Assessment and management of hare impact on high-altitude vegetation

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Abstract

In New Zealand, introduced brown hares (*Lepus europaeus*) are present in many sub-alpine and alpine habitats. In 1995, five Department of Conservation Conservancies documented their concerns that hares may be causing unacceptable damage to such areas, particularly in the alpine grasslands. It was acknowledged, however, that hare impacts are difficult to separate from those of rabbits, possums and larger grazing mammals. In response, the Department of Conservation commissioned this review of the existing literature on assessment and management of hare impacts on high altitude vegetation.

The average density of New Zealand's hare population is estimated to be 0.1 hares ha^{-1}. Densities are highest in sub-alpine areas and much lower in alpine areas. Hares are most abundant along the dry, eastern side of the Southern Alps, where densities of 2–3 hares ha^{-1} are reached. Hare diet tends to reflect the composition of the vegetation community that they are feeding in, although preferences for certain plant species are evident. To date, three studies have attempted to quantify hare impacts on high altitude vegetation. These suggest that hares reduce plant growth and inhibit regeneration in some habitats but have relatively little impact in others.

In certain parts of their range, hares are probably the 'main' introduced herbivore, in that they consume more forage per hectare than possums, chamois, thar, deer or domestic livestock. In many other areas, however, the impact of these other grazers is likely to exceed that of hares.

If conservation managers require specific information about hare impacts in areas of high conservation value, then additional studies on hare diet and density assessment, and experiments using exclosure plots and population reduction techniques, will be needed. A critical issue for managers will be to determine how intensively hares need to be controlled to achieve conservation goals in an area—this needs to be known before the appropriate methods and likely costs can be evaluated. Any expenditure on hare control should be supported by long-term vegetation monitoring to assess the benefits of such control. Hares are only one of numerous issues affecting high altitude habitat management, and so need to be considered within a broad management framework for such areas.

1. Introduction

The potential impact of hares on New Zealand's high altitude vegetation is of concern to the Department of Conservation. In most regions, it has been a traditional view that hares have relatively minor effects on such vegetation due to their low, stable densities in these habitats. In recent decades, however, overall numbers of large grazing mammals have significantly decreased in most alpine and sub-alpine catchments, yet vegetation condition in some of these grasslands continues to degrade. Consequently, increasing attention is being directed to the problems in these habitats of weed invasion and ongoing herbivory by the smaller mammals (i.e., rabbits, possums and hares).

Field staff in several regions have suggested recently that active management of hare impacts may be justified in certain high altitude catchments. To date, however, the Department of Conservation has designated hares as 'critical pests' only at Mt. Taranaki and two small nature reserves in inland Canterbury. To properly evaluate the impacts of hares and other small herbivores in these and other areas, reliable methods for assessing hare abundance and impact are required.

The objectives of this report are therefore to:

- Review the existing literature on hare impacts on high altitude vegetation;
- Recommend methods for assessing hare abundance, and for identifying and scoring hare browse.

Methods of hare control are also considered briefly. This report was prepared for, and funded by, the Science and Research Division of the Department of Conservation.

1.1 THE HISTORY OF HARES IN NEW ZEALAND

Brown hares *Lepus europaeus occidentalis* (also called common hares, European hares, and field hares), were first liberated in New Zealand in 1851 (Wodzicki 1950). The majority of introductions occurred in the 1860s and 1870s at major ports around the country. Sport and harvesting for food were the primary motivations behind these introductions. During the late 1800s hares spread rapidly throughout most of the North and South Islands. They were protected from unrestricted hunting from 1861 until 1866, when landholders were given permission to control them as pests (Flux 1990).

Hare distribution has remained largely unchanged since this initial rapid increase in numbers and distribution. They are now present throughout both the North and South Islands in suitable habitat (see section 2.2) from sea level to 2000 m elevation, except for parts of South Westland, most of Fiordland (Parkes et al. 1978) and an area from Auckland city to about 80 km north. They are absent from all other New Zealand islands. The highest densities of hares now occur in sub-alpine grasslands along the eastern side of the Southern Alps (Wodzicki 1950; Parkes 1981).

1.2 HIGH ALTITUDE VEGETATION

This report defines high altitude vegetation as being the alpine and sub-alpine vegetation types, which encompass tussock lands, forests, shrub lands and herb fields. Indigenous vegetation still dominates most of these landscapes, but these communities have been heavily modified in many areas (Newsome 1987). The tussock grasslands and associated communities are the main habitat of hares in New Zealand at high altitude, and so are the foci of this report.

Indigenous grasslands at high altitudes are dominated by *Festuca novae-zealandiae* and *Poa colensoi* at lower altitudes and by various species of *Chionochloa* tussock at higher ones. Such grasslands are widespread in the mountain ranges of both main islands, descending to sea level in southern regions. Where undisturbed, *Chionochloa* tussocks can form dense stands with thick litter beneath, but usually other grasses and herbs form the lower tiers. Depending on drainage and fertility, these vegetation communities range from typical grassland assemblages to those associated with wet-heath and bog. The proportion of forbs and small herbs increases on rocky ground, on steep topography and along watercourses. *Chionochloa* grasslands below the treeline occur at certain sites, for example where there are poorly drained soils or past deforestation (Wardle 1991).

Other important plant genera in New Zealand's alpine and sub-alpine tussock grasslands include: mountain daisies *Celmisia,* speargrass *Aciphylla*, *Anistome,* buttercups *Ranunculus*, various herbs of the genera *Ourisia*, *Forstera*, *Lobelia*, *Hebe* and *Geum*, tussocks of *Astelia*, summer-green bulbous geophytes *Bulbinella,* and various mosses and liverworts (Wardle 1991).

1.3 HARES AND LAND MANAGERS

Hare impact on high altitude vegetation in New Zealand has generally been considered an issue of relatively low conservation priority. However, in 1995 five Department of Conservation Conservancies (Nelson/Marlborough, Canterbury, Southland, Hawkes Bay and Wanganui) documented their concerns that hares may be causing unacceptable damage to high altitude vegetation in parts of their regions, particularly in alpine grasslands. It is, however, difficult to separate hare impact from that of rabbits, possums and larger grazing mammals. Conservancy staff suggested, therefore, that there was a need for new research on the issue.

Each of the five Conservancies reported having particular concerns about hares. For example, in the Nelson/Marlborough Conservancy, an expansion of hare range had been noted by the Forest Research Institute in mid-eighties (Hawes et al. 1986). Hares have spread into some alpine tussock grasslands in this area during the past decade and some catchments appear to still be free of hares (K. Walker pers. comm.).

Field staff at Mt Cook in the Canterbury Conservancy have in recent years observed the progressive destruction of herbs throughout the alpine grasslands and in particular a decrease in the prominence of *Celmisia.* On-going change in these grasslands seem to be associated with a local increase in hare numbers (R. Bellringer pers. comm.).

Southland Conservancy staff were concerned about hare impact in sub-alpine mixed shrubland, grassland and herbfield. Areas of particular concern include the Blue Mountains, Mt Bee, South Argries and the Mavora Lakes (C. West pers. comm.).

The three central North Island Conservancies (Hawkes Bay, Wanganui, and Tongariro/Taupo) were concerned at continuing degradation of red tussock grasslands and associated herbfields as a result of hare browsing (G. Walls, C. Speedy and B. Fleury pers. comm.). In many parts of the montane grasslands east of the volcanoes, including the alpine area of Mt Taranaki, hares appear to have become the main grazers (B. Fleury pers. comm.).

This review has been commissioned by the Department of Conservation in response to these Conservancies' concerns. It aims to review the known effects of hares on high altitude vegetation and identify shortfalls in this knowledge. Methods of hare impact research are also reviewed. At present, the relative importance of hare impact, and thus the priority for hare control, is largely unknown. However, if control of hares were deemed necessary, then improved control methods would need to be developed. Therefore, this review also briefly considers future management options.

2. Hare biology and habitat use

2.1 BIOLOGY

Hares are similar in appearance to rabbits but can be distinguished by their larger size, proportionally larger hind legs, more rakish build, richer tawny colour, black-tipped ears and their characteristic loping, tail-down gait when disturbed (King 1990; Wodzicki 1950). Weight and body measurements of adult hares are shown in Table 1.

2.1.1 Field sign

Hares can be identified from their distinctive footprints where the large hind feet overreach the forepaws. Tracks made at slow speed show asymmetrically placed hind foot prints, unlike rabbits which have the hind footprints side by side. Tracks made by hares travelling at high speed show a completely symmetrical gait. On soft surfaces such as snow the five hind toes are spread, leaving prints like a dog's, and the four toes on the small forepaws are kept close

TABLE 1. AVERAGE BODY MEASUREMENTS OF ADULT HARES IN NEW ZEALAND (FROM FLUX 1990).

	FEMALE	MALE
Weight (kg) (range)	3.8 (2.4–4.8)	3.3 (2.4–4.4)
Hind foot length (mm)	143.8	144.1
Skull length (mm)	96.6	97.3
Skull width (mm)	46.1	46.1

together to give a pear-shaped print; forefoot prints follow each other in line, about 10–20 cm apart (Flux 1990).

Hares are primarily nocturnal (Flux 1990). During daylight hours they spend much time crouched in a 'form', an oval shaped depression in vegetation or soft ground approximately 200 x 400 mm in size (Parkes 1984; Flux 1990). Hares typically begin feeding at dusk (earlier in spring) and may move some distance, often downhill, to find grazing (Parkes 1984). They habitually use the same paths or 'runs'. In deep grass these may become conspicuous depressions 100–200 mm wide, running along ridges and up and down slopes.

