HARE NUMBERS AND DIET IN AN ALPINE BASIN IN NEW ZEALAND

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INTRODUCTION

Hares (*Lepus europaeus*) have often been blamed for contributing to accelerated erosion of alpine grasslands in New Zealand (Riney 1957; Logan 1956; Batcheler and Logan 1963; Holloway 1965). In 1962 a three-year joint project by D.S.I.R. and N.Z. Forest Service was started to investigate the effects of red deer (*Cervus elaphus*), chamois (*Rupicapra rupicapra*) and hares on alpine vegetation in Cupola Basin, Nelson Lakes National Park.

The study area of approximately 3,100 acres between Mt Cupola and Mt Hopeless, ranges in altitude from 2,600 to 7,400 ft. Hares were mainly restricted to about 300 acres of north-facing slopes within the basin from about 4,000 to 5,500 ft. The area is well described in the recent Park Handbook (Host 1965). In general it is composed of shattered greywacke with beech forest reaching from the valley floor to 4,500 ft., giving way to alpine grassland without a distinct scrub zone (Fig. 1). Christie (1964) classified the vegetation of the area in three main types which may be summarised with minor changes as follows:

1. Beech forest, dominated by mountain beech (*Nothofagus solandri* var. *cliffortioides*).
2. Shrubland, including mountain beech scrub and a mixed scrub of species such as *Podocarpus nivalis, Coprosma pseudocuneata, Aristotelia fruticosa* and *Hymenanthera alpina.*
3. Alpine grassland, with three major communities, snowgrass (*Chionochloa pallens, Chionochloa flavescens*), short tussock (*Poa colensoi, Festuca mathewsii*), and carpet grass (*Chionochloa australis*); and two minor communities dominated by *Schoenus pauciflorus* and *Chionochloa rubra* respectively.

The rainfall is about 120 inches per annum, and night frosts are common. From June to September the area is normally snow-covered, but isolated heavy falls occurred in all months of the three-year study except January and February. Summer temperatures occasionally reach 70°F.

FIGURE 1. *Cupola Basin showing observation hide, main grassland used by hares with scattered patches of scrub, and bare screes below the 6,500 ft. ridge.*

The aim of the hare study was to find out how many were present, what they ate, and how important this was in relation to the damage caused by other species.

METHODS

Snow tracking

In winter, hare tracks in fresh snow could be followed next day to record the number of bites on each plant eaten. In especially favourable con-

ditions after a little fresh snow had fallen during the night it was possible to count the tracks of hares returning to their forms after a night's feeding and so estimate the number of hares present.

Hide observations

In summer, hares in Cupola Basin were not so strictly nocturnal as they were in winter and could be watched from a hide with 16×56 and 20×60 binoculars from about 3 p.m. to 8 p.m. Each place where a hare had been seen feeding was carefully examined next morning to note the species of plants eaten and number of bites.

Faecal pellets

Hare pellets were counted on various vegetation types in May each year, to investigate their use in assessing the abundance of hares. Two hundred square feet (100 throws of a 1 sq. ft. hoop, and 25 throws of a 4 sq. ft. hoop) were sampled on a 50-yard line through chosen vegetation types in eight localities within the range occupied by hares in Cupola Basin, the same patches of vegetation being sampled each year.

The decay rate was measured of 15 sets of 50 pellets, whose age was known by watching the hares defecating. Three were at Travers Flats (2,000 ft. altitude), two at John Tait Hut (2,600 ft.), and the remainder in Cupola Basin at 4,200 and 4,800 ft. They were left exactly as the animal dropped them, on bare soil or various vegetation types, except that a few pellets were added or removed to make the number up to 50 and surrounding pellets were cleared to avoid confusion.

Samples of fresh pellets were collected each month for food analysis and preserved in 10% formalin. Equal quantities of material from each hare available for that month were mixed thoroughly and a miscroscope slide prepared in Hertwig's mountant (Dusi 1949). The slide was systematically scanned at a magnification of 100× until 300 plant fragments were identified as *Poa colensoi, Chionochloa, Celmisia* or "unidentified" by comparison with reference slides of these plants prepared in the same way. Fragments larger than the microscope field were recorded as two, so that the totals would be roughly proportional to the volumes of the species eaten.

