 2020). Such differences in mobility between treatments could have affected the comparisons of transect count abundances because the open sites would be subject to more statistical variability than the fenced site. Additionally, permanent immigration or emigration of grasshoppers from a site violates the assumption that CMR was carried out on a closed population. To mitigate the effect of grasshopper mobility on CMR and transect counts in future monitoring, a barrier to grasshopper movement across the road at the ends of each site could be erected.

Temperature may also have confounded my ability to detect a *B. robustus* response to predator exclusion because these grasshoppers seek refuge during very high and low ground temperatures which affects their detectability (Thorsen 2010). At Patersons Terrace, high temperatures were recorded, and there was an apparent temperature threshold above which grasshoppers were less abundant (Appendix 5). Because of the action taken to reduce the effect of ground surface temperature on detectability (see 3.2), I am confident that it did not systematically bias *B. robustus* counts. However, ground temperature could not be included as a co-variate for analysis of transect counts, so it may have increased the unexplained variability in the models, potentially reducing their ability to detect a significant effect and contributing to *B. robustus* initially showing no response to predator exclusion fencing. For the Crau Plain grasshopper (*Prionotropis rhodanica*), an ecologically similar species to *B. robustus*, temperature and wind speed had no impact on capture or recapture probability (Bröder et al. 2019), in contrast to the likely relationship for *B. robustus*. As such, the effect of ground temperature on *B. robustus* detectability needs further investigation to inform suitable monitoring conditions.

3.4.1.3 Time lags

Time lags in *B. robustus* numerical response to mammal exclusion may explain why grasshopper abundance did not increase immediately after fencing was installed. This is because insect response to mammalian predator removal may only become apparent after two or more generations because the effect of predation accumulates over the course of a generation (Van Aarde et al. 2004). Robust grasshoppers have a two-year life cycle, so a response could take up to four years to be observed.

Additionally, the timing of predator exclusion in relation to the stages of *B. robustus* lifecycle is important for understanding their abundances. Eggs are laid in summer and must overwinter before hatching in late summer the following year (Mason 1971) (Figure 3.6 A). Nymphs grow through approximately six instars (White 1994), although this may be higher and may vary by sex (Schori et al. unpublished), reaching adulthood the following summer when they produce eggs and then die. Even though the adults present at the end of 2018 were protected for the last two months of their life (Figure 3.6 B) their abundance was not affected, possibly because the majority that were going to be preyed on had already been consumed. The remaining adult grasshoppers would also have been slowly dying of natural causes, having reproduced. The abundance of the first protected juvenile generation in 2019 did not respond to protection from mammalian predators either. The eggs they hatched from were laid in 2017 by adults which were subject to mammalian predation for their whole life (Figure 3.6 B), potentially limiting 2019 egg abundance and therefore juvenile abundance at all sites because of the historic effect of predators or environmental conditions on adult abundance. A lack of 2019 juvenile response could also indicate that mammalian predators do not cause significant mortality for small individuals which would be consistent with optimal foraging theory that suggests predators selectively consume large bodied individuals (Pyke et al. 1977). In either case, a response of the population within the fenced area to mammalian predator removal in later generations would still be possible. For example, an increase in survival of larger juveniles and adults would provide more eggs which should increase juvenile abundance provided it is not strongly limited by density dependent processes, as can occur in more common grasshoppers (Kemp and Dennis 1993). Such density dependent limitation is less likely for *B. robustus*, at least initially, because of their rarity. All else being equal, increased abundance would occur in the 2021 juvenile generation, as the adults that laid their eggs in late 2019 experienced mammalian predator exclusion for their whole life (Figure 3.6 B). Although, this response would be very small because of the current rarity of grasshoppers. If such a delayed increase did occur it would be in line with that seen in New Zealand forest dwelling insects, which may take up to ten years to respond to predator exclusion (Watts et al. 2014). However, rather than showing no or little change in the second year after predator exclusion as predicted by a delayed response, *B. robustus* abundance decreased.

3.4.1.4 Increased skink abundance

Skink abundance increased within the fenced area at Patersons Terrace in the year following fence construction, likely in response to predator exclusion (Chapter 2). The skink species found at Patersons Terrace (*Oligosoma maccani* and *Oligosoma polychroma*) primarily consume arthropods (Hare et al. 2016), so an increase in their abundance could have contributed to the decline in adult *B. robustus* abundance in the second year after predator exclusion occurred (Figure 3.6 C). It is unclear whether the observed skink release at Patersons Terrace would occur in braided rivers where *B. robustus* are naturally found. However, increased skink abundance may represent a return to 'natural' conditions, under which robust grasshoppers are thought to have been more abundant (White 1994), at odds with their observed decline. Decline may have occurred in this situation because their present-day populations are much smaller than they were historically and can no longer sustain this skink predation. Small population size could also indicate the population is at risk of, or is already entering an extinction vortex where mutually reinforcing effects of environmental and demographic stochasticity, inbreeding, and breakdown of behaviour related processes lead to extinction (Gilpin and Soulé 1986, Fagan and Holmes 2006, Bell and Gonzalez 2009). Alternatively, grasshopper decline may be because skink abundance has increased in addition to increased bird abundance that may have prevented the initial response to mammalian predator exclusion (Figure 3.6 C). Furthermore, because time lags in *B. robustus* response may have caused the effect of mammals to persist after their exclusion, increased skink abundance may have added to the effect of mammalian predation in the short term, rather than replacing it (Figure 3.6 C).

