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CHANGES IN THE DENSITY AND DISTRIBUTION OF RED DEER AND WAPITI IN NORTHERN FIORDLAND

Summary: Deer density indices were estimated in 1969, 1975, and 1984 in the core of the Wapiti Area of Fiordland National Park. Between 1969 and 1984, density above timberline was reduced to near zero by commercial airborne hunting, with smaller decreases in the forest. Overall density declined by 81%. An estimated 2007 ± 385 deer were present in the 850 km² survey area in 1984, with an average density in the forest of $3.47 \pm 0.66/\text{km}^2$. The highest densities remained in the most completely forested sub-area (Catseye). Deer distribution within the forests became more clumped as densities decreased and, in 1984, was determined by slope, forest type, and terrain. The proportion of deer considered to be wapiti decreased from 100% in the 1920s to 17.7% in 1982-83. The decline is thought to be due to hybridisation and competition with the sympatric red deer, and not the result of differential harvesting. Most remaining wapiti are concentrated between George and Bligh Sounds and eastwards, including the George, Edith, Wapiti, and Glaisnock catchments.

Keywords: *Cervus elaphus nelsoni*; *Cervus elaphus scoticus*; population census; population density; hybridisation; hunting; wapiti; red deer; Fiordland; New Zealand.

Introduction

Wapiti (*Cervus elaphus nelsoni*) were liberated in northern Fiordland in 1905, and red deer (*C. e. scoticus*) colonised the area in the 1930s (Batcheler and McLennan, 1977). The resulting population provides the only opportunity to hunt wapiti in New Zealand. This causes conflict between those wanting the herd retained as a special hunting resource and those wanting the deer removed to allow vegetation recovery in accordance with National Park policy. Proposals to introduce an endangered flightless bird, the takahe (*Notornis mantelli*), to part of the area occupied by wapiti have added to this conflict. Although takahe are at present found only in the Murchison Mountains (Fig. 1), they were once present over much of Fiordland (Mills, Lavers and Lee, 1984), and competition from deer is likely to have contributed to their decline (Mills and Mark, 1977). Successful attempts to re-establish takahe in their former range may therefore require low deer densities.

Staff of the Forest Research Institute surveyed north Fiordland three times, in 1969, 1975 and 1984. This paper documents changes in deer density and distribution in the core of the area occupied by wapiti between the surveys, and describes some relationships of deer with their habitat in 1984. We also studied hunting pressure and the extent of cross-breeding between wapiti and sympatric red deer in light of the conflicting management options mooted for the area.

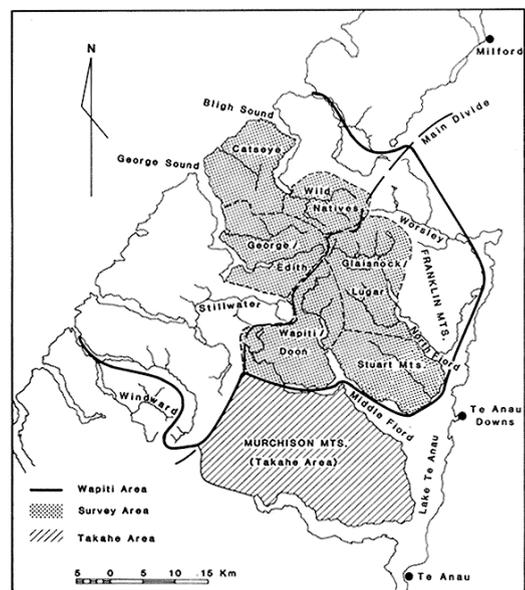


Figure 1: The location of the survey area, showing the six sub-areas, and its relation to the Wapiti and Takahe areas, northern Fiordland National Park.