RESULTS

Number of hares

The best estimates of the number of hares in Cupola Basin were probably those made from tracks in overnight snow followed on 16 August 1963 and 31 August 1964 when seven and six hares respectively were counted. There was no evidence that hares moved from Cupola Basin to lower ground in winter. During snowfalls in the beech forest at many times of the year no tracks were found except within about 400 ft. of open grassland, and no pellets were ever found on the two clearings on the obvious route for any hares running between Cupola Basin and the valley floor. Even in 1964 when over 10 ft. of snow fell and the deer left the Basin, hares remained in forms within the bush edge and fed with the chamois on exposed vegetation on cliffs at 5,500 ft. on the face of Mt Cupola.

In summer, the numbers of hares seen from the hide in 19 evening and 24 morning counts were as follows:

	No. hares seen				
	0	1	2	3	4
Evenings	5	3	4	3	4
Mornings	5	9	5	4	1

The different patterns of numbers seen in the evening and morning probably arise from differences in hare behaviour and will be discussed elsewhere. Both series, however, indicate that the maximum number of adult hares present in summer was four. Juvenile hares are very secretive and were not seen from the hide. Since the age ratio of hares in autumn rises to about 50% young of the year (Flux 1964), these adults would be expected to produce about four young, bringing the autumn population to eight.

The number of dead hares on an area provides another clue to the number of animals present. For example, on a 1.5 sq. mile study area in Scotland, with a pre-breeding population of 165 hares (*L. timidus*), I found 82 carcases during the year: in other words there were about twice as many live hares as bodies on the area. The number of dead hares found each year in Cupola Basin were as follows:

	Year of death				
	1961	1962	1963	1964	Total
Adult	3	1	1	6	11
Juvenile (full grown)	2	1	1	0	4

Most hares died in the winter, presumably of starvation as they have no predators, and were found the following summer. It is probably significant that the winters of 1961 and 1964 had far heavier snow than those of 1962 and 1963. The average number of dead hares found per year was

3.8 which, on the basis of the Scottish results, would indicate very roughly 8 live hares present in Cupola Basin.

Faecal pellet counts may be used to assess the number of hares present if the daily production of pellets per hare, the average decay rate, and the number of pellets in the area are known. Two captive hares measured over 24 days averaged 388 pellets each daily (extremes 157 and 603), on a natural diet supplemented with concentrated rabbit food. To check if this level of pellet production held for wild hares in Cupola Basin, five hares were tracked in snow over their whole night's travels and the number of pellets counted. The average per hare was 434 with extremes of 296 and 671. Consequently, the best available estimate was taken to be 410 pellets per hare per day although in such a small, and not necessarily representative, sample the true average might well be anywhere between 300 and 600 per day.

The decay rate of pellets of known age was not correlated with height of vegetation but decay rates decreased markedly with altitude (Fig. 2). Pellets do not usually disintegrate until they are overgrown by vegetation, and this takes far longer at high levels. Moore (1956) makes the comparison vividly: Alpine fescues in the Waimakariri take three years to double in size, whereas rye grass under optimum lowland conditions can do this in a week. Since most of the hare pellets in Cupola Basin lay between 4,200 and 5,000 ft., an average decay time of three years seems the best available estimate from Figure 2, although anything in the range from 6 months to 5 years is possible.