Hares may travel 15 km while feeding in one night in snow above the timberline (Flux 1967a), however most are relatively sedentary. In the sub-alpine Avoca River valley, west of the Craigieburn Range in Canterbury, five adult hares had home ranges varying from 30 ha (for a female) to 70 ha (for a male) and averaging 53 ha (Parkes 1984). Most of the hares' time was spent in small centres of activity; half their time was spent within 10% of their home range. During March to May, the non-breeding season, hares extended their ranges from lower mountain slopes down onto river terraces (Parkes 1984). Hares showed little emigration from an area, moving on average 280–640 m from their initial capture site over two breeding seasons (Douglas 1970).

Hare pellets (also referred to as faecal pellets, pellets, faeces and scats) are typically flattened spheres, 15 mm x 10 mm in size, with a slight 'tail' on one side. They are similar to rabbit pellets, but larger, paler and more fibrous in appearance (Flux 1990), and less rounded in shape (Horne 1979). Rabbit pellets tend to be found in small piles whereas hare pellets tend to be scattered widely, although they do accumulate at favoured stopping places.

Hares clip vegetation with a characteristic 45° cut. The tips of plants are often left on the ground with a few pellets nearby (Flux 1990). *Chionochloa* tussocks are grazed one tiller at a time in a semi-circle that is distinctive from all other introduced herbivores except possums. Hares often eat only the more nutritious bottoms of tussocks and leave the tops intact and lying on the ground, unlike deer which tend to graze tussocks more evenly (J. Parkes pers. comm.).

2.1.2 Reproduction and population dynamics

In New Zealand, hares start breeding soon after the shortest day of the year. The breeding season extends from early July until mid March (Parkes 1989), with over 90% of females pregnant from August to February (Flux 1990). The average litter size in one New Zealand study (Flux 1967b) was 2.14, allowing for pre- and post-implantation loss, and the average number of successful litters per year was 4.59. This gave an annual production of 9.8 young per female.

Hare population densities appear to be self-regulated through behavioural mechanisms and so their populations do not undergo the kinds of irruptions seen in rabbits (Flux 1990). Their densities do not exceed 3 per hectare, but it is uncertain why this is so. There is no evidence that they are limited by food, they are not territorial, and direct aggressive interactions seem to be rare (Flux 1981a).

2.1.3 Predators and parasites

Adult hares are remarkably free from predation in New Zealand (Flux 1990), although they are occasionally taken by harrier hawks, stoats, ferrets, weasels and feral cats. As with most mammals, it is the young that are most vulnerable to such predators (Douglas 1970).

Hares are also relatively free of parasites (as are many other wild mammal species in New Zealand). Many of the diseases which affect or can be transmitted by hares in Europe—including European brown hare syndrome, plague, rabies, tularaemia, brucellosis and myxomatosis—are not present in New Zealand populations (Flux 1990).

2.2 HABITAT USE

Hares are found in most pastoral and grassland areas of New Zealand. The average density of the national population is c. 0.1 hares per hectare (Flux 1981), with highest densities occurring in sub-alpine areas. Densities are much lower in alpine areas. At their highest numbers along the dry, eastern side of the Southern Alps, densities of 2–3 hares per hectare have been recorded (Parkes 1984; J. Parkes unpubl. data). In areas where hares are at high densities they are often the most important mammalian herbivore present, particularly in areas where domestic stock have been removed and/or commercial hunting has markedly reduced the number of wild ungulates (Parkes 1981). There are relatively few hares at the highest altitudes, but in such habitats they survive well given the lack of competition from other herbivores (Flux 1990).

In Nelson Lakes National Park hares are more common on short grass swards than on dense tall tussock areas, and prefer the dry north- and northwest- facing slopes (Hayward 1977). In grasslands above the timberline in west Nelson, hares used the red tussock *Chionochloa rubra* association significantly less than the *C. flavescens* and *C. pallens* tall tussock association. Few hare faecal pellets were found in forest and none were found on fell-field plots (Hickling 1985). Nevertheless in winter hares will shelter by day in forest adjacent to grassland (they produce few pellets during the day). In Wairau catchment, Nelson, hare density was positively correlated with the proportion of grassland in an area. Alpine carpet grasslands, particularly those depleted by other grazers and erosion, are particularly favored by hares (Bathgate 1974).

As previously mentioned, northwest Nelson is one area in New Zealand into which hares may still be spreading. In the mid 1980s hares were found to be slowly spreading along the alpine tops of the Domett Range and extending their distribution south along the Marshall and Morgan Ranges (Hawes et al. 1986). It is thought that hares are continuing to expand their distribution in this area by establishing on suitable open valley-floor sites, and that densities in those areas where they were uncommon or occasional in the 1980s are likely to now be higher (K. Walker pers. comm.). In some areas it is possible that range expansion has been confounded by, or confused with, periodic re-invasion of high altitude habitats after local eradication by snow freeze (J. Flux pers. comm.). Hare populations on mountain tops are sparse so that gaps in their distribution are common. For example, some peaks in the Tararua mountains, North Island, remain free of hares for 1–5-year periods before being recolonised (J. Flux pers. comm.)

2.2.1 Diet

Hares feed on numerous plant species. The primary information on hare diet in New Zealand high altitude vegetation comes from three studies—one in alpine tussock on Mt Ruapehu (1100–1600 m elevation) (Horne 1979), one in the alpine tussock grassland of Cupola Basin in Nelson Lakes National Park (1200–1700 m) (Flux 1967a), and one on a modified fescue tussock (*Festuca novae-zealandiae*) grassland on the Avoca River flats in central Canterbury (600–700 m) (Blay 1989).

In the two alpine grasslands studies, the main species eaten by hares were *Chionochloa* tussocks, followed by *Celmisia* species and *Poa colensoi*. Numerous herbs, other grasses, shrubs, mosses and seeds comprised the remainder of the diet. The diet composition of hares at these sites is contrasted in Table 2 (there, and in the associated text, species introduced to New Zealand have been marked with an asterisk*).

In the sub-alpine grassland study, *Hieracium pilosella** was the most common item in the hares diet (32.3%), followed by grasses (*Anthoxanthum odoratum**, *Agrostis tenuis**, *Holcus lanatus)* (22.2%), and tussocks (*Festuca novae-*

TABLE 2. AVERAGE PERCENTAGE OF PLANT SPECIES IN THE ANNUAL DIET OF HARES IN TWO NEW ZEALAND ALPINE GRASSLANDS.

PLANT SPECIES	CUPOLA BASIN[1] (1200–1700 m)	MT RUAPEHU[2] (1100–1600 m)
Chionochloa spp.	26	44
Poa colensoi	31	4
Celmisia spp.	11	24
Senecio bidwillii	0	15
Other species	32 *Schoenus pauciflora,* *Celmisia allanii* *Celmisia. coriacea,* *Coprosma brunnea,* *Dracophyllum uniflorum,* *Anisotome filifolia,* *Trifolium repens*,* *Celmisia spectablis,* *Gaultheria depressa,* *Hebe pauciramosa,* *Holcus lanata*,* *Phorium colensoi,* *Aristotelia fruticosa,* *Hymenanthera alpina,* *Coprosma psuedo cuneata,* *Oreomyrrhis colensoi,* *Pittosporum divaricatum,* *Wahlenbergia albomarginata,* *Nothofagus solandri* var. *cliffortoides,* *Aciphylla colensoi,* *Helichrysum selago,* *Muehlenbeckia axillaris,* *Viola cunninghamii.*	13 moss, seeds, grass, *Notodanthonia setifolia,* *Schoenus pauciflora,* *Aciphylla squarrosa,* bark, *Hebe odora,* *Calluna vulgaris*,* *Nothofagus solandri.*

[1] Flux (1967a) [2] Horne (1979) * introduced species

zealandiae and *Poa colensoi*) (16.2%). Other species consumed were *Rhacomitrium lanuginosum*, *Carex coriacea*, moss, *Trifolium** spp., *Carmichaelia* spp., *Corokia cotoneaster*, *Rumex acetosella**, *Hypochaeris radicata*, *Digitalis purpurea**, *Luzula crinita*, *Schoenus pauciflorus*, *Taraxicum officianale*, *Juncus effusus*, *Epilobium melanocaulon* and *Rosa rubiginosa**.

Seasonal variability in hare diet was identified in two of the three studies and was attributed to seasonal changes in plant availability. In Cupola Basin (Flux 1967a) hares favoured short grasses in summer, and shrubs and tussocks in winter. In the Avoca River (Blay 1989) grasses were favoured over tussock in all seasons except summer; the utilisation of other minor plant species also varied seasonally. On Mt Ruapehu hare diet was similar year round, but differences were found at different elevations. This was again attributed to changes in the plant community, in this case with altitude (Horne 1979).

Differences in diet between habitats thus appears to result primarily from differences in the composition of the vegetation communities in those areas. Blay (1989) and Horne (1979) concluded that hares were relatively unselective grazers. Horne (1979) found selection against several strongly aromatic species and Blay (1989) detected small preferences for *Carmichaelia* spp. in summer and for *Carex coriacia* and *Rumex acetosella* during winter. These differences demonstrate that it is difficult to extrapolate hare diet information between areas, to the same area at different hare densities, or in different years (Flux 1967a).

Hares often show preferences for particular parts of plants, such as the base of tussocks and new growth or seedlings (J. Parkes pers. comm.). Horne (1979) found that hares increased their consumption of *Festuca* during the period of new shoot growth in early summer.

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* In Table 2 and in the associated text, species introduced to New Zealand have been marked with an asterisk.