Study Area and Deer History

Study Area

Our study was confined to the 850 km² area of north Fiordland between George and Bligh Sounds in the west, and North and Middle Fiords, Lake Te Anau, in the east. This area was divided into six sub-areas (Fig. 1). It is part of a heavily glaciated upland rising to 1800 m a.s.l., and is characterised by generally narrow valleys and fiords with steep, near vertical sides. Forest covers 70% of the area, with generally well-defined timberlines at about 1100-1200 m a.s.l. in the east, and about 900 m a.s.l. in the west. Silver beech (*Nothofagus menziesii*) is the dominant canopy tree, but others are locally important. Forest composition varies with altitude, soil type, and rainfall, with the simplest forests (both structurally and compositionally) occurring at high altitudes and on the poorer soil types, particularly in the low rainfall areas to the east. Above timberline a narrow discontinuous belt of subalpine shrubland merges with alpine grassland dominated by two species of snowgrass (*Chionochloa crassiuscula*, *C. pallens*), which in turn grades into fellfield and cushion herb field vegetation at high altitudes. There is a marked rainfall gradient across the survey area, shown by the long-term average annual rainfall of 6300 mm at Milford to the north-west of the study area, and 1300 mm at Te Anau to the east. Precipitation is heavy throughout the year, but tends to be greatest in summer (New Zealand Meteorological Service, 1983).

Deer History

After their release at George Sound in 1905, wapiti spread slowly until the late 1930s, when they met red deer dispersing from liberations near Lake Manapouri in the south, and possibly Olenorchi in the north. Red deer continued to spread through the area occupied by wapiti, and the two subspecies together colonised the eastern Stuart Mountains, the Franklin Mountains, the Doon River, the Worsley River, and the area north of Bligh Sound. Hybridisation was reported on numerous occasions soon after the two subspecies became sympatric (Murie, 1966).

Management of the wapiti and red deer populations of the study area has undergone a number of changes. The wapiti herd was completely protected until 1922, but after this some trophy hunting was allowed under the jurisdiction of the Southland Acclimatisation Society. In 1934 the government took control of hunting in the area and the first cull by the Department of Internal Affairs took place in 1938. By

1948, when the department next culled the herd, only red deer and hybrid animals were shot. From 1954 to 1962 the New Zealand Deerstalkers Association organised hunting. The Wapiti Area yielded 112 wapiti trophies during this period, as well as 3952 culled red deer and red-wapiti hybrids (Henderson, 1965). After 1965 hunting was controlled by the Fiordland National Park Board.

Commercial venison recovery, aimed at red deer and hybrids, was permitted between 1971 and 1981, but an unknown number of deer, including wapiti, were taken illegally over this period. After 1978 an increasing proportion of the animals taken were captured alive for farming. During 1982-83, as part of a plan to relocate the wapiti herd (Davis, 1985), all animals were taken regardless of type. Little hunting occurred during 1984, but the recovery of red deer and hybrids recommenced in 1985.

Methods

Pellet Surveys

The study area was surveyed in the summers of 1969/70, 1975/76, and 1984/85 (cited as the 1969, 1975, and 1984 surveys). During each survey the disappearance rate of deer faecal pellet groups (Hickling, 1985) was measured in two locations, one each side of the main divide (summarised in Appendix 1). Trends in deer density over time, and deer densities in 1984, were inferred from pellet densities using two different counting techniques:

1. Pellet density indices (PDIs), calculated by the presence/absence technique for single pellets (Baddeley, 1985), were used to described changes in deer density. Plots of 1.26 m radius (1969 and 1975) and 1.14 m radius (1984) were placed along transects located semi-randomly throughout the area. The 23 forest transects all began at valley bottom and finished at or near timberline, with plots spaced 15 m apart. On the 19 transects above timberline, groups of eight (1984) or 10 (1969, 1975) plots were sited randomly within 20 x 20 m vegetation plots placed every 61 m a.s.l. up the slope. Disappearance rates were similar in 1969 and 1984, but were lower in 1975 (Appendix 1). Changes in the indices between 1969 and 1984 therefore reflected equivalent changes in deer density, but the 1975 indices were biased high.
2. In 1984, pellet group densities (PGDs) were derived from counts of pellet groups on 2.5 m radius plots spaced 15 m apart along 57 forest transects (including the 23 above). The PGDs

