

## Cleared and uncleared pellet plots as indices of brown hare density

Michael E. Perry\* and Alastair W. Robertson

Ecology Group, Institute of Natural Resources, Massey University, Private Bag 11222, Palmerston North 4474, New Zealand

\*Corresponding author (perrym@landcareresearch.co.nz)

Published on-line: 28 May 2012

**Abstract:** Faecal pellet counts are commonly used as indices of lagomorph abundance but uncertainty over variation in decay rates among sites has led to most researchers recommending the use of pellet accumulation rates in previously cleared plots rather than the simpler and quicker method of counting uncleared plots. We use data from cleared and uncleared 0.1-m<sup>2</sup> brown hare pellet plots at six sites in the central North Island of New Zealand to test the reliability of the two methods. The sites varied considerably in hare pellet density and also varied in altitude and rainfall, but the initial cleared count was extremely tightly correlated with the subsequent pellet accumulation rate ( $r = 0.987$ ) suggesting there is minimal bias from differential decay rates in uncleared plot counts. Our results show that the simpler and less time-consuming uncleared-plot method is an adequate index of hare density across a range of hare densities and climates and is not unduly biased by differential decay rates. This should simplify the work of land managers interested in assessing relative abundance. At one site (the area round Manson Hut on the Kaweka Range) where the plots were followed for a year in a variety of habitat types, there were strong seasonal changes in hare abundance (peaking in summer and declining through winter), and strong habitat preferences for exotic grasslands and grassland–herbfield mixes, while pure herbfield, and particularly rocky scree and southern beech forest were not favoured. We estimated that based on published defecation rates of hares, population densities at our six sites varied from 0.03 to 3.93 hares per hectare and that they consumed between 1.4 and 188 kg ha<sup>-1</sup> of biomass annually.

**Keywords:** animal density; census techniques; habitat use; *Lepus europaeus*; New Zealand; pellet counts

### Introduction

A wide variety of techniques have been developed for assessing the number of individuals in free-ranging mammalian populations such as of hares (Wong & Hickling 1999), including the direct counts of animals (Flux 1967; Langbein et al. 1999; Hochachka et al. 2000), shooting rates (Flux 1969), trapping rates including mark-recapture methods (Krebs et al. 1987, 2001), or the observation of animal sign such as faecal pellets (Parkes 1981; Krebs et al. 1987, 2001). Compared with other population census techniques, pellet counts have the advantage that they are not labour intensive, are able to be completed by a single fieldworker, and can provide robust data for assessing relative abundance (Horne 1979). Pellet counts can be used to calculate both absolute and relative population estimates (Parkes 1981; Krebs et al. 1987, 2001), habitat and range use (Rao et al. 2003), biomass consumption (Hansen 1972), and even sex structure and population biomass (Putman 1984). In New Zealand, pellet counts are commonly used for monitoring long-term trends in pest populations (e.g. Riney 1957; Batcheler 1975; Pekelharing 1979; Jenkins 1982).

Pellet counts are based on either uncleared plots or cleared plot methodology. In uncleared plots, the density of pellets present in the environment (i.e. pellets m<sup>-2</sup>) or the presence/absence of a pellet group (sometimes with a measure of the nearest neighbour group to correct for contagion) is recorded. Cleared pellet plots involve clearing all pellets within a fixed plot, then recounting the plot after a period of time to obtain the number of pellets recruited over time (recruitment rates). There are advantages and disadvantages to each method. Pellet group analysis is most appropriate for ungulates where pellets are dropped in groups rather than singly and so individual pellets are not independent. For lagomorphs pellets

are deposited singly and so contagion is less of a problem. Recruitment rates are more time consuming to obtain since they require at least two visits to each site and the plots must be permanently marked, but will be more regionally comparable than initial counts if the decay rate of pellets varies with habitat (Wallmo et al. 1962; Prugh & Krebs 2004; Murray et al. 2005). Measuring pellet recruitment also allows an estimate of the total forage consumption in an area and of the density of animals, assuming that assimilation efficiency and daily per-animal defecation rates are available (Bailey & Putman 1981). However, counting just the standing crops of pellets for animals like hares is much quicker and may actually be more effective than recruitment rates when the density of animals is low since the counts will generally be higher (and the standard errors lower) because pellets typically last much longer than the recruitment interval used in most studies. The constant-decay-rate assumption, though, is critical if standing crops are to be used to compare regions. Local climate may affect the decay rate – pellets in wet and warm sites may decay faster than pellets from cool and dry sites. To date, however, there have been few tests of the assumption of constant decay rates for hare pellets (Murray et al. 2005).