3. Grazing impacts on high altutude vegetation

Until European settlement, New Zealand's alpine grasslands were browsed only by flightless indigenous birds and invertebrates (Rose & Platt 1987). Now, almost no New Zealand grassland has escaped the effects of grazing by wild and feral mammals (e.g., Wardle 1991). Most high altitude grasslands are subject to grazing by various combinations of domestic and feral sheep, cattle, horses and goats, and by wild hares, rabbits, deer, chamois, thar, wallabies, pigs and possums.

Such grazing affects the survival, growth and reproduction of plant communities. Grazing can influence species richness, the relative abundance of species, and the physical structure of the community (Crawley 1983; Rose & Platt 1987), but its effects in high altitude vegetation communities are complex. For example, species richness and vigour can either increase or decrease in response to grazing (Rose & Platt 1987; Huntly 1991; Wilson 1994).

Evidence that grazing can depress plant diversity is widespread (Wilson 1994). Selective feeding can modify competitive relationships between plant species by allowing a normally uncompetitive species to replace its more palatable competitors. Even non-selective feeding can mean that tall plants suffer little damage while small herbs are completely defoliated (Crawley 1983). In extreme cases heavy grazing could lead to extinction of preferred species (Wilson 1994), however, there is no known example of grazing-induced plant extinction in the New Zealand's high altitude grasslands.

Where grazing is less extreme preferred species may persist at a greatly reduced abundance. Examples of grazing decreasing plant diversity include: alpine grasslands in northern Fiordland, where there was a significant recovery in the diversity and growth of plants preferred by deer when deer numbers were reduced (Rose & Platt 1987); sub-alpine herbaceous vegetation in the Australian Snowy Mountains, where nine species of herbs were found to be present only in plots that excluded rabbits (Leigh et al. 1987); and sub-alpine meadows in Colorado, where plant species richness increased following exclosure of herbivorous pikas (*Ochotona princeps*; Huntly 1987).

In contrast, when grazing is gap-forming an increase in plant diversity can occur. Selective feeding on a previously dominant species can reduce its vigour and open spaces that are then colonised by less competitive species (Carr & Turner 1959; Crawley 1983; Gibson & Kirkpatrick 1989; Wilson 1994). A New Zealand example is the sub-alpine, highly modified short tussock *Poa cita* grassland of the Port Hills, Canterbury, where sheep grazing has maintained indigenous plant species by suppressing the growth of introduced grasses between tussocks (Lord 1990).

Heavy grazing can reduce plant vigour. For example, mountain hares *Lepus timidus* caused heather plants to remain in, or revert to, a juvenile, non-flowering physiological state (Moss & Hewson 1985). Grazing by hares, as well as rabbits, in inland Canterbury is thought to prevent *Hebe armstrongii* from flowering (R. Smith pers. comm.). Artificial defoliation of mid-ribbed snow tussock *Chionochloa pallens* (to simulate deer grazing) in the Murchison Mountains, Fiordland caused an increase in tiller density, but depressed tiller size and total tussock biomass (Lee et al. 1988). Lee et al. concluded that the severe effects of defoliation on *C. pallens* tussocks, and their slow rate of recovery, meant that two decades would be required for the tussocks to recover from a single defoliation event.

Where grazing is less severe an increase in vigour can sometimes occur. For example, bushes that had been heavily browsed by snowshoe hares *Lepus americans* in Kluane, Yukon recovered rapidly after hare numbers declined (Smith et al. 1988). In this ecosystem, where the plants are adapted to the native herbivores, hare browsing had a stimulatory effect on the growth of the woody plants.

3.1 HARE GRAZING IMPACT

Despite the ubiquity of hares in New Zealand their impact on the native grasslands has received little attention. Hares have generally been perceived to have minimal impact on the environment because they live at relatively low densities, hedge palatable plants without killing them, graze only a few leaves from many plants over a wide area, and do not dig burrows (Flux 1990). The only published work quantifying hare impact on high altitude vegetation details their effect on snow tussock regeneration (Rose & Platt 1992), while an unpublished report describes hare impact in three central North Island habitats (Rogers 1994) and an unpublished thesis (Blay 1989) describes hare impact in a sub-alpine, fescue tussock grassland.

Rose & Platt (1992) found browsing by hares alone was sufficient to inhibit snow tussock *Chionochloa macra* recovery in montane-sub-alpine, formerly forested sites in the Avoca and Harper River valleys, where sheep had long been excluded. Hare browsing pressure was intense, as hare densities in the study area were the highest recorded in New Zealand (Parkes 1984). Almost all the snow tussocks (97%) showed browsing damage. Snow tussock lengths in this hare-browsed stand were similar to those in a similar stand nearby that had been grazed only by sheep, with 17% of tussocks senescent. Within a hare-exclosure enclosure at the study site, snow tussocks showed pronounced recovery after 10 years; tussocks >5 cm in diameter were about twice as tall as those on the stand grazed only by sheep and only 2% of tussocks were senescent. No seedlings were found in either of two hare-affected area and in both of these areas juvenile tussocks made up <10% of each population (compared with 12% and 67% in two similar areas that had been retired from sheep grazing for 20 and 33 years, respectively). Lack of seedling regeneration was reflected in the low basal area of tussocks remaining as seed sources, high seedling mortality rates, and low seed production as a result of poor tussock vigour (Rose & Platt 1992).

Rogers (1994) investigated impacts of hares in different habitat types in the Moawhango Ecological District, central North Island, by measuring the vegetation within and outside of plots subdivided to exclude hares on one side and large ungulates and hares on the other. In a *Schoenus pauciflora* wetland plot established in 1989 hares appeared to have slowed the recovery of native sedges, exotic grasses and native herbs relative to that seen in the area free of introduced grazers. In two plateau, red tussock/hard tussock grassland plots the exclosure of hares did not affect tussock biomass, stature or recruitment; in this area hares appeared to feed on exotic grasses. However, on a hillslope plot established hares and rabbits had a substantially reduced the rate of recovery of red tussock, hard tussock and exotic grasses. Three other similar subdivided exclosure plots have been constructed in the central North Island, two in mountain beech forest and one in manuka-inaka scrub, but as yet no data are available from these (G. Rogers pers. comm.).

Blay (1989) excluded hares from a fescue tussock, sub-alpine grassland in central Canterbury and during two successive, six month periods found 18.5% and 19.9% more plant material inside the exclosures compared with equivalent hare-affected plots.

These three studies, which are relatively short-term and limited in terms of replication, thus suggest that hares reduce the growth and inhibit regeneration of vegetation in some high altitude habitats but in other habitats have little measurable effect.

In some situations hares may be beneficial to New Zealand grasslands, in particular when their grazing suppresses exotic grasses (as described above) or introduced weeds. For example, Blay (1989) suggests that hare grazing of *Hieracium pilosella* in the Avoca Valley is beneficial to the native flora. White (1991) studied moth communities in montane, tussock grasslands of the Waimakariri River valley and observed that areas with numerous hare pellets had a greater frequency of low herbs and low shrubs, and a more diverse moth fauna, than did surrounding areas dominated by rank *Agrostis.* He suggested that an optimised level of hare grazing of *Agrostis* could help conserve indigenous insect fauna in these modified grasslands without overgrazing the endemic plant species.

Another positive aspect of hare browsing is that their defecations have a fertilising effect on the plants in their feeding areas. Furthermore, hares transfer nutrients from their low-altitude feeding grounds to the higher slopes that they return to after feeding (Flux 1990). This will tend to mitigate the natural leaching of nutrients out of high-altitude soils, however the relative magnitudes of such nutrient flows remain unknown.

3.2 RELATIVE IMPACTS OF GRAZING BY HARES AND OTHER INTRODUCED HERBIVORES

It is often very difficult to differentiate the impact of hares on grasslands from the impacts of other mammalian grazers, such as deer, chamois, thar and possums. The distribution of hares overlaps with rabbits at lower altitudes, with chamois, thar and deer at high altitudes, and with wild horses and possums (Blay 1989; Hawes et al. 1986; Horne 1979). Hares also share their habitat with many insect species.

Compared to the grazing ungulates, which tend to pull tussocks out by the roots, cut the soil with their hooves, and have high per capita forage requirements, individual hares do less damage (Flux 1967a). Compared to rabbits, hares seldom graze as closely and occur at much lower densities (Flux 1967a). Nevertheless, in several areas of New Zealand hares are reported to be the main mammalian grazer, greatly outnumbering the larger ungulates. These areas include the parts of the high country of the west coast of the South Island (T. Farrell pers. comm.) and some of the montane grasslands of the central North Island (B. Fleury pers. comm.).

A comparison of relative metabolic requirements and forage intake of various introduced herbivores, given in Table 3, suggests that hares could be responsible for a relatively high proportion of total grazing pressure in some areas, depending on the abundance of other species present. Before controlling one or more herbivore species in a particular high altitude area, managers may wish to consider these types of calculations as an aid in identifying the species that should be prioritised for control in that area. (Diet selectivity of the various species is a further consideration that is discussed in section 4.)

Rabbits have been observed to dominate hares in 45 of 55 encounters on a communal feeding area (Flux 1981a). If rabbits numbers are substantially reduced by Rabbit Haemorrhagic Disease (RHD) or other sustained control

TABLE 3. PREDICTED BASAL METABOLIC RATES (BMR), ABUNDANCE AND FORAGE INTAKE OF VARIOUS INTRODUCED HERBIVORES IN NEW ZEALAND'S HIGH ALTITUDE AREAS.

SPECIES	WEIGHT (kg)[1]	BMR ($kcal.day^{-1}$)[2]	BMR RELATIVE TO HARES	ABUNDANCE WHERE PRESENT (ha^{-1})[3]	MINIMUM INTAKE RELATIVE TO HARES[4]
Rabbit	1.7	104	0.6	1–10	3.5
Possum	2.8	105	0.6	0.1–1	0.3
Hare	**3.5**	**179**	**1**	**0.01–3**	**1.0**
Chamois	31	920	5.1	0.01–1	0.3
Goat	33	972	5.4	0.1–0.5	3.1
Thar	45	1216	6.8	0.02–1	0.8
Red deer	97	2163	12.1	0.01–0.1	0.7

[1] Average of female and male (adapted from King 1990).