were used to assess deer distribution and numbers. As the highest deer densities were expected at low altitudes, sampling intensities of one plot per 0.16 km² and 0.10 km² were used above and below 600 m a.s.l. respectively to increase sampling precision. The greater sampling intensity below 600 m a.s.l. was achieved by ending some of the new transects at that altitude. Altitude, aspect, slope, terrain, and vegetation were recorded, and the distance from timberline was estimated for each plot. The vegetation types are described briefly in Table 2, and are based on the forest types in Wardle, Hayward and Herbert (1971). Differences in PGD between sub-areas or site types were assumed to reflect differences in deer density as pellet group disappearance rates in the west did not differ significantly from those in the east, despite the steep rainfall gradient across the area (Appendix 1.) Nor did they differ between the three major ground cover types (Appendix I). To compare deer distribution patterns between site types for sub-areas with different overall deer densities, we used a relative use index (Parkes, Tustin and Stanley, 1978), where

$$\text{Relative Use (RU)} = \frac{\text{PGD for the site type}}{\text{PGD for the sub-area}}$$

Standard errors for these indices were estimated by a non-parametric bootstrap technique (Efron, 1981). Deer numbers were estimated by combining pellet group density and disappearance rate estimates (Baddeley, 1985) and assuming a defecation rate of 12.5 ± 1.4 pellet groups/deer/day (Neff, 1968).

Hunting Statistics

The number and location of deer taken by airborne and ground-based hunters and the hours spent flying by the major deer recovery operator working the study area in the 1982-85 period were obtained from Fiordland National Park Board records. Deer can be subjectively typed as red, wapiti, or hybrid from a combination of body size, pelage and size and shape of the rump patch (Batcheler and McLennan, 1977). Such assessments were made in the field in 1948 (Banwell, 1966), during the 1969 survey, and from all females older than 10 months captured during 1982 and 1983 when animals were taken regardless of type. The proportions of each type from these three assessments are compared with a sample shot in 1966/67 and typed, more objectively, by craniometric methods (Caughley, 1971; Batcheler and McLennan, 1977).

Presentation of Results

The following conventions are used. All areas and distances are planar estimates. Sampling error is presented as 95% confidence limits (95% C.L.s) about means in tables and text. Where a series of means are compared in detail, these are presented graphically with an associated Least Significant Interval (LSI). Any two means whose LSIs do not overlap are regarded as significantly different ($p < 0.05$). This criterion was used to test differences in PDIs, PGDs and RUs and is a close approximation of the Least Significant Difference test for means with different sample sizes (Andrews, Snee and Sarner, 1980).

Results

Changes in Deer Density and Distribution 1969-1984

Deer densities decreased significantly ($p < 0.05$) both above and below timberline between 1969 and 1984 (Fig. 2). Overall they showed an 81 % decline, calculated by weighting PDIs by the area above (252 km²) and below (598 km²) timberline. The greatest decline occurred before 1975. Deer were initially at highest densities above timberline, but this had reversed by 1975, and in 1984 no pellets were found on any of the plots in this zone. However, nine deer were seen above timberline during the 1984 survey (about 250 were seen in 1969) and deer were still being shot or captured there (J. von Tunzelman, pers. comm.).