Skinks supressing *B. robustus* abundance is consistent with the effects of other lizards on grasshoppers. For example, in California meadows, grasshopper density declined with increased proximity to structures inhabited by western fence lizards (*Sceloporus occidentalis*) (Chase 1998). There are also cases of New Zealand skinks affecting invertebrate abundance. For example, at a New Zealand South Island dry grassland site, ground-dwelling invertebrate abundance was strongly negatively correlated with skink abundance (Norbury et al. 2013). However, in contrast to my result, Norbury et al. (2013), found that predator suppression (cats, *Felis catus*; ferrets, *Mustela furo*; stoats, *Mustela erminea*), which appeared to increase lizard abundance where mice were not present, largely had no effect on invertebrate abundance. These invertebrates were not threatened which could explain the differing response of *B. robustus*. Meso-predator release like that at Patersons Terrace has also inhibited conservation efforts in New Zealand. For example, Pacific rats (*Rattus exulans*) were released from predation after cats were eradicated from Little Barrier Island, with negative effects on Cook's petrel (*Pterodroma cookii*), the target of the conservation intervention (Rayner et al. 2007).

It is unclear whether *B. robustus* abundance will increase as the effect of mammalian predators within the fenced area fades in future generations, or whether their population will stabilise or even decrease further. A further decline would be possible because skinks are omnivores (Hare et al. 2016) so their abundance, and therefore predation intensity on *B. robustus*, will be largely independent of grasshopper population density (Pech et al. 1995, Sinclair and Pech 1996). This could allow skinks to reduce grasshopper populations to zero and then switch to a different food source because they do not rely on *B. robustus*. To facilitate *B.* robustus recovery and avoid exacerbating their current decline, I recommend that skinks are removed from within the exclusion fence site at Patersons Terrace and released in another area, and that skink and *B. robustus* abundance continue to be monitored.

3.4.1.5 Microclimate alteration

Temperature can influence aspects of insect development such as growth rate, sex ratio, larval fitness, and timing of egg hatching (Potter et al. 2009, Chuche and Thiéry 2012, Zuo et al. 2012). At Patersons Terrace, minimum ground temperature differed slightly between sites in summer but, as this appeared to be a site effect, it would have been accounted for by the BACI study design. More importantly, microclimate in autumn inside the exclusion fence may have been affected by the fence itself, or possible changes to vegetation (Chapter 2). For *B. robustus*, ground surface temperature is important because this species regulates its temperature by basking. Cooler 2019 autumn ground surface temperature within the exclusion fence could have reduced juvenile growth, caused prolonged basking and therefore higher mortality from predation, and increased mortality from fungal pathogens by preventing individuals from attaining high temperatures (Inglis et al. 1996). In all cases this could have contributed to reduced November and December 2019 adult abundance compared with unfenced sites.

Norbury et al. (2009) found that changes in rabbit abundance and resulting changes to vegetation and therefore microclimate at a South Island dryland site were not generally responsible for changes to ground dwelling invertebrate number, species richness, or species diversity. They concluded that large scale climatic variations were likely controlling invertebrates more than rabbit abundance. However, *B. robustus* are thermophilic and adapted to open braided riverbeds, not grasslands, potentially explaining why the response observed here was different. Furthermore, grasshopper specific research in a Hungarian grassland found that microclimate was strongly correlated with the abundance of thermophilic species (Kenyeres and Cservenka 2014), consistent with my possible result. If reductions in temperature are truly widespread in the fenced area at Patersons Terrace then controlling vegetation, particularly on the gravel road, could help mitigate any ongoing detrimental effects on *B. robustus*, even if the fence is also affecting microclimate. Such vegetation control will likely be necessary at all sites on the gravel road as vegetation succession continues because, unlike in a braided river, vegetation is not periodically removed by flooding.

3.4.2 Management trade-offs

If skink, bird, and vegetation control are undertaken simultaneously, then it may be difficult to determine which action is responsible for any change to grasshopper abundance. As such, a trade-off may exist between guaranteeing that a population of this species is secured against extinction in the short term, important given its threat status, and fully understanding the effect of mammals, skinks and other factors; information that could guide future conservation of *B. robustus* or other similar species. Management that utilizes ongoing *B. robustus* monitoring in response to interventions that can be analysed and adapted will allow balanced research and protection to be sustained, providing the best outcome for the species. For example, this could be achieved by staggering implementation of different control measures, i.e. controlling skinks immediately, and implementing vegetation control later, provided possible delays in response of *B. robustus* abundance are accounted for when interpreting results.

