

REVIEW

Impacts of introduced mammalian predators on New Zealand's alpine fauna

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Abstract: Alpine zones are threatened globally by invasive species, hunting, and habitat loss caused by fire, anthropogenic development and climate change. These global threats are pertinent in New Zealand, with the least understood pressure being the potential impacts of introduced mammalian predators, the focus of this review. In New Zealand, alpine zones include an extensive suite of cold climate ecosystems covering c. 11% of the land mass. They support rich communities of indigenous invertebrates, lizards, fish, and birds. Many taxa are obligate alpine dwellers, though there is uncertainty about the extent to which distributions of some species are relicts of wider historical ranges. The impacts of introduced mammalian predators are well described in many New Zealand ecosystems, though little is known about the impacts of these predators on alpine fauna. Here we review the importance of alpine habitats for indigenous fauna and the impacts of introduced mammalian predators; and develop a conceptual model explaining threat interactions. Most evidence for predation is anecdotal or comes from studies of species with wider ranges and at lower altitudes. Nevertheless, at least ten introduced predator species have been confirmed as frequent predators of native alpine species, particularly among birds and invertebrates. In the case of the endangered takahē (*Porphyrio hochstetteri*) and rock wren (*Xenicus gilviventris*), stoats (*Mustela erminea*) are primary predators, which are likely to be impacting significantly on population viability. We also document records of mammalian predation on alpine lizards and freshwater fish. While the precise impacts on the long-term viability of threatened species have not been evaluated, anecdotal evidence suggests that predation by mammals is a serious threat, warranting predator control. Future research should focus on predicting when and where mammalian predators impact on populations of indigenous fauna, furthering our understanding of the alpine predator guild particularly through adaptive management experiments, and exploring interactions with other threats.

Keywords: alpine; conceptual model; mast seeding; mustelids; possums; predation; rock wren; rodents; threatened species; weasels

Introduction

Alpine environments and many of the specialist species that inhabit these zones are threatened globally (Franzén & Molander 2012; Scridel 2014). The alpine zone can be broadly defined as the altitudinal area above the climatic timberline (or equivalent elevations in non-forested environments) (Mark & Dickinson 1997; Mark et al. 2000). Alpine ecosystems are challenging environments for plants and animals, and their inhabitants display a range of physiological and behavioural adaptations to this environment. For example, some animals display greater longevity, relatively large body sizes (Scridel 2014) and physiological advantages such as high-elevation haemoglobin genotypes (Dragon et al. 1999) or the ability to survive freezing (Ramløv et al. 1996). Alpine species are subject to a large number of constraints imposed by extremely low temperatures – hypoxia, long and variable periods of snow and ice loading, and limited food availability (Sandercock et al. 2005; Scridel 2014). Such characteristics lead to shortened breeding seasons and relatively low fecundity, and exacerbate the vulnerability of alpine species to anthropogenic threats.

Alpine habitats and their specialised biodiversity are threatened by a wide range of factors including browsing,

predation (MacDonald & Bolton 2008), hunting (Sandercock et al. 2005) and habitat loss through land use changes (Laiolo et al. 2004), anthropogenic development (Rolando et al. 2007; Patthey et al. 2008), fire, and the emerging threat of climate change (Dirnböck et al. 2011; Chamberlain et al. 2013). Northern Hemisphere climate models generally predict massive contraction in the ranges of some alpine bird species, and elevational shifts in habitats for a wide range of taxonomic groups (Chen et al. 2011; Dirnböck et al. 2011).

In New Zealand, alpine areas form one of the most widespread environments (c. 11% of the land area; Fig. 1). They encompass an altitudinal belt of c. 1000 m over much of the country that is generally subdivided into low-alpine and high-alpine zones, each with their own vegetation communities; and above this belt is the nival zone, which is characterised by permanent snow, ice and rock (Mark & Dickinson 1997; Mark et al. 2000). These zones are altitudinally compressed at higher latitudes (e.g. an altitudinal belt of c. 500 m on Stewart Island). Tall tussock grasslands dominated by one or more species of the genus *Chionochloa* characterise the low-alpine zone (Connor 1991), with shrubs and large herbs often co-dominating within c. 200 m of the timberline (Mark et al. 2000). Above the upper altitudinal limit of the low



Figure 1. Estimated extent of the New Zealand alpine zones using ArcGIS for Desktop Spatial Analysis Tools. Spatial extent was estimated by creating a minimum height raster based broadly on a regression in treeline altitude of -100 m elevation for every degree in latitude southwards, starting at 2100 m.a.s.l. at the northern tip of the North Island (Cieraad & McGlone 2014). A 25 metre digital elevation model (DEM) provided by Landcare Research NZ with the minimum height raster was then overlaid to find all areas where the DEM value was above the minimum height value. The resulting area was extracted to a polygon, extracting the following land cover areas provided from the NZ Land Cover Database (LCDB v 4.1): Permanent snow and ice, gravel or rock, landslide, alpine grass/herbfield, sub alpine shrubland, and tall tussock grassland.

alpine zone, tall tussock species give way to shorter grasses, dwarf shrubs and cushion or turf-forming herbs in fellfields; growth forms indicative of the high alpine zone (Mark & Dickinson 1997). As a consequence of relatively recent rapid tectonic activity and glaciations, phylogenetic radiations of plants and animals have been extensive in the alpine zone, especially among plant and invertebrate communities, but including reptiles and birds (Wallis & Trewick 2009). Floral diversity throughout the alpine zone is high, with >600 species of vascular alpine plants, the majority of which (c. 93%) are endemic (Mark & Adams 1995).

Global threats to alpine ecosystems are also pertinent in New Zealand, particularly the effects of invasive browsers and predators, climate change, and to a lesser extent, fire and anthropogenic development (e.g. ski resorts, wind farms). Introduced mammalian herbivores, particularly Himalayan

tahr (*Hemitragus jemlahicus*), chamois (*Rupicapra rupicapra*), red deer (*Cervus elephas*), brushtail possums (*Trichosurus vulpecula*) and hares (*Lepus europaeus*) browse a wide variety of alpine plants, usually with each species feeding primarily on particular plant species or groups of species. Goats (*Capra hircus*), high country sheep and other ungulates contribute locally to browsing pressure in some places. However, the absolute impacts of browsers on alpine plant species and regeneration remains uncertain (Flux 1967; Lavers et al. 1983; Rose & Platt 1987, 1992; Wong & Hickling 1999; Hickling & Forsyth 2000; Parkes & Forsyth 2008) and identifying them is complicated by the extinction of many indigenous avian browsers (Holdaway 1989; Horrocks et al. 2004; Lee et al. 2010; Wood et al. 2012). The impacts of climate change in the alpine zone are likely to revolve around changes in habitat suitability, seasonality of food sources, changes in both indigenous and introduced species abundance, increased fire frequency, and potentially new diseases and pathogens (Christie 2014). Many pests that currently have upper altitudinal limits are likely to extend to higher elevations under predicted warming (Christie 2014).

At least 13 species of introduced mammals have been recorded as significant predators of indigenous threatened wildlife across a range of taxonomic groups in forest, river, coastal and wetland habitats (Ramsay 1978; Dowding & Murphy 2001; Sanders & Maloney 2002; Baker 2006; Innes et al. 2010; Reardon et al. 2012; O'Donnell et al. 2015). In alpine areas, there is little understanding of the potential impacts of these predators, despite their presence there (Wilson et al. 2006; Smith et al. 2007). Understanding these factors is important, because there may be a need to control predators in alpine areas if vulnerable indigenous taxa are to persist, just as is done in other ecosystems in New Zealand (Baber et al. 2009; O'Donnell & Hoare 2012; Reardon et al. 2012; Cruz et al. 2013). We focus this review on indigenous fauna that characteristically feed, shelter and/or breed in the alpine zone, but exclude species that are merely vagrants to alpine habitats. The objectives of this review are to: (1) describe the significance of alpine faunal communities in New Zealand; (2) examine the anecdotal and published evidence for predation by introduced mammalian predators on fauna characteristic of the alpine zone; (3) summarise information on the presence and abundance of mammalian predators in alpine areas and factors that drive predation risk; and (4) indicate future directions for research and conservation management, on the basis of a conceptual ecological model.

Value of alpine habitats for indigenous fauna

Birds

We record 24 indigenous bird species as characteristic of the alpine bird community, of which 17 are threatened or at risk (Table 1; Robertson et al. 2013). A species can be categorised as restricted to the alpine zone for at least part of its life history (obligate user), as living in a range of lowland, montane and alpine habitats of which the alpine zone is an important habitat (primary user), or present incidentally or locally in the alpine zone but not dependent on alpine habitat (facultative user). Only three species are obligate users of the alpine zone (i.e. restricted to it for at least part of their life history): Hutton's shearwaters (*Puffinus huttoni*), takahē (*Porphyrio hochstetteri*) and rock wrens (*Xenicus gilviventris*). Hutton's shearwaters

Table 1. Characteristic indigenous vertebrate fauna of the New Zealand alpine zone