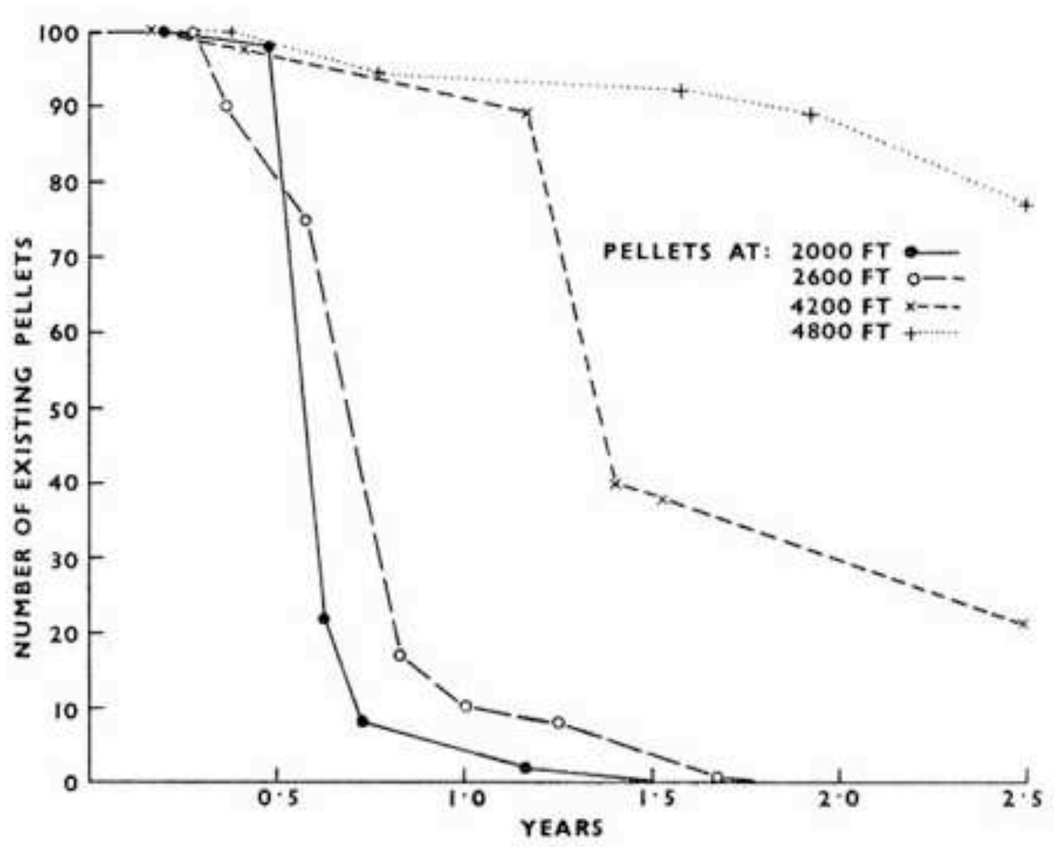

FIGURE 2. *Decay rate of hare pellets at various altitudes.*

Although hare pellets are deposited singly, and not in heaps as are rabbit pellets, they are not distributed at random. They accumulate wherever hares spend the longest time, which may be either at a favoured plant or look-out point. None are produced during the day while the hares are in their forms. Most pellets are produced in the evening as the animals start feeding, so that the distribution of pellets largely coincides with the favoured feeding areas. Pellets were counted on 1,600 sq. ft. of the same patches of vegetation each year. Table 1 illustrates the wide variation in the results, much of which is attributable to random counting errors: compare, for example, Area 3 in 1965 and Area 6 in 1964; and the decline in Area 7

TABLE 1. *Number of hare pellets on various vegetation types each year.*

		NUMBER OF PELLETS PER 100 SQ. FT.					
		1963		1964		1965	
	Vegetation	Size of Frame		Size of Frame		Size of Frame	
Area	Cover	1 sq. ft.	4 sq. ft.	1 sq. ft.	4 sq. ft.	1 sq. ft.	4 sq. ft.
1	*Poa colensoi*	23	16	76	122	43	37
2	Bare scree	0	1	2	0	0	0
3	*Poa* and scree	27	42	55	30	68	27
4	*Poa*, scree and *Hymenanthera*	82	98	151	128	179	119
5	*Poa* and scree	114	105	73	97	74	71
6	Deep *Chionochloa*	6	5	26	61	13	6
7	Deer grazed *Chionochloa*	200	133	53	58	49	40
8	*Chionochloa pallens*, *C. australis*	21	11	18	28	34	36
Total pellets per 800 sq. ft.		473	411	454	524	460	336

* About half of the unidentified material from this hare was *Aciphylla* sp.

is more rapid than the decay rate and hence must be caused by factors other than a reduction in animal use. Of the 0.38 sq. miles of Cupola Basin calculated to be used by hares from a map of their movements, about half was unfavourable habitat (bare scree and deep snow-tussock) which had an average pellet density of 10 per 100 sq. ft. The other half averaged 71 pellets per 100 sq. ft. This gives a total of 4.29 million pellets in the Basin; but, for a guess, the true figure could well be anywhere in the range 2–6 million.