[2] Basal metabolic rate assumed equal to $70W^{0.75}$ for eutherians and $48.6W^{0.75}$ for marsupials (Robbins 1983).

[3] Figures based on King (1990), J. Parkes pers. comm. and personal observations. Different estimates will apply in each management area.

[4] Calculated from BMR x minimum local density, assuming a mean hare abundance of 0.176 hares per hectare. Relative intake will obviously vary between management areas depending on the relative abundance of each species in each management area. Relative intake will be at least an order of magnitude *higher* when a species is near the upper end of its abundance range.

methods, then it is likely that hare numbers and impacts will increase in such habitats. Hare numbers in the UK are known to have increased in the late 1950s and early 1960s following the spread of myxomatosis in the rabbit population there (Tapper 1992).

The main insect herbivores that hares share their habitat with are grasshoppers. Grasshoppers are low-volume grazers, but are selective on certain ground cover species of low biomass to the extent that such species may be under high grazing pressure (White 1974). In low-productivity tussock grasslands, a paucity of inter-tussock vegetation sometimes reflects persistent grazing pressure on preferred plant species by grasshoppers (White 1974). Grasslands are presumably well-adapted to grazing by these indigenous fauna, but since hares may have their greatest impact in these same inter-tussock areas (G. Rogers pers. comm.), it is possible that the impacts of vertebrate and invertebrate grazers will sometimes be confounded.

3.3 Hare impact studies: key findings

- Hares can inhibit the recovery, regeneration and recruitment of snow tussocks.
- Hares can affect the recovery of native sedges, exotic grasses and native herbs in wetlands.
- In some red tussock-hard tussock grasslands hares can affect the rates of recovery of red tussock, hard tussock and exotic grasses.
- Hares can reduce the available plant material in fescue tussock, sub-alpine grassland.
- In some parts of their range, hare populations are likely to be consuming more forage per hectare than possums, chamois, thar or deer. However, elsewhere, the impact of these other grazers is probably far more significant than that of hares.

4. Research needs

Research on hare impact in high altitude vegetation in New Zealand is very limited, but it is likely that hares are causing grassland degradation in at least some areas (see above). There are many gaps in our knowledge of hare impact in New Zealand, including population estimation, diet composition and selection, habitat use, and the long term impact on our indigenous vegetation communities. Research that could help fill these knowledge gaps is discussed in this section. Methods of hare control are also reviewed briefly, with the proviso that their use would need to first be justified by appropriate impact studies.

4.1 HARE ABUNDANCE ASSESSMENT

The objective of any attempt to actively manage hares should be to limit their impact on ecological communities and processes. Nevertheless, the evaluation of specific management actions such as hare control is likely to require monitoring of hare abundance. Methods used to estimate abundance are reviewed below.

4.1.1 Direct counts

It is seldom, if ever, possible to obtain a total count of hares by direct observation over an entire survey area. Direct counts of hares in small areas have been made in New Zealand by hide observations and dead hare counts (Flux 1967a), and overseas by flushing (e.g. Lechleitner 1958; Flux 1970; Hewson 1976), spotlighting (Lord 1961; Anderson & Shumar 1986), from an aircraft (Windberge & Keith 1977) and by line transect sampling (Webb 1942).

Flux (1967a) observed hares from a hide overlooking Cupola Basin, Nelson for 19 evenings and 24 mornings during summer; a maximum of four adult hares was seen in a 120ha area. The evening counts averaged 1.9 hares, with all four seen on only six occasions. Morning counts averaged 1.5 hares, with all four seen on only one occasion. Juvenile hares were secretive and were not seen from the hide. In autumn, about 50% of the population is the young of the year, so Flux estimated the autumn population of his study site to be about 8.

Dead hares numbers in an area can provide an indication to the numbers of live animals present (Flux 1967a). In Cupola Basin, an average of 3.8 dead hares were found during each year of the study, with most dying in winter. Based on mortality data from a population of mountain hare *Lepus timidus* in Scotland (Flux 1970), this again indicated that about eight hares were present.

Spotlighting has been used to obtain estimates of relative hare numbers by Anderson & Shumar (1986) and Lord (1961). This method requires the survey area to be free from high vegetation and easily accessible, which is rarely the case in New Zealand alpine and sub-alpine areas (e.g., Horne 1979). It has, however, been used to monitor rabbit populations over time, with reasonable results (e.g. Frampton & Warburton 1994).

Counts made from aircraft can be accurate in very low vegetation or after snow, but are not be feasible under most New Zealand conditions. Aerial counts using a forward-looking infrared (FLIR) camera has recently been trialed on New Zealand possums with some success (Livingstone 1995), and so would probably be effective for hare survey if the considerable expense and night-time flying could ever be justified.

Using a line of field staff to move across an area on foot to 'flush' all the hares present is labour-intensive and produces poor abundance estimates, as there is extreme variation in flushing distances and some hares do not flush at all (J. Parkes pers. comm.).

A more sophisticated flushing procedure, based on line transect sampling methods (Webb 1942; Lancia et al. 1994), involves individual staff walking transects of designated length set out randomly within the area to be sampled. Counts of all hares seen are made as the observer travels along the transects (a maximum observation distance beyond which animals are not counted is sometimes established). The proportion of animals present that are actually seen is then calculated and the counts adjusted accordingly. Either perpendicular distance data, or sighting distance and angle, are required to estimate sighting probabilities. The effort required to apply this technique to hares in New Zealand is unknown, but is likely to be considerable.

4.1.2 Trapping and shooting

Standard ‘mark and recapture’ methods (reviewed in Seber 1982) involve tagging live-trapped hares, releasing them, and then estimating the proportion of tagged hares that are either retrapped, or at least seen again on some subsequent occasion. This method can produce reliable estimates of hare numbers and densities (e.g. Krebs et al. 1986a), but would be very labour-intensive as hares are difficult to trap in alpine grasslands, where their densities are low and runs indistinct (J. Parkes pers. comm.).

Trapping and hunting methods that involve capture without release can also be used to estimate hare abundance. Removal methods can provide an absolute estimate of abundance and density, and kill-rate data (e.g. hares caught per 100 trap nights or shot per hunter-hour) can provide indices of relative abundance. Flux (1969) used ‘minutes to shoot one hare’ as an index of hare population density in three study areas in East Africa. This index correlated well with estimates based on spotlight counts from a vehicle. Difficulties associated with these methods include the effort required to catch or shoot an adequate sample of hares, and potential biases due to weather, season, visibility and different observers. Such biases must be carefully controlled for comparisons of indices generated from different surveys to be valid.

4.1.3 Sign counts

It is often easier to work with animal sign than to attempt to catch-fast moving individuals.

Counts of hare tracks on snow (e.g. Flux 1967a; Shibata 1985; Thompson et al. 1989) can provide a measure of hare abundance, but the necessity for winter surveys has obvious disadvantages. Flux (1967a) found that tracking hares in snow was most successful after a fresh snowfall during the night, as it was then possible to count only the tracks of the hares returning to their forms after the night’s feeding. Track counts from consecutive years in Cupola Basin, Nelson were found to consistently indicate seven and six hares, respectively.

Faecal pellet counts have been used with mixed success to estimate hare numbers in New Zealand (e.g. Flux 1967a; Horne 1979; Parkes 1984) and overseas (e.g. Johnson & Anderson 1984; Krebs et al. 1986a). Pellet-count surveys can be based on ‘standing crop’ or ‘cleared plot’ methodology.

In New Zealand, calculations of hare densities from the standing crop of pellets have been attempted, but the results are too imprecise to be useful. For example, in Cupola Basin, Flux (1967a) estimated hare numbers from the standing crop of pellets using the calculation:

$$N = \frac{\text{total number of faecal pellets}}{\text{defecation rate x decay rate}}$$

A daily defecation rate of 410 pellets was estimated from the average production of pellets by captive hares and by hares tracked hares in the snow over a whole night's travel (hares do not produce pellets during the day while in their forms). The average pellet decay time (3 years) was measured from different sets of fresh pellets at different altitudes. The number of pellets in the catchment (4.29 million) was calculated by counting the number of pellets in quadrats along line transects situated in representative vegetation types and then extrapolating the densities in favourable and unfavourable habitats over the whole area occupied by hares (total = 4.29 million pellets). Thus:

$$N = \frac{4\ 290\ 000}{410 \times (3 \times 365)}$$

$$= 9.5 \text{ hares}$$

This estimate was close to Flux's other estimates of population size (discussed above). Unfortunately, given the low precision of each estimate, the final estimate had a potential range of 2–109 hares.

In Tongariro National Park, Horne (1979) used similar methods to Flux (1967a) and also had problems estimating pellet decay rates and defecation rates with sufficient accuracy. Neither Flux nor Horne considered their pellet-count methods to be sufficiently accurate to be useful.