Common name	Scientific name	Threat status ¹	Dependence on alpine zone ²	Use ³	Mammalian predation in alpine habitat confirmed ⁴	Mammalian predation in non-alpine habitats confirmed ⁵	Alpine distribution
Birds							
Haast tokoeka	<i>Apteryx australis</i> "Haast"	Nationally critical	Primary	F, B, S	Yes	Yes	Haast Range
Great spotted kiwi	<i>Apteryx haastii</i>	Nationally vulnerable	Primary	F, B, S		Yes	North of Arthurs Pass, South Island only
Fiordland tokoeka	<i>Apteryx australis</i>	Nationally vulnerable	Primary	F, S	Yes	Yes	Fiordland mountains
Hutton's shearwater	<i>Puffinus huttoni</i>	Declining	Obligate	B	Yes		Seaward Kaikoura Range
Black shag	<i>Phalacrocorax carbo</i>	Declining	Facultative	F			Tarns and streams, throughout
Paradise shelduck	<i>Tadorna variegata</i>	Not threatened	Facultative	F, S		Yes	Tarns and streams, throughout
Whio	<i>Hymenolaimus malacorhynchos</i>	Nationally vulnerable	Facultative	F, B, S		Yes	Alpine streams throughout
Grey duck	<i>Anas superciliosa</i>	Nationally critical	Facultative	F, B, S		Yes	Tarns and streams, throughout
NZ scaup	<i>Aythya novaeseelandiae</i>	Not threatened	Facultative	F, B, S		Yes	Throughout
Australasian harrier	<i>Circus approximans</i>	Not threatened	Facultative	F, B, S			Throughout
NZ falcon	<i>Falco novaeseelandiae</i>	Nationally vulnerable	Primary	F, B, S			Throughout
Western weka	<i>Gallirallus australis</i>	Not threatened	Primary	F, B, S		Yes	Fiordland, northern South Island
Takahē	<i>Porphyrio hochstetteri</i>	Nationally critical	Obligate, relict	F, B, S	Yes		Fiordland
Southern New Zealand dotterel	<i>Charadrius o. obscurus</i>	Nationally critical	Primary, relict	F, B, S	Yes		Stewart Island
Banded dotterel	<i>Charadrius bicinctus</i>	Nationally vulnerable	Primary	F, B, S		Yes	Canterbury, Otago, Stewart Island
Southern black-backed gull	<i>Larus dominicanus</i>	Not threatened	Primary	F, B, S			Throughout
Black-fronted tern	<i>Chlidonias albostriatus</i>	Nationally endangered	Facultative	F, B,		Yes	South Island mountains
Kea	<i>Nestor notabilis</i>	Nationally endangered	Primary	F, B, S	Yes	Yes	South Island mountains
Kākā	<i>Nestor meridionalis</i>	Nationally vulnerable	Facultative	F		Yes	Throughout
Silvereye	<i>Zosterops lateralis</i>	Not threatened	Primary	F		Yes	Throughout
Rock wren	<i>Xenicus gilviventris</i>	Nationally endangered	Obligate	F, B, S	Yes		South Island mountains
NZ pipit	<i>Anthus novaeseelandiae</i>	Declining	Primary	F, B, S		Yes	Throughout
Fernbird	<i>Bowdleria punctata</i>	Declining	Primary	F, B, S		Yes	Otago, Canterbury, northern South Island
Tomtit	<i>Petroica macrocephala</i>	Not threatened	Primary	F, B, S		Yes	Throughout
Lizards							
Cascade gecko	<i>Mokopirirakau "Cascades"</i>	Declining	Primary	F, B, S	Yes		South Westland, Fiordland
Cupola Basin gecko	<i>Mokopirirakau "Cupola"</i>	Data deficient	Obligate, relict?	F, B, S			Nelson Lakes

Common name	Scientific name	Threat status ¹	Dependence on alpine zone ²	Use ³	Mammalian predation in alpine habitat confirmed ⁴	Mammalian predation in non-alpine habitats confirmed ⁵	Alpine distribution
Orange spotted gecko	<i>Mokopirirakau</i> "Roys Peak"	Nationally vulnerable	Primary	F, B, S			Otago
Takitimu gecko	<i>Mokopirirakau cryptozoicus</i>	Nationally vulnerable	Primary	F, B, S			Southland
Forest gecko	<i>Mokopirirakau granulatus</i>	Declining	Facultative	F, B, S			Mount Taranaki -Lewis Pass
Black-eyed gecko	<i>Mokopirirakau kahutarae</i>	Nationally vulnerable	Obligate, relict?	F, B, S			Northern South Island
Harlequin gecko	<i>Tukutuku rakiurae</i>	Nationally vulnerable	Obligate, relict?	F, B, S			Stewart Island
Mini mac gecko	<i>Woodworthia</i> "Marlborough mini"	Not threatened	Facultative	F, B, S			Malborough and southern North Island
Kahurangi gecko	<i>Woodworthia</i> "Mount Arthur"	Naturally uncommon	Obligate, relict?	F, B, S			Kahurangi
Kōrero gecko	<i>Woodworthia</i> "Otago/Southland large"	Declining	Facultative	F, B, S			Otago
Southern Alps gecko	<i>Woodworthia</i> "Southern Alps"	Not threatened	Primary	F, B, S			Canterbury
Short-toed gecko	<i>Woodworthia</i> "southern mini"	Not threatened	Primary	F, B, S			Southern South Island
Raukawa gecko	<i>Woodworthia maculata</i>	Not threatened	Facultative	F, B, S			North Island and northern South Island
Mackenzie skink	<i>Oligosoma</i> aff. <i>lineoocellatum</i> "Mackenzie Basin"	Nationally vulnerable	Facultative	F, B, S			Canterbury
Canterbury spotted skink	<i>Oligosoma</i> aff. <i>lineoocellatum</i> "central Canterbury"	Nationally vulnerable	Facultative	F, B, S			Canterbury
Pukuma skink	<i>Oligosoma</i> aff. <i>longipes</i> "Rangitata"	Nationally critical	Obligate, relict?	F, B, S			Canterbury
Southern long-toed skink	<i>Oligosoma</i> aff. <i>longipes</i> "Southern"	Declining	Facultative	F, B, S			Canterbury
Cryptic skink	<i>Oligosoma</i> <i>inconspicuum</i>	Declining	Facultative	F, B, S			Southern South Island
Speckled skink	<i>Oligosoma</i> <i>infrapunctatum</i>	Declining	Facultative	F, B, S			North Island, northern South Island
Barrier skink	<i>Oligosoma judgei</i>	Nationally endangered	Obligate, relict?	F, B, S			Fiordland
McCann's skink	<i>Oligosoma maccanni</i>	Not threatened	Facultative	F, B, S			Throughout South Island south of Lewis Pass, east of divide
Southern skink	<i>Oligosoma notosaurus</i>	Not threatened	Primary	F, B, S			Stewart Island
Sinbad skink	<i>Oligosoma pikitanga</i>	Nationally endangered	Obligate, relict?	F, B, S			Fiordland
Northern grass skink	<i>Oligosoma polychroma</i>	Not threatened	Facultative	F, B, S			Mount Ruapehu, north-west South Island - Lewis Pass
South Marlborough skink	<i>Oligosoma</i> aff. <i>polychroma</i> Clade 3	Declining	Facultative	F, B, S			Inland South Marlborough

Common name	Scientific name	Threat status ¹	Dependence on alpine zone ²	Use ³	Mammalian predation in alpine habitat confirmed ⁴	Mammalian predation in non-alpine habitats confirmed ⁵	Alpine distribution
Canterbury grass skink	<i>Oligosoma aff. polychroma</i> Clade 4	Declining	Facultative	F, B, S			Canterbury foothills
Southern grass skink	<i>Oligosoma aff. polychroma</i> Clade 5	Declining	Facultative	F, B, S			Banks Peninsula, South Canterbury, Otago, Fiordland
Eyres skink	<i>Oligosoma repens</i>	Nationally vulnerable	Primary, relict?	F, B, S			Southland
Small-eared skink	<i>Oligosoma stenotis</i>	Naturally uncommon	Primary	F, B, S			Stewart Island
Scree skink	<i>Oligosoma waimatense</i>	Nationally vulnerable	Primary	F, B, S			Marlborough, Canterbury
Fish							
Alpine galaxias	<i>Galaxias paucispondylus</i>	Naturally uncommon	Facultative	F, B, S			>1200 m, Mackenzie Basin
Dusky galaxias	<i>Galaxias pullus</i>	Nationally endangered	Facultative	F, B, S			>1050 m, Taieri Catchment
Clutha flathead galaxias	<i>Galaxias "species D"</i>	Nationally critical	Facultative	F, B, S			>1070 m, Clutha Catchment
Canterbury galaxias	<i>Galaxias vulgaris</i>	Declining	Facultative	F, B, S			>1100 m, Ashburton Catchment
Koaro	<i>Galaxias brevipinnis</i>	Declining	Facultative	F, B, S			To 1390 m, Kahurangi
Upland longjaw galaxias	<i>Galaxias prognathus</i>	Nationally vulnerable	Facultative	F, B, S			>1200 m, Mackenzie Basin
Gollum galaxias	<i>Galaxias gollumoides</i>	Nationally vulnerable	Facultative	F, B, S			1060 m, Nevis Catchment
Upland bully	<i>Gobiomorphus breviceps</i>	Not threatened	Facultative	F, B, S			>1200 m, Ashburton Catchment

1. Source: Goodman et al. 2013; Robertson et al. 2013; Hitchmough et al. 2016.

2. Dependence on alpine zone: Obligate = Restricted to the alpine zone for at least part of its life history; Primary = Lives in a range of lowland, montane and alpine habitats but the alpine zone is an important habitat; Facultative = Can occur incidentally or locally in the alpine zone but is not dependent on it.

3. Use code: F = Feed, B = Breed, S = Shelter.

4. See text of this review for detail. Blank spaces indicate no confirmation of mammalian predation was found.

5. See Basse et al. 1999; Dowding & Murphy 2001; McLennan & McCann 2002; Sanders & Maloney 2002; Baker 2006; Innes et al. 2010; Keye et al. 2011; Reardon et al. 2012; O'Donnell et al. 2015.

use the zone only for breeding, foraging at sea for the rest of the year (Cuthbert & Davis 2002), and takahē nest in alpine habitat during the spring and forage there until late autumn, when they move down and utilise forest habitats during the winter (Mills et al. 1980). Only rock wrens are truly confined to the alpine zone, except perhaps when dispersing between suitable sites (Weston et al. 2016).