Assuming that pellets last for three years, each hare is represented by $410 \times 365 \times 3 = 448{,}950$ pellets on the ground. Then the 4.29 million pellets in Cupola Basin indicate that an average of 9.5 hares is present. This is very close to the estimate by other methods; but the wide range in each of the measurements used gives no confidence in the result. From the extremes given (300–600 pellets per day; half life of 0.5–5 years; number of pellets 2–6 million) the number of hares in the area could be anything from 2 to 109. To bolster the result with statistical confidence limits would merely be misleading, because several factors which could affect the measurements have not been allowed for. To give but three examples: pellets produced after eating the hairy leaves of *Celmisia* may swell and disintegrate in the first shower of rain; an unknown number of pellets is lost on scree faces and in rivers; and the number of pellets produced daily may vary by a factor of 9:1 on different diets (Cochran and Stains 1961, working on *Sylvilagus*).

TABLE 2. *Number of hare bites on plant species in Cupola Basin, recorded by observation in summer and snow tracking in winter.*

	SUMMER (Oct.–Mar.)	WINTER (Apr.–Sept.)
Aciphylla colensoi		5
Anistome filifolia	16	
Aristotelia fruticosa	1	117
Astelia cockaynei		5
Celmisia allanii		100
Celmisia coriacea		54
Celmisia spectabilis		8
Chionochloa flavescens		547
Chionochloa pallens	160	1063
Chionochloa rubra		2107
Coprosma brunnea		7
Coprosma pseudocuneata		34
Dracophyllum uniflorum		20
Gaultheria depressa	6	1
Hebe pauciramosa		6
Helichrysum selago		5
Holcus lanatus	5	
Hymenanthera alpina	75	
Muehlenbeckia axillaris	1	
Nothofagus solandri var. *cliffortioides*		10
Oreomyrrhis colensoi	29	
Phormium colensoi		1
Pittosporum divaricatum		18
Poa colensoi	12067	5
Schoenus pauciflorus	46	555
Trifolium repens	10	
Viola cunninghamii	1	
Wahlenbergia albomarginata	15	
Unidentified plants	7	10
Soil, roots, etc.		6

Food of hares

The species of plants eaten by hares were recorded on seven days after hide observations of feeding in summer (October to March), and by following 15 miles of tracks on 10 days following fresh snowfalls in winter (April to September). The number of leaves or twigs eaten (Table 2) shows the seasonal change in diet from *Poa* in summer to snowgrass (*Chionochloa*) in winter.

The plants eaten, especially in winter, in general reflected their availability, although *Chionochloa flavescens* seemed to be preferred to *Chionochloa pallens* which is far commoner; and *Poa colensoi* was much preferred to other tussock species, as Cockayne (1919) found for rabbits. Certain species such as *Podocarpus nivalis* and *Phyllocladus alpina*, which are strongly aromatic, were never eaten although abundant, and mountain beech was eaten only on a few days following a 10 ft. snowfall when little else was available. *Podocarpus nivalis*, however, is eaten by chamois in Cupola Basin (Christie 1964), and red deer eat large quantities of *Phormium colensoi*, although it seems unpalatable to hares. Only three times during the study were hares recorded drinking from streams.

Pellets from hares watched defecating were available for analysis from all months except April, June and November. The only items looked for were *Poa colensoi*, *Chionochloa* spp. and *Celmisia* spp. which are reasonably distinct; anything else was classed as "unidentified". The percentage of these items for each month is shown in Table 3, and the complementary nature of the winter and summer diet is illustrated in Figure 3. *Chionochloa* and *Celmisia coriacea* are both available on ridges cleared of snow by the wind, and the abrupt change to *Poa* in October when the snow melts is striking. The hare fur shown in Table 3 is a normal constituent of the diet (Aldous 1935), probably eaten while the animal grooms.

TABLE 3. *Percentage occurrence of food items in 300 microscope fields of view of each monthly sample of hare pellets from Cupola Basin.*

	PERCENTAGE OCCURRENCE									
	Jan.	Feb.	Mar.	May	Jul.	Aug.	Sept.	Oct.	Dec.	Mean
Poa colensoi	67.3	52.6	39.4	4.6	0.9	0	0	61.7	57.7	31.2
Chionochloa spp.	10.4	20.8	23.9	33.5	51.3	51.0	24.9	8.7	5.3	25.8
Celmisia spp.	0	0	0.6	31.7	19.0	12.3	26.4	4.5	3.7	11.0
Unidentified	21.0	24.8	32.7	28.9	28.8	36.8	47.9*	24.8	33.3	31.0
Hare fur	1.2	1.8	3.3	1.2	0	0	0.9	0.3	0.3	1.0
No. hares examined	3	1	2	2	6	6	1	3	3	27

* About half of the unidentified material from this hare was *Aciphylla* sp.

