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RECOVERY OF NORTHERN FIORDLAND ALPINE GRASSLANDS AFTER REDUCTION IN THE DEER POPULATION

Summary: A significant recovery of food plants preferred by introduced deer *(Cervus elaphus)* occurred between 1969 and 1984 on 57 permanent plots in the alpine grasslands of northern Fiordland. During this period the deer population was reduced markedly by hunters operating from helicopters.

Deer showed a strong preference for grasslands characterised by *Chionochloa pallens* and large-leaved herbs. These occur on fertile soils, and have shown the most recovery, especially at low altitude *(c.* 900-1100 m a.s.l.). Little change occurred in the less-favoured grasslands characterised by *C. crassiuscula* and *C. acicularis* on infertile soils.

Several studies suggest the vegetation preferred by deer was some of the best former habitat of the takahe *(Notornis mantelli),* an endangered rail. Little competition from deer would now occur if takahe were reintroduced on to these sites, providing intensive aerial hunting continued.

Keywords: tussock grasslands; browsing damage; wildlife management; red deer; wapiti; takahe; hunting; Fiordland; Notornis mantelli; Cervus elaphus nelsonii; Cervus elaphus scoticus

Introduction

Until the period of European settlement, the alpine grasslands of northern Fiordland were browsed only by flightless indigenous birds (Mills, Lavers and Lee, 1984) and invertebrates. However, by the 1930s interbreeding populations of wapiti *(Cervus elaphus nelsonii)* and red deer *(C.e. scoticus)* were present, having been liberated for recreational hunting in the early part of this century (Nugent, Parkes and Tustin, 1987). Damage to the grasslands was reported as deer numbers rose (e.g., Poole, 1951), and by the late 19605, high levels of deer had strongly modified grassland composition and structure (G.R. Evans, unpubl.).

Commercial aerial hunting of red deer and hybrids began in the study area (Fig. 1) in 1973, rapidly reducing animal numbers and initiating vegetation recovery (Nugent *et al.,* 1987; G.R. Evans, unpubl.). Continued hunting, including recent live' capture of wapiti, has reduced current deer numbers in the alpine grasslands to near zero.

The effects of high numbers of deer, and of their subsequent reduction, have been measured in three grassland surveys by the Forest Research Institute. Permanent plots were established throughout northern Fiordland in 1969, when animal numbers were high, and were remeasured in 1975, soon after the onset of commercial hunting (G.R. Evans, unpubl.). A further remeasurement of a subset of these plots within the central range of the wapiti herd (the central Wapiti Area, Fig. 1) in 1984 provided the opportunity to assess the recovery patterns after II years of intensive aerial hunting.

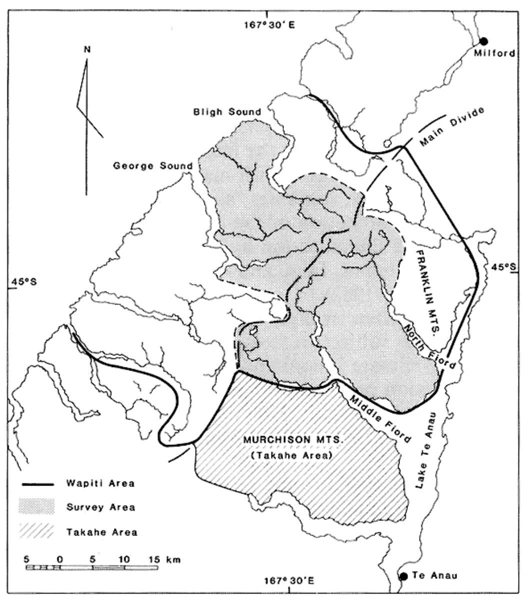

Figure 1: *Location of the survey area.*

The takahe *(Notornis mantelli),* an endangered rail, was once widespread in the study area, but is currently almost totally restricted to the Murchison Mountains to the south (Lavers *et al.,* 1980; Fig. I). Competition from deer for food, particularly snow tussocks *(Chionochloa*[1] spp.), was first implicated by Kean (1956) as contributing to the takahe's demise. Other studies on diet and habitat use by deer or takahe also show an overlap in preferred foods (Mason, 1951; Mills and Mark, 1977; Lavers, 1978; Lavers *et al.,* 1983; Mills *et al.,* 1984; Evans, unpubl.). After identifying a high proportion of good quality potential takahe habitat in the study area, and with the drastic reduction in deer numbers, the New Zealand Wildlife Service has advocated the reintroduction of captive-reared takahe into the area (e.g., Lavers *et al.,* 1980). Recreational hunters have concurrently advocated the reintroduction of a wapiti herd (e.g., Bamford, 1985). A further objective of our study was, therefore, to assess the recovery of preferred foods of takahe, and to comment on the implications for takahe management.

Study Area

The central Wapiti Area of Fiordland National Park consists of *c.* 85 000 ha of deeply dissected upland, with peaks rising to over 1800 m (Fig. 1).

The main rocks are highly indurated gneiss, granite, and granodiorite, which are resistant to physical and chemical weathering. The alpine landscape strongly reflects the impact of Pleistocene and Holocene glaciations, with many ice-cut benches and bedrock slopes, moraines, and cirque basins. Subsequent modification of the landscape by mass movement and fluvial action has resulted in landforms such as debris cones, fans, and block fields (Wood, 1960; McKellar, 1982).