The brown hare (*Lepus europaeus occidentalis* de Winton, 1898) was first introduced into New Zealand in 1851 and by the late 1800s hares were found throughout most of New Zealand in open country and grasslands (Flux 1990). Although they are widespread, the traditional view has been that hares have a relatively minor effect on the vegetation when compared with larger ungulates, possums or rabbits (Wong & Hickling 1999) since they live at relatively low densities, hedge palatable plants without killing them, graze a few leaves from many plants over a wide area, and do not dig burrows (Flux 1990). However, in some parts of their range, hare populations appear to be dense

and may, at some sites, consume more forage per hectare than other introduced herbivores (Wong & Hickling 1999).

Understanding the full impact of hares in New Zealand has been hampered by the lack of data on hare abundance and of a standard technique for assessing hare population densities (Wong & Hickling 1999). Several methods have been tried: direct observations from a hide (Flux 1967); counts of the number of hares seen along transects, often by means of spotlights at night (Norbury et al. 2002); counts of dead hares found in a season (Flux 1967) and of tracks in the snow (Flux 1967); and the time taken to shoot one hare (Flux 1969). Pellet counts have only been used three times in New Zealand. Horne (1979) used the standing crop method to assess hare abundance on Mt Ruapehu in the central North Island, while cleared pellet plots were used by Parkes (1981) to successfully show a reduction in pellet recruitment after a poisoning operation in Craigieburn Forest Park. They were also used in the Borland Saddle area of Fiordland National Park by Wilson et al. (2006) as part of a study of alpine small mammals. But aside from those studies there have been few data published investigating how faecal pellets counts could be used as a monitoring tool. Consequently, Parkes (2001) and Wong and Hickling (1999) recommend that the cleared-plot technique be developed for assessing hare population density and determining habitat use for New Zealand conditions.

We used the cleared-pellet-plot technique to obtain pellet recruitment rates of hares at six locations in the central North Island of New Zealand, to (1) test the relationship between recruitment rates and standing crops across sites, (2) determine habitat use at one site—the Manson Hill area of the central Kaweka Range, and (3) relate recruitment rate to absolute hare abundance and to estimate biomass consumption in these systems.

## Materials and methods

### Study area

Pellet plots were established in six locations in the central North Island, New Zealand (Table 1). At most locations, a single site was chosen, but in the Manson area of the Kaweka Ranges five sites were chosen spanning a range of habitat

types. Three sites were located in zones of the Moawhango Ecological District, one each at Awapatu, Argo Road (Upper) and Motumatai, and two sites were in Tongariro National Park, at Tukino and Turoa. We have also included data from the south of New Zealand from the Borland Valley site used by Wilson et al. (2006), to compare with our sites (Table 1). The sites varied in altitude from 900 to 1550 m above sea level and were mostly located in short-stature vegetation. Mean annual temperature and annual rainfall estimates for each site were obtained from the corresponding polygons in the *Land Environments New Zealand* classification GIS (Leathwick et al. 2003), which uses thin-plate splines fitted to meteorological stations to interpolate climate at a kilometre-grid scale. The predicted climate varies among the sites from cool and mesic (Argo Road and Awapatu) to cold and wet (Turoa and Borland) (Table 1).

### Regional comparisons

At each site, we established five transects between February and March 2002, each with 20 circular sampling points of 0.1 m<sup>2</sup> (radius = 17.8 cm). The transect origins were spaced 40 m apart and were permanently marked using aluminium poles. Sampling points were spaced at 5-m intervals along each transect and permanently marked using an aluminium tree tag pegged to the ground using high tensile fencing wire. The plot size (0.1-m<sup>2</sup>) was selected as recommended for use in New Zealand (Parkes 2001), and to be consistent with the sizes used elsewhere in New Zealand (Parkes 1984; Wilson et al. 2006). Where the terrain was flat, we ran the transects parallel to each other using a compass bearing while on sloping ground we followed the contour of the slope. During the initial measurement, we recorded the aspect, slope, physiography, and vegetation type of each plot, and all pellets present were counted and then removed. For the subsequent pellet recruitment survey, we followed the recommendation of Parkes (1981, 2001) to use a remeasurement interval of 60 days, which is considered short enough to prevent any chance of pellet decay in the interval between measurements. We aimed to have two remeasurements but this was not always possible at some sites due to periods of heavy snow cover in winter.

**Table 1.** Environmental conditions of the New Zealand study sites, number of plots established and how many times they were remeasured after the initial survey.