The decrease in deer density in the forest was less dramatic, although still significant ($p < 0.05$), and a

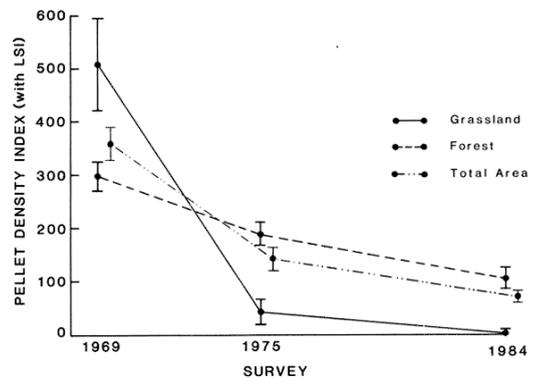


Figure 2: Overall changes in deer density within the survey area (1969-1984) and changes above and below timberline.

greater proportion of the overall decline occurred after 1975 in contrast to the earlier decline above timberline (Fig. 2). Four sub-areas yielded sufficient comparable data. Overall deer density in the forest did not change significantly in Catseye, the most western and completely forested sub-area, but decreased significantly ($p < 0.05$) in the remaining three sub-areas (Fig. 3). The earliest decrease occurred in the least forested sub-area. These results are consistent with the rapid removal of deer during the early commercial harvests from the more accessible and less forested sub-areas, and a shift in impact in later years (as deer became scarce) to the more remote and difficult western sub-areas.

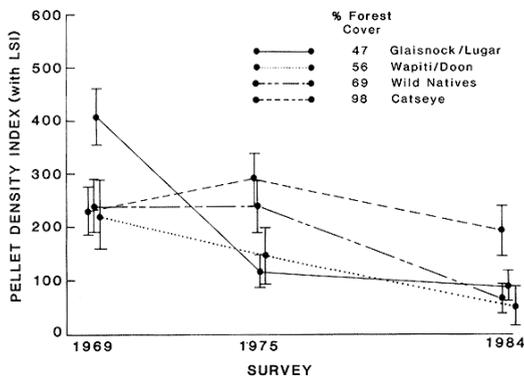


Figure 3: Changes in deer density within the forests (1969-1984) of four survey sub-areas, showing the relationship between the timing of hunting impact, and the percentage of forest cover in each sub-area.

Deer density decreased significantly at all altitudes within the forest between 1969 and 1975 (Fig. 4). The greatest decrease was in the upper forest (64%), with lesser reductions in the mid (49%) and lower forest (44%). In 1984 more of the remaining deer were concentrated in the mid-altitude forest than in the earlier years. In the three sub-areas showing significant declines between 1969 and 1984 (see Fig. 3), the coefficient of variation (CV) of the PDIs for 19 forest transects was 54%, 84% and 137% in 1969, 1975, and 1984 respectively. The greater variation in 1984 shows that deer were more unevenly distributed between transect locations than in 1969 and that deer in some forest areas were more vulnerable to airborne hunters than in others.

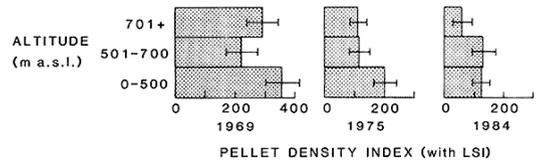


Figure 4: The distribution of deer in three altitude classes within the forest in 1969, 1975, and 1984. There were significant decreases in all classes between 1969-1975, and a further significant decrease in the low altitude class (0-500 m) between 1975-1984 ($p < 0.05$). Data are from the 18 transects starting below 500 m a.s.l.

Deer Density and Distribution Within the Forest in 1984

Deer were at significantly higher densities in Catseye than in the other sub-areas ($p < 0.05$; Table 1), and deer were more evenly distributed ($CV = 47%$ for PGDs on nine transects in Catseye compared with 83% for the remaining 48 transects). The differences in deer density between the other sub-areas are relatively small, with a continuum of overlapping 95% confidence intervals. This similarity occurred in spite of differences in the timing of the declines (Fig. 3). There was no significant correlation between the proportion of forest cover and deer density in 1984 ($r = 0.58$, Table 1), indicating that the magnitude of the declines within sub-areas was at least partly independent of the proportion of forest cover.

Table 1: Forest pellet group densities for each sub-area in 1984.