A popular misconception is that kea (*Nestor notabilis*) use only alpine habitat, perhaps the result of their common description as ‘the world’s only alpine parrot’. While alpine areas constitute an important component of kea habitat, kea are sequential foraging specialists, commonly found in coastal and montane forests and moving among numerous seasonally available food sources (O’Donnell & Dilks 1994; Greer et al. 2015). In addition, Jackson (1963) dispelled the myth that kea nest in alpine areas, describing 33 of 36 nests below the timberline in high altitude montane forests, and the remaining three in subalpine scrub. The New Zealand pipit (*Anthus*

novaeseelandiae) specialises in grassland and open habitats, with a breeding range extending from coastal dunes up to high altitude alpine fellfields (Higgins et al. 2006; Beauchamp 2009); consequently, alpine areas are an important habitat for this species. The alpine zone also supports a number of species that exploit high altitude habitats but are not confined to them. These include wetland species that use high altitude fens, flushes, lakes, tarns and streams and shrubland species (e.g. grey duck (*Anas superciliosa*), black-fronted tern (*Chlidonias albostriatus*), NZ scaup (*Aythya novaeseelandiae*), fernbird (*Bowdleria punctata*), tomtit (*Petroica macrocephala*), silvereye (*Zosterops lateralis*); Table 1). Similarly, whio (*Hymenolaimus malacorhynchos*) frequently feed and sometimes breed in alpine streams (Harding 1990, 1994).

Several threatened species are now restricted to local distributions in the alpine zone (Table 1). Haast tokoeka (*Apteryx australis* ‘Haast’) are confined to forests and alpine areas in the Haast Range, South Westland; Hutton’s

shearwaters breed only in the Kaikoura Ranges at elevations between 1200 and 1800 metres; takahē occur naturally only in the Murchison Mountains, Fiordland; and southern New Zealand dotterels (*Charadrius o. obscurus*) breed only on the Tin Range and Table Hill on Stewart Island (Dowding 1999). Other species use the alpine zone seasonally, and perhaps not every year (e.g. kākā (*Nestor meridionalis*) when mountain flax (*Phormium cookianum*) flowers; P. Wilson & T. Greene, DOC Christchurch, pers. comm.).

It is uncertain how many of these restricted distributions are relicts of wider distributions in the past. There is no evidence that Hutton's shearwaters nested beyond the Kaikoura Ranges (Cuthbert 2001). However, in pre-historic times, takahē were distributed throughout the South Island and were not confined to the alpine zone (Worthy & Holdaway 2002). Similarly, breeding southern New Zealand dotterels were widespread in the alpine areas of the South Island when Europeans arrived in the country (Stead 1927; Dowding 1999). Fernbirds are widespread in some regions but not others. For example, they are common in alpine tussock and shrublands in the Paparoa Range, north-west Nelson and the central North Island, and occasionally in other alpine areas (Authors, pers. obs.; Robertson et al. 2007), but it is not known if they were distributed more widely in alpine zones in the past. Further, some bird species are now locally extinct in alpine areas; for example, kea have disappeared from the North Island (Tennyson et al. 2014). It has not been confirmed whether rock wrens were once present in the North Island, though a specimen labelled as *X. gilviventris* held at the Natural History Museum at Tring in the United Kingdom is recorded as being collected in the Rimutaka Ranges. If this is an accurately labelled rock wren specimen, then rock wrens have become extinct in alpine areas of the North Island since the 1930s. Kākāpō (*Strigops habroptilus*) were also found in subalpine scrub and tussocklands in Fiordland and on Stewart Island up until the 1980s (Powlesland et al. 2006).

There is little doubt that the alpine bird fauna was more diverse prior to the arrival of humans in New Zealand (Worthy & Holdaway 2002), although there is scant information available on the community composition or the relative importance of alpine habitats compared with other zones. It is unlikely that any extinct species were obligate alpine species, although it may have been a primary habitat for several. South Island snipe (*Coenocorypha iredali*) were thought to be found primarily in tussockland above the timberline (Tennyson & Martinson 2006), similar to extant *Coenocorypha* spp., which are common breeders in alpine-like tussocklands and herbfields in subantarctic New Zealand (Miskelly et al. 2006). The long-billed wren (*Dendrocansor decurvirostris*) was also thought to inhabit high altitude montane forests, subalpine scrub and tussock (Worthy & Holdaway 2002). A number of moa species (*Dinornis*, *Pachyornis*, *Megalapteryx* spp.), Lyall's wrens (*Traversia lyallii*), Haast's eagles (*Harpogornis moorei*), Eyles's harriers (*Circus eylesi*) and others were probably present in fellfields and high altitude shrublands, at least seasonally (Worthy & Holdaway 2002).

Some indigenous birds fulfil an important ecological role in the alpine zone as pollinators and seed dispersers. For example, rock wrens consume nectar from mountain flax, thus acting as pollinators, as well as feeding on a range of alpine fruits (Michelsen 1982; O'Donnell et al. 2011). New Zealand falcons (*Falco novaeseelandiae*) eat fruits of *Gaultheria depressa* and *Leucopogon fraseri* (Young & Bell 2010), New Zealand pipits have been observed feeding on fruits (Young et al. 2012) and who frequently pass faeces entirely composed

of *Coprosma* spp. (Harding 1990). In addition, birds of prey may act as secondary seed dispersers when they prey on other fruit/seed eaters (Young & Bell 2010). The relative importance of indigenous birds as pollinators and seed dispersers in the alpine zone is uncertain due to few quantified studies. Compared with invertebrates, alpine birds are likely to play an incidental role as pollinators, but they appear more important as seed dispersers (Primack 1978). Kea are the most important alpine avian frugivore (Young et al. 2012), however numerous other alpine frugivores are now extinct (Worthy & Holdaway 2002). Earlier research indicated that kea were primarily seed destroyers in forests (O'Donnell & Dilks 1994) and sometimes seed destroyers in the alpine zone (Clarke 1970), but Young et al. (2012) demonstrated through faecal analysis that in two alpine areas, rates of seed predation were extremely low; with seeds of >20 plant species passing through the gut and remaining viable. In addition, kea make frequent long distance movements on a scale of tens of kilometres (Clarke 1970), potentially making them effective seed dispersers.

Lizards

Alpine areas of New Zealand have a diverse lizard fauna, with at least 13 gecko and 17 skink species recorded (Table 1; based on NZ Herpetofauna database). However, populations are generally poorly surveyed and understood. Distributions of most taxa appear highly localised, and like many other reptile taxa in New Zealand, are probably relicts of former, more widespread distributions (Worthy 1987). About one quarter of alpine lizards may be obligate alpine species (seven taxa; Table 1), and the majority of other taxa are widespread at lower altitudes. It has been argued that the black-eyed gecko (*Mokopirirakau kahutarae*) is New Zealand's only truly alpine lizard, inhabiting cliffs and bluffs between 1250 and 2200 m.a.s.l. in eastern Marlborough and at Mt Arthur in Kahurangi National Park (Whitaker 1984, 1997; Whitaker et al. 1999). However, several newly identified taxa also appear restricted to the alpine zone between 1200 and 1500 m, such as the Mt Arthur and Roy's Peak geckos (Nielsen et al. 2011), and the Barrier and Sinbad skinks (*Oligosoma judgei*, *O. pikitanga*) (Bell & Patterson 2008; Patterson & Bell 2009). It remains uncertain whether these taxa are true alpine obligates, or if lower altitude populations have been extirpated in the past (Whitaker et al. 1999; Bell & Patterson 2008; Patterson & Bell 2009). Several species formerly considered to be alpine specialists have been discovered at low elevation, making us re-evaluate habitat choices and suggesting that the alpine zone provides refugia for formerly widespread species. For example, the range of the Takitimu gecko (*M. cryptozoicus*) was recently extended to include low altitude forest in the Waitutu area (Bell & Patterson 2008).

Lizards may play an important role as pollinators, being more local dispersal agents for alpine plants, though little is known in general of their effectiveness (quantity and quality) for most New Zealand flora (Whitaker 1987; Young & Kelly 2014; Wotton et al. 2016). Several alpine lizard taxa are known to visit flowers to feed on nectar and also remove and ingest fruits, excreting viable seed of several montane grassland species (Whitaker 1987; Lawrence 1997). A recent study of alpine fruit removal rates in the central Southern Alps showed the contribution of lizards to be unexpectedly high; constituting on average 50% of total fruit removal (Young & Kelly 2014).

Invertebrates

The New Zealand alpine zone supports a rich and extensive array of endemic invertebrate groups; some of the most notable include wētā and short-horned grasshoppers (Orthoptera), cockroaches (Blattodea), cicadas (Homoptera), weevils (Coleoptera), butterflies and moths (Lepidoptera), giant wingless stoneflies (Plecoptera), spiders (Araneae) and giant carnivorous snails (Mollusca). Many of these taxa possess specialised adaptations to survive the extreme alpine conditions such as dark colouration, flightlessness and freeze tolerance (Buckley & Simon 2007; McCulloch et al. 2009; Wharton 2011). Patterns such as low levels of endemism within the volcanic mountainous areas of the North Island, and high levels of endemism in the alpine areas of north-west Nelson and west Otago have been identified, as well as hotspots of local endemism on individual mountain ranges, though detailed information on alpine fauna distributions across New Zealand remains lacking (Goldberg et al. 2008; Buckley et al. 2015).

Amongst wētā, perhaps the most charismatic alpine dwellers are those from the genus *Deinacrida* (giant wētā). Of the eleven giant wētā species, six are classified as alpine, three of which are obligate alpine inhabitants and restricted to localised regions of the South Island mountains (Morgan-Richards & Gibbs 2001). *Deinacrida talpa* is known only from the central Paparoa Range, on the West Coast of the South Island (Gibbs 1999), and *D. parva* survives as a relict in the Kaikoura Ranges of the northern South Island (Gibbs 1998). Each species of giant wētā is specialised to use different alpine microhabitats, ranging from rocky crevices and bluffs, to scree slopes and self-excavated underground burrows (Morgan-Richards & Gibbs 2001). Only two species, *D. connectens* and *D. pluvialis*, are not classified as at risk, attributed to their relative wide ranges throughout the Southern Alps (Trewick et al. 2012). Several species of Rhaphidophoridae (cave wētā), such as the iconic 'Mount Cook Flea' *Pharmacus montanus*, are also obligate alpine dwellers, found only in some of the highest alpine-nival zones of the Southern Alps (Richards 1972). Some wētā species, such as *D. connectens* and ground wētā *Hemiandrus maculifrons*, are thought to be seed dispersers of alpine plants (Burns 2006; Larsen & Burns 2012). However, the overall contribution of wētā to effective alpine seed dispersal is thought to be low (Morgan-Richards et al. 2008; Young & Kelly 2014).