Site	Latitude	Longitude	Altitude (m)	Mean annual temp. (°C)	Annual precipitation (mm)	General vegetation type	Plots (N)	No. times remeasured
Tukino	39°16.6' S	175°41.9' E	1120	7.2	1901	Alpine gravelfield with scattered vegetation	100	2
Manson	39°17.8' S	176°15.7' E	1180–1350	7.6	1724	Modified native grassland and herbfield	500	5
Motumatai	39°18.6' S	176°00.2' E	1300	6.6	1587	Tall tussock grassland	100	1
Turoa	39°18.6' S	175°31.5' E	1550	4.9	2654	Alpine fellfield	100	1
Awapatu	39°23.6' S	175°49.2' E	900	8.4	1222	Tall tussock grassland	100	2
Argo Rd	39°27.3' S	175°50.4' E	1070	8.3	1175	Tall tussock grassland	100	2
Borland (Wilson et al. 2006)	45°44' S	167°23' E	1000–1200	4.3	2190	Tall tussock grassland	600	4

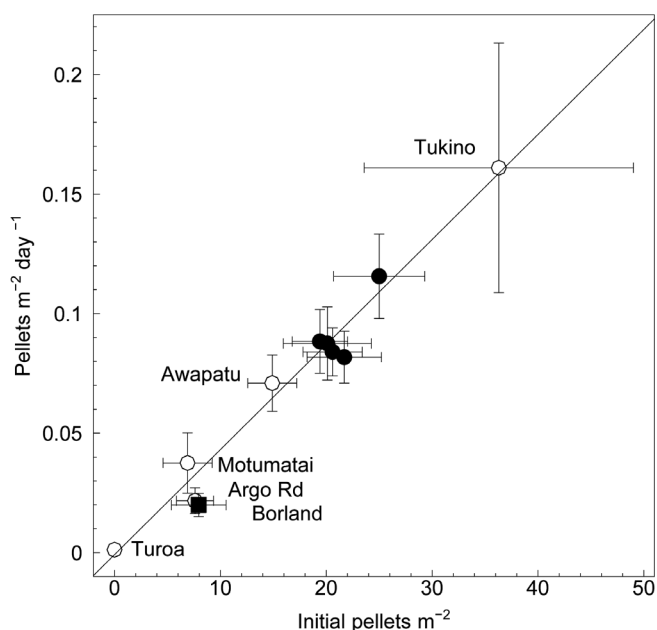
At each remeasurement of the site, pellets were counted and cleared from each sample point.

**Habitat use in the Manson area**

More intensive sampling occurred in March 2002 in the Manson region where we studied five separate sites and re-measured each transect five times. Here we classified the habitats, by the dominant vegetation type in a 1-m radius around the plot, into five categories: **Herbfield** – habitat dominated by species such as the moss *Racomitrium lanuginosum*, the daisy *Celmisia spectabilis*, the small tussock grass *Poa colensoi*, and the subshrub *Leucopogon fraseri*; **Grassland** – a sward of introduced and native grasses such as *Anthoxanthum odoratum*, *Holcus lanatus*, *Rytidosperma* spp. and *Poa* spp.; **Herbfield/Grassland** – a mixture of the above two habitat types; **Mountain Beech** – *Nothofagus solandri* var. *cliffortioides* dominated forest; **Scree** – scree and gravel.

**Pellet weights**

We collected 113 fresh pellets from near the Tukino study site in May 2012, oven-dried them, and weighed them to get average pellet weight.



**Figure 1.** Averages and standard errors for recruitment rate and standing crop of brown hare pellets calculated on the pooled data from all five transects run at each of seven New Zealand sites. The closed circles are the five sites at Manson and the square is data from the Borland site studied by Wilson et al. (2006). The line is a simple linear fit to the means excluding the Borland data ( $r = 0.987, n = 10, P < 0.0001$ ).

**Analysis**

We performed all the analyses on the per-plot counts, but for presentation, we calculated the number of pellets per square metre for comparison with other studies, and included the Borland data (Wilson et al. 2006), which was not included in the statistical analysis. We divided the number of pellets recruited at each measurement by the number of days between measurements to obtain a daily recruitment rate and analysed these data and the initial pellet density with analyses of variance. To test the relationship between initial standing crops and subsequent recruitment rates, the recruitment rates at each of the succeeding measurements were averaged to obtain a single value for each plot. We used analysis of covariance of the standing crop of pellets per plot with recruitment rates grouped by region as the predictor. Since the  $x$ - and the  $y$ -variates are both measured with error, we also fitted model II regressions using major axis regression and standard major axis regression (Legendre 2008), but the fitted lines differed only in trivial ways from ordinary least-squares regression and so are not presented here.

We analysed the Manson data for variation in plot-average recruitment rates among habitat types, using a GLM where the sites were first fitted as blocks, followed by habitat, slope and aspect (absolute degrees from North) and the interactions between the latter three variables. We used the statistical program R ver. 2.9.0 for all analyses (R Development Core Team 2009).