'Cleared plot' methods avoid the problem of unknown, and variable, decay rates that make standing crop pellet counts very difficult to interpret. 'Turd transects' have been used to estimate the population density of snowshoe hares *Lepus americanus* near Kluane Lake, Yukon Territory Canada (Krebs *et al.* 1987). Pellets were cleared from each of 50 optimally-sized quadrats (5.08 x 305 cm = 0.155m^2) in six areas of variable habitat. The quadrats were counted annually for seven years, clearing the pellets from each quadrat as it was counted. Optimal quadrat size was determined by measuring fifty quadrats of five different shapes (square, rectangular) and sizes (0.25 - 0.8m^2) and selecting the size that produced low-variance estimates and that could be effectively sampled by one or two field staff. Plots were cleared each year and all pellets all lasted at least that long, so there was no need to estimate pellet decay rates. The Yukon turd counts were highly correlated (r = 0.94) with the estimates generated by Jolly-Seber mark-recapture techniques (Krebs *et al.* 1986a, Seber 1982). Since the two techniques provided similar data, the much less laborious pellet count method was favoured thereafter by the researchers.

A similar cleared-plot method was used to estimate the densities of mountain hares *Lepus timidus* in Sweden (Angerbjorn 1983), also with successful results. Parkes (1981, 1984) used cleared plots in New Zealand to estimate a change in hare density after poisoning and to determine hare habitat use (see section 4.5). Cleared plot methods can be biased by hares being attracted to and defecating around plot pegs (J. Flux pers. comm.). Some diets produce pellets that disintegrate quite rapidly (e.g. *Celmisia*), and pellets can blow onto plots after they have been cleared.

The advantages and disadvantage of the abundance survey methods described above are summarised in Table 4.

TABLE 4. ADVANTAGES AND DISADVANTAGES OF VARIOUS HARE ABUNDANCE ESTIMATION METHODS.

METHOD	ADVANTAGES	CONCERNS	EXAMPLES[1]
Direct counts			
Observations from hide	Most reliable in the evenings	Unsuitable for large areas; requires many days	*Flux 1967a*
Dead hare counts	Carcasses can be searched for without disturbance effects	The relationship between carcass numbers and live hare numbers may vary from year to year	Flux 1970, *Flux 1967a*
Spotlight counts	Suits large areas; can provide low-precision indicies of abundance	Can be biased by weather, season & observer; requires low vegetation with easy access	*Frampton & Warburton 1994*, Anderson & Shumar 1986, *Horne 1979*, Lord 1961
Aerial counts	Suits very large areas; requires very low vegetation	New Zealand vegetation rarely suitable; expensive	Windberg & Keith 1978
Flushing counts	Requires only 1 trip to the study site	Requires numerous staff; results often inaccurate	Flux 1970, Hewson 1976, Lechleitner 1958
Line transect counts	One observer can cover large areas	Assumes all hares directly on the transect will be seen; distances and angles must be measured accurately	Lancia et al. 1994, Webb 1942
Trapping and shooting			
Mark-recapture	Can provide an estimate of absolute density	Very labour-intensive given likely low trap success; unsuitable for large areas	Krebs et al. 1986a, Flux 1970
Shooting	Contributes to hare control; provides material for diet analysis	Huge effort required to obtain an adequate sample size; can be biased by weather, season and observer	Flux 1969
Sign counts			
Counting tracks	Successful after fresh snow falls	Requires extended periods of winter fieldwork	*Flux 1967a*
Pellet counts (i) standing crop	Can be performed by one person on one sampling occasion over large areas	Very low precision	*Horne 1979, Flux 1967a*
Pellet counts (ii) cleared plots	Can be performed by one person; avoids the need to assess pellet decay rate	Need at least two sampling occasions; need to mark and relocate the plots	Krebs et al. 1986a, Parker 1984, Angerbjorn 1983

[1] New Zealand examples are in italics.

4.2 DIET COMPOSITION

The plant species that hares impact upon can be investigated by assessing the composition of their diet, although such studies obviously cannot provide information on species that have already disappeared from an area (Flux 1967a). Research to date (Flux 1967a; Horne 1979; Blay 1989) suggests that hare diet primarily reflects plant availability, but that a degree of selectivity is shown towards certain species (see section 3.2.1).

Casual observations of plants eaten by hares can give a misleading impression of their importance in the diet, as some plants show bite marks readily or recover slowly from hare damage. For example, *Hymenanthera alpina* show severe hedging in Cupola Basin, Nelson, yet are not a major food item (Flux 1967a). Hares rarely killed such hedged plants, although they did take most of the current growth year after year.

Quantitative data on hare diet in a particular area can be obtained by sampling the plant material before, during or after digestion. Direct observation of feeding hares is one pre-digestion method of diet assessment. As an example, Flux (1967a) used a hide at Cupola Basin, Nelson, to record hare feeding localities. Each locality was then further examined for the number of bites taken from each plant species (Flux 1967a). To locate where hares had fed during winter, Flux (1967a) followed tracks made by hares after fresh snow falls. A similar technique was used to determine the winter diet of mountain hares *Lepus timidus* in Finnish Forest Lapland (Pulliainen & Tunkkari 1987). Mountain hares were followed by radiotelemetry to determine their diet in Norway (Johannessen & Samset 1994). Horne (1979) attempted to use an infra-red night viewer to locate and observe feeding hares, but was unsuccessful. A major problem with direct observations of browse damage is differentiating between the browse marks of hares and those of other species such as possums, particularly when the plant material is soft.

Diet determination during digestion involves detailed examination of stomach contents from hares that have been shot or trapped (e.g. Sparks 1968; Homolka 1986; Blay 1989). Plant material sampled from the stomach is identified with a microscope by cuticle analysis; a time-consuming process that requires reference collections and training in cuticle identification. There is considerable variation in the stomach contents of individual hares, so numerous hares must be killed to obtain reliable data (Horne 1979). Analysis of stomach samples will tend to underestimate the contribution to the diet of species that are rapidly digested or difficult to identify. A detailed review of the methodology, as applied to rabbits in New Zealand, is provided by Reddiex (1998).

Faecal pellet analysis is a simple and frequently-used method of analysing hare diet (e.g. Horne 1979; Johnson & Anderson 1986; Daniel et al. 1993). Pellets can be readily obtained from most habitats throughout the year. Plant remains in each pellet are identified by microscope (Sparks & Malecher 1968; Horne 1979); as with stomach content analysis this is time consuming and requires training. Data obtained by pellet analysis are similar (both quantitatively and qualitatively) to that obtained by stomach content analysis (Homolka 1986). It is also fairly similar to pre-digestion analysis data, although Flux (1967a) found that in winter the ratio of *Chionochloa* to *Celmisia* was higher by field observation than by pellet analysis (the two methods gave similar results in summer).

The most common method of pellet analysis involves the establishment of plots that are cleared at regular intervals so that pellets of known age can be analysed. Depending on how frequently pellets can be collected, they can be used to assess monthly or seasonal variation in diet.

Of the dietary analysis methods reviewed (Table 5) analysis of pellets collected from plots located randomly within stratified habitats is probably the most practical technique for use in New Zealand. Pellets can be collected and carried by a single person so that time in the field is minimised using this technique.

TABLE 5. ADVANTAGES AND DISADVANTAGES OF HARE DIET ANALYSIS METHODS.

METHOD	ADVANTAGES	CONCERNS	EXAMPLES[1]
Before digestion Observations from a hide, following tracks in snow, radiotracking	Plants are easily identified; little lab work required	May be difficult to differentiate between browse by hares versus other species; requires long hours in the field	Johannessan & Samset 1994, Pulliainen & Tunkkari 1987, *Flux 1967a*
During digestion Stomach content analysis	Provides detailed qualitative and quantitative information; reduced time in field	Requires an adequate sample of shot hares, staff experienced in cuticle identification, and long hours in the laboratory; will underestimate the contribution of readily digested plant species	*Blay 1989*, Homolka 1986, Sparks 1968
After digestion Faecal pellet analysis	Easily collected; minimal time in the field	Requires experienced staff; long hours in the laboratory; will underestimate readily digested species	Daniel *et al.* 1993, Johnson & Anderson 1984, *Horne 1979*

[1] New Zealand examples are in italics

4.3 DIET SELECTION AND HABITAT USE

An assessment of hares' diet *selection* behaviour requires a comparison of diet *composition* (see above) with plant species availability in the habitat they are using. Diet selection and habitat preference studies involve similar techniques and so are combined in this section.

Direct methods of habitat assessment include observation and radiotracking. Indirect methods are dependent on signs of hare activity within an area; for example browsed vegetation, pellets or tracks (Litvaitis *et al.* 1994). Hare presence or absence can be most readily determined by the presence or absence of their pellets (Hawes *et al.* 1986, Hayward 1977, Bathgate 1974, Flux 1967a). Pellet abundance can also provide some information on broad habitat preferences of hares, e.g., between forest and grassland in west Nelson (Hickling 1985). However, since pellets may persist for months or years, 'standing crop' counts are not suitable for assessing short-term or seasonal shifts in habitat use.

Cleared plot pellet-count techniques can provide better habitat preference information. For example, Parkes (1981) used cleared, relocatable, 0.09m^2 circular plots counted at 60-day intervals to determine seasonal changes in habitat use in the Avoca River catchment, Canterbury. Pellet counts were also used to provide a measure of the effect of a poisoning program in the catchment. A similar technique was used by Hewson (1989) to determine grazing preferences of mountain hares *Lepus timidus* on heather moorland and hill pastures in Scotland. In Nevada, USA, monthly counts of blacktailed jackrabbits *Lepus californicus* pellets were used as an index of jackrabbit use of new rangeland (McAdoo et al. 1987); the number of jackrabbit pellets was assumed proportional to jackrabbit grazing intensity.

The optimum plot size and counting interval for any given habitat will give pellet counts with homogeneous variances and should be able to be easily sampled by one person. These need to be determined by a pilot study. The counting interval needs to take into account hare diet, as certain diets produce pellets that disintegrate more rapidly than others. A suitable plot size is likely to be 0.1 m^2 (J. Parkes *pers. comm.*).