Solitary bees (Hymenoptera), native flies (Diptera) and moths comprise the majority of insect pollinators within the New Zealand alpine zone (Primack 1978, 1983; Bischoff 2008; Bischoff et al. 2013). Unlike in the alpine regions of Europe and North America, native social bees (Hymenoptera) are absent and butterflies are scarce, with only five described obligate alpine dwellers; the endemic black mountain ringlet (*Percnodaimon merula*), Butler's ringlet (*Erebiola butleri*), and alpine boulder butterflies *Lycaena* spp. (Gibbs 1980; Newstrom & Robertson 2005; Patrick & Patrick 2012). Most of New Zealand's short-horned grasshoppers (Orthoptera: Acrididae) are confined to alpine or subalpine habitats and hence as a group, they are generally referred to as alpine grasshoppers, despite some species being only primary or facultative in their dependence on the alpine zone (Bigelow 1967; Trewick 2008). The Homer grasshopper (*Sigaus homerensis*) is only known from the Earl Mountains of Fiordland (Morris 2003) and is ranked as nationally critical under New Zealand threat ranking criteria (Trewick et al. 2012). Only one species, *S. piliferus*, has been recorded from alpine areas of the North Island (Bigelow 1967). As a group, the short-horned grasshoppers represent

a significant guild of herbivores in the New Zealand alpine zone (Batcheler 1967; White 1975).

Within the New Zealand cicada genus *Maoricicada*, there are 14 described species, nine of which can be considered either alpine or subalpine (Dugdale & Fleming 1978; Buckley & Simon 2007). The genus has speciated extensively in the South Island mountains and several species are severely range restricted. For example, *M. otagoensis maceweni* is known only from the Takitimu Range in Southland (Dugdale & Fleming 1978). These cicadas utilise a diversity of habitat types, ranging from subalpine scrub and scree, to boulder and herbfields adjacent to the permanent snow line (Buckley & Simon 2007). Similarly, within the cicada genus *Kikihia*, many species are found in specific habitats (e.g. *K. horologium* are mostly found on subalpine shrubs). It is likely that new species were formed by adaptation to new alpine habitat types during the rapid uplift of the Southern Alps 3–5 Ma (Arensburger et al. 2004). Similar patterns with hotspots of local endemics are found among the alpine stoneflies (McLellan 1977; McCulloch et al. 2010). The *Lyperobius* or 'speargrass' weevils are predominantly found in higher montane, subalpine and alpine grasslands, or herbfields and rocky habitats in the South Island (Craw 1999). These large flightless weevils feed exclusively on herbaceous plants from the family Apiaceae in two genera – *Aciphylla* and *Anisotome* (Craw 1999). At least one obligate alpine species, *L. carinatus*, is currently listed as threatened, attributed to being uncommon throughout its range (Leschen et al. 2012). Carnivorous land snails belonging to the genus *Powelliphanta* are also found throughout the alpine areas of New Zealand, with the greatest diversity of species in the mountains of north-west Nelson (Walker 2003). At least ten *Powelliphanta* species are obligate users of subalpine scrub and alpine tussock grasslands, some spending up to 5 months of the year under snow and able to withstand below-freezing conditions (Walker 2003).

Freshwater fish

Overall, there are few records of freshwater fish in alpine areas. With >34 000 survey records in the NZ Freshwater Fish Database (NZFFD), only 203 were in alpine areas above 1000 m.a.s.l., and fish were recorded on only 63 of these 203 sites (NZFFD, August 2015). Eight of the 56 New Zealand indigenous freshwater fish taxa (Goodman et al. 2013) have been recorded in the alpine zone (Table 1; NZFFD), but none are obligate alpine species. Koaro (*Galaxias brevipinnis*) have been recorded to 1390 m.a.s.l. in Kahurangi National Park. Two taxa were recorded as common or abundant at a few sites (upland longjaw galaxias *G. prognathus* and alpine galaxias *G. paucispondylus*), but most taxa were recorded in only one or few reports.

Bats

New Zealand bats are essentially forest dwelling species (O'Donnell et al. 1999; O'Donnell 2001). There have been reports of long-tailed bats (*Chalinolobus tuberculatus*) foraging up to the timberline, but not above it (Dwyer 1962; Daniel & Williams 1984).

Distribution and ecology of alpine mammalian predators

Studies documenting mammalian predator ecology above the timberline are sparse and distribution records are not formally collated anywhere. Trap catch data collated from several alpine sites, combined with anecdotal records from managed alpine sites, show that almost the full suite of predators known to be present below the timberline are also present in the alpine zone (Fig. 2). These predator control programmes include a range of trap-box entrances and trap types, which may have been optimised for different predators; consequently, the number of captures may not reflect actual composition (Fig. 2). Alpine tracking tunnels (Gillies & Williams 2013) have mainly recorded stoats and house mice (*Mus musculus*) (DOC, unpubl. data). However, in situations where mustelid or rodent detectability and/or density is low, such as has been suggested for alpine zones in general, tracking tunnels are not always sensitive enough to confirm presence/absence (Choquenot et al. 2001; Gillies & Williams 2013; Pickerell et al. 2014). The lack of alpine records of feral ferrets (*Mustela furo*) and the apparent patchiness of other predators, is not evidence for absence of these taxa, largely because of the paucity of studies at high altitude. Although most mammalian predators are present in the alpine zone, there is little information available on actual or relative abundance compared with other habitat types.

Mustelids

Stoats (*Mustela erminea*) are widespread throughout New Zealand and are able to live in any habitat where they can find prey (King & Murphy 2005). Both trapping and tracking tunnel studies indicate stoats are common in alpine areas (Fig. 2; Smith et al. 2005; Wilson et al. 2006), which is not surprising given that they are cold-adapted animals (King & Powell 2007) with the majority of their global range lying north of latitude 45° and associated with boreal and subalpine biomes (King & Powell 2007; Frey & Calkins 2014).

Population densities of stoats are considered to be lower and more stable in non-beech-forest habitats (King & Murphy 2005), though within an alpine Hutton's shearwater colony in the Kaikoura Ranges stoat density was the highest recorded in any habitat (c. 17 stoats per km²) during the shearwater nesting season, when prey were superabundant (Cuthbert & Sommer 2002). Limited trapping data (Fig. 2) indicate that stoat capture rates vary markedly from year to year in South Island areas adjacent to beech sites, compared with Mt Taranaki where adjacent forest is podocarp-hardwood; this difference may be related to mast seedfall events within the alpine zone or in adjacent beech forests.

Standard tracking tunnel indices have been used to investigate differences in stoat abundance between alpine grassland and beech forest in the Murchison Mountains and Borland Valley of Fiordland (Smith & Jamieson 2005; Wilson et al. 2006). In the Murchison Mountains in a summer following two consecutive heavy beech seedfall events and a weak *Chionochloa* seed mast, stoat densities were significantly higher at beech forest sites (Smith & Jamieson 2005), but in the Borland Valley where no heavy beech or *Chionochloa* tussock seedfall events had occurred, no significant difference in stoat tracking between alpine and beech forest habitats was detected (Wilson et al. 2006). In the Borland Valley, stoat density (c. one stoat per km²) and body weights were similar between alpine and forest habitats (Smith et al. 2008), and stoats preferentially selected alpine grassland habitat over adjacent lower elevation beech forest within their home ranges (Smith et al. 2007).

In the Murchison Mountains, mice were the most common prey of stoats, following a heavy beech and tussock seedfall event (Smith et al. 2005). While the limited diet studies to date imply geographical variation in the contribution of alpine invertebrates to stoat diet, there is strong evidence that wētā are the most common invertebrate prey of alpine stoats (Lavers & Mills 1978; Cuthbert et al. 2000; Smith et al. 2005, 2008), particularly during years when no heavy seeding of beech or *Chionochloa* occurs and rodents are scarce (Smith et al.

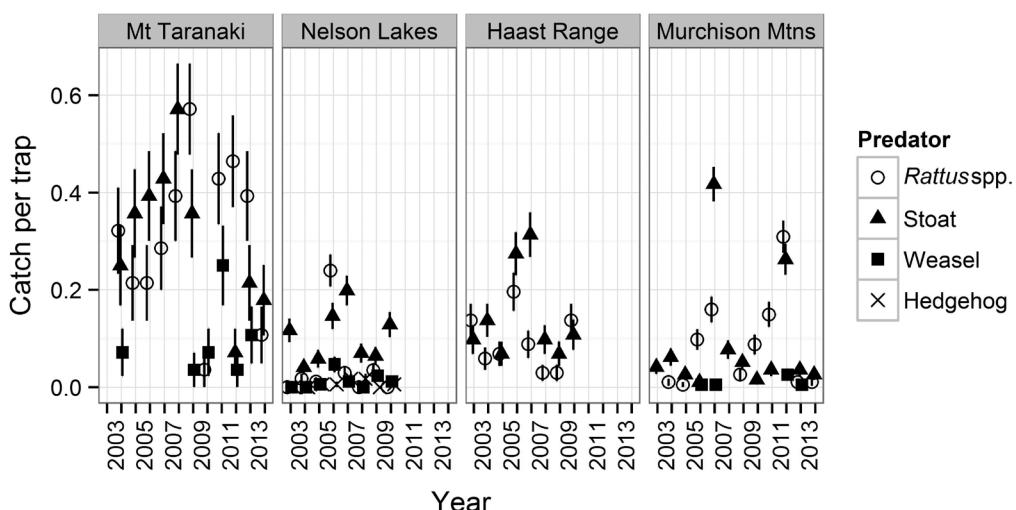


Figure 2. Trapping rates (uncorrected trap catch ± SE) of mammalian alpine predators from Mt Taranaki (1290–1540 m.a.s.l; n = 191 captures; 28 double DOC180 traps; 2004–2014), Nelson Lakes National Park (1320–1880 m.a.s.l; n = 224 captures; 171 single DOC200 traps; 2003–2010), Haast Range, South Westland (980–1470 m.a.s.l; n = 195 captures; 102 double DOC200 traps; 2003–2010) and Murchison Mountains, Fiordland (1000–1390 m.a.s.l; n = 193 captures; 194 double DOC150 traps; 2003–2014). (See Poutu & Warburton 2005, for further detail on DOC series trap design).