Soils are often strongly developed and infertile except on sites subject to frequent deposition of fresh debris. The climate is cool and humid, with much of the preciptation occurring in early summer. Annual rainfall increases from *c.* 3000 mm in the east to 6000 mm in the west (New Zealand Meteorological Service, 1983).

The alpine zone is most extensive in central regions near the main divide and in the east, where the grasslands extend from the *Nothofagus* timberline *(c.* 900-1200 m) to about 1500 m a.s.l. Their distribution is frequently interrupted by steep, bare, bedrock slopes. In the west the topography is of lower relief and the alpine grasslands are confined to the few ridges which rise above timberline.

The alpine grasslands are dominated by five species of snow tussock: *Chionochloa crassiuscula, C. pallens, C. flavescens, C. acicularis,* and *C. oreophila. C. ovata,* a species endemic to Fiordland, also occurs as a minor component. Near timberline the grasslands merge with a narrow, discontinuous belt of subalpine shrubland containing genera such as *Dracophyllum, Coprosma,* and *Olearia*. Fellfield and cushion herb field genera such as *Phyllachne, Donatia* and *Oreobolus* are prominent near the upper limits of grassland.

Methods

One hundred and seventy-four permanent grassland plots were established throughout northern Fiordland in the 1969-70 summer (1969 survey) and were remeasured in 1975-76 (1975 survey). The plots were spaced at 61 m (200 ft) altitudinal intervals along lines whose origins had been chosen on a restricted random basis and had been marked on aerial photographs.

Before the 1984 survey the major grassland types on the 174 plots were identified by an agglomerative clustering technique (Allen, Rose and Evans, 1983; Hall and Allen, 1985). Eighty-six of the original plots were in the restricted area surveyed in 1984, and 57 of these, covering the range of grassland types, were selected for remeasurement (Fig.1). Priority was given to those containing *Chionochloa pallens* or *C. flavescens,* preferred foods of both deer and takahe (e.g., Mills and Mark, 1977). Plots were also chosen for ease of access on foot from base camps established using a helicopter.

The following measurements were recorded on the standard FRI 20 x 20 m plots (Allen *et al.,* 1983):

1. Specific frequency (percent frequency of occurrence) in 50 circular subplots of 15 cm diameter located at 40 cm intervals along a 20 m transect running through the centre of each plot. Two transects not found in 1975 were remeasured in 1984.
2. Percent frequency of bare ground as a first point intercept at 40 cm intervals along the 20 m transect.
3. Top cover of vegetation and bare ground. Stereo pairs of colour transparency photographs, taken from a height of c. 1 m and parallel to the slope and contour, were repeated at eight random but permanently fixed photocentres on 23 of the plots (poor weather prevented photographing at the rest of the plots). Each photograph covered an area of about 1 m^2. Only one photograph from

[1]Nomenclature follows Allan (1961), Dawson (1961, *Anisotome),* Zotov (1963, *Chionochloa),* Moore and Edgar (1970), Connor and Edgar (1979, *Rytidosperma),* and Given (1984, *Celmisia verbascifolia).*

each stereoscopic pair was required for analysis in this study.

4. Tussock stature (maximum extended leaf length) of the tussock of *Chionochloa pallens* or *C. flavescens* nearest the photocentre and of its nearest conspecific neighbour. Tussock stature was not recorded in 1969.
5. Deer density index, calculated from the presence of intact faecal pellets in 10 randomly located circular subplots on each plot. The index allows for different subplot diameters (1.26 m in 1969 and 1975 and 1.14 m in 1984; Baddeley, 1985; Nugent *et al.,* 1987).
6. Site factors. Altitude, aspect, slope, drainage, and landform.

Specific frequency data from the 1984 survey were used to refine the initial classification of the 57 plots. The composition and site factors of the resulting four main grassland types were then summarised and compared (Allen *et al.,* 1983; Hall and Allen, 1985).

Changes in specific frequency, bare ground, cover, tussock stature, and deer density index between surveys were examined for each grassland type. The mean specific frequencies of selected visually conspicuous species, species recognised as preferred by deer or takahe (see Table 4), and the frequency of bare ground were compared between the three surveys using analysis of variance (ANOVA) and Duncan's new multiple range test after arcsine square root transformation (Wilson, 1979). Mean tussock stature was compared between 1975 and 1984 using ANOVA.

For each photocentre a single transparency was projected, with the length of the diagonals of the image adjusted to 66 cm. The earlier surveys' images were compared against the 1984 image, using two slide projectors. Percentage cover classes for six vegetation categories and proportion of bare ground were visually estimated, requiring consensus between the same two observers throughout. Classes were: 1 = < 1% or apparently absent; 2= 1- 5%; 3=6-25%; 4=26-50%; 5=51-75%; 6= 76-100%. Reference cards showed the area of each class. If a change in cover was marginal or disputed, the class indicating 'no change' between surveys was assigned. Where images were not comparable, for example because of poor lighting, the photocentre was abandoned for all three surveys.