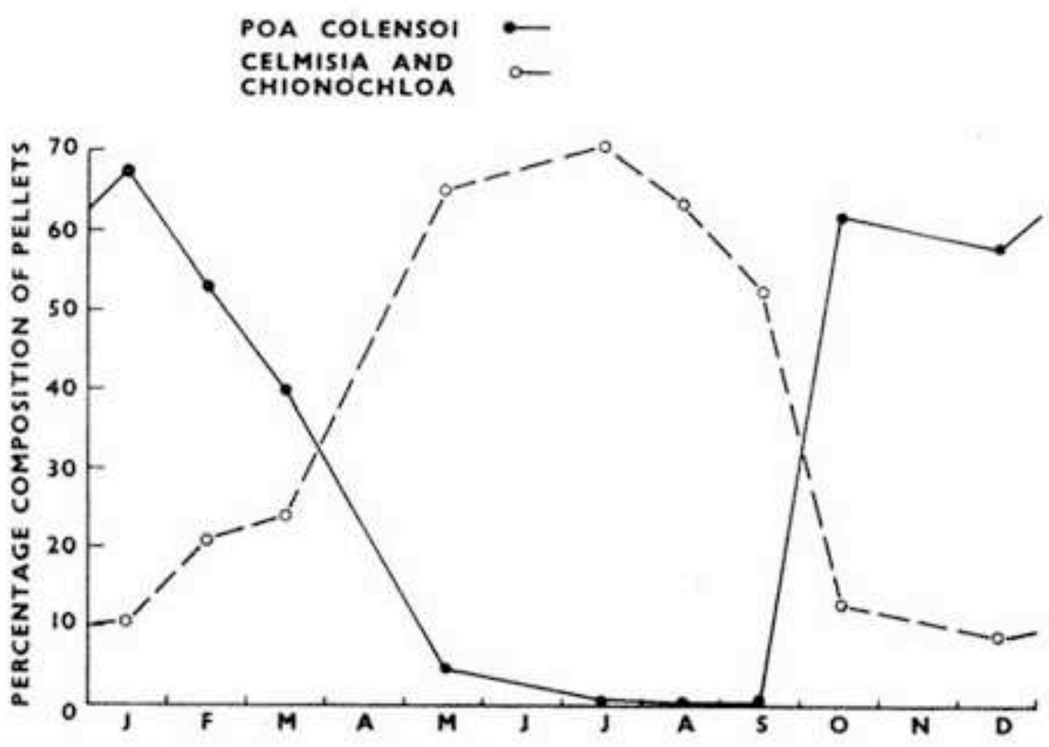

FIGURE 3. *Seasonal change in diet of hares in Cupola Basin from* Chionochloa *and* Celmisia *in winter to* Poa colensoi *in summer.*

To compare the results of the two methods of estimating diet, the "bites" counted must be converted to quantity eaten. Representative weights of the parts of *Poa colensoi*, *Chionochloa*, and *Celmisia coriacea* eaten by hares were in the ratio 14.4:1:0.4 respectively. Using these conversion factors, estimates of the summer diet were similar by both methods, but the proportion of *Chionochloa* to *Celmisia* in winter was higher by field observation than by pellet analysis (Table 4).

TABLE 4. *Comparison of the relative percentage of food items in the diet of hares in Cupola Basin recorded by two methods.*

	PERCENTAGE IN DIET		
	Poa colensoi	*Chionochloa*	*Celmisia*
SUMMER			
Pellet analysis	78	19	3
Field observation	84	16	0
WINTER			
Pellet analysis	2	63	35
Field observation	0	90	10