2005, 2008). Supplementary feeding experiments with stoats in alpine habitat also indicate that stoats may alter the rate at which they prey upon wētā in alpine grasslands, when other food sources are abundant (Smith et al. 2011).

Weasels (*Mustela nivalis*) are less common and more patchily distributed across New Zealand than stoats, and prefer thick ground cover to more open country (King 2005). However, weasels are caught regularly in alpine trapping programmes (Fig. 2). Dietary studies of weasels in alpine habitat have not been undertaken, though the few data available from lowland habitats indicate that mice comprise much of weasel diet and that larger prey items such as rats and lagomorphs are consumed less frequently (King et al. 1996; Murphy et al. 1998). When supplied with abundant food, weasels are capable of producing up to three litters per season and can breed in the year of their birth; by contrast, stoats do not produce their first litter until they are 12 months old and produce only a single litter per season (King 2005). Therefore, weasels are more closely adapted than stoats to exploit irruptions in small mammals, and consequently their New Zealand distribution and rapid fluctuations in abundance are closely correlated with the distribution and abundance of mice (King 2005). Weasels cannot be reliably distinguished from stoats using tracking tunnel footprints (C. Gillies, DOC Hamilton, pers. comm.), so it is uncertain how extensively they occupy alpine environments.

Rodents

House mice are found throughout the New Zealand mainland, from the coast to high altitudes (Ruscoe & Murphy 2005). They generally reach higher population densities in areas with dense ground cover, and habitat choice is a trade-off between access to food and safety from predation (Ylönen et al. 2002; Ruscoe & Murphy 2005). We are aware of only one published assessment of mouse diet in the alpine zone (alpine

grasslands, Borland Valley, Fiordland) (Wilson et al. 2006; Wilson & Lee 2010). In this habitat, mouse diet appeared to be dominated by invertebrates during non-tussock-mast years and by *Chionochloa* tussock seed during a mast seedfall year, when mouse density increased from 4 ha⁻¹ to 39 ha⁻¹ (Wilson & Lee 2010). Mouse populations also irrupt in beech and podocarp-hardwood forest following moderate to high seedfall because this abundant food supply facilitates winter breeding (King 1983; Murphy 1992; Fitzgerald et al. 1996; O'Donnell & Phillipson 1996; Choquenot & Ruscoe 2000; Ruscoe et al. 2004). The extent to which alpine mice respond to tussock mast seeding, compared with their response to seedfall events in adjacent forests, has been documented only once in New Zealand (Wilson & Lee 2010). There is uncertainty also as to whether there is spillover of mice into alpine habitat from adjacent forest in high beech seedfall years, or indeed, vice versa during *Chionochloa* mast or other pulsed seeding events in alpine vegetation. In the Borland Valley, densities of mice were consistently higher in alpine habitat compared with adjacent montane beech forest in years prior to tussock seeding, but mice were not monitored in adjacent forest during or after the *Chionochloa* mast seeding year (Wilson & Lee 2010).

We found confirmed reports of all three rat species (ship rats (*Rattus rattus*), Norway rats (*R. norvegicus*) and Pacific rats (kiore, *R. exulans*)), in alpine areas (Table 2). However, misidentification and failure to identify rats to species during alpine trapping programmes impedes knowledge about distribution (Ruscoe 2004). Consequently, in this review, we refer to '*Rattus* spp.' where the species of rat is unknown. All three rat species are omnivorous generalists, each consuming a wide range of invertebrates and plant parts including seeds and fruits, and, less often, lizards and birds (Atkinson & Towns 2005; Innes 2005a, b). As with mice, rat populations irrupt in beech and podocarp-hardwood forest due to increased food supply following moderate to high seedfall (King & Moller 1997; Harper 2005a).

Table 2. Known records of mammalian predators from selected New Zealand alpine sites

	Stoat	Weasel	Feral cat	Hedgehog	Pacific rat	Norway rat	Ship rat	House mouse	Feral pig	Deer spp.	Brushtail possum	Source
Mount Taranaki	Yes	Yes	-	-	-	-	-	Yes	-	-	-	Monitoring & trapping data, DOC Taranaki
Kahurangi	Yes	Yes	-	-	-	-	-	Yes	Yes	Yes	-	Authors unpubl. data; Friends of Flora; Friends of the Cobb; J. Kemp pers. comm.
Kaikoura Ranges	Yes	-	Yes	-	-	-	-	Yes	Yes	-	-	G. Taylor pers. comm.; Cuthbert & Davis 2002; Cuthbert 2002
Nelson Lakes	Yes	Yes	-	Yes	-	-	-	Yes	Yes	-	-	J. Mace pers. comm.; Monitoring & trapping data, DOC Nelson Lakes
Haast Range	Yes	-	-	-	-	-	-	Yes	Yes	-	Yes	Authors unpubl. data; Monitoring & trapping data, DOC Haast
Arthurs Pass	Yes	-	Yes	-	-	-	-	Yes	Yes	Yes	Yes	Authors unpubl. trail camera data
Aoraki/Mount Cook	Yes	-	Yes	-	-	-	-	Yes	-	-	Yes	A. Warren pers. comm.; P. Hondelink pers. comm.
Homer-Gertrude Cirque	Yes	-	-	-	-	-	-	Yes	Yes	-	Yes	Authors unpubl. data; NZAC trapping data
Murchison Mountains	Yes	Yes	-	-	Yes	-	Yes	Yes	-	Yes	-	Monitoring & trapping data, DOC Te Anau; J. Christie pers. comm.
Stewart Island	-	-	Yes	-	-	Yes	-	-	-	Yes	-	Monitoring & trapping data, DOC Rakiura

Norway rats were widespread on the mainland in the nineteenth century, but now tend to survive best in wetland habitats and are generally absent from high elevations (Innes 2005a). On Stewart Island, they are still found in alpine areas (K. Richardson, DOC Stewart Island, pers. comm.) and at large distances from water (Hickson et al. 1986; Harper 2005b).

Ship rats are generally found from coast to timberline (Innes 2005b), though trap catch data collected across an altitudinal gradient shows a negative effect of increasing elevation (Studholme 2000; Christie et al. 2017). Although ship rats were previously reported to be absent from alpine tussock (Innes 2005b), recent trap catch data (Fig. 2) reveals that *Rattus* spp. are frequently present above the timberline, including within tussock grassland habitat, albeit in low numbers. Given that on the mainland kiore are now apparently confined to parts of Fiordland, Southland and South Westland, and Norway rats are generally absent from higher elevations, it is most likely that the *Rattus* spp. captured from the northern alpine sites (Taranaki and Nelson Lakes) were ship rats (Fig. 2). Like stoats, numbers of *Rattus* spp. trapped above the timberline fluctuate among years and within seasons (Fig. 2). Predicted rising temperatures associated with climate change will further facilitate the invasion of ship rats into higher altitude areas, though the interplay between temperature and other drivers of rat abundance such as invertebrate activity and mast seeding of grasses, herbs or shrubs remains unclear (Studholme 2000; Christie et al. 2017).

Possums

Brushtail possums are present throughout most of New Zealand (Clout & Erickson 2000), but little information is available on their distribution and ecology in alpine areas. In the North Island, they are absent only above 2400 m on the upper slopes of Mts Taranaki and Ruapehu, whereas in the South Island, they are absent above 1800 m (Cowan 2005). It seems likely that the spread of possums into alpine areas, particularly in Fiordland and South Westland, has been slowed by the topography and harsh climatic conditions. Possum habitat studies in the central Southern Alps indicate that possums are common, albeit at low densities, in sub-alpine shrubland and occur less commonly within alpine grassland habitats (Coleman et al. 1980; Hickling & Forsyth 2000). Shrubland is likely preferred over alpine grasslands because the heterogeneity of shrubland habitat provides more suitable den sites for shelter and alpine grasses are rarely eaten by possums (Hickling & Forsyth 2000; Parkes & Forsyth 2008; Glen et al. 2012).

In the north east of the South Island, possum capture rates declined with increasing altitude, from 600 to >1600 m, and also towards wetter western areas (Glen et al. 2012). Home ranges in high-altitude habitat were larger compared with those typical of forested areas, which was again attributed to more sparsely distributed resources such as food and den sites in open, high-altitude habitat (Glen et al. 2012). In spite of these perceived differences in habitat quality, mean body weights of adult possums in the central Southern Alps are the largest recorded for a New Zealand population, suggesting it is den sites, as opposed to food, that is limiting (Hickling & Forsyth 2000). Survival rates in high-altitude habitat were also similar to those elsewhere in New Zealand (Glen et al. 2012).

Although possums are primarily folivores, they eat flowers, fruit, fungi and small quantities of invertebrates in all habitats (Nugent et al. 2000) and occasionally birds and eggs (Brown et al. 1993). Limited evidence suggests that possums select non-foliar foods for their high nutritional value, and that

possum carrying capacity may be linked to the availability of these foods in different habitats (Nugent et al. 2000). How much possums prey on alpine fauna is unknown.

Hedgehogs

European hedgehogs (*Erinaceus europaeus occidentalis*) are abundant throughout lowland New Zealand, particularly in coastal areas (Brockie 1975; Jones & Sanders 2005). They are thought to be limited by climate at higher elevations and their abundance generally decreases with altitude; however, they have been recorded as high as 2000 m.a.s.l. in the mountains of the South Island (Brockie 1975). Trap catch data indicate they can be trapped regularly in certain alpine areas (Fig. 2). Hedgehog habitat is largely associated with the availability of invertebrate prey and dry nest sites; warmer, drier areas with fewer and milder frosts tend to be favoured (Jones & Sanders 2005). Dietary studies from a range of habitats, but not alpine areas, indicate that invertebrates comprise much of hedgehog diet, though vertebrates such as lizards, birds (particularly eggs) and carrion are also eaten where available (Berry 1999; Jones & Sanders 2005; Jones et al. 2005). Thus, where hedgehogs dwell above the timberline they are likely to pose some level of threat to alpine fauna.