The categories used for cover analysis were:

TUSSOCKS: mostly species of *Chionochloa,* but including tall sedges or rushes such as *Schoenus pauciflorus* or *Marsippospermum gracile.*

DICOTS: the large-leaved dicotyledonous herbs *Anisotome haastii, Ranunculus lyallii, R. buchananii, Senecio lyallii, S. scorzoneroides, Ourisia macrophylla, O. macrocarpa, Geum parviflorum,* and *G. uniflorum.*

CELMISIA: visually conspicuous and other readily indentifiable species of this genus (*C. walkeri,* C. *verbascifolia, C. ramulosa, C. petriei, C. du-rietzii, C. holosericea, C. bonplandii*).

SHRUBS: *Coprosma cheesemanii,* C. *crenulata,* C. *pseudocuneata, Hebe odora, H. hectori, Dracophyllum uniflorum, D. menziesii, Gaultheria crassa, Olearia crosby-smithiana,* O. *colensoi.*

MAT: low growing species, including bryophytes, many of which were not readily distinguished or identifiable (e.g., *Poa colensoi/ Rytidosperma setifolium).*

LITTER: dead plant material not attached to living plants. Leaf tip dieback of *Chionochloa* species, which shows considerable seasonal variation, was included in TUSSOCKS.

BARE: bare soil or rock, also recorded individually.

Cover was also recorded for individual species in the DICOTS, CELMISIA and SHRUBS categories, but not for TUSSOCKS because of difficulty in distinguishing *C. pallens* from *C. crassiuscula.* In cool, moist weather *C. crassiuscula* leaves resembled those of *C. pallens* because they were no longer curled. When *C. pallens* was heavily grazed its stunted habit resembled that typical of *C. crassiuscula.*

The data from cover analysis formed a 3 (surveys) x c (cover classes, up to six) frequency table for each vegetation category and bare ground. Changes in cover and bare ground were then analysed by the X^2 or G test of independence. A repeat scoring, by the same two observers, of 55 randomly selected images from the 1984 survey indicated a high degree of consistency, varying from $0.1 < p < 0.5$ for LITTER and BARE to $0.975 < p < 0.995$ for TUSSOCKS and CELMISIA.

Results

Composition and distribution of the grassland types

Four major grassland types identified from cluster analysis of the 1984 transect data accounted for 51 of the 57 plots. Type PC1 (*Chionochloa pallens - C. crassiuscula - C. flavescens* grassland) consisted mainly of stands where *C. pallens* was dominant, or co-dominant with *C. crassiuscula* but also included some stands dominated by C. *flaveseens*. Type PC2 (*C. pallens - C. erassiuseula - Celmisia du-rietzii)* was dominated by *C. pallens, C. crassiuseula* or a mixture of both species, and included a few stands dominated by *C. oreophila*. Types CA1 (*C. erassiuseula - C. aeieularis - C. flaveseens)* and CA2 (*C. crassiuseula* - C. *acieularis - Donatia novae-zelandiae*) were usually dominated by C. *erassiuseula* (Table 1).

Table 1: *Mean specific frequency of species with ≥10% frequency in at least one type on transects in the four major grassland types in 1984 (+ = <1%).*

Grassland type	PC1	PC2	CA1	CA2
Number of transects	17	13	14	7
Species most frequent in types PCI and PC2				
Poa colensoi	36	38	9	3
Chionochloa pallens	35	28	4	0
Anisotome haastii	17	13	8	1
Microlaena colensoi	16	10	4	0
Celmisia walkeri	16	9	3	+
Bulbinella gibbsii ssp. *balanifera*	15	9	+	+
Senecio Iyallii	13	10	+	+
Uncinia divaricata	9	14	3	0
Craspedia uniflora	6	13	1	0
Species most frequent in types CA1 and CA2				
Chionochloa crassiuscula	22	35	69	78
Astelia linearis	7	9	49	33
Chionochloa acicularis	+	+	13	6
Pentachondra pumila	0	+	16	42
Oreobolus impar	+	+	6	26
Forstera sedifolia	3	3	16	22
Drapetes dieffenbachii	+	+	8	12
Species most frequent in type PC1				
Oxalis lactea	27	11	+	0
Coprosma cheesemanii	25	+	15	+
Blechnum penna-marina	14	1	+	0
Gentiana spp.	14	1	9	4
Chionochloa flavescens	13	+	6	1
Pratia angulata	11	+	+	0
Species most frequent in type PC2				
Coprosma pumila	7	49	19	18
Celmisia du-rietzii	+	36	2	1
Oreomyrrhis colensoi	4	36	1	0
Anisotome flexuosa	+	21	6	+
Rytidosperma setifolium	+	20	+	+
Celmisia verbascifolia	3	19	+	+
Wahlenbergia albomarginata	+	10	+	0
Species most frequent in type CA1				
Celmisia petriei	3	+	24	8
Dracophyllum kirkii	0	+	10	2

Table 1 Cont.