3.4.3 Robust grasshopper analysis issues

A working model was established that allowed *B. robustus* abundance in response to predator exclusion to be assessed based on transect counts. However, model singular fit issues precluded testing of more complex interaction effects, such as grasshopper sex, and were initially problematic for testing the models I did analyse. This was caused by a high number of zero values in the data and was overcome through forsaking true replication, which was impossible anyway with only one exclusion fence. I split transects into 20 m units and including repeated sampling within a month to give a higher number of 'replicates', reducing the proportion of zero values. I opted to continue existing transect counts, despite this only giving five adjoining pseudo-replicates within the fenced site, because the valuable pre-existing data from those transects allowed for a robust BACI study design (Christie et al. 2019). These challenges to analysis, and limited replication as described for robust grasshoppers are not unusual in threatened species research (Radford et al. 2018). At Patersons Terrace, there was an opportunity to install a single predator exclusion fence and installation costs were too high to construct multiple fences to provide spatial replication. Future monitoring could continue the transect monitoring method and accept that data will be difficult to work with and patchy, or another method could be selected that intensively searches each area to increase detection probability. However, the latter would forsake valuable historical data.

Analysis of CMR monitoring was unsuccessful because few adult individuals could be detected to mark. The marking protocol used did not capitalize on having grasshoppers in the hand by marking all individuals that were caught because of the use of separate mark and recapture periods. However, CMR could be a valuable tool for monitoring populations if the method is adjusted. Optimized CMR was trialled for the Crau Plain grasshopper (*Prionotropis rhodanica*), another cryptic grasshopper species, providing a template that could be applied for *B. robustus* (Bröder et al. 2019). These methods could be trialled as part of *B. robustus* detection and monitoring testing, which is ongoing (T. Murray, *pers. comm.*), potentially allowing for better outcome monitoring for this and other elusive threatened species.

3.4.4 Can predator exclusion fencing be utilised for insect conservation in non-forest environments?

Superficially, this study provides more evidence that predator exclusion fencing does not achieve the goals it set out to, providing weight to the same assertion made by Scofield et al. (2011), and may actually be detrimental to target species survival. However, as described above, further monitoring must take place so that the future trajectory of *B. robustus* abundance can be understood. Additionally, a beneficial effect of predator exclusion fencing on *B. robustus* may only become apparent when combined with other management actions, such as meso-predator control. Based on the early outcomes of this predator exclusion fence trial I cannot make a conclusive recommendation as to whether predator exclusion fencing should be or should not be further utilized to protect other non-forest insects like *B. robustus*. If the decision is made to implement predator exclusion fencing for future insect conservation, populations must be monitored with refined techniques for an extended period because insect response to predator exclusion may be delayed or inhibited by unintended consequences of predator control. Such delays would be consistent with that seen in New Zealand forest dwelling insects, which may take up to ten years to respond to predator exclusion (Watts et al. 2014). Extended monitoring incurs an expense, but will ultimately allow for adaptation of management plans, ensuring that conservation spending eventually results in success and can inform future conservation projects. The net result of extended monitoring and management for non-forest insects will be maximization of the benefit for threatened species while minimizing the cost, allowing sparse conservation funds to be spread as widely and effectively as possible.

Chapter 4 General discussion

Invasive species are one of the major drivers of biodiversity loss worldwide (IPBES 2019). They are particularly important in New Zealand where, out of all drivers of biodiversity loss, invaders represent the greatest threat to terrestrial biodiversity (Craig et al. 2000, Department of Conservation 2000). In New Zealand, fencing is commonly used for invasive species control, allowing for exclusion of invasive mammalian predators from an area and enabling their local eradication (Innes et al. 2012). However, predator exclusion fencing is expensive (Scofield et al. 2011) and, because it has been primarily established for bird conservation around forest fragments in New Zealand, little is known about its effect on non-forest species, especially invertebrates (Burns et al. 2012).

I tested whether a low-cost, low-height predator exclusion fence (Agnew and Nichols 2018) could exclude mammalian predators, and monitored the effect of mammal exclusion and unintended effects of fencing on a population of Nationally Endangered robust grasshoppers (*Brachaspis robustus*), a braided river grasshopper (Trewick et al. 2012). In Chapter 2 I showed that the area inside the fence was mammal-free, and that low-height predator exclusion fencing had successfully excluded hedgehogs and mustelids, as well as lagomorphs, but still needed to be robustly field tested for rats and mice. A lack of response in vegetation biomass in the absence of lagomorphs also suggested that plant communities may take more than one year to respond to lagomorph exclusion where conditions are harsh. When I compared it to unfenced sites (Chapter 3), *B. robustus* abundance did not change immediately after predators were excluded but declined in the second year after fencing was installed. My use of a BACI design provided a rigorous assessment given the constraints of a single fence, but the very low number of *B. robustus* means that long term monitoring is required to fully evaluate the effects of the fence. My evidence for meso-predator release (Chapter 2) due to increased native skink abundance does go some way towards explaining the decline, but other unintended effects of the predator exclusion fencing may have contributed. These effects included an apparent change in bird behaviour, and possible changes to microclimate, although it is unlikely these were sufficient to cause a decline.

Here I discuss how the observed response of *B. robustus* compares with the response of other New Zealand invertebrates to invasive mammalian predator control, and the possible implications of my research for larger predator control projects such as Predator Free 2050, the New Zealand Government target to eradicate, rats, stoats, and possums through large scale predator control (Section 1.6).