Cats

Feral cats (*Felis catus*) are distributed throughout New Zealand and can live in most habitats, including sand dunes, pasture, tussock, scrub, exotic plantations and native forest (Gillies & Fitzgerald 2005). They have been recorded from sea-level to 3000 m (Collins & Charleston 1979). In lower altitude tussock grassland and braided riverbed habitats, lagomorphs (mainly rabbits (*Oryctolagus cuniculus*)) are cats' most frequent prey; with birds, rodents, invertebrates and lizards also consumed depending on their local availability (Murphy et al. 2004; Gillies & Fitzgerald 2005). On Stewart Island, where lagomorphs are absent, ship rats are the primary prey of cats, regardless of their abundance, and birds are their main alternative prey (Harper 2005b). However, there appear to be no data on cat density or prey consumed in alpine areas.

Feral cat home ranges in high country braided river valleys include steep sided slopes adjacent to riverbeds, and several radio tracked individuals have been recorded in the alpine zone (1100–1700 m.a.s.l.) in winter, including in tussock dominated alpine valleys and amongst scree (Recio et al. 2010). They may range in the alpine zone in search of juvenile hares during the peak of the hare breeding season (Recio et al. 2014).

Pigs

Feral pigs (*Sus scrofa*) occupy approximately a third of New Zealand and are still expanding in range (Fraser et al. 2000). Preferred habitats are native and exotic forests, regenerating farmland, river flats and tussock grasslands with patches of scrub for shelter, which therefore limits pigs' use of alpine areas (McIlroy 2005). They are opportunistic omnivores, and feed on a range of plants above the timberline such as the roots of *Aciphylla* spp., grasses, and the lower part of *Chionochloa* tillers, as well as digging and churning surface substrates. Animal material constitutes an important component of their diet, particularly when breeding, and includes invertebrates, lizards, ground-nesting birds and their eggs, mice, *Rattus* spp., young rabbits, and carrion (Cuthbert 2001; McIlroy 2005), so alpine fauna are likely to be under threat where pigs are present.

Deer

Deer are adaptable herbivores that both browse and graze, but white-tailed deer (*Odocoileus virginianus*) have also been recorded preying on the eggs of southern New Zealand dotterels, in their alpine breeding grounds on Stewart Island (K. Richardson, DOC Stewart Island, pers. comm.). Although other deer species commonly use alpine habitat, there appear to be no other records of them preying on fauna. However, it has been shown that deer impact indirectly on takahē in the Murchison Mountains of Fiordland, by competing for *Chionochloa* tussock as food (Mills & Mark 1977; Parkes et al. 1978; Lavers et al. 1983).

Evidence for the impacts of mammalian predators

Birds

Direct evidence for impacts of introduced mammalian predators on avifauna in the alpine zone is limited and often anecdotal, and is largely derived from studies of threatened species that have been a priority for research. Mammalian predators have been identified as nest predators of seven bird species in alpine habitats (Table 1). For the remaining 16 characteristic alpine bird species, there have been no studies of nesting that we know of in the alpine zone, though mammalian predation has been recorded as a threat in other ecosystems (Table 1).

Mice and stoats have been identified as frequent predators on rock wren eggs, nestlings, and adults (Authors, unpubl. data; Michelsen-Heath 1989; Willans & Weston 2005; Willans 2007). In the McKenzie Burn area of the Murchison Mountains, Fiordland, Michelsen-Heath (1989) found that eight (24%) of 33 nests failed because of predators, five being preyed on by stoats and three by mice. Similarly, in the Murchison Mountains, two (17%) of 12 nests monitored in the Mystery Burn and two (13%) of 16 nests in the McKenzie Burn failed due to predation (Willans & Weston 2005; Willans 2007). Where the predators could be identified, stoats preyed on two nests and mice on one nest. However, while it was concluded that predation was having some impact on rock wren populations, these studies were carried out simultaneously with low intensity predator trapping programmes, either to identify the presence of mammalian predators (Michelsen-Heath 1989) or to protect takahē (Willans 2007). The biases caused by the stoat trapping potentially mask the true impact of these predators on rock wrens because an unknown number of predators may have been killed before they could prey upon rock wrens.

More recently, using infrared video monitoring, stoats have been identified as important predators of adult rock wrens at nests (2011–2015; Authors, unpubl. data). In three untrapped areas of Fiordland and South Westland, 60–80% of nests were preyed upon, including many on bluff systems, and all predation events captured on camera were by stoats (Authors, unpubl. data). Stoats frequently preyed upon cliff-nests, and in one case a stoat jumped across a metre-wide gap to reach a nest. There is only one confirmed record of a weasel killing rock wrens; a fixed trail camera showed an individual weasel killing nestlings in Kahurangi National Park in 2015 (T. Rawlence, DOC Nelson, unpubl. data). Likewise, a *Rattus* spp. was recorded killing rock wren nestlings, also in Kahurangi National Park (T. Rawlence, unpubl. data). However, Reischek (1884) mentioned heavy predation by Norway rats during the nineteenth century when rat plagues were common in the Southern Alps.

Stoats are known to prey upon takahē eggs, chicks, and adults in their natural range in the Murchison Mountains, Fiordland (Reid 1967; Lavers & Mills 1978; Crouchley 1994; Maxwell & Christie 2005), although it has also been reported that in at least one instance an adult takahē has successfully fended off and actually killed a stoat (Lavers & Mills 1978). Predation on eggs appears to be low (3–6% of fertile eggs; Maxwell & Christie 2005). Predator impacts can also be inferred from benefits of predator control programmes in takahē habitat in the Murchison Mountains. Annual adult takahē survival increased significantly from 78% to 85% in the presence of low density stoat trapping, but was still low relative to the survival rates of translocated takahē populations on predator-free offshore islands (Hegg et al. 2012). Further, numbers of takahē in Fiordland almost halved (from 168 known individuals to 93) as a consequence of a stoat plague during the winter of 2007 (Hegg et al. 2012). During the winter, takahē are also at risk of predation from stoats inhabiting beech forest at lower altitudes (Smith & Jamieson 2005) because they move into these forests and grub for the roots of *Hypolepis millefolium* when access to alpine tussock food resources becomes limited by snowfall (Maxwell 2001).

While there have been no specific studies of predation on whio in alpine habitats, video monitoring of nests identified stoats as the primary nest predator in Fiordland valley ecosystems (Whitehead et al. 2008). Further, low intensity stoat control year-round (10 traps per linear km) significantly reduced stoat abundance in trapped whio habitat compared with untrapped habitat. During the same period, whio nesting success and productivity increased significantly within trapped areas (Whitehead et al. 2008). In central North Island rivers, population viability modelling indicates that cessation of predator trapping would rapidly lead to local extirpation of whio (Simpkins et al. 2015).

Stoats, feral cats and feral pigs prey on Hutton's shearwater in the Kaikoura Ranges (Cuthbert 2002; Cuthbert & Davis 2002). Stoats were the major cause of shearwater mortality, with evidence of stoat predation found on 58% of carcasses (30 of 52); feral cats were likely responsible for 14% of mortality (7 of 52) (Cuthbert 2001). Overall, stoats were estimated as killing 0.25% of breeding adults and 12% of chicks produced annually, resulting in a predicted 0.86% reduction in population growth per annum (Cuthbert & Davis 2002). However, because most predation was targeted at chicks, stoat control may not be warranted to protect this species, especially given that natural variation in breeding success due to environmental factors is greater than the effects of predation (Cuthbert 2002). In general, long-lived seabirds like Hutton's shearwaters are much more sensitive to the loss of adults than to the loss of chicks or eggs (Cuthbert 2001). Further, the presence of feral pigs within six extinct colonies of Hutton's shearwaters and at the boundaries of the two extant colonies strongly suggests that pigs were responsible for the historic contraction in breeding range (Cuthbert 2002).

Predation is recognised as the main threat to the southern New Zealand dotterel (Dowding & Murphy 1993), resulting in the implementation of annual predator control in the dotterels' alpine breeding grounds on Stewart Island (Dowding 1995). However, there are few direct observations of predation to support this assertion (Hope 2014; M. Dobbins, pers. comm.). Feral cats are believed to be the primary predator of these dotterels, responsible for the decline of the population from an estimated 350 individuals in 1955 to 62 individuals in 1992 (Dowding & Murphy 1993). Subsequent predator control

may have enabled the slow recovery of the population since the early 1990s (Dowding & Murphy 1993; Dowding 1999; Hope 2014). *Rattus* spp. are also thought to have some impact (Dowding 1999) and there is a recent trail camera record of a Norway rat preying on southern New Zealand dotterel eggs (K. Richardson, DOC Stewart Island, pers. comm.). White-tail deer and swamp harrier (*C. approximans*) have also been recorded taking eggs. Predation on adult dotterels has reduced their life expectancy to approximately 5 years and there is now a female biased sex ratio of 2:1, largely because males are more susceptible to predation as they undertake most of the nocturnal incubation (Dowding 1997 cited in Hope 2014).

Three species of kiwi inhabit alpine areas (Table 1). However, there is little direct evidence of predation on alpine kiwi, largely because studies are few and are predominantly conducted in the lower altitude regions of their range (Keye et al. 2011). Thus, evidence for predation is inferred from these lower altitude studies. Great spotted kiwis have disappeared from lowland sites, probably because of habitat loss and predation. The main agent of decline appears to be predation on chicks and juveniles by stoats (McLennan & McCann 2002). Stoats are also the main predator of young Fiordland tokoeka, with 24% of 34 predation events recorded in the Murchison Mountains between 2003 and 2009 occurring above the timberline (Tansell 2009; Edmonds 2015). During this same period, Fiordland tokoeka chick survival was significantly greater in trapped areas of the Murchison Mountains (37%) than in non-trapped areas (17%) (Tansell 2009). Modelling of this population indicates a slow decline (-1.3% per annum) in the absence of trapping, whereas trapping results in a stable or very slightly increasing population size (1.1% per annum) (Edmonds 2015). Stoats are also a major predator of the closely related northern brown kiwi (*Apteryx mantelli*) (Basse et al. 1999). In lowland forests, ferrets and dogs were the main predators of adult brown kiwi and possums and mustelids were the main egg predators, while stoats (77% of confirmed predations) and cats were largely responsible for the deaths of young kiwi (McLennan et al. 1996). Haast tokoeka frequently nest above the timberline along the Haast Range in South Westland, and in the few instances where causes of mortality have been confirmed, stoats have been identified preying upon chicks (Gardner 2010).