**Results**

**Standing crop vs recruitment**

At the site level, including each of the Manson sites as separate sites, the correlation between the site averages of standing crops and daily recruitment rate was remarkably tight ( $r = 0.987$ , Fig. 1) and even the Borland data, which came from a very different site a long way from any of our study sites, fitted this pattern closely. A generalised linear model that included all the plots partitioned by location (‘regions’) showed that around 46% of the variation in recruitment rate could be predicted by the initial standing crops, with only a very small amount of variability attributable to regional differences in this overall relationship (Table 2). The Motumatai, Awapatu, and one of the Manson sites had slightly more recruitment than expected from the standing crop of pellets, while Argo Rd, Borland, and two of the Manson sites had slightly less recruitment than expected. Although these departures were small, they were statistically significant, with about 0.7% and 2.4% of the variation attributable to region and region  $\times$  standing crop interaction respectively (Table 2).

**Table 2.** Analysis of covariance of brown hare pellet recruitment rate per plot among the six New Zealand ‘regions’. Significant effects are shown in bold.

	d.f.	Deviance	R <sup>2</sup> (%)	F	P
<b>Standing crop</b>	<b>1</b>	<b>0.1906</b>	<b>46.0</b>	<b>892.70</b>	<b>&lt;0.0001</b>
<b>Region</b>	<b>5</b>	<b>0.0027</b>	<b>0.7</b>	<b>2.58</b>	<b>0.0252</b>
<b>Recruitment rate:Region</b>	<b>4</b>	<b>0.0099</b>	<b>2.4</b>	<b>11.65</b>	<b>0.0008</b>
Residual	989	0.2111			

### Regional comparisons

There were highly significant regional variations in both measures (standing crops,  $F_{5, 994} = 8.00$ ,  $P < 0.001$ ; daily recruitment rates,  $F_{5, 994} = 9.26$ ,  $P < 0.001$ ). The pellet density was highest at Tukino where the initial density approached 40 pellets  $m^{-2}$  and the recruitment rate was approximately 0.16 pellets  $m^{-2}day^{-1}$ , and lowest at Turoa where zero pellets were found initially and the subsequent daily pellet recruitment rate was extremely low (0.0012  $m^{-2}day^{-1}$ ). The recruitment rates obtained from the cleared-pellet-plot method can be converted to hare densities with knowledge of pellet production (Table 3). There are two reported pellet production rates for hares in New Zealand that are in remarkably close agreement. Flux (1967) reported 410 pellets hare $^{-1}day^{-1}$  averaged from captive hares fed wild forage and observations of wild animals tracked and closely observed over a single night, while Horne (1979) reported 409 pellets day $^{-1}$  from captive hares. Therefore, using the figure of 410 pellets per day and the daily pellet recruitment rates obtained in this study, the population densities for the regions in this study were estimated to range from 0.03 to 3.93 hares ha $^{-1}$  (Table 3). Since the error associated with the daily pellet production rate is not known, an associated error cannot be given to these values. Pellet production has been shown to accurately reflect actual hare densities in other countries (Krebs et al. 2001; Murray et al. 2002; Berg & Gese 2010), but ideally a validation study (such as mark-recapture; Berg & Gese 2010) should be conducted in New Zealand to calibrate the pellet densities with known hare densities to confirm these estimates.

Pellet recruitment rates can also be used to estimate biomass consumption (see e.g. Hansen 1972). The pellets collected at Tukino weighed 0.144 on average (SE 0.004,  $n = 113$ ). Typically, hares digest about 45% of wild forage consumed (Hansen 1972; Shoemaker et al. 1976; Rodgers

& Sinclair 1997; Kuijper et al. 2004). Using these figures and the rates of pellet recruitment observed in this study, we estimate that vegetation consumption by hares ranges from just 1.4 kg ha $^{-1}year^{-1}$  at Turoa to about 188 kg ha $^{-1}year^{-1}$  at the Tukino site (Table 3).

### Seasonal and habitat effects at the Manson sites

At Manson, significant variation in pellet recruitment also occurred among the five habitat types (Table 4). Grasslands were a strongly preferred habitat in this area, less so when mixed with herbfield, and rocky scree and mountain beech forest habitats were scarcely used (Fig. 2). There were also strong seasonal patterns, with a general decline through the winter and spring (June to October) and a recovery in summer when hares reoccupied the grassland in high numbers. There were smaller effects on pellet recruitment attributable to aspect (Table 4) with a tendency of pellets to be concentrated in more northerly aspects especially in grasslands, resulting in a significant aspect  $\times$  habitat interaction.