4.1 New Zealand invertebrate response to predator control

Numerous mammal control and eradication projects have been undertaken on mainland New Zealand (Burns et al. 2012, Russell et al. 2015). These projects are rarely implemented specifically for protection of invertebrates but are often expected to benefit invertebrates as well as the taxa they aim to protect (Bennett et al. 2015, Towns et al. 2019). Large-bodied invertebrates, like *B. robustus*, may benefit more from mammal control than their small-bodied counterparts because mammals may preferentially consume larger species (St Clair 2011), as predicted by optimal foraging theory (Pyke et al. 1977). There is some evidence for this in forest and shrub environments, where mammalian predator control carried out to suppress bovine tuberculosis has benefited the large bodied Auckland tree wētā (*Hemideina thoracica*) and juvenile *Placostylus* landsnails but did not affect the abundance of smaller invertebrates (Byrom et al. 2016). Similarly, within the forested Maungatautari sanctuary several medium and large bodied wētā species increased in abundance after mammals were eradicated for bird protection (Watts et al. 2011), and at Macraes Flat, a South Island grassland, medium-bodied ground wētā (*Hemiandrus* spp.) benefited from hedgehog removal for lizard protection (Jones et al. 2013). Given the positive response to mammal control previously observed for large and medium sized wētā, why did *B. robustus*, a large bodied grasshopper, not respond similarly?

One explanation is that, in contrast to wētā, the *B. robustus* population is so small that it cannot support the multiple unintended effects related to predator exclusion (Chapter 3). Equally plausible is that the time since mammal exclusion was not sufficient for robust grasshopper abundance to increase. Alternatively, this difference could be related to insect behaviour. Mammalian predators in New Zealand are generally nocturnal (Alterio and Moller 1997, Innes 2005a, b, Jones and Sanders 2005, Ruscoe and Murphy 2005), so would encounter wētā and robust grasshoppers at night. This is because wētā are nocturnal (Lewis 1999, Monteith and Field 2000) and, contrary to expectations, *B. robustus* may not seek refuge at night (Schori 2020). Abundance of some meso-predators increased with mammal control in the aforementioned studies (Iles 2012, Jones et al. 2013), but almost all (except low numbers of North Island brown kiwi, *Apteryx mantelli*, at Maungatautari, Smuts-Kennedy and Parker 2013) are diurnal (Cree and Hare 2016). These diurnal predators would have had little impact on wētā, which take refuge during the day, but *B. robustus* would have relied only on crypsis for protection from skinks. Crypsis is never perfect, and skinks may partially overcome this using chemosensory cues (Nicoletto 1985, Hoare et al. 2007). As such, the total predation pressure on wētā was likely greatly reduced with mammal control, while, to some extent, mammals may have been replaced with skinks for *B. robustus*.

Other studies have observed invertebrate responses to mammalian predator control that are unexpected based on their body size. For example, in Zealandia, another forested and fenced sanctuary, beetle abundance (including medium and large bodied species) declined for six years after mammals (except mice) were eradicated (Watts et al. 2014). In New Zealand drylands, top-predator control largely did not affect the abundance of invertebrates at dry grassland/shrubland sites (Norbury et al. 2013). Furthermore, Schori et al. (2019) found that a very small grasshopper species, *Sigaus minutus* increased in abundance in the presence of predator control. These responses, along with the response observed in robust grasshoppers highlight that the relationship between body size and invertebrate response to mammalian predator control may not be strong and may be heavily influenced by species behaviour, the environment, the type of meso-predator species that are released from predation, or other factors, either independently or in combination. The varied response of invertebrates also reinforces that assumed invertebrate benefit from predatory mammal control would be erroneous. This could have important management implications for threatened invertebrates as the scale of predator control increases towards Predator Free 2050.

4.2 Implications for invertebrates under Predator Free 2050

There are 1343 threatened or at risk terrestrial invertebrate species in New Zealand, although a further 1247 are data deficient and could also be threatened, an increase since the last New Zealand Threat Classification System assessment was published (Stringer and Hitchmough 2012). Additionally, the majority of invertebrate species have not yet been assessed (McGuinness 2001). Arguably, there is a moral imperative to conserve these species because of their intrinsic value (Silvertown 2015), as well as the ecosystem services they provide (Prather et al. 2013). As invasive predator removal progresses toward Predator Free 2050 goals, more invertebrate species are expected to benefit, but there is the potential for as yet unknown repercussions for some species because of unintended consequences of control (Linklater and Steer 2018, Peltzer et al. 2019). My research found evidence for mechanisms by which interactive effects of predator elimination and the methods used to achieve predator elimination can reduce the abundance of a threatened invertebrate. Could these mechanisms impact threatened dryland or other invertebrates more broadly with predator control towards Predator Free 2050?