For kea, predation in adjacent high altitude forests appears to be a significant threat. Although Jackson (1963, 1969) found no evidence of predators preying on adult kea or their nests, Elliott and Kemp (2004) found that predators, mainly stoats and possums, had reduced kea populations in the St Arnaud Range in Nelson Lakes National Park, and increased the likelihood of local extinction. In 2010, remote cameras recorded both possums and stoats attacking and killing kea at their nests in South Westland (B. Barrett, pers. comm.).

Lizards

About 75% of alpine lizards are threatened or at risk (Table 1; Hitchmough et al. 2016) but as with other alpine species groups, there are few data on impacts of predators on alpine lizards. There is a perception that high altitude lizard sites are rarely visited by mammalian predators (Patterson & Bell 2009). However, stoats, possums and mice are present on the sheer rock walls >1100 m.a.s.l. occupied by Sinbad and cryptic skinks (*O. inconspicuum*) and Cascade geckos (*Mokopirirakau 'Cascades'*) in Sinbad Gully, Fiordland (Bell & Patterson 2008; J. Reardon, DOC Te Anau, pers. comm.). Almost all impacts of predators on alpine lizards are inferred from studies at lower

altitude, where the impacts of a wide range of mammalian predators have been implicated in declines of several species (Towns & Daugherty 1994; Tocher 2009; Jones et al. 2013). However, during a recent dietary analysis of stoats in alpine habitat on the Haast Range in South Westland, a Cascade gecko was recovered from the gut of a freshly-trapped stoat (Authors, unpubl. data).

Most evidence for predator impacts on population viability of lizards comes from studies where their numbers increased following predator control. For example, in mid-altitude populations of endangered grand (*Oligosoma grande*) and Otago skinks (*O. otagense*), the greatest increase in abundance occurred at the centre of a predator trapping treatment area and inside a mammal-proof fence (Reardon et al. 2012). Similarly, survival in a coastal population of McCann's (*Oligosoma maccanni*) skinks also increased in areas enclosed by predator-proof fences (Lettink et al. 2010).

Invertebrates

Evidence for predation by introduced mammalian predators on alpine invertebrates is derived mainly from dietary studies. Lavers and Mills (1978) found that in montane to alpine areas of the Murchison Mountains, ground wētā (*Hemiandrus* spp., particularly *H. focalis*) were common in the scats of stoats (55% of samples). At the same sites, Smith et al. (2005) confirmed that ground wētā were an important dietary component, comprising up to 59% of stoat stomachs. Ground wētā (predominantly *H. maculifrons*) were also identified as the most common prey item of stoats in alpine grasslands in the Borland Valley (Smith et al. 2008). Gibbs (1998) suggested that large alpine *Deinacrida* wētā were highly vulnerable to predation due to their ground-dwelling life style, but were not threatened because their habitats are above the elevational limit of rat invasion. However, in an alpine breeding colony of Hutton's shearwaters, *D. parva* were common in stoat diets, particularly once the majority of young shearwaters had fledged and departed the colony (Cuthbert et al. 2000). Other invertebrate prey items consumed by stoats include Orthopterans (grasshoppers) and representatives of the orders Coleoptera, Diptera, Hymenoptera, Lepidoptera, Araneae and Gastropoda (Smith et al. 2005, 2008).

Greater numbers of invertebrates are consumed by individual mice when *Chionochloa* tussock species are not mast-seeding (Wilson & Lee 2010). Invertebrate groups eaten by alpine mice include ground wētā (36% of stomachs), spiders (34%), caterpillars (Lepidoptera) (15%) and grasshoppers (13%) (Wilson & Lee 2010).

Possums, *Rattus* spp. and hedgehogs are known to prey upon *Powelliphanta* snails in forests, but there is no direct evidence for predation on high-altitude *Powelliphanta*. Alpine-dwelling *Powelliphanta* are currently considered less vulnerable to the impacts of most mammalian predators relative to their congeners from forested areas, due to their smaller size and reduced conspicuousness (K. Walker, DOC Nelson, pers. comm; Meads et al. 1984; Walker 2003).

It is unknown if invertebrates form an important component of the diet of feral cats in alpine areas. Invertebrates, particularly orthopterans and coleopterans, are commonly eaten by cats, especially kittens, though contribute little mass in cat diet overall (Gillies 2001; Harper 2005b). Some authors have suggested that in tussock grassland habitat, cats may consume more alternative prey such as invertebrates when rabbits or rodents are scarce, or when kittens have not yet developed the hunting skills to catch rabbits (Pierce 1987; Norbury et

al. 1998; Murphy et al. 2004). In alpine habitat, short-horned grasshopper (Acrididae) remains have been identified in feral cat scats along Bealey Spur in Arthurs Pass National Park (K. Weston, pers. obs.).

Freshwater fish

We found no reports of mammalian predation on freshwater fish in the alpine zone, which is not surprising given the paucity of research on alpine fish. Anecdotes from lowland situations throughout New Zealand show that mammalian predators regularly take freshwater fish. For example, mice have been video-recorded consuming all eggs of inanga (*Galaxias maculatus*) from spawning sites (Baker 2006; Hickford et al. 2010), and mice along with *Rattus* spp., hedgehogs and stoats are likely to feed on nests of other galaxids such as short-jawed, banded and giant kōkopu (*G. postvectis*, *G. fasciatus*, *G. argenteus*) (D. Jack, DOC Dunedin, pers. comm.; Allibone & Caskey 2000; Charteris et al. 2003). *Rattus* spp. have been observed taking freshwater mussels (*Hyridella menziesii*) (M. Brady, DOC Napier, pers. comm.; P. Ravenscroft, DOC Dunedin, pers. comm.). Cats have been seen taking eels (*Anguilla* spp.) and kōkopu (*Galaxias* spp.) in Northland (P. Warren, DOC Wellington, pers. comm.) and koi carp (*Cyprinus carpio*) at Whangamarino wetland when water levels decline (M. Brady, pers. comm.). Stoats have been recorded eating banded kōkopu on Banks Peninsula (S. Bowie, DOC Christchurch, pers. comm.) and dragging live and freshly dead eels and a live lamprey (*Geotria australis*) along tracks, presumably after catching them (Waikato, Arthur's Pass and the West Coast; C. Annandale, DOC Hamilton, pers. comm.; C. Golding, DOC Motueka, pers. comm.; COD, pers. obs.). Fish were a regular dietary item of stoats at Okarito and Te Urewera, present in up to 5% of gut samples in some seasons

(Rudolph 1999; Murphy et al. 2008). Stoats have also been seen taking freshwater crayfish (Murphy et al. 2008; B. Rance, DOC Invercargill, pers. comm.). Ferrets have been observed catching spawning sockeye salmon (*Oncorhynchus nerka*) in the Canterbury high country (P. Ravenscroft, DOC Dunedin, pers. comm.) and scavenging stranded brown trout (*Salmo trutta*) on the Lindis River (Fish & Game Cromwell, pers. comm.). Based on these observations, we suggest that alpine predators are likely to prey upon freshwater fish at times.

Interactions with other threats – an alpine conceptual model

Conceptual ecosystem modelling provides a framework for deciding on and declaring clear and specific conservation targets for ecosystem management (Margoluis et al. 2009). Although the focus of our review is on threats posed by introduced mammalian predators, conceptual modelling exposes interactions among threats and information gaps when there is a high degree of uncertainty about specific pressures (c.f. more data rich approaches; e.g. Price & Gawne 2009; Ramsey & Norbury 2009). We developed a conceptual model to illustrate the major threats to alpine biodiversity, how they are likely to interact with predation, and their relationships to different biodiversity conservation objectives, other ecosystem drivers, and associated management actions, as a way of identifying priority research needs (Fig. 3; based on two workshops).

For alpine ecosystems, broad conservation targets revolve around restoring browse sensitive flora, predator sensitive fauna, and community structure and function (Fig. 3). Although trajectories for these targets are unknown, conceptually they encompass increasing the condition, richness, and/or abundance

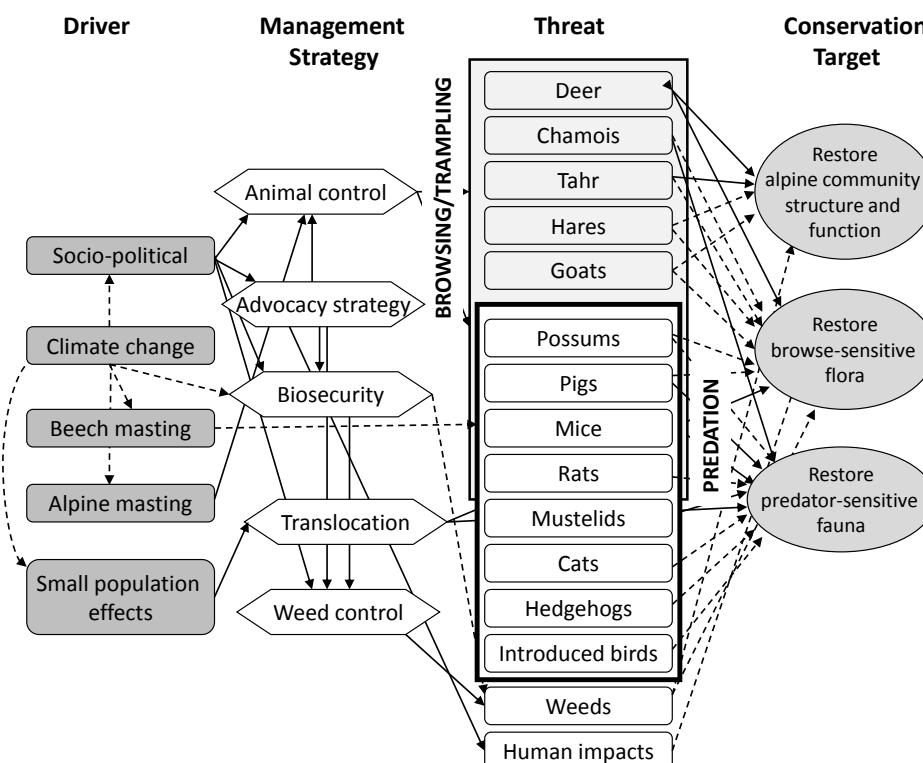


Figure 3. Conceptual model for threats to alpine biodiversity in New Zealand, where a Conservation Target = a specific target or outcome that needs to be achieved to enhance ecological integrity; Threat = a major threat to achieving the conservation target or targets; Management Strategy = a management strategy to alleviate threats; and Driver = major ecological or social drivers influencing threats to the ecosystem or ability to manage threats. Arrows depict cause and effect relationships between different components. Solid arrows indicate the relationship has been established or is well known, whereas dashed lines depict uncertainty, thus signalling priority research gaps that should be addressed before effective management strategies can be implemented. Under threats, the top box includes browsers/trampers, whereas the bottom (solid lined) box lists predators, four of which also overlap the browsers/trampler box.