Grassland type	PC1	PC2	CA1	CA2
Number of transects	17	13	14	7
Species most frequent in type CA2				
Celmisia glandulosa	+	+	2	47
Donatia novae-zelandiae	0	0	1	39
Drosera stenopetala	+	0	2	38
Oreobolus pectinatus	0	0	+	21
Celmisia graminifolia	5	+	+	19
Drosera arcturi	0	0	+	14
Hemifues suffocata	0	0	+	14
Cyathodes pumila	0	0	+	12
Rytidosperma nigricans	+	0	+	12
Carpha alpina	+	0	4	11
Other species				
Schoenus pauciflorus	44	12	33	44
Caltha novae-zelandiae	2	19	2	14
Gaultheria depressa	2	13	13	1
Euphrasia zelandica	4	10	7	6
Lycopodium fastigiatum	3	12	18	17
Myrsine nummularia	8	0	11	2

Table 1 highlights the importance of *C. pallens* and *C. acicularis* in the classification, with one virtually restricted to type PC and the other to CA. Fifteen other common species showed similar patterns. For example, *Poa colensoi, Microlaena colensoi, Bulbinella gibbsii* ssp. *balanifera,* and *Celmisia walkeri* characterised types PC1 and PC2. *Astelia linearis, Pentaehondra pumila, Oreobolus impar, Forstera sedifolia,* and *Drapetes diejjenbaehii* were virtually restricted to types CA1 and CA2.

Type PC1 was distinguished from all other types by high frequencies of *Blechnum penna-marina* and *Pratia angulata,* and type PC2 by *Celmisia du-rietzii, Oreomyrrhis colensoi, Anisotome flexuosa, Rytidosperma setifolium, Celmisia verbaseifolia,* and *Wahlenbergia albomarginata*. Type CA1 was distinguished by *Celmisia petriei* and *Draeophyllum kirkii,* and CA2 by low-growing and mat-forming species like *Donatia novae-zelandiae, Drosera arcturi* and *Carpha alpina*.

Type PC grasslands occurred almost exclusively on well-drained soils derived from talus on alluvial fans, debris cones, and colluvial sideslopes (Tables 2 and 3). Such sites typically have an active drift regime causing soil rejuvenation. In contrast, type CA grasslands were markedly more common than PC on stable landforms, such as interfluves or sideslopes on strongly indurated bedrock. The quality of drainage was poorer on these landforms, and type CA2 was

Table 2: *Proportion (%) of plots of the four main grassland types on various landforms.*

	Grassland type			
	PC1	PC2	CA1	CA2
Number of plots	17	13	14	7
Alluvial fan and debris cone	65	15	0	0
Colluvial sideslope	29	77	57	43
Interfluve	0	0	36	29
Bedrock sideslope	6	8	7	28

Table 3: *Proportion (%) of plots of the four main grassland types by drainage class.*

	Grassland type			
	PC1	PC2	CA1	CA2
Number of plots	17	13	14	7
Good	82	92	64	14
Moderate	12	8	21	29
Poor	6	0	14	57

seldom present on well-drained sites (Table 3). These differences in drainage were partly a function of slope angle. Although types PC and CA occurred over a similar range of slopes (0-50∞), type CA was more common on slopes of 20∞ (50% of plots) than type PC (16%).

Type PC1 generally occurred at lower elevations than type PC2 (mean elevation 1017 and 1107 m a.s.l. respectively). Similarly, type CA2 (1034 m a.s.l.) tended to occur at lower elevation than type CA1 (1100 m a.s.l.). All types occurred over a wide range of aspects.

Use of vegetation types by deer

Deer were widespread and numerous in the alpine grasslands in 1969 and clearly preferred types PC1 and PC2 (Fig. 2). However, 2 years of aerial hunting had significantly lowered deer numbers by 1975 (Nugent *et al.,* 1987). Preferences for vegetation types were similar, but less obvious in 1975. Least use was made of CA2 grasslands, and PC1 grasslands were more preferred than CA1. An apparently larger decrease in use of PC2 grasslands than PC1 grasslands between 1969 and 1975 may have reflected the increasing vulnerability of deer with increasing distance from the shelter of timberline forest. No deer pellets were recorded in the grasslands in 1984, indicating a continued decrease in browsing pressure (Nugent *et al.,* 1987).

Overall changes on the transects

The main feature of the 55 transects measured in all three surveys was a large increase between 1969 and 1984 in the frequencies of the large-leaved herbs *Anisotome haastii, Celmisia verbascifolia, Gentiana* spp., and *Senecio lyallii/S. scorzoneroides* (Table 4). Similar, but less significant trends occurred for *Aciphylla takaheal A. lyallii,* and *Celmisia petriei,* as well as for *Coprosma cheesemanii, Microlaena colensoi,* and *Ranunculus lyallii.* Most of the largest increases occurred between 1975 and 1984, the period when deer numbers declined to near zero. The frequency of *Ourisia macrophyllala. macrocarpa* was lowest in 1975, possibly reflecting depletion by deer between 1969-1975 and subsequent recovery. Little