Alterations to microclimate or bird abundance at Patersons Terrace were likely related to the fence itself, so the magnitude of these effects would diminish with increasing distance from the fence structure. The role of predator exclusion fencing under Predator Free 2050 will mostly be confined to protecting much larger areas from re-invasion than those tested here (Murphy et al. 2019). As such, the area within which microclimate or bird abundance is altered will be small compared to the size of the protected area and will only impact species near the structure itself. Any impact on threatened invertebrates could be mitigated by planning the path of a fence to avoid proximity with populations of threatened invertebrates. Therefore, the indirect effects of predator exclusion that may have occurred at Patersons Terrace as a direct result of the exclusion fence, rather than predator exclusion itself are unlikely to be significant issues with landscape level predator eradication. However, predator exclusion fencing will continue to be important for exclusion of species not targeted under Predator Free 2050, particularly hedgehogs and mice that have a large impact on endemic insect and lizard species (St Clair 2011, Jones et al. 2013). As such, some fencing may still be needed on a small scale so the potential detrimental indirect effects of fencing must be measured, and appropriate mitigation action taken.

Unlike rats, stoats and possums, lagomorphs are not directly targeted by Predator Free 2050 goals. Unless separate control is undertaken, mammalian predator removal will likely have little effect on rabbit populations because, in New Zealand, mammalian predators have a small impact on rabbit population regulation compared with other factors such as disease, and burrow flooding and collapse (Norbury and Jones 2015). However, a feasibility study for rabbit eradication in the Mackenzie Basin is in progress as part of the Te Manahuna Aoraki project (TMA 2019). My research suggests that, if rabbit eradication is undertaken, then changes to vegetation in the Mackenzie Basin may not be observed immediately because of the harsh environmental conditions. However, there is good evidence that long term vegetation composition and biomass changes in response to rabbit exclusion are likely (Walker et al. 2015). It is possible this will include the release of invasive weed species that already require extensive control in the Mackenzie Basin (such as wilding pines, and russel lupins- *Lupinus polyphyllus*), with potentially disastrous effects for species like *B. robustus* that rely on open habitats. As such, tools for large scale weed control must be developed and implemented in conjunction with rabbit control so that open habitats are maintained for threatened species that rely on them.

In Chapter 2 of this thesis, I provided evidence of increased skink abundance, likely because of release from mammalian predators, that could be responsible for reduced robust grasshopper abundance either on its own or in conjunction with other factors (Chapter 3). Longer term monitoring is required to determine whether *B. robustus* abundance continues to decline, stabilises at a lower level, or eventually increase within the fenced site. However, reducing the population of a threatened species, even temporarily, can increase the risk of that population entering an extinction vortex where mutually reinforcing effects of environmental and demographic stochasticity, inbreeding, and breakdown of behaviour related processes lead to extinction (Gilpin and Soulé 1986, Fagan and Holmes 2006, Bell and Gonzalez 2009). This is obviously an undesirable outcome for conservation management. While predator exclusion at Patersons Terrace was small scale, it is possible skink abundance will increase even more if control is undertaken on a larger scale, provided mice remain at low abundances as they are in the Mackenzie Basin (Norbury et al. 2013, Hunt 2018). This would provide a mechanism by which predator control in pursuit of Predator Free 2050 could have a wide detrimental effect on threatened invertebrate species in dryland environments. For example, another threatened grassland invertebrate, the Canterbury knobbled weevil (*Hadramphus tuberculatus*) which only exists in one population of less than 100 individuals (Young et al. 2008), could also be affected. It is not yet known if skinks are a major predator of knobbled weevils. If they are, could mammalian predator eradication subject the knobbled weevil population to meso-predator release? Like *B. robustus*, Canterbury knobbled weevils must have evolved in the presence of skinks. However, this did not prevent an apparent decline in *B. robustus* abundance when skink abundance increased. Similarly, the knobbled weevil population is now so small that it may not be able to cope with a return to ‘natural’ predation regimes or may also be affected by several pressures that suppress abundance at the same time. The worst-case scenario for this species would be local, and therefore global extinction; an unacceptable side effect of predator control. Further investigation would be required to determine to what extent increased skink abundance at Patersons Terrace was responsible for decreased *B. robustus* abundance with mammal exclusion. If skinks are largely responsible, appropriate management of these native meso-predators must be incorporated into predator control for Predator Free 2050 in dryland ecosystems, at least in the short term, to allow recovery of *B. robustus* and other threatened invertebrate species.

4.3 Conclusions

Several important lessons were learned from this study where I aimed to assess whether low cost, low-height predator exclusion fencing can exclude mammalian predators, identify unintended effects of exclusion, and determine if that exclusion benefitted a population of *B. robustus*. As well as highlighting that predator exclusion fencing was an efficient and relatively low-cost way of testing the hypothesis that predatory mammals are impacting *B. robustus* compared with maintaining widespread trapping, my results suggest that low-cost conservation interventions may be just as effective as more expensive versions. This has potential to reduce the cost of conservation and allow limited conservation funding to benefit more threatened species. However, I also found that the complexities of trophic interactions may prevent conservation management from benefitting some species; in my research, one management tool alone (exclusion fencing) caused unintended consequences at multiple levels with apparent detrimental effects for the target species. Consequences included meso-predator release, change in non-target predator behaviour, altered microclimate and likely future direct and indirect effects of weed release. Given predator control and exclusion fencing are commonly used for conservation around the world (Hayward and Kerley 2009), the potential for similar detrimental effects on other threatened species is significant. Adding different predator control tools or other management action to the mix could further increase unintended changes that affect target species. Where widespread alteration to communities is undertaken in the name of conservation management, as could be the case in New Zealand’s near future, we must remember that the complexity of biological interactions may cause the response of threatened species to be equally complex. As such, the challenge for conservation practitioners is to understand how the interactions across multiple trophic levels control target species response to management and adapt that management as required.