Selection for particular plants by hares is determined by comparing dietary composition to vegetation abundance in a particular area (e.g. Blay 1989; Horne 1979). A wide range of food preference indices are available and are reviewed by Norbury & Sanson (1992). Reddiex (1998) applied the technique to New Zealand rabbits, and provides numerous up-to-date references.

Plant selection can also be determined by estimating the amount of foliage consumed from the amount of pellets produced. For example, in a northeastern Colorado rangeland, USA, the amount of herbage that blacktailed jackrabbits were consuming was determined by sampling at 3-month intervals 20 permanent plots (30 x 50 cm). These were distributed in a regular-random pattern to serve as sub-sample units for assessment of total pellet production (Hansen 1972). The plots were initially cleared and newly deposited pellets collected, dried and weighed to give a measure of herbage intake. The relative abundance of plants in the diet was calculated by examination of pellets contents under a microscope (Sparks & Malecher 1968). A digestion index (Arnold & Reynolds 1943) was used to calculated the total amount of foliage removed. Similar methods were used in a study of hares grazing heather moorlands in northeast Scotland (Welch 1984), with hare damage estimated by assessing the percentage of shoots and leaves grazed in plots and relating this to pellet density. Diet selection of the mountain hare in Finnish Forest Lapland was determined by measuring the size of 'cut' twigs and comparing the amount of twigs consumed (measured by weight) with the amount of material available (Pullianinen & Tunkkari 1987).

In New Zealand, a method for estimating the proportion of foliage eaten by introduced herbivores was developed by Nordmeyer & Evans (1985) in west Nelson. This involved stripping the leaves of plant species, drying and weighing them. Plant height—leaf biomass relationships were then determined by linear regression and used to generate forage biomass estimates from plant height data obtained from field surveys. The 'available biomass' estimates were then compared with herbivore dry matter intake rates obtained from the literature.

Plant selection can also be assessed from browsing sign, provided that the marks left by hares can be distinguished from the browse marks of other animals. This is difficult in New Zealand but has been achieved in overseas studies. For example, a study of snowshoe hares *Lepus americanus* in two Canadian forests measured their browse selection by randomly selecting plots in different forest types (Telfer 1972). Within each plot hare browsing was distinguished from deer browsing by the way twigs were clipped. The number of browsed twigs was estimated for each plant species and related to estimates of the amount of browsable plant material that remained to obtain a measure of food plant preference. Such data can also be used to determine habitat use. The extent of blacktailed jackrabbit *Lepus californicus* browsing of desert shrubs in New Mexico, USA was measured by classifying the number of branches browsed on shrubs as none, low (1–5 branches browsed) or high (>5 branches browsed) (Ernest 1994). Krebs et al. (1986b) used a photographic technique to assess the amount of woody twigs browsed by snowshoe hares *Lepus americanus* in southwestern Yukon.

Measurements of foliage consumption could also record the part or age class of a particular plant that has been grazed. This aspect of diet selectivity has not been investigated in New Zealand, but is likely to be important in impact studies.

Hares can be followed by radiotracking and spotting scopes to determine their diet selection. Spotting scopes give better detail than radiotracking (J. Flux pers. comm.). The amount of each species grazed is estimated and then compared to the availability of each plant species in the area. The proportions of different food plants grazed is assumed to represent the hares' diet. Diet selection of mountain hares *Lepus timidus* in a low-alpine area in southern Norway was assessed in this way, with radiocollared hares being tracked at dawn and dusk (Johannessen & Samset 1994). Studies confined to dawn and dusk are likely to be misleading, however, as J. Flux (pers. comm.) found that the diet of Scottish hares on the way to and from their feeding grounds at dawn and dusk was 80% heather, whereas at night they prefered to forage for white clover or grass seed-heads.

Radiotracking was used by Parkes (1981) to assess hares' seasonal use of different parts of his study area in the Avoca river catchment. Twenty five hares were fitted with radio transmitters and their movement was monitored using two fixed double-yagi aerials set about 800m apart along the river edge of the valley flats. The hares were tracked for four 24 hr periods each month for a year. The results from the radiotelemetry were similar to those obtained by cleared plot pellet counts.

A summary of the methods used to determine habitat use and diet selection of hares is given Table 6.

4.4 LONG TERM VEGETATION IMPACTS

4.4.1 Field experiments

Hares have been present throughout much of their New Zealand range for many decades. Their past impacts may have been significant in some areas, but in many cases will have been confounded by the presence of other introduced grazers. Their present impact may not seem great, but the full effects of hare browsing now or in the past may not yet be evident. For example, hares inhibit the regeneration of snow tussock (Rose & Platt 1992). These long-lived plants may only show the consequences of this grazing many years later; for example, if lack of regeneration means that affected snow tussock stands eventually die out. Hares may be preventing regeneration of the threatened *Hebe armstrongii*; in recent years the only known individual to flower in the wild was surrounded by wire mesh (R. Smith pers. comm.). Other plants, such as *Hymenanthera* bushes, may show marked damage from hare grazing, despite being a minor component of their diet (Flux 1967a). Thus, it is crucial to evaluate not only the

TABLE 6. SUMMARY OF METHODS FOR MEASURING HABITAT USE AND DIET SELECTION BY HARES.

METHOD	ADVANTAGES	CONCERNS	EXAMPLES[1]
Direct			
Observation	Provides information on exact foraging locations	Only feasible in a small areas; differential visibility among habitats can bias results; labour-intensive	*Flux 1967a*
Radiotelemetry	Provides information on activity centres and movement patterns	Time-consuming; small sample sizes; provides only an approximate indication of where feeding is taking place	Johannessen & Samset 1994; *Parkes 1984, 1981*
Indirect			
Track counts	Can sample a large area in a short time; adults more easily seen than juveniles	Requires snow cover and low vegetation	*Flux 1967a*
Pellet counts (i) standing crop	Samples all segments of a population; provides simple presence/absence information	Defecation rates vary with activity; decay rates vary with altitude, habitat and season	*Hawes et al. 1986*; *Hayward 1977; Bathgate 1974*; *Flux 1967a*
Pellet counts (ii) cleared plot	Samples across all individuals in a population; provides information on seasonal patterns	Defecation rates vary with activity	McAdoo et al. 1987; Welch 1984; Hansen 1972
Browse scores	Samples all age groups; also provides information on impacts on vegetation	Restricted to sites where food plants are available	Ernest 1994; Telfer 1972

[1] New Zealand examples are in italics

immediate impact of hares but also their likely long term impact on high altitude vegetation.

One way of measuring long-term grazing impacts is to experimentally exclude the grazer from small areas and then compare the vegetation community inside and outside the exclosures over time. The best examples of hare exclosure plots in New Zealand are those of Rogers (1991, 1994) in the Moawhango Ecological District, central North Island. The plots are 20 x 20 m in size and subdivided to exclude large grazing mammals from one half and all grazers (including hares) from the other. Thus, half the plot provides information on hare damage while the other half provides information of damage caused by the hares together with larger herbivores. Possums have the ability to get into such enclosures, but can be removed from the area by regular poisoning (J. Parkes pers. comm.).

A different approach to exclosure plots was used by Rose & Platt (1992) in their study of snow tussock in montane–sub-alpine, formerly forested sites in the Avoca and Harper river valleys. Their plots ranged in size from 24 to 900 m^2, so as to include exactly 30 tussocks in each.

Three exclosure plots have been set up in Canterbury in a stand of the threatened *Hebe armstrongii* to investigate the effect of different herbivores. One plot excludes all herbivores, another excludes pigs, cattle and sheep but allows hares and rabbits to graze, and the other is a control plot. No results have come from this work as yet (R. Smith pers. comm.).

Three issues that need to be considered when installing exclosure plots are their initial placement, subsequent maintenance, and potential effects on grazing. Firstly, plots need to located in areas where hares are having an impact, which can be determined from studies of diet, habitat use and diet selection. Plot placement is of particular importance in the alpine zone where hare habitat is often patchy. In recent thar impact studies, photopoint monitoring is being used to supplement exclosure plot data to increase the extent of habitat being sampled (Miller 1995). The second issue is the importance of continually maintaining exclosures in alpine areas; these are often subject to avalanches and rockfall and exclosures seldom last for more than a year (J. Parkes pers. comm). The third issue is that hare behaviour may be altered by the plot pegs and markers.

An alternative approach to measuring long term hare impact, which has not been used in New Zealand, is to reduce hare numbers in large treatment areas and compare subsequent changes in the vegetation with non-treatment areas where hare numbers remain uncontrolled. Reduction in pest numbers, rather than complete eradication, is the most likely scenario for hare control programs so this type of study could prove data on vegetation responses (or lack thereof) that is more helpful to managers than the data on complete removal of hares that is provided by exclosure studies. A reduction in hare numbers may significantly change the impact they are having on the environment, e.g. a study of snowshoe hares *Lepus americans* in Kluane, Yukon (Smith et al. 1988), found heavily browsed bushes rapidly recovered after a natural decline in hare numbers.

A critical issue for managers is how much control is needed to achieve conservation goals in an area, which in turn will determine the methods and costs that would be involved. Only one study (Parkes 1981) has investigated hare population recovery after control. In a 120ha control block in the Avoca River valley, inland Canterbury, c.100 hares were poisoned and a further 200 shot over an 8-month period in 1980. Pellet surveys suggested that this control work reduced hare numbers on the block by 60%. There was, however, substantial recovery in hare numbers during the subsequent breeding season, which emphasises that localised, one-off hare control operations will only provide a brief respite from hare impacts. This is discussed further in section 4.5.