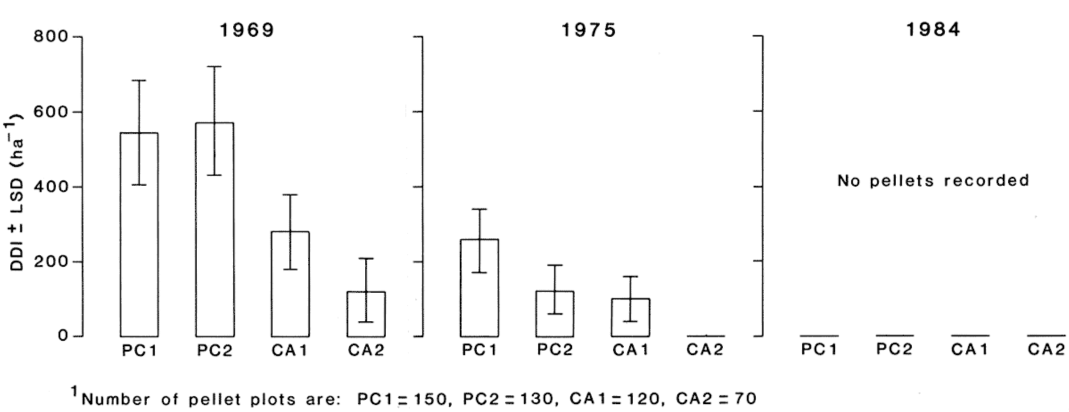

Figure 2: *Deer density index (DDI ±LSD) by grassland type, calculated from the frequency of intact faecal pellets. For DDI = 0, LSD varies from* 6-13 *ha.*

change occured in the frequencies of all four snow tussocks and bare ground.

Changes within each grassland type

(a) Transects

The plants showing marked changes in overall frequency were also those which changed markedly within vegetation types (Table 5). By far the most significant increases occurred in PCI grasslands, affecting *Aciphylla takahea/A. Iyallii, Anisotome haastii, Celmisia verbascifo/ia,* and *Gentiana* spp. *Senecio Iyallii/S. scorzoneroides,* and *Ourisia macrophylla/O. macrocarpa* were least frequent in 1975.

The only other increases which approached or reached significance were: *Celmisia verbascifolia* in PC2, *Aciphylla Iyallii* in CAI, and *Gentiana* spp. in CA2. Although the frequency of *Celmisia petriei* showed an upward trend in types PCI and CAI, neither change was significant. In addition to the 20 taxa tested in Table 4, no change was recorded for *Astelia nivicola* in PC2 or *Dracophyl/um uniflorum/D. kirkii* in CAI.

(b) Photocentres and tussock stature

The most significant changes in cover also occurred in type PCI (Table 6). In 1969 the average cover of TUSSOCKS was about 50070 in this type. Significant recovery was evident by 1975, and by 1984 tussock cover was over 75% at most photocentres (Fig. 3). Between 1975 and 1984 the mean maximum extended leaf length of *Chionochloa pallens* increased by about 50% and of C. *flavescens* by almost 20% (Table 7). The cover of mCOTS (mainly *Anisotome haastii* and *Ranunculus Iyallii)* was less than I % on almost all photocentres in both 1969 and 1975, but by 1984 establishment of new plants and an increase in size of existing plants resulted in a significant increase in cover (Table 6, Fig. 3). Overtopping by TUSSOCKS was mainly responsible for decreases in MAT, LITTER, and BARE, and sometimes mCOTS were also obscured. The decrease in BARE was also caused by invasion by MAT species such as *Poa colensoi* and *Rytidosperma setifolium*. Cover of CELMISIA (mainly C. *petriei* and C. *walkeri)* in PCl showed little change. C. *verbascifo/ia,* which increased in frequency, was a minor cover component.

In PC2 grasslands, the mean maximum extended leaf length of *Chionochloa pallens* increased by about 30% between 1975 and 1984, but was not reflected in increased cover of TUSSOCKS (Tables 6, 7). The

Table 4: *Overall changes in mean specific frequency (%) of selected taxa and bare ground on 55 transects measured in* 1969, 1975 *and* 1984. [1]*n = number of transects on which a taxon has occurred.* [2]*Results of analysis of variance after arcsine square root transformation.* [3]*Within a row means which are significantly different are indicated by different letters (Duncan's new multiple range test on transformed data, p = 0.01)*

	n[1]	1969 $\bar{x}$	1975 $\bar{x}$	1984 $\bar{x}$	F[2]	P[2]
Anisotome haastii	44	11.44a[3]	9.4a	19.9b	6.2	0.01
Celmisia verbascifolia	36	5.2a	4.7a	11.3b	5.9	0.01
Gentiana spp.	46	4.7a	6.6a,b	10.4b	7.4	0.01
Senecio lyallii/S.scorzoneroides	45	9.la	6.8a	15.lb	6.7	0.01
Ourisia macrophylla/O. macrocarpa	20	6.0a	1.3b	4.5a	8.2	0.01
Celmisia petriei	27	11.9	11.3	19.5	3.2	0.05
Aciphylla takahea/ A. Iyallii	30	3.3	4.9	6.9	3.3	0.05
Coprosma cheesemanii	31	14.9	16.2	23.1	1.6	NS
Microlaena colensoi	36	10.9	15.3	17.3	1.5	NS
Ranunculus Iyallii	18	2.9	1.8	4.7	2.5	NS
Bulbinella gibbsii ssp. *balanifera*	39	19.3	12.7	13.1	1.0	NS
Celmisia du-rietzii	25	21.1	21.4	26.9	0.5	NS
Celmisia walkeri	28	24.1	22.2	28.1	0.3	NS
Chionochloa acicularis	16	22.3	22.0	25.3	0.1	NS
Chionochloa crassiuscula	49	45.9	44.8	51.5	0.7	NS
Chionochloa flavescens	20	24.0	25.5	28.8	0.2	NS
Chionochloa pallens	39	21.6	27.3	29.4	1.4	NS
Craspedia uniflora	25	17.4	13.3	21.9	0.6	NS
Geum unifiorumlG. parviflorum	19	5.4	4.5	7.4	1.0	NS
Schoenus pauciflorus	50	33.4	31.2	38.4	1.5	NS
Bare ground	55	5.9	5.4	5.1	0.2	NS