## Discussion

### Standing crops vs recruitment rate

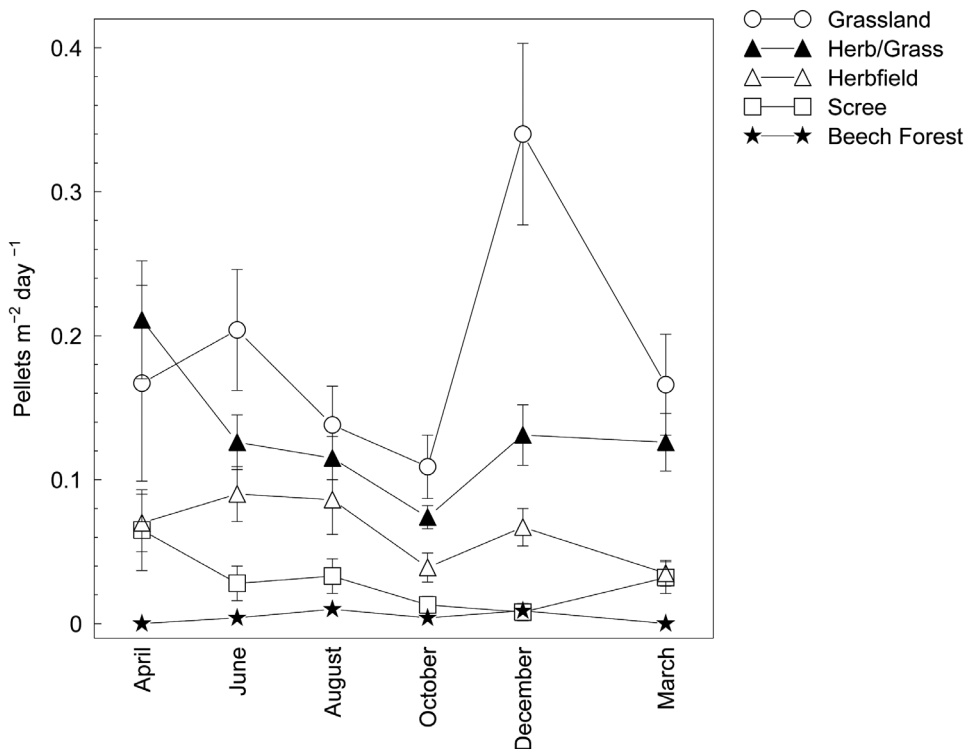
The standing crop uncleared-pellet-plot method has generally not been considered suitable for population studies of hares in New Zealand or elsewhere and other researchers have generally advocated the use of recruitment rates into cleared plots to estimate abundance (Flux 1967; Horne 1979; Murray et al. 2005). However, the outstanding result from this study is the very tight relationship between pellet recruitment and standing crop, indicating that the standing crop provides a useful index of hare densities that is broadly applicable across

**Table 3.** Estimates of the brown hare population density and biomass consumption in our New Zealand sites. The values were calculated assuming a daily pellet production rate of 410 pellets per hare, pellet dry weight of 0.144 g, a digestibility rate of the diet of 45%, and the pellet recruitment rates from our study.

Region	Pellet recruitment rate (pellets $m^{-2} day^{-1}$ )	Hares per hectare	Annual biomass consumption (kg ha $^{-1}$ )
Tukino	0.161	3.93	188.0
Manson	0.091	2.23	106.8
Awapatu	0.071	1.73	82.8
Motumatai	0.035	0.91	43.8
Argo Road	0.022	0.53	25.3
Turoa	0.001	0.03	1.4

**Table 4.** Analysis of covariance of brown hare pellet recruitment rates at the five Manson sites, Kaweka Range, New Zealand. Site was fitted as a block followed by habitat class, slope, aspect – degrees from north, and the interactions between these variables. Significant effects are shown in bold.

	d.f.	Deviance	R <sup>2</sup> (%)	F	P
Site	4	0.00074	0.79	1.29	0.2726
<b>Habitat</b>	<b>4</b>	<b>0.01750</b>	<b>18.60</b>	<b>30.38</b>	<b>&lt;0.0001</b>
Slope	1	0.00017	0.18	1.17	0.2804
<b>Aspect</b>	<b>1</b>	<b>0.00114</b>	<b>1.22</b>	<b>7.95</b>	<b>0.0050</b>
Habitat:Slope	4	0.00131	1.39	2.28	0.0600
<b>Habitat:Aspect</b>	<b>4</b>	<b>0.00313</b>	<b>3.32</b>	<b>5.43</b>	<b>0.0003</b>
Slope:Aspect	1	0.00018	0.20	1.28	0.2583
<b>Habitat:Slope:Aspect</b>	<b>1</b>	<b>0.00147</b>	<b>1.57</b>	<b>2.57</b>	<b>0.0375</b>
Residual	475	0.06840			



**Figure 2.** Habitat and seasonal variation in brown hare pellet recruitment rates (averages and standard errors) at the Manson sites, Kaweka Range, New Zealand.

the New Zealand grasslands we surveyed. The relationship is not perfect – there were small but significant departures from the expected values, with some populations yielding more pellet recruits than expected from the initial standing crop and vice versa. This could be due to changing hare densities before, compared with after, the initial sampling, or to variation in pellet deposition or decay rates. However, there was no discernible relationship between the size and direction of the departures from the line and the local climate, which might be expected if decay rates do vary; i.e. warm, wet conditions might be expected to raise the decay rate compared with that at dry cool sites (Murray et al. 2005). Of the sites with more recruitment than expected, Motumatai is moderate in both rainfall and temperature and Awapatu is relatively warm but dry (Table 1). Of the sites with less recruitment than expected and therefore perhaps with relatively low decay rates, Borland is one of the wettest sites but does have low mean temperatures, while Argo Rd is the warmest but driest site. It may be that hare population densities are changing at these sites and it is this that has altered the ratio of standing crop to recruitment, rather than climate.