The unintended consequences of the predator exclusion fence and the short period of this research meant that I could not definitively determine whether mammalian predators are the key driver suppressing *B. robustus* populations. For the reasons outlined in this thesis, answering this question will require longer term monitoring of at least two generations to determine whether predator exclusion results in an eventual increase in *B. robustus* abundance. To improve conservation management of this species, my research indicates that management and a better understanding of native meso-predators is required, and that the same may be true for weeds. I recommend that, in addition to continued *B. robustus* monitoring, skinks be removed from the predator exclusion fence area, addressing what appears to be an immediate threat, and that vegetation control be undertaken on the gravel road at a later date, because vegetation appears to be responding slowly in comparison to skinks. Ideally, as well as securing a population of this species against threatening processes, such management will allow for analysis of the effects of skinks and vegetation on *B. robustus* survival, allowing management and further research to be adapted as necessary.

Appendix 1 Mackenzie Basin weather

Table A1 Monthly summaries of mean rainfall (mm), temperature (°C) and wind speed (km h^{-1}) from 2004 to 2019 at the Lake Tekapo Airfield (weather station 4970 from the CliFlo database) approximately 6 km from the centre of the Patersons Terrace study site.

Measurement	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Mean total rainfall (mm)	43	40	31	49	68	54	54	42	33	48	46	39
Mean air temperature (°C)	15	15	13	10	6	3	2	4	7	9	11	14
Mean daily maximum air temperature (°C)	22	22	20	15	11	7	7	9	13	15	18	20
Mean daily minimum air temperature (°C)	9	8	6	4	1	-2	-3	-1	1	3	5	7
Mean wind speed (km h^{-1})	16	13	13	12	12	11	12	12	14	16	16	14
Maximum gust speed (km h^{-1})	111	109	109	113	105	96	101	105	116	126	114	107

Appendix 2 Predator exclusion fence specifications

A 1.2 m high predator exclusion fence was constructed by Central Fencing LTD, centred around the central transect on the gravel road at Patersons Terrace (Figure A1 A). Construction specifications are as follows (Nigel Broadbridge - Central Fencing, *pers. comm.*)

- Posts: 1.8 m x 150 mm uniformly lathed tantalised pine posts at 2 m spacing (Figure A1 B).
- Mesh: 1.6 mm wire mesh imported from China, welded style (rather than woven) with 6.3 mm aperture (measurement from centre to centre of the wire) giving a 4.7 mm space between wires (inside to inside measurement). This mesh was only available in 800 mm wide rolls, so a mid-rail was required to join 2 widths of mesh to obtain the required height.
- Skirt: A 400 mm wide mesh skirt was created by burying mesh 100 mm deep at the base of posts and 160 mm deep at the outer edge.
- Capping: 1.2mm Z600 galvanised steel. 0.9 mm capping would normally be used but could not be sourced in the time available (Figure A1 B).

Construction commenced in September 2018 and was completed in November 2018. Work involved 540 labour hours, including 39 tractor hours to drive posts and 48 hours of 1.7 tonne digger to dig and backfill mesh ditch.