Table 5: Changes in mean specific frequency (0/0) of selected taxa by grassland type on transects measured in 1969, 1975 and 1984. [1]n = number of transects on which a taxon has occurred. [2]Results of analysis of variance after arcsine square root transformation. [3]Within a row means which are significantly different are indicated by different letters (Duncan's new multiple range test on transformed data, p=0.01)

	N[1]	1969 $\bar{x}$	1975 $\bar{x}$	1984 $\bar{x}$	F[2]	P[2]
TYPE PC1						
Aciphylla takaheal A. lyallii	8	0.5a[3]	0.5a	4.0b	9.9	0.01
Anisotome haastii	15	9.2a	8.0a	22.5b	6.1	0.01
Celmisia verbascifo/ia	13	1.2a	1.9a	4.5b	6.0	0.01
Gentiana spp.	16	6.8a	10.5a,b	15.3b	5.4	0.01
Ourisia macrophyllala. macrocarpa	10	4.8a	0.8b	3.6a,b	6.8	0.01
Senecio lyallii/S.scorzoneroides	17	10.7a,b	7.5a	19.7	5.0	0.05
Celmisia petriei	7	9.7	10.3	17.7	0.5	NS
TYPE PC2						
Celmisia verbascifo/ia	13	11.1	9.4	20.9	3.6	0.05
Aciphylla takahea/A. lyallii	5	15.2	5.6	19.2	0.0	NS
Anisotome haastii	10	14.0	10.6	22.0	2.2	NS
Gentiana spp.	7	4.3	4.3	4.0	0.0	NS
Senecio lyallii/S.scorzoneroides	11	13.8	8.6	18.0	1.0	NS
TYPE CA1						
Aciphy//a lya//ii	12	1.5a	4.8a,b	5.5b	4.4	0.05
Anisotome haastii	11	9.5	8.7	13.8	0.5	NS
Celmisia petriei	11	14.0	14.9	24.6	2.0	NS
Gentiana spp.	12	4.0	6.8	10.5	2.8	NS
Senecio lya//ii/S.scorzoneroides	9	5.8	4.9	9.3	1.9	NS
TYPE CA2						
Gentiana spp.	5	0.8	2.8	7.2	4.8	0.05
Celmisia petriei	6	7.7	4.3	12.0	2.5	NS

trend of increasing frequency of preferred herbs in this type was, however, reflected in a significant increase in cover of DICOTS (mainly *A. haastii, R. lyallii,* and *Senecio lyallii,* Fig. 4). The dominant species of CELMISIA were C. *du-rietzii* and *C. verbascifolia,* and the increase in this category (Table 6, Fig. 4) was almost solely the result of establishment and growth of *C. verbascifolia,* which also doubled on the transects. Little change occurred in MAT, LITTER, or BARE in this type.

In CA1, a significant increase in cover of DICOTS (Table 6) was mainly the result of an increase in size of *Anisotome haastii,* a species which showed an increasing trend on the transects. The decrease in LITTER may partly reflect a small, non-significant increase in TUSSOCKS, although extended leaf length of *Chionochloa flavescens* changed little between 1975 and 1984 (Table 7). No change was recorded for CELMISIA (mainly *C. petriet),* MAT, SHRUBS (mainly *Dracophyllum uniflorum),* or BARE.

Little change in cover was recorded for type CA2, apart from a marginally significant decrease in MAT (Table 6).

Discussion

In 1969, the large numbers of deer using the alpine grasslands showed a strong preference for grassland types PC1 and PC2. These types naturally contain the highest diversity and biomass of preferred food plants, including the snow tussocks *Chionochloa pallens* and *C. flavescens,* and large-leaved herbs such as *Anisotome haastii* and *Celmisia verbascifolia*. These plants were heavily browsed, were reduced in size, and may have been eliminated on some sites. Diet studies in Fiordland and elsewhere have similarly concluded that snow tussocks and large herbs are major components of deer diet in alpine grasslands (Gibb and Flux, 1973; Lavers, 1978; Lavers *et al.,* 1983).

By the 1975 survey, 2 years of aerial hunting had significantly lowered the browsing pressure. Although the type PC grasslands were still preferentially browsed, the initial stages of recovery were also most apparent here, largely involving vegetative regrowth of preferred snow tussocks. At this stage, large herbs had shown little response.