DISCUSSION

As Taylor and Williams (1956) stress in their careful analysis of the use of pellet counts for estimating rabbit numbers, an accurate knowledge of decay rate is essential. At the rate of decay of *L. californicus* pellets in Kansas (Brown 1947), the number of pellets in Cupola Basin would indicate the presence of over 300 hares! Factors known to affect decay rate include the type of food eaten, ground cover, climate, amount of trampling, and breakdown agents such as invertebrates, bacteria or fungi. To this list may be added altitude, which probably exerts its effect through slower plant and bacterial growth with increasing height, and which has previously been overlooked. For example, Riney (1957) states: "it would be expected, from the decomposing effect of weather on [deer] pellets, that fewer faeces per 100 plots would be found in the higher parts of the drainage where rainfall is much heavier. As more faeces were counted at the higher elevations, there can be little doubt that this indicates a higher concentration of deer in those areas". Since we now know that pellets last six times as long at 5,000 ft. as at 2,000 ft., and this holds for red deer as well as for hare pellets (R. H. Taylor pers. comm.), Riney's conclusion is open to question, and results of many other pellet studies may require reappraisal. In general, to measure the number of pellets on the ground, their decay rate, and the daily production of pellets with the necessary degree of accuracy is so time-consuming and involves so many sources of error that I have more confidence in a direct count of the number of live or dead hares on the area, multiplied by an appropriate factor gained from experience.

Casual observations of plants eaten by hares may give a misleading impression of their relative importance in the diet. For example, *Hymen-*

anthera alpina is very palatable and all the bushes in Cupola Basin are severely hedged, yet it is not a major food item. This plant shows bite marks readily and grows very slowly — one protected from hares produced shoots less than one inch long during a year. Hares rarely kill such hedged plants although they take most of the current growth year after year (Fig. 4). On the other hand, it may be argued that more palatable and less resistant species have already disappeared. Plant palatability to grazing mammals varies with a host of factors (see Tribe and Gordon 1950) and it is not likely that the list for Cupola Basin is valid in other areas, or even in the same area with hares at different densities, or in different years. For example, no hares ate *Chionochloa rubra* during the first two years of the study, but in Table 2 this species heads the list of snow tussocks because in the following winter two hares ate over 2,000 leaves in one night. Neither is it safe to argue from the preferences of penned animals: three captive hares ate mountain beech avidly, but wild hares in Cupola Basin ignored it almost completely, although McConochie (1966) records a hare eating large numbers of beech seedlings in a neighbouring forest.

Hares bite through large plants such as snow-grass about six inches above ground level, and eat from there towards the leaf tip, which is often discarded. Only once in hot weather was a hare found eating the lower, more succulent stalks of *Chionochloa* to within an inch of the ground. After nibbling a few leaves the animal moves on to the next tussock, and this does relatively little harm to the plant. *Poa* and fine grasses may be eaten from the top down, although hares seldom graze as closely as rabbits do, and nowhere in Cupola Basin did they establish a short turf. The seed heads of *Poa* are particularly favoured by hares, but whether this assists in, or limits, the spread of *Poa* would be difficult to discover. Weight for weight of vegetation eaten, hares almost cer-