Sub-area	Total Area (km ²)	Percent Forest	No. Plots	Forest PGD/ha ($\pm 95\% C.L.$)
Catseye	126.6	98	965	88 \pm 15
George/Edith	144.2	81	838	35 \pm 11
Wild Natives	84.3	69	425	45 \pm 18
Glaisnock/Lugar	179.5	47	970	48 \pm 12
Wapiti/Doon	197.2	56	936	31 \pm 11
Stuart Mountains	136.9	75	831	32 \pm 9

Deer use decreased as the steepness of the terrain increased (Fig. 5). Use recorded on slopes greater than 500 reflects a few plots placed on deer trails between bluffs which give spurious estimates of the slope actually used by deer. The relative use of slopes greater than 400 was significantly higher in Catseye than in sub-areas east of the main divide ($RU = 0.65 \pm 0.26, 0.20 \pm 0.22$; $p < 0.05$), again

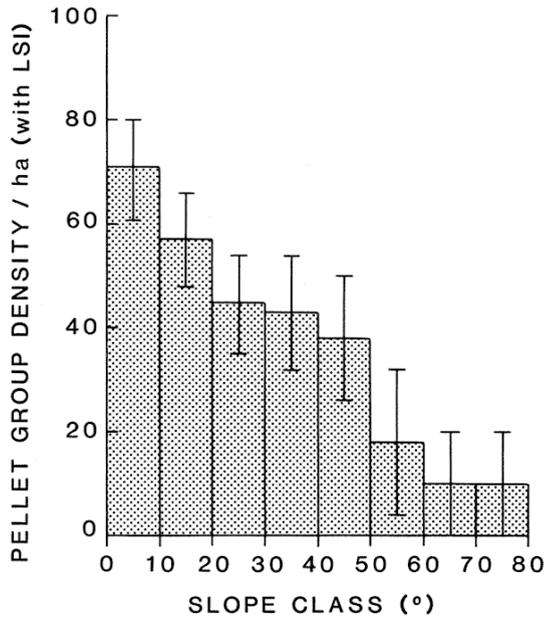


Figure 5: Distribution of deer in 1984 within the forest in relation to slope.

evidence that deer used more of their range where densities were high. Deer avoided blockfields (areas of large jumbled rocks) and were absent from some habitable areas between bluffs; about 15% of the area was not used by deer. Deer were at significantly higher densities on, or near, the valley floor (terraces and lower slopes) than on the valley sides (faces, gullies, spurs, main ridges, and benches) ($PGD = 74 \pm 13$; 45 ± 6 ; $p < 0.05$). On the valley sides, main ridges and benches were favoured over other sites ($PGD = 63 \pm 16$; 40 ± 6 ; $p < 0.05$). PGD estimates were consistently (but not significantly) lower on south-eastern aspects in low altitude forests.

Overall deer were most numerous within 100 m of the valley floor ($PGD < 100\text{ m} = 66 \pm 12$; $> 100\text{ m} = 42 \pm 6$; $p < 0.05$). However, analysis of individual sub-areas revealed three different patterns of deer distribution in relation to valley floor (Fig. 6). In Catseye, deer were numerous near timberline and near the valley floor (as in 1969, Fig. 4). In the three sub-areas with extensive timberlines and steep mid-slopes (Glaisnock/Lugar, George/Edith, Wild Natives), deer were most numerous near the valley floor. In the two

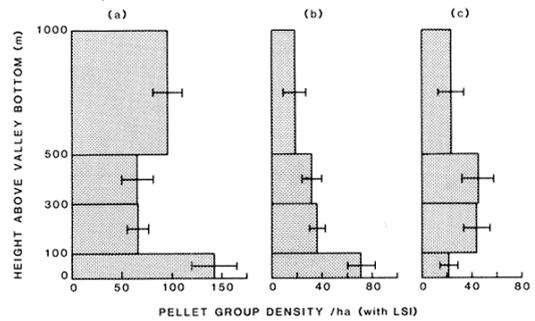


Figure 6: Distribution of deer in 1984 in relation to height above valley floor for (a) Catseye, (b) Glaisnock/Lugar, George/Edith, and Wild Natives and (c) Wapiti/Doon, and Stuart Mountains.

south-eastern sub-areas (Wapiti/Doon, Stuart Mts.), which have extensive timberlines but generally less steep mid-slopes, deer were most numerous on the mid-slopes.