Table 6: *Changes in six vegetation categories and bare ground on photocentres measured in 1969, 1975 and 1984. See also Figs. 3 and 4.*

Grassland Type	Cover Category	X^2	df	p<	Direction of change
PC1	TUSSOCKS	24.5	6	0.01	increase
(n = 60)	CELMISIA	0.8	2	NS	
	DICOTS	25.7	2	0.01	increase
	MAT	28.6	6	0.01	decrease
	SHRUBS	0.8	2	NS	
	LITTER	17.5	4	0.01	decrease
	BARE	9.4	2	0.01	decrease
PC2	TUSSOCKS	6.0	10	NS	
(n = 79)	CELMISIA	17.7	6	0.01	increase
	DICOTS	21.8	2	0.01	increase
	MAT	6.9	10	NS	
	SHRUBS	N/A			
	LITTER	6.4	4	NS	
	BARE	2.7	6	NS	
CA1	TUSSOCKS	2.8	4	NS	
(n = 51)	CELMISIA	0.8	4	NS	
	DICOTS	27.5	2	0.01	increase
	MAT	4.4	6	NS	
	SHRUBS	1.8	2	NS	
	LITTER	15.7	2	0.01	decrease
	BARE	3.4	4	NS	
CA2	TUSSOCKS	1.1	2	NS	
(n = 16)	CELMISIA	0.0	2	NS	
	DICOTS	N/A			
	MAT	8.9	2	0.05	decrease
	SHRUBS	N/A			
	LITTER	1.7	2	NS	
	BARE	1.6	2	NS	

Table 7: *Changes in mean maximum extended leaf length (cm) of* Chionochloa pallens *and* C. flavescens *in three grassland types over nine years.*

	1975			1984			
	n	x	s.e.	x	s.e.	F	P<
C. *pallens*							
Type PC1	48	43.1	2.0	65.8	2.2	59.8	0.01
Type PC2	65	31.5	1.3	41.7	1.5	26.6	0.01
C. *flavescens*							
Type PC1	46	76.0	3.7	88.9	3.9	5.8	0.05
Type CA1	10	79.5	9.2	81.9	11.4	0.0	NS

As browsing pressure was further reduced between 1975 and 1984, vegetation recovery continued, and was again most marked in the type PC grasslands, especially at low altitude (type PC1). Further vegetative regrowth of *C. pallens* and *C. flavescens* occurred. We also observed prolific establishment of *C. pallens* seedlings on a few sites. This later phase of recovery involved establishment of new plants and increased growth of existing plants of the favoured large herbs. Vegetation recovery was sufficient on some sites in type PC1 to cause a decrease in the proportion of bare ground. Recovery trends involving preferred snow tussocks and large herbs have also been observed in other parts of Fiordland (Mills and Mark, 1977; G.R. Evans, unpubl.; A.F. Mark, unpubl.) and further north in Mt Aspiring National Park (Mark, 1978).

Landform and drainage data from this study, as well as previous work on the site requirements of snow tussocks, suggest that the differences in composition, use by deer, and degree of recovery of the four main grassland types largely reflect an underlying gradient of decreasing soil fertility from type PC to type CA. Recent soils rapidly develop through to gleyed or podzolised yellow-brown earths on stable sites in humid alpine zones. The associated large reduction in levels of total inorganic and calcium-bound phosphate and development of poor soil drainage can occur in less than 1000 years (Archer, 1973, 1976; Williams, *et a1.,* 1976; Williams *et a1.,* 1978; O'Connor, 1980, 1984; Basher, Tonkin and Daly, 1985). *C. pollens* is associated with the earlier stages, and both *C. crassiuscula* and *C. acicularis* with the later stages of this sequence (Burrows, 1969; Williams, 1975; Williams *et a1.,* 1976; Williams *et a1.,* 1978). In addition, both *C. crassiuscula* and *C. acicularis* are associated with infertile, poorly-drained, organic soils (Williams *et a1.,* 1976).

In this study, type PC grasslands were associated with well-drained soils on relatively unstable landforms, where frequent soil rejuvenation is likely. In contrast, type CA grasslands occurred on stable landforms with poorer soil drainage. The dominant soils beneath type PC grasslands are therefore inferred to be relatively fertile recent and yellow-brown soils. Those beneath type CA are inferred to be relatively infertile, stronger developed, or organic soils.

Deer preferentially browsed the grasslands typical of fertile soils where the abundant preferred tussocks *C. pallens* and C. *flavescens* contain high levels of nutrients (Mills and Mark, 1977; Williams *et a1.,* 1978). The large herbs characteristic of these grasslands may also be nutrient-rich. Deer also select individual tussocks with high nutrient levels (Mills and Mark, 1977), probably explaining the greater