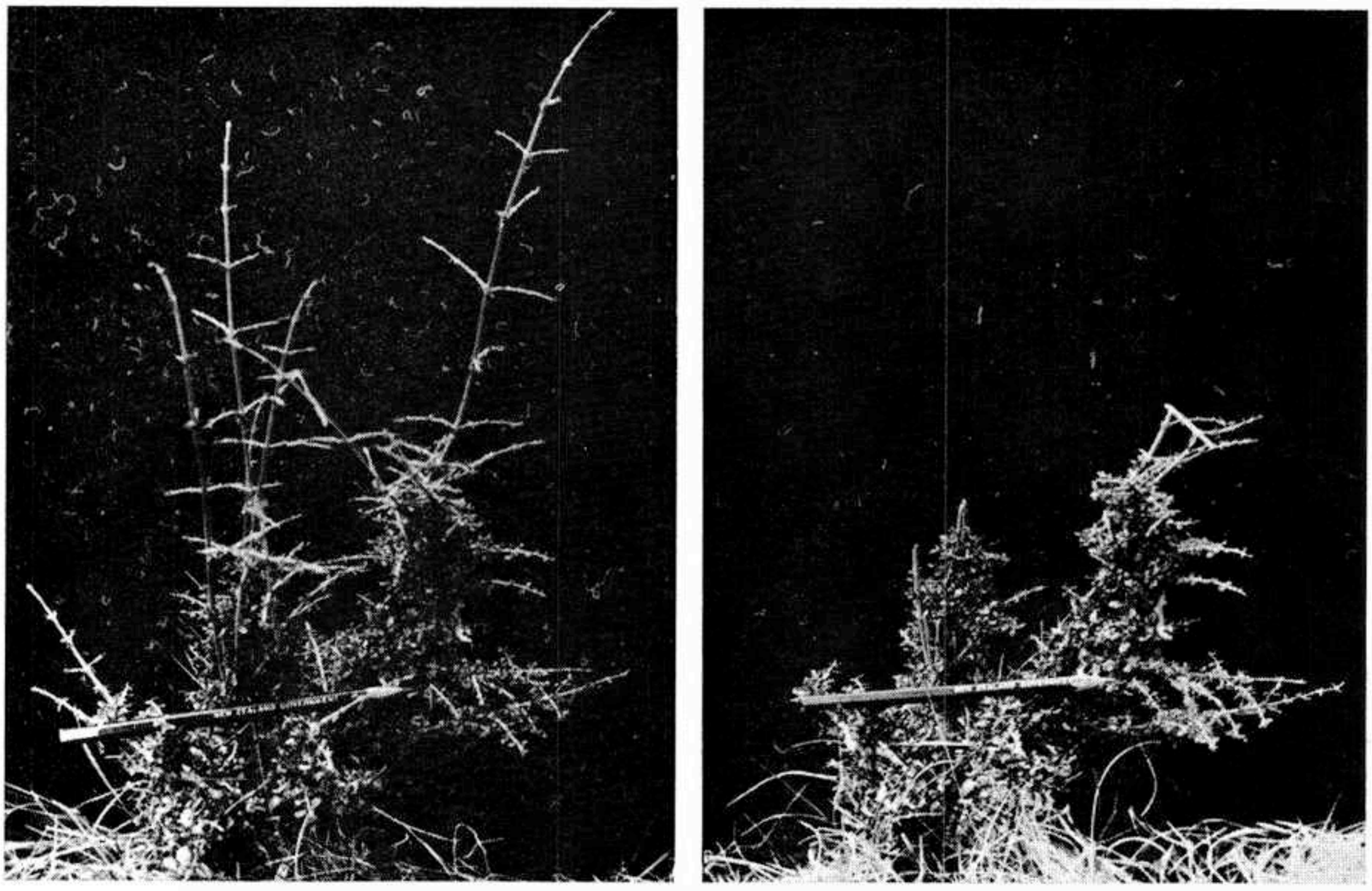

FIGURE 4. Coprosma parviflora *scrub at 2,600 ft. in Travers Valley showing summer growth (May, left) before removal by hares overwinter (November, right).*

tainly do less damage than deer or chamois, which tend to pull tussocks out by the roots and cut the soil with their hooves. Since, in America, somewhere between 5.8 (Currie and Goodwin 1966) and 30 (Vorhies and Taylor 1933) *L. californicus* eat as much vegetation as one sheep, we may assume the eight hares in Cupola Basin are having little effect relative to the 40–60 deer and chamois present: the damage they cause could be relieved by shooting one deer. In areas like the Harper and Avoca watersheds, however, where deer have been severely controlled and hares are far more numerous, they could have a significant effect on the vegetation as Holloway (1965) suggests, although Batcheler and Logan (1963) report satisfactory regeneration despite the high number of hares.

SUMMARY

The number of hares (*Lepus europaeus*) and their diet above the tree line in a 3100-acre basin at 4000–6000 ft. were assessed by tracking in snow, observing from a hide, and counting and analysing faecal pellets. About 8 hares lived on 300 acres of north-facing slopes, feeding chiefly on *Chionochloa* tussock and shrubs in winter and *Poa colensoi* in summer. These are dominant species of the grassland and hares are causing little damage relative to the 40–60 deer (*Cervus elaphus*) and chamois (*Rupicapra rupicapra*) present. The decay rate of faecal pellets decreased with altitude from a half-life of 7 months at 2000 ft. to over 3 years at 5000 ft. Population assessment by pellet counts involved so many variables and unknowns that it was better to count the hares, or their tracks or carcases, directly.

ACKNOWLEDGMENTS

I am very grateful to Dr. P. C. Bull, project leader, for overcoming problems of administration; to Mr. A. H. C. Christie and Mr. C. M. H. Clarke for identifying plants; to Messrs. I. R. Fryer, R. G. Keightley, R. E. R. Porter and G. D. Ward for assistance in the field; and to Mr. G. Lyon and the Nelson Lakes National Park Board for transport on Lake Rotoiti and the use of Park facilities. Dr. J. A. Gibb and Mr. R. H. Taylor made helpful comments on the text.

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