In sub-areas with few deer, they were concentrated on the lower and middle reaches of main catchments ($PGD = 49 \pm 12$, 47 ± 9), with significantly fewer in the headwaters ($PGD = 29 \pm 9$; $p < 0.05$). This difference was not apparent in Catseye, where deer were evenly spread throughout the catchments. The marked overall increase in deer density away from timberline (Fig. 7) was also not apparent in Catseye. Deer used the timberline in Catseye significantly more often than in the eastern sub-areas (Fig. 7; $p < 0.05$), indicating their greater vulnerability at timberline in the areas with extensive unforested zones. In the eastern sub-areas, the sharp increase in deer use within 0.5 km of timberline (Fig 7; $p < 0.05$) indicates an avoidance of timberline, as, in the absence of hunting, deer living 0.5 km from timberline would range up to timberline.

Deer density also varied between vegetation types (Table 2). Because of hunting, no pellet groups were found above timberline (A), or in the short shrub associations at timberline (S1, S2). The high altitude silver beech (*Nothofagus menziesii*) forest comprised approximately 23% of the total forest area and had lower than average deer densities. The relative use of this type was significantly higher in Catseye than east of the main divide ($Ru = 0.40 \pm 0.39$, 0.33 ± 0.16 , $p < 0.05$), indicating that the low use was at least partly the result of hunting. The remaining forest types were generally so closely interspersed that the

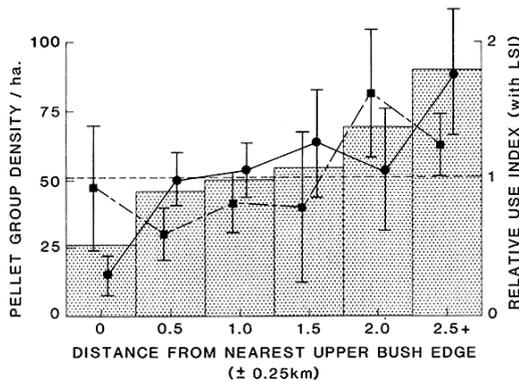


Figure 7: Distribution of deer in 1984 in relation to timberline, showing (a) Pellet group density for the whole survey area (histograms); (b) Relative Use within the Catseye sub-area (●----●) and (c) Relative Use east of the main divide (●—●). The horizontal line (----) represents both the average density for each sub-area (RU = 1.0) and overall (PGD = 51.3 gps/ha).

differences in deer density reflect deer preferences rather than the effects of hunting.

Deer densities were highest in the seral forest associations (P1, P2, P3), but these comprised only 5.9% of the forest area. The widespread, low altitude silver beech associations (C3, C4) had near average deer densities, and, as they comprised 45% of the forest area, were the most important deer habitat. The mountain beech (*Nothofagus solandri* var. *cliffortioides*) associations (M1, M2, M3) were mainly in the east where overall deer densities were low. Two of these (M2, M3) characteristic of sites of poor fertility with few palatable species (Wardle *et al.*, 1971), had the lowest deer densities of all forest associations. The other association (M1) was on more fertile sites and had average deer densities for the sub-areas in which it occurred. At the low densities prevailing east of the main divide, deer were more selective of the preferred seral forest types than deer in the high density Catseye sub-area (RU = 2.64 ± 0.97, 1.38 ± 10.60; $p < 0.05$).

Table 2: Differences in deer density between vegetation types. ¹With the exception of association A and O these associations are fully described in Wardle *et al.*, 1971.