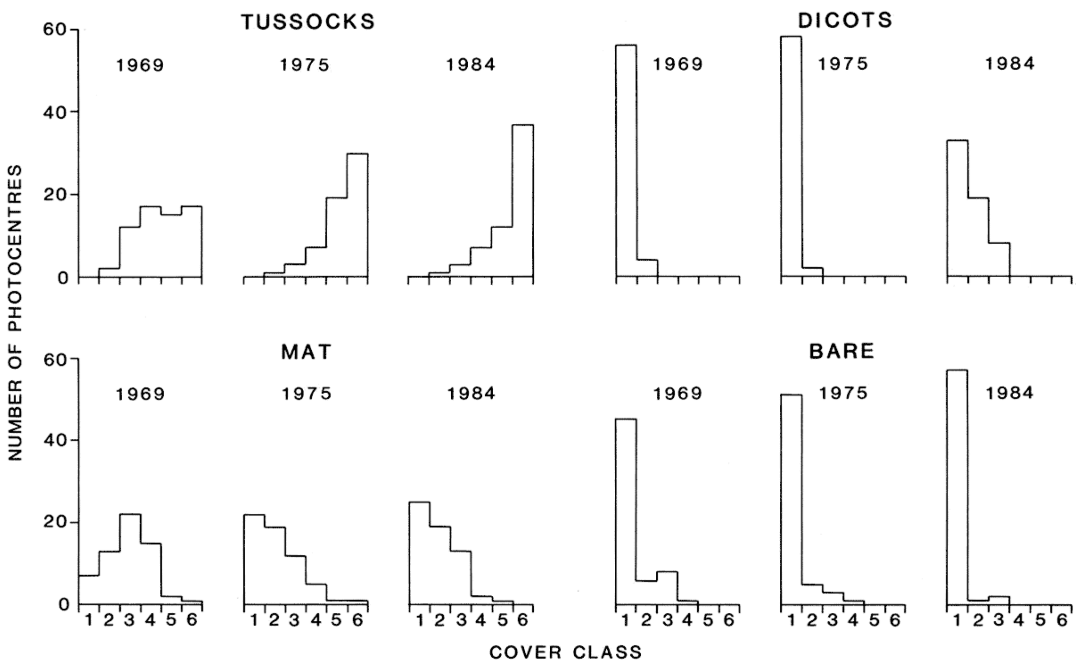

Figure 3: *Examples of significant changes in cover estimated from photocentric analysis, type PC1 grassland. See also Table 6. Cover classes are: 1 = <1%; 2 =1–5%; 3 = 6–25%; 4 = 26-–50%; 5 = 51–75%; 6 = 76–100%.*

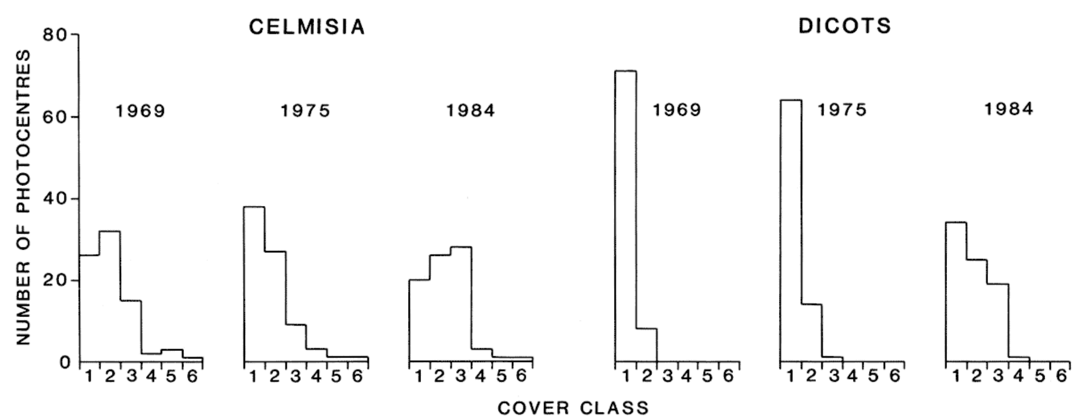

Figure 4; *Examples of significant changes in cover estimated from photocentre analysis, type PC2 grasslands. See also Table 6. Cover classes are defined in Fig.* 3.

preference for *C. flavescens* in type PC1 than in CA1.

Recovery of grassland was also most apparent on fertile sites. It could be argued that browsing pressure by relatively low numbers of deer on the few preferred plants in type CA grasslands was greater than on the same species in type PC, because of their low availability. This would be clarified by a later remeasurement. Clearly, however, type PC grasslands received the greatest overall browsing pressure in terms of amount of foliage consumed per unit land area. Subsequent recovery of the vegetation resource begins relatively rapidly on these fertile sites, especially at low elevation. As a result they are sensitive sites for monitoring the impact of deer in the grasslands.

Chionochloa pallens and *Chionochloa flavescens* are the staple food resources for takahe in the Wapiti Area, and type PC grasslands would be among the most preferred and productive takahe habitat (Lavers *et al.,* 1980). Results of this study support the contention that high deer numbers seriously depleted this resource, contributing to the decline of the takahe (Kean, 1956; Williams *et al.,* 1976; Mills and Mark, 1977; Mills *et al.,* 1984). Other, lesser, components of takahe diet may also have been depleted (e.g., *Celmisia petriei),* but most were too infrequent to show clear trends on the plots.

Lavers *et al.* (1980) and Mills (pers. comm.) have recently advocated liberation of takahe into areas of outstanding habitat within their former range. The recovery in type PC grasslands after 11 years of intensive deer control suggests reintroduction of takahe may succeed in these areas, as long as intensive aerial hunting of deer (including wapiti) continues above timberline, and the deer population and its impact is regularly monitored.

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