of sensitive indicator species until they eventually reach a yet-to-be-defined asymptote representative of a reference ecosystem (Matthews et al. 2009). The targets reflect thinking that is now common among many restoration ecologists in New Zealand. That is, an awareness of the profound effects of introduced browsers and mammalian predators on indigenous biodiversity and a broad aim to restore ecological integrity as much as is practicable (Atkinson 2001; Saunders & Norton 2001).

The model identifies many potential threats to achieving biodiversity restoration targets in the alpine zone (Fig. 3). However, the numerous dashed lines in the model indicate our uncertainty about many relationships. For example, between 'browsers' and the 'restore community structure and function' and 'restore browse-sensitive flora' targets, the dashed lines indicate uncertainty about the absolute impacts of ungulates, possums and hares on regeneration, and the influence of rodents on seed predation. We consider the primary threats to alpine fauna to be mice and stoats (solid arrows; see earlier) but this review highlights uncertainty about the current importance of *Rattus* spp., cats, pigs, hedgehogs, and possums as predators in this ecosystem. There are other potential predators, such as introduced blackbirds (*Turdus merula*) and song thrushes (*T. philomelos*), which prey upon threatened snails at high altitude (K. Walker, DOC Nelson, pers. comm.) and whistling frogs (*Litoria ewingii*) which are likely to prey upon alpine invertebrates. Conversely, native avian predators are likely to be important natural predators, which should be recognised when restoring functioning ecosystems. Weed spread is a threat to restoring the integrity of alpine ecosystems in some locations (for example, *Calluna vulgaris*, *Pinus contorta* and *Salix* spp. in the central North Island, *Juncus squarrosus* in damp, low fertility sites, and some *Hieracium* spp. in alpine marble ecosystems; S. Moore, DOC Nelson, pers. comm.; R. Burns, DOC Rotorua, pers. comm.).

Whether there are interactions between browsers, mammalian predators and weeds that influence the intensity of these pressures is unknown, although such interactions are evident in dryland, braided river and forest ecosystems (Norbury et al. 2013; Tompkins et al. 2013; Pickerell et al. 2014). In addition to pests, human impacts have in the past impacted on alpine areas through intensive farming and burning, and contemporary threats may impact local alpine sites directly, for example, through the development of ski fields, wind farms and alpine roads, and by lighting fires.

There is also uncertainty about the importance of some of the key drivers of threats in the alpine zone. The primary drivers are likely to include beech masting and consequent fluctuations in pest densities in adjacent forests that may have flow-on effects to pest densities above the timberline. The relationship between beech masting, subsequent plagues of rodents and stoats, and increased predation on sensitive species is well documented in forests (King 1983; Murphy & Dowding 1995; O'Donnell & Phillipson 1996; O'Donnell et al. 1996; Dilks et al. 2003), but the form of such interactions in the alpine zone is unclear. Similarly, periodic heavy seeding of tussocks, and the fruiting and seeding of other alpine plants, may also drive predator cycles above the timberline, though only one study to date has documented these relationships (Wilson et al. 2006; Wilson & Lee 2010). Thus, there are several questions around the way in which predation risk might vary in time and space, how impacts might vary among vulnerable species, interactions among guilds of alpine predators, and impacts of mammalian predators relative to other environmental threats. For example, it has been postulated that predation risk will

increase under future climate change scenarios because ship rats will invade high altitude areas and likely irrupt in numbers more frequently (Christie 2014). Socio-political factors are also major drivers, particularly as they influence the acceptability of different toxins for pest control and of different ground or aerial hunting strategies for ungulates.

Small-population processes refer to genetic and random stochastic events that have disproportionate impacts on viability of populations once they become very small (Lande 1993). Diseases can become more significant when populations are small and under stress. Disease issues in the model specifically reflect the presence of the viral Psittacine beak and feather disease (PBFD), which affects parrots in New Zealand forests, although its potential influence on alpine kea is uncertain (Massaro et al. 2012). There is also strong evidence that increasing temperatures are associated with expanding mosquito-borne diseases into higher altitude areas worldwide (Epstein et al. 1998). In Hawaii, avian malaria has devastated the native avifauna and it is predicted that warming temperatures will enable mosquito vectors to invade into the few remaining mountain refugia of several endangered species (van Riper III et al. 1986; Benning et al. 2002; Freed et al. 2005). Vectors of avian malaria in New Zealand are known to be extending in range, signalling a real risk of disease emergence in alpine ecosystems with further climatic warming (Tompkins & Gleeson 2006; Cross 2014). Extreme weather events, in the form of markedly higher or lower winter temperatures, adversely affect survival of birds and bats in adjacent forests (Dilks 1999; Pryde et al. 2005), so may also influence survival of alpine species. Extreme events are being reflected in the duration and extent of the winter snow pack and increased erosion (McGlone & Walker 2011).

We identified five areas where management interventions are likely to be required (Fig. 3). The primary strategy is to control pests directly through animal and weed control, with a second management strategy being translocations for reintroducing key species (e.g. kiwi) to some areas, despite the poor understanding of species loss in the alpine zone. Although aerial hunting techniques are well developed for ungulate browsers (Rose & Platt 1987), they are absent for hare control. There is also uncertainty about whether 'best practice' predator control would be effective in the alpine zone. Current 'best practice' for stoat control in forests involves intensive trapping (O'Donnell et al. 1996; Dilks et al. 2003) and/or secondary poisoning where *Rattus* spp. are the primary vector of the toxin 1080 (Gillies & Pierce 1999; Murphy et al. 1999). However, whether such techniques are effective in the alpine zone is unknown. The practicality of large-scale trapping above the timberline is limited because of difficulties in servicing traps at appropriate densities in rugged terrain with seasonal access. Capitalising on secondary poisoning via aerial application of toxins is likely to be more cost effective than trapping, but suitable vectors may not be present in sufficiently predictable numbers. Ship rats, which are the primary vector for poisoning stoats in forests, are rare at higher altitudes and above the timberline (Innes 2005b; Efford et al. 2006). Mice would be likely vectors for secondary poisoning in alpine areas when their densities are high, though whether mice can act as a vector for secondary poisoning of stoats on a large scale remains poorly understood. Other food sources may be equally important as vectors, especially in low rodent years (e.g. wētā, Smith et al. 2008; or perhaps hares). New toxins, such as para-aminopropiophenone (PAPP) for controlling stoats (Dilks et al. 2011), have potential to solve

some of the challenges of predator control in the alpine zone (although development of a bait matrix for aerial delivery and regulatory approval are both required in this case).

The role of mice as alpine predators, and therefore the importance of controlling mice, is also uncertain. While there are records of mice preying on invertebrates and rock wren, their importance relative to other threats is unknown. Further, it has often been postulated that mice may compete with native fauna for food, though empirical evidence for such competition is lacking (Wilson et al. 2006). Understanding the impacts of mice and factors that influence variation in their numbers in space and time are fundamental research needs. It is likely that mouse numbers vary considerably seasonally, annually and among different alpine habitats (Wilson et al. 2006; Wilson & Lee 2010). There is some evidence that periodic heavy seeding of tussocks (Kelly et al. 2000; Wilson & Lee 2010) and potentially other alpine plants (Clarke 1968) strongly influences mouse cycles above the timberline. However, it is not known if best practice toxin applications could control mice, which appear to have different sensitivities to toxins compared with ship rats and potentially reach higher densities (J. Kemp, DOC Nelson, pers. comm.).

Conclusions

A wide range of introduced mammalian predators occupy the alpine zone of New Zealand. Although there are examples of these predators killing alpine invertebrates, lizards and birds, the impact of predation on population viability of these taxa is unknown. The strongest evidence for unsustainable impacts comes from a few relatively well-studied threatened bird species (takahē, rock wren and kiwi). While the precise impacts of mammalian predators on the long-term viability of threatened species have not been evaluated, anecdotal evidence suggests that predation is a serious threat, warranting predator control.

There is substantial diversity and pattern within and between alpine communities throughout New Zealand, largely driven by differences in climatic conditions affected by latitude, local topography, substrate patterns, west-east climatic gradients and geological history. Thus, the few studies indicating impacts of predators require replication across alpine ecosystems if we are to understand fully the threats and how to manage them. There is also little understanding of how food resources, climate change, and pest densities in adjacent lower altitude forest drive alpine predator populations. Understanding these factors is important before appropriate pest management techniques can be developed and initiated at the right scale. Future research should focus on predicting when and where mammalian predators impact on populations, furthering our understanding of the alpine predator guild, particularly through adaptive management experiments, and exploring interactions with other threats. Development of robust and logically feasible monitoring methods for predators and their prey above the timberline is also urgently required.

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