Vegetation Type ¹	Description	No. Plots	Pellet Group Density/ha (± 95% C.L.)
A	Above timberline, unforested	72	0
S1, S2	Subalpine shrubland, with no silver beech (<i>Nothofagus menziesii</i>)	26	0
S3	Subalpine shrubland with silver beech	77	7 ± 10
P1, P2	Seral forest dominated by <i>Hoheria glabrata</i> and <i>Polystichum vestitum</i>	124	98 ± 40
P3	Seral forest dominated by <i>Melicactus ramiflorus</i> , <i>Cyathea smithii</i> , and <i>Schefflera digitata</i>	181	97 ± 38
C1, C2	High altitude silver beech forest with <i>Coprosma pseudocuneata</i> , and <i>Archeria traversii</i>	914	24 ± 8
C3	Low altitude silver beech forest characterised by <i>Blechnum discolor</i> and <i>Pseudowintera colorata</i>	1656	63 ± 10
C4	Low altitude silver beech forest with some <i>Metrosideros umbellata</i> and <i>Weinmannia racemosa</i>	892	68 ± 14
M1	Forest with a high mountain beech (<i>N. solandri</i> var. <i>cliffortioides</i>) component	695	42 ± 12
M2, M3	Mountain beech forest with <i>Leptospermum scoparium</i> and <i>Lepidothamnus intermedius</i>	206	15 ± 12
0	Unforested slips and valley flats below timberline	122	38 ± 30

1984 Population Size

The estimates of deer numbers in Table 3 and those discussed below are taken to represent the population present just before the season of births in December 1984. The population of the survey area was estimated at 2007 ± 385 , with an average density in the forest of $3.47 \pm 0.66/\text{km}^2$. These estimates were consistent with the harvest data from the 2-year 1982-83 operation, which were about 50% (i.e., 25% p.a.) of the 1984 density estimates (Table 3).

Sub-species Composition of the Herd

Wapiti alone were present in the three eastern sub-areas before 1935. By 1948, however, only 31% of 268 deer seen there were classed as wapiti (Banwell, 1966), and in 1969, 24% of 386 deer seen. A significant decline in the proportion of wapiti was also evident between 1966-67 and 1982-83 (Table 4, $X^2 = 29.1$, $df = 1$, $P < 0.05$) in these sub-areas.

The proportions of wapiti and hybrids across the whole Wapiti Area in 1982-83 are shown in Table 5. Only in the Catseye sub-area and the George, Edith, Glaisnock, and Wapiti catchments were more than 35% of the animals wapiti or hybrids. This was the wapiti stronghold. Of the 192 adult females taken from this 485 km² area in 1982-83, 33% were classed

as wapiti. For the remainder of the Wapiti Area there were significantly fewer (11 %) wapiti ($n=422$; $X^2=43.7$, $df= 1$, $p<0.01$).

The adult female deer taken from throughout the survey area in 1982-83 ($n=313$) included 22% wapiti. Assuming binomial confidence limits about this percentage and using population estimates from Table 3, we estimated that there were 456:139 wapiti remaining there in 1984, with 89% of them living in the stronghold area.

Hunting Pressure and Known Harvests

Intensive commercial hunting began in the survey area in 1973. Most of the deer taken before 1977 were harvested east of the main divide. Thereafter the pattern reversed (Table 6). From December 1982 to March 1985, the major airborne hunter working the survey area average 1.36 deer per flying hour ($n = 522$ hours). Most effort (45%) was spent in the Catseye sub-area, with 44% of all deer being taken there (2.6/km² of forest). Fewer deer were taken from the George/Edith and Wild Natives sub-areas (1.2/km²) and fewest in the eastern sub-areas (0.7/km²); i.e., the harvest rate per unit area appeared to be partly related to deer density. However, there was no correlation between deer density in the forest and harvest rate per

Table 3: Estimated total deer population and density in 1984 compared with the known harvest in 1982-83. ¹ The 95% C.L.s incorporate only the sampling error associated with measuring pellet group densities and disappearance rate, but no allowance for error in the assumed defecation rate, or in the underlying model. ² The total population is calculated from the entire data set pooled, ignoring slight differences in sampling intensity between sub-areas so that the sum is slightly less than the sub-area totals.