4.4.2 Vegetation trend assessment

Interpretation of the impact of introduced browsing animals requires that changes in the population structure and seedling regeneration of browsed grassland communities be measured over time (Rose & Platt 1990). Successful vegetation monitoring requires methods that are able to accommodate the problems associated with sampling New Zealand native tussock grassland and shrubland. Firstly, large and small plants occur together and an adequate sampling of both is required; in the tussock grassland the tussocks themselves determine the structure and microclimate of the vegetation community, but much of the forage for hares is provided by the smaller plants. Secondly, the canopy spread of large plants varies at different levels within the vegetation, and hence needs to be measured at a range of different heights. This is particularly important in areas that receive deep winter snow cover that allows hares to browse much higher in the vegetation than is possible for them in summer.

Thirdly, most study areas will include areas where the vegetation needs to be sampled on steep slopes (Scott 1965).

Frequency sampling is often used in vegetation reconnaissance survey because it is a simple field technique that integrates several aspects of a plant's abundance. However, frequency is a complex characteristic determined by plant density, cover, and pattern, and by quadrat size, so frequency sampling is seldom suitable for intensive work (Scott 1965). When intensive sampling is required, the point analysis method is often used. This method can be extended to measure plant height. However, the point analysis method is time-consuming and requires that the plants remain stationary and hence it is often unsuitable for work in windy New Zealand (Scott 1965).

The Scott height-frequency sampling method is a variation of point analysis that measures plants' vertical distribution by recording species frequency in successive layers within a vegetation community (Scott 1965). Rogers (1991, 1994) successfully used this technique for hare damage monitoring and recommended it for future studies (see also Dickenson et al. 1992). To date, the Scott height frequency method has provided the best information on vegetation community response to hare browse.

Rose & Platt (1990, 1992) used a sampling approach that involved mapping each tussock. For each, the basal diameter, height, number of flowering culms and the presence/absence of recent browsing damage were recorded. Crown death was estimated for tussocks >5 cm in diameter and tiller counts were made for a sample of individuals <15 cm in diameter. Population structures were then analysed by determining diameter class and age-state distributions. Rose and Platt (1990) recognised four putative age states—seedling, juvenile, mature and senescent—that differed in basal diameter, number of tillers, leaf length and crown depth. Other species were not accounted for, although the approach could be adapted to do so.

A simpler and less time-consuming method of monitoring vegetation uses indicator species, and this has been suggested for monitoring thar impact in New Zealand (Miller 1995). Indicator species must be carefully chosen; an ideal indicator species should be common enough to find and measure, be impacted on by the target herbivore and not by others, and show measurable changes over the range of pest densities under study (J. Parkes pers. comm.). Common species such as tussocks can provide a general indication of community condition but do not necessarily reflect impacts on less common plants. However, rare plants do not usually meet the criteria listed above (D. Given pers. comm.). Possible indicator species for hare impacts include the *Aciphyllas,* which are primarily grazed by hares (J. Parkes pers. comm.) although also by rabbits (Reddiex 1998).

A further important consideration of hare impact studies is the slow growth of many indigenous plants in alpine and sub-alpine environments, which means that monitoring will need to be conducted over a long periods. Adequate baseline data should be collected in both treatment and non-treatment areas before hares are excluded or controlled. Replication of treatments is obviously important, but will be costly to achieve.

Table 7 summarises the points made above.

TABLE 7. ADVANTAGES AND DISADVANTAGES OF METHODS FOR MEASURING THE LONG TERM IMPACTS OF HARES ON THE ENVIRONMENT.

METHOD	ADVANTAGES	CONCERNS	NEW ZEALAND EXAMPLES
(i) Reduce hare numbers in control areas	Information is directly relevant to managers	Costly to maintain the population at a low level	None
(ii) Exclude hares from semi-permanent plots	Easily monitored over a long period of time	Does not provide information on the benefits of hare *control* (as distinct from eradication)	Rogers 1994, 1991; Rose & Platt 1992
Exclosure plot type			
(i) Exclude all mammals (including hares)	Maximises the potential vegetation response	Does not differentiate between hare and other animal damage; may require possum control	Rose & Platt 1992; Blay 1989
(ii) Bisected—exclude all mammals on one side, and all mammals except hares on the other	Provides information of damage done by both hares and other mammals	Extra cost and effort; may require possum and rabbit control	Rogers 1994, 1991
Vegetation sampling method			
(i) Scott height-frequency	Provides comprehensive details on plant composition, and structure	Does not specifically measure tussock condition	Rogers 1994, 1991, Scott 1965
(ii) Tussock mapping	Provides detail on tussock condition	Need to combine with measurements of intertussock flora	Rose & Platt 1992 Rose & Platt 1990
(iii) Indicator species	Quick to monitor	Does not necessarily indicate impacts on all species	Miller 1995
(iv) Photo-point analysis	Quick to monitor	Does not provide detail on individual species	Miller 1995

4.5 HARE CONTROL

Hares have been controlled on agricultural land since soon after their introduction to New Zealand because they feed on a wide variety of shrubs, herbaceous plants, crops and young plantation trees. In contrast, there have been a few attempts to control hares in sub-alpine environments and no attempts in alpine environments. This section briefly reviews methods of hare control and previous control attempts. It does not attempt to deal comprehensively with the many problems associated with the control and eradication of introduced mammal pests in New Zealand (see Parkes 1993 for an overview).

Methods that have been used for hare control include shooting, snaring, hare-proof fencing, poisoning, and biological control with predators or pathogens.

Shooting is a reasonably cost-effective method of controlling hares on agricultural land, where access and visibility for shooters is good. In alpine basins, however, the rugged terrain poses both access and visibility problems for shooters. Therefore, while it may be technically possible to control hares by shooting (J. Parkes pers. comm.), the cost is likely to be prohibitive and the level of population reduction achieved might not be sufficient to provide significant conservation benefits.

Snares placed in hares' runs and checked on a daily basis have been used in lowland areas where hares occur in high densities. In the alpine areas, however, hare populations are low and their runs indistinct so snaring is unlikely to be efficient (J. Parkes pers. comm.).

Hare-proof fencing (e.g. a netting fence at least one metre high with mesh no larger than 8–10 cm, or electric fencing with the lower four wires about 10 cm apart) can be effective for small horticultural blocks or nurseries but is obviously of limited use in the alpine environment. Fencing has been used since 1948 in an attempt to exclude hares, rabbits and other grazing mammals from rare plant communities in the 6 ha Lance McCaskill Nature Reserve in inland Canterbury (McCaskill 1980, 1982) near Castle Hill. The current fencing is 17 gauge, 1066 mm wide, 41 mm mesh netting rising 900 mm above the ground with the remaining netting bent out along the ground. A further 450 mm wide strip of netting laid along the ground is attached to the fence.

The fences around the Nature Reserve plots have not proven sufficient to completely exclude rabbits and hares, which have either dug under the fence or climbed over it during periods of deep snow cover. Periodic shooting is consequently required to keep the reserve free of these animals (R. Smith pers. comm.). The nearby Enys Scientific Reserve (also 6 ha) is fenced to protect a rare species, *Hebe armstongii*. Similar problems have been encountered there, so additional fencing has been used inside the reserve to protect transplanted seedlings (R. Smith pers. comm.).

Poison baiting of hares has been trialed on a few occasions. Previous attemps on river terraces in sub-alpine basins (Logan 1956; Batcheler & Logan 1963; Parkes 1981) used boiled oats as bait; these were dyed green and impregnated with sodium monofluoroacetate (1080). The trials were undertaken in winter, when natural food was assumed to be in shortest supply. Radiotracking of hares during the 1980/81 trial suggested, however, suggested that autumn was the season when hares were most likely to encounter poison baits laid on river terraces. Even then, only two of five hares monitored over a year in the Avoca River basin study site used the river terraces (Parkes 1984, 1981). Thus, baits would need to be either long-lasting or else spread on the hill slopes as well as the terraces for the majority of the hare population to be placed at risk.

Other toxins used for rabbit and possum control (e.g. pindone) are more costly than 1080 and there are no published reports of their efficacy on hares in New Zealand.

Similarly, there are no New Zealand studies on the impact of poisoned oats on non-target species, such as birds or insects. There was no evidence that birds were taking the bait in the Avoca Basin poison trial (J. Parkes pers. comm.), however species such as kea, kahu and chukar would probably be at risk from such baits if they were present in a control area. In lowland areas, birds are known to feed on and die from the chaff from cereal and carrot 1080 baits (Spurr 1994).

As mentioned previously, an attempt at controlling hares on the Avoca Valley river flats (Parkes 1981) through a combination of 1080 poisoning and shooting achieved an initial 60% population reduction, but substantial recovery in numbers occurred during the subsequent breeding season. Recovery of hare numbers through increased breeding, immigration, and perhaps enhanced survival means that hare control programs will need to be sustained if conservation benefits are to be achieved. Managers aiming to reduce such impacts by hare population reduction will therefore need to plan for substantial, ongoing, investment in regular control work. Planning for such control programmes will require better information on the likely rates of hare immigration into control areas from surrounding habitats, as this will have implications for the optimal size of control areas.

Predators such as feral cats and ferrets, originally introduced into high country areas in an attempt to control rabbits, probably kill some hares, but it is unlikely that they have any regulatory effect on hare populations. It is difficult to see how predator numbers could be enhanced to reduce hare numbers without having an unacceptable impact on non-target species.

Biological control using pathogens is a possible long-term solution to New Zealand's hare problems. In Europe, widespread death of hares has been attributed to European brown hare syndrome (EBHS) (e.g. Sostaric et al. 1991; Duff et al. 1994). This host-specific disease was first isolated from hares in 1982 and has symptoms comparable to Rabbit Calicivirous Disease (RCD). However Gavier & Morner (1993) reported that in spite of EBHS, the number of hares shot in Sweden in the recent years has increased, which suggests that the disease is not causing a marked reduction in the overall population. It is also questionable whether EBHS, or any other pathogen, could spread effectively among the sparse hare populations found in New Zealand's high altitude habitats.