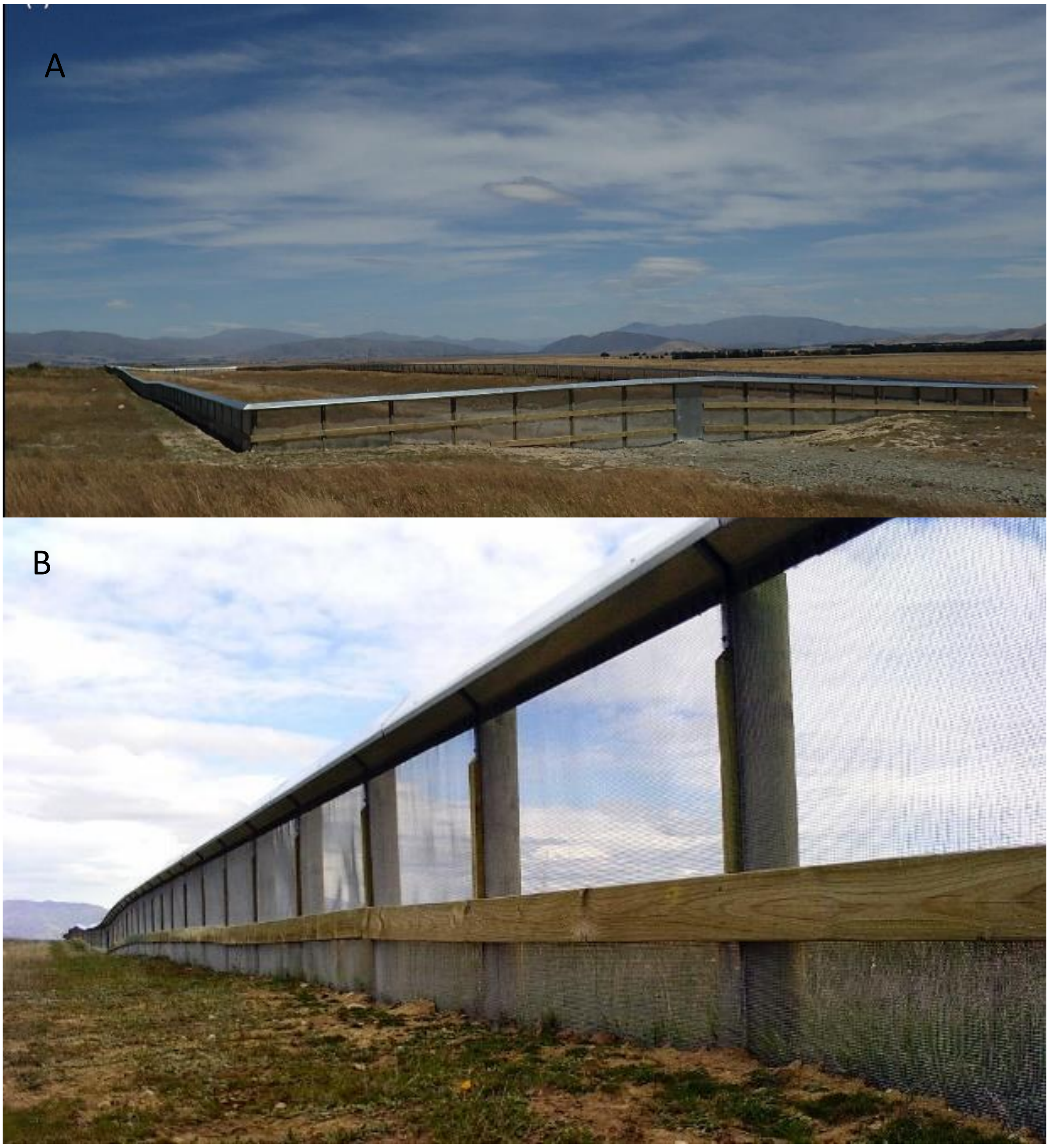

Figure A1 The new design predator exclusion fence constructed at Patersons Terrace showing (A) its setting in the landscape, and (B) a section of the fence.

Appendix 3 Vegetation at Patersons Terrace

Table A2 The vegetation present (marked with an x) at Patersons Terrace in February 2019 and January 2020 at two open sites (O_s and O_n) and one fenced site (F). Site O_n was not assessed in January 2020.

	Road surface					Road verges				
	2019			2020		2019			2020	
Plant Species/Group	O_s	O_n	F	O_s	F	O_s	O_n	F	O_s	F
Achillea millefolium			x		x	x		x	x	x
Cytisus scoparius		x								
Trifolium repens									x	x
Coprosma petriei				x				x	x	x
Epilobium hectorii	x	x		x						
Geranium sessiliflorum	x				x					x
Hieracium pilosella	x	x	x	x	x	x	x	x	x	x
Leucopogon fraseri							x	x		x
Muehlenbeckia axillaris								x		x
Raoulia australis	x	x		x	x					
Raoulia subulata	x					x	x			
Rosa rubiginosa			x							
Rumex acetosella	x	x	x	x	x	x	x	x	x	x
Sedum acre		x					x			
Stellaria species				x	x	x			x	
Trifolium arvense						x			x	
Wahlenbergia albomarginata									x	
Grasses	x	x	x	x	x	x	x	x	x	x
Lichens	x	x	x	x	x		x	x	x	x
Total number	8	8	6	8	8	7	7	8	10	10

Appendix 4 Vegetation pairwise contrasts

Table A3 Pairwise contrasts of vegetation group estimated marginal means for each significant interaction for the models of vegetation frequency and vegetation relative composition on the gravel road and the vegetated verges at two sites (O_s = open south and F= fenced) in two years (2019-20).