Overall, we have no reason to doubt the usefulness of the standing crop uncleared-plot method, which is much easier and quicker to perform than the cleared-plot method, and which provides a valuable and simple index for population studies of hares. While uncleared plots cannot provide detailed information on seasonal fluctuations within sites or reveal declining or growing populations, our results indicate that they are suitable for comparing regional densities within the range of climates that hares inhabit in New Zealand. Concerns about differential deposition or decomposition rates biasing the estimates (Murray et al. 2002, 2005) do not appear to be a serious issue in these New Zealand systems. It is possible that increased decay rates at mesic sites are compensated for by an increase in defecation rates at these sites, but since we did not measure decay rates or defecation rates ourselves we can only speculate about this. Most researchers working with snowshoe

hare (*Lepus americanus*) in the United States and Canada have advocated using cleared plots rather than uncleared plots to avoid the decay-rate bias (Murray et al. 2002, 2005; Prugh & Krebs 2004; Mills et al. 2005) (though this method does not avoid variable defecation rates), but even there, a recent study has also found a high correlation ( $r = 0.91$ ) between uncleared- and cleared-plot pellet densities (Hodges & Mills 2008), suggesting that uncleared plots may provide useful estimates of hare abundance in North America too.

#### Seasonal and habitat effects in recruitment rates

The cleared plots at Manson showed significant reductions in pellet recruitment rates over the winter period, and that habitat-use changes significantly with season. In all habitat types pellet recruitments peaked in summer and autumn and then fell steadily until spring. Parkes (1981) also showed a decrease in pellet recruitment over winter, spring and early summer in the Avoca Valley in the South Island of New Zealand over several concurrent years, with recruitment rates that fell from 0.20 pellets  $m^{-2} day^{-1}$  during autumn (March to May) to 0.12  $m^{-2} day^{-1}$  in spring (September to November) and early summer (November to January). Both the trend and values reported there are consistent with the data from this study and presumably reflect the recruitment of leverets after the breeding season, seasonal shifts in habitat preferences, and an overall increased mortality rate over winter.

The use of the grassland habitat at Manson showed a marked peak in spring perhaps coinciding with a strong flush of growth. While the other vegetation types did not undergo large absolute fluctuations in pellet recruitment, during winter, pellet recruitment in the herbfield and herbfield/grassland habitats increased relative to the grass habitat indicating that use of these habitats was relatively higher in winter. Seasonal shifts in habitat preferences by hares have been reported before in overseas studies (Hulbert et al. 1996; Rodgers & Sinclair 1997; Rao et al. 2003) and in the New Zealand literature (Flux 1967; Horne 1979). Hare use of the mountain beech habitat

was consistently low, with the average recruitment only 0.3% of the total for the region. This agrees with Parkes (1984), who reported that radio tagged hares in the Craigieburn State Forest Park avoided the beech forest habitat and spent only 2% of their time there, and with Wilson et al. (2006), who found that pellet counts in forests were almost always zero. Horne (1979) suggests that hares only use the forest habitat as shelter during periods of stormy weather, or as a route from one grassland area to another.

### Ecosystem impacts

Our data suggest that some New Zealand grasslands support relatively high densities of brown hares (up to 3.9 per hectare, consuming up to 188 kg dry matter ha<sup>-1</sup> year<sup>-1</sup>). These are higher figures than is typically found in the brown hare's native range in Europe but are fairly comparable with snowshoe and jackrabbit (*Lepus californicus*) densities in North America. Flux (2001) states that brown hares seldom exceed 2 per hectare in Europe and that the highest density recorded is 3.4 per hectare on an island with favourable habitat. Smith et al. (2005) report that across a wide range of sites in Europe, arable land supported the highest densities of hares but averaged only 0.80 per hectare, and in Britain, arable land supports 0.07 per hectare (Hutchings & Harris 1996), a figure that is exceeded by all our sites other than the high-alpine Turoa site. Upland sites in Britain average only 0.01 per hectare (Hutchings & Harris 1996). In contrast, Snowshoe hares reach about 5 per hectare in Wyoming (Berg & Gese 2010) and Hansen (1972) estimated that Jackrabbits consumed about 142 kg dry matter ha<sup>-1</sup> year<sup>-1</sup> in Colorado pastures.