5. Hare management in high altitude vegetation

Hare impact is only one component of high altitude vegetation management, and so needs to be integrated into a general conservation framework for these areas (Figure 1).

5.1 IDENTIFICATION OF CONSERVATION VALUES

The first question that land managers need to ask is: what areas of high conservation value, such as localities containing rare plant species or communities, are possibly under threat from browsing mammals?

As there is no national list of such areas, each Department of Conservation Conservancy needs to identify rare plants and habitats that are potentially at risk from hares, using tools such as lists of threatened plants (e.g. Cameron et al. 1995) combined with geographic information systems once these become more readily available. Possums and goats are currently considered the greatest threats to New Zealand's vegetation, so the habitats considered most at risk are predominantly forests (J. Parkes pers. comm.). If hares do pose a threat to indigenous flora, and there now exist many high altitude areas where hares outnumber the larger ungulates, then these areas may deserve increased attention.

5.2 VEGETATION TREND ASSESSMENT

The Department of Conservation, Landcare Research, and some other groups monitor a range of vegetation in selected high altitude grasslands, primarily in areas where past or present grazing by domestic stock is an issue. However, vegetation trends in most areas are not currently formally assessed and concern about hare impact is consequently based largely on anaecdotal evidence (see Section 3).

Any expenditure on hare control should be supported by long term vegetation monitoring to the benefits of such control (see Section 4).

5.3 IDENTIFICATION OF CRITICAL PESTS

A regime of 'priority place—critical pest' has been proposed by Parkes & Nugent (1995) as a basis for an integrated national pest control strategy. They stipulate that the following be considered:

- The need to maintain conservation gains achieved under the present 'worst pest—priority place' model (i.e. funding for hare control should not undermine any existing goat or possum control programme)

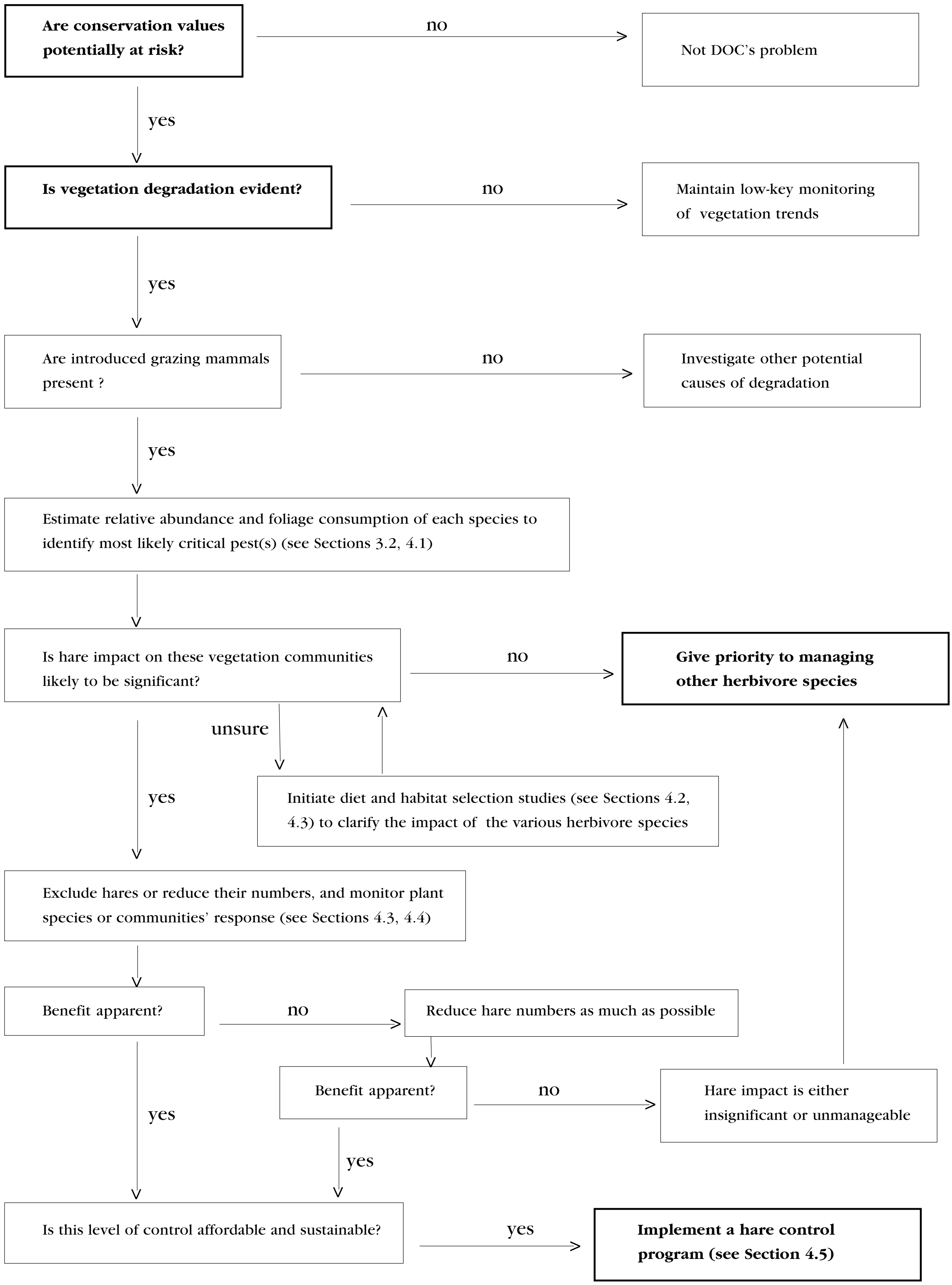

Figure 1. Flowchart of decisions involved in the management of the impact of hares on high-altitude vegetation.

- The need for any system to provide sustained action, and the need for research to identify critical pests

A preliminary identification of critical pests can be made from distribution maps of introduced herbivores being compiled by Landcare Research. If abundance data are available, Section 3.2 describes one approach to assessing pest species status (i.e. by estimating foliage consumption using relative abundance and metabolic rate data). Dietary studies can provide further information on critical pests, by determining which herbivore is most likely to be targeting particular plant species. This approach has been used to investigate the damage that three different pest species (thar, deer, and possums) are responsible for in the Rangitata/Rakaia area of the Southern Alps (Parkes & Thomson 1995). The three species were found to be partitioning their food resources, with thar eating mainly grass, chamois eating mainly shrubs and herbs, and possums eating various species of shrubs and herbs, plus fruit when available.

At present, it would seem that there are few places where hares are clearly the main cause of grazing damage. One such place is the alpine area of Mt Taranaki, where possums have been controlled so that hares are now the most significant introduced herbivore (J. Parkes pers. comm.). In many other areas, the relative impact of hares remains uncertain.

5.4 OPTIONS FOR HARE MANAGEMENT

Parkes (1993) has highlighted the need for managers to clearly separate questions of control *strategy* (e.g. should the objective of management be eradication or sustained control?); control *tactics* (e.g. should shooting or 1080 oats be used?); and control *logistics* (e.g. how much will it cost and how long will it take?). The main strategies available for hare control, ordered by decreasing benefit for conservation values, are:

Local eradication

If there are any isolated areas where hares could be eradicated (i.e., the entire population could be targeted and the prospects of recolonisation are negligible) then a one-off eradication programme might be worthwhile.

Prevention of range expansion

It may be easier to prevent colonisation of where hares have not yet invaded or have undergone local extinction(e.g., parts of Nelson and Fiordland) than to control hares in the many areas where they are already established.

Sustained control

In priority areas for hare control, the level of control necessary must be determined. Exclosures will be of limited use in addressing this question, because complete eradication of hares is unlikely to be a feasible option for managers. The benefits (or otherwise) of sustained control need to be assessed by controlling hare numbers in treatment areas and comparing vegetation responses with untreated areas. The self-regulatory nature of hare populatios poses problems for any control program, because they are likely to recover quickly. Adequate baseline data, and long term monitoring, will be essential to these studies.

Do nothing

New Zealand has a high degree of endemism in its indigenous vascular flora and between 10–15% of these are considered to be at risk of extinction (Norton 1991). Until the impact of hares on these species is clarified it would unwise to assume that we can afford to do nothing. Nevertheless, we predict that once better impact data come to hand the conclusion will be that, in areas of low to moderate conservation priority, active hare management programmes will not be justifiable in the face of the many competing demands for scarce conservation funds.

6. Recommendations

The following methods are recommended for hare research in areas of high conservation value:

- Development and validation of a suitable cleared plot technique for assessing hare population density and determining habitat use (Sections 4.2, 4.3)
- Diet composition and selection studies, using stomach contents or faecal pellet analyses, that can be related to vegetation availability data obtained by field survey (Sections 4.1, 4.3)
- Investigation of long-term hare impact using exclosure-plot and population reduction techniques (Section 4.4)
- Integration of data about hares and other introduced herbivores into an integrated pest management framework for a selected catchment, as a case study of the ‘priority place—critical pest’ approach (Section 5.1)

Three Conservancies have previously offered to support field studies on hares: Hawke’s Bay Conservancy has offered to provide sites and logistic support for field research; Southland Conservancy could contribute materials for construction of exclosures within the conservancy, study site access and expertise for monitoring; and Nelson/Marlborough Conservancy could help establish and maintain hares exclosures.

Any planned implementation of these recommendations should therefore take advantage of the enthusiasm of these Department of Conservation Conservancies and the staff who helped initiate this review.

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