			Road								Vegetated Verges							
			Frequency				Relative composition				Frequency				Relative composition			
interaction	Contrast	group	estimate	SE	z ratio	*p*	estimate	SE	z ratio	*p*	estimate	SE	z ratio	*p*	estimate	SE	z ratio	*p*
site:species	O_s-F	Achillea millefolium	-	-	-	-	-	-	-	-	-1.685	0.499	-3.374	<0.001	-0.8923	0.49	-1.822	0.069
		grass	-1.362	0.219	-6.222	<0.001	-0.719	0.209	-3.44	<0.001	-0.931	0.121	-7.708	<0.001	-0.372	0.078	-4.767	<0.001
		Hieracium pilosella	-1.017	0.152	-6.999	<0.001	-0.7	0.153	-4.568	<0.001	-0.757	0.132	-5.737	<0.001	0.059	0.084	0.698	0.485
		lichen	0.612	0.272	2.249	0.025	1.568	0.273	5.752	<0.001	-	-	-	-	-	-	-	-
		Rumex acetosella	0.917	0.28	3.276	0.001	1.752	0.285	6.139	<0.001	0.461	0.187	2.469	0.0135	1.347	0.156	8.66	<0.001
species:year	2019-20	grass	-0.752	0.166	-4.526	<0.001	-0.278	0.209	-1.329	0.184	-	-	-	-	-	-	-	-
		Hieracium pilosella	-0.411	0.097	-4.265	<0.001	0.088	0.153	0.576	0.5649	-	-	-	-	-	-	-	-
		lichen	0.415	0.242	1.717	0.086	1.051	0.273	3.856	<0.001	-	-	-	-	-	-	-	-
		Rumex acetosella	-0.85	0.253	-3.336	<0.001	-0.418	0.285	-1.465	0.143	-	-	-	-	-	-	-	-

Appendix 5 Effect of Ground temperature on robust grasshopper abundance

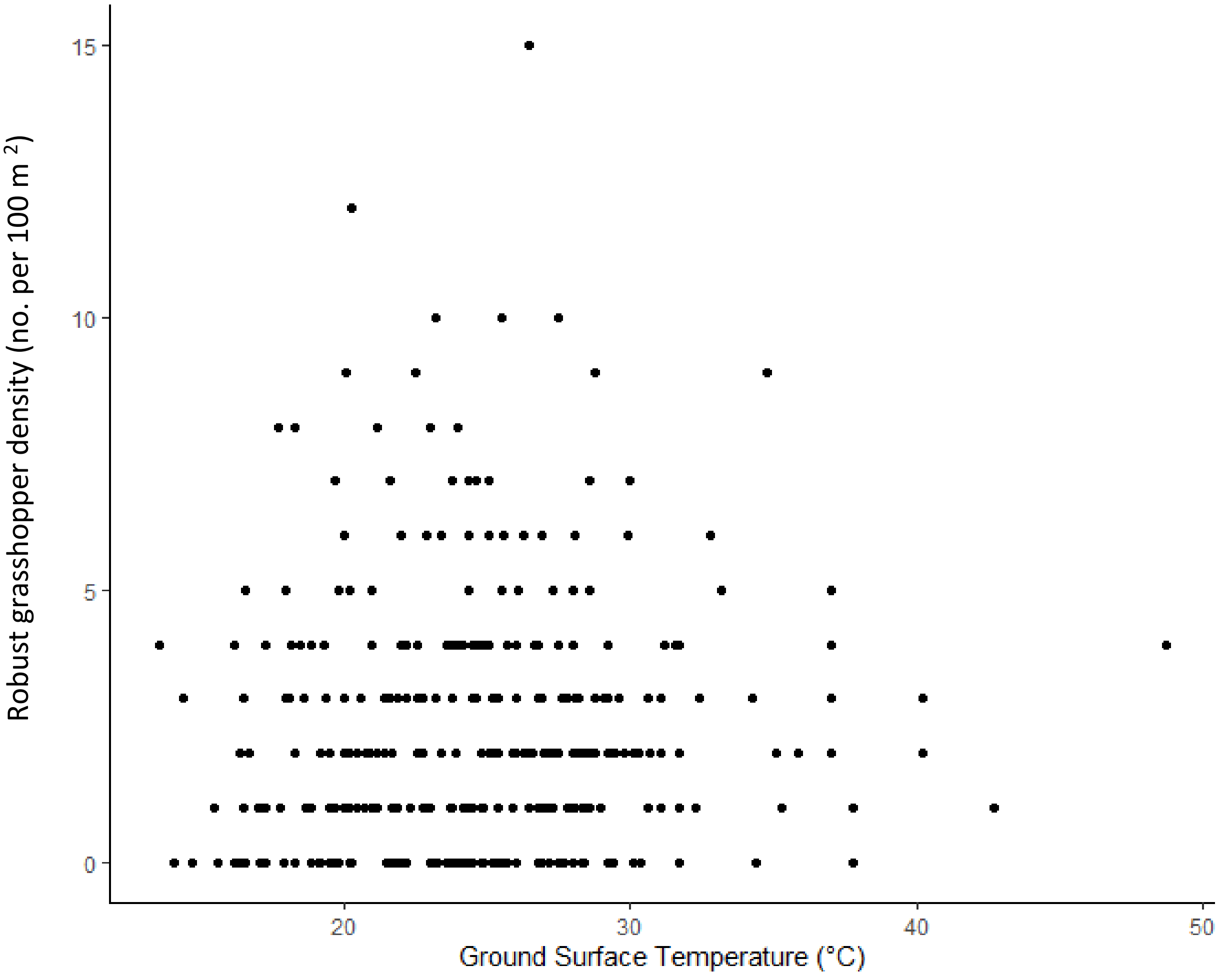

Figure A2 The relationship between robust grasshopper abundance from each straight-line distance transect count and ground surface temperature recorded before starting each transect in every sampling session this was recorded between 2015 and 2020.

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