### Management implications

Our data suggest that uncleared plots are an efficient method of inferring hare densities for regional comparisons. Counts of above about 25 pellets m<sup>-2</sup> represent high population densities (>3 hares ha<sup>-1</sup>), while counts of less than about 10 pellets m<sup>-2</sup> are indicative of low densities (<1 per hectare). For sites such as Manson with moderate pellet densities (average 21.4 pellets m<sup>-2</sup>, SE 1.6,  $n = 500$ ), a relatively small number of 0.1-m<sup>2</sup> plots, for example 100, would be sufficient to give a reasonably accurate picture of hare densities with relatively little effort. However, for measuring changes in hare densities over relatively short time-frames, e.g. following population control, recruitment plots are more appropriate since they sample only the period between surveys and therefore track short-term changes. As an indication of how many plots are

**Table 5.** Power analysis of the number of 0.1-m<sup>2</sup> brown hare pellet plots required in each New Zealand 'region' to significantly detect a change in recruitment rates 95% of the time using a one-tailed *t*-test with significance level of  $P < 0.05$ . The Turoa site was omitted from this analysis since it had almost no pellets.

Site	75% reduction	50% reduction	25% reduction
Manson	46	103	406
Awapatu	56	118	465
Argo Road	111	262	874
Tukino	203	460	1835
Motumatai	205	476	1710

needed to show significant reduction in pellet densities, we conducted a simple power analysis assuming reductions of 25%, 50%, and 75% in five of the regions (Table 5). The appropriate sample size will vary depending upon heterogeneity of the habitat and population size along with the detail required from the study. For a high density hare population in homogeneous habitat, a sample size of 100 plots would be perfectly adequate to show changes. However, in heterogeneous habitat, or where population densities are low, a sample size of 200–300 plots would be needed, and if detailed sampling of all habitats is required, 500 plots would be more suitable.

### Acknowledgements

The authors thank the New Zealand Defence Force and the Department of Conservation for permission to work on their lands, the Miss E. L. Hellaby Indigenous Grasslands Research Trust for funding, and R. Fordham, P. van Essen, and R. Duncan and two anonymous referees for comments on earlier drafts.

### References

- Bailey RE, Putman RJ 1981. Estimation of fallow deer (*Dama dama*) populations from faecal accumulation. *Journal of Applied Ecology* 18: 697–702.
- Batcheler CL 1975. Development of a distance method for deer census from pellet groups. *Journal of Wildlife Management* 39: 641–652.
- Berg ND, Gese EM 2010. Relationship between fecal pellet counts and snowshoe hare density in Western Wyoming. *Journal of Wildlife Management* 74: 1745–1751.
- Flux JEC 1967. Hare numbers and diet in an alpine basin in New Zealand. *Proceedings of the Ecological Society of New Zealand* 14: 27–33.
- Flux JEC 1969. Current work on the reproduction of the African hare, *Lepus capensis* L., in Kenya. *Journal of Reproduction and Fertility Supplement* 6. Pp. 225–227.
- Flux JEC 1990. Brown hare. In: King CM ed. *The handbook of New Zealand mammals*. 1st edn. Oxford University Press in association with the Mammal Society, New Zealand branch. Pp. 161–172.
- Flux JEC 2001. Evidence of self-limitation in wild vertebrate populations. *Oikos* 92: 555–557.
- Hansen RM 1972. Estimation of herbage intake from Jackrabbit feces. *Journal of Range Management* 25: 468–471.
- Hochachka WM, Martin K, Doyle F, Krebs CJ 2000. Monitoring vertebrate populations using observational data. *Canadian Journal of Zoology* 78: 521–529.
- Hodges KE, Mills LS 2008. Designing fecal pellet surveys for snowshoe hares. *Forest Ecology and Management* 256: 1918–1926.
- Horne RSC 1979. Seasonal and altitudinal variations in diet and abundance of the European hare (*Lepus europaeus* Pallas) in Tongariro National Park, New Zealand. Unpublished thesis, Massey University, Palmerston North, New Zealand. 141 p.
- Hulbert IAR, Iason GR, Racey PA 1996. Habitat utilization in a stratified upland landscape by two lagomorphs with different feeding strategies. *Journal of Applied Ecology* 33: 315–324.
- Hutchings MR, Harris S 1996. The current status of the brown hare (*Lepus europaeus*) in Britain. Peterborough, UK,

- Joint Nature Conservation Committee. 78 p.
- Jenkins C 1982. The animals & vegetation of Kaweka State Forest Park. Palmerston North, New Zealand Forest Service. 60 p.
- Krebs CJ, Gilbert BS, Boutin S, Boonstra R 1987. Estimation of snowshoe hare population density from turd transects. *Canadian Journal of Zoology* 65: 565–567.
- Krebs CJ, Boonstra R, Nams V, O'Donoghue M, Hodges KE, Boutin S 2001. Estimating snowshoe hare population from pellet plots: a further evaluation. *Canadian Journal of Zoology* 79: 1–4.
- Kuijper DPJ, van Wieren SE, Bakker JP 2004. Digestive strategies in two sympatrically occurring lagomorphs. *Journal of Zoology* 264: 171–178.
- Langbein J, Hutchings MR, Harris S, Stoate C, Tapper SC, Wray S 1999. Techniques for assessing the abundance of brown hares *Lepus europaeus*. *Mammal Review* 29: 93–116.
- Leathwick JR, Overton JMcC, McLeod M 2003. An environmental domain classification of New Zealand and its use as a tool for biodiversity management. *Conservation Biology* 17: 1612–1623.
- Legendre P 2008. lmodel2: Model II regression. R package version 1.6-3. <http://CRAN.R-project.org/package=lmodel2>.
- Mills LS, Griffin PC, Hodges KE, McKelvey K, Ruggiero L, Ulizio T 2005. Pellet count indices compared to mark-recapture estimates for evaluating snowshoe hare density. *Journal of Wildlife Management* 69: 1053–1062.
- Murray D, Ellsworth E, Zack A 2005. Assessment of potential bias with snowshoe hare fecal pellet-plot counts. *Journal of Wildlife Management* 69: 385–395.
- Murray DL, Roth JD, Ellsworth E, Wirsing AJ, Steury TD 2002. Estimating low-density snowshoe hare populations using fecal pellet counts. *Canadian Journal of Zoology* 80: 771–781.
- Norbury G, Heyward R, Parkes J 2002. Short-term ecological effects of rabbit haemorrhagic disease in the short-tussock grasslands of the South Island, New Zealand. *Wildlife Research* 29: 599–604.
- Parkes JP 1981. Hare control in the high country. *What's New in Forest Research* 97: 1–4.
- Parkes JP 1984. Home ranges of radio-telemetered hares (*Lepus capensis*) in a sub-alpine population in New Zealand: implications for control. *Acta Zoologica Fennica* 171: 279–281.
- Parkes JP 2001. Methods to monitor the density and impact of hares (*Lepus europaeus*) in grasslands in New Zealand. DOC Science Internal Series 8. Wellington, Department of Conservation. 13 p.
- Pekelharing CJ 1979. Fluctuation in opossum populations along the north bank of the Taramakau Catchment and its effect on the forest canopy. *New Zealand Journal of Forestry Science* 9: 212–224.
- Prugh LR, Krebs CJ 2004. Snowshoe hare pellet-decay rates and aging in different habitats. *Wildlife Society Bulletin* 32: 386–393.
- Putman RJ 1984. Facts from faeces. *Mammal Review* 14: 79–97.
- R Development Core Team 2009. R: A language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing.
- Rao SJ, Jason GR, Hulbert IAR, Daniels MJ, Racey PA 2003. Tree browsing by mountain hares (*Lepus timidus*) in young Scots pine (*Pinus sylvestris*) and birch (*Betula pendula*) woodland. *Forest Ecology and Management* 176: 459–471.
- Riney T 1957. The use of faeces counts in studies of several free-ranging mammals in New Zealand. *New Zealand Journal of Science and Technology* 38B: 507–532.
- Rodgers AR, Sinclair ARE 1997. Diet choice and nutrition of captive snowshoe hares (*Lepus americanus*): Interactions of energy, protein, and plant secondary compounds. *Ecoscience* 4: 163–169.
- Shoemaker VH, Nagy KA, Costa WR 1976. Energy utilization and temperature regulation by Jackrabbits (*Lepus californicus*) in the Mojave Desert. *Physiological Zoology* 49: 364–375.
- Smith RK, Vaughan Jennings N, Harris S 2005. A quantitative analysis of the abundance and demography of European hares *Lepus europaeus* in relation to habitat type, intensity of agriculture and climate. *Mammal Review* 35: 1–24.
- Wallmo OC, Jackson AW, Hailey TL, Carlisle RL 1962. Influence of rain on the count of deer pellet groups. *Journal of Wildlife Management* 26: 50–55.
- Wilson DJ, McElrea GJ, McElrea LM, Heyward RP, Peach RME, Thomson C 2006. Potential conservation impacts of high-altitude small mammals: a field study and literature review. DOC Research & Development Series 248. Wellington, Department of Conservation. 51 p.
- Wong V, Hickling GJ 1999. Assessment and management of hare impact on high altitude vegetation. *Science for Conservation* 116. Wellington, Department of Conservation. 40 p.

Editorial Board member: Wayne Linklater

Received 22 August 2011; accepted 23 February 2012