Sub-area	Forest area (km ²)	Deer density km ² ($\pm 95\%$ C.L.) ¹	Population size ($\pm 95\%$ C.L.) ¹	1982-83 Harvest (deer/km ²)
Catseye	124.2	6.35 \pm 1.84	789 \pm 230	2.9
George/Edith	97.7	2.70 \pm 1.32	264 \pm 129	1.3
Wild Natives	58.4	3.20 \pm 1.86	187 \pm 109	1.7
Glaisnock/Lugar	84.5	3.25 \pm 1.17	275 \pm 98	1.6
Wapiti/Doon	111.0	2.80 \pm 1.10	311 \pm 124	1.3
Stuart Mountains	102.6	2.40 \pm 1.10	246 \pm 111	0.9
Total ²	578.4	3.47 \pm 0.66	2007 \pm 385	1.6

Table 4: Proportions of wapiti in two samples from north Fiordland. ¹Adult females only ²Data from table 3, Caughley (1971).

	1966/67 Sample ²		1982/83 Sample	
	N ¹	% Wapiti \pm 95% C.L.	N ¹	% Wapiti \pm 95% C.L.
Wapiti/Doon	66	32 \pm 12	49	10 \pm 15
Stuart Mountains	47	27 \pm 13	41	0 \pm 9
Glaisnock/Lugar	43	71 \pm 14	48	29 \pm 10
Above three sub-areas	156	41 \pm 8	138	13 \pm 8

Table 5: Proportions of wapiti and hybrid deer in the 1982-83 sample of adult female deer taken from the entire Wapiti Area. ¹ Includes 13 from unknown locations within the Wapiti Area.

Catchment or Sub-area	N Deer	% Wapiti	% Hybrids	% Wapiti + Hybrid
Bligh Sound-North (west of Main Divide)	72	8.3	9.7	18.0
Franklin Mountains	29	3.4	6.9	13.3
Worsley	47	17.0	2.1	19.1
Wild Natives	39	12.8	12.8	25.6
Catseye	95	30.5	22.1	52.6
George/Edith	41	41.5	12.2	53.7
Glaisnock	29	41.4	17.2	58.6
Wapiti	27	18.5	18.5	37.0
Lugar	19	10.5	15.8	26.3
Stuart Mountains	41	0	4.9	4.9
Doon	22	0	0	0
Stillwater	18	16.7	5.9	22.6
George Sound-South (west of Main Divide)	135	16.3	8.1	25.4
Total ¹	627	17.7	11.2	28.9

Table 6: Known harvest of deer shot or captured by airborne hunters in the Survey area, 1970-1985. ¹ Locations of kills not clear for this year. ² Hunting permitted in December only.

Year	No of Deer Taken		Total
	Eastern blocks	Western blocks	
1970	0	0	0
1971	47	0	47
1972	0	0	0
1973	1481	156	1637
1974	-	-	700 ¹
1975	271	117	388
1976	398	270	668
1977	757	920	1677
1978	423	861	1284
1979	282	563	845
1980	167	348	515
1981	29	74	103
1982	222	383	605
1983	144	278	422
1984 ²	24	42	66
1985	120	246	366

flying hour in the six sub-areas ($r = -0.47$). The harvest rate per unit hunting effort was therefore a poor indicator of deer density.

Hunters on foot had little effect on the total harvest, at least in the early 1980s. For example, in the year to April 1981, hunters on foot accounted for less than 10% (50 animals) of the known harvest ($n = 584$) from the survey area. The Wapiti Area is divided into 17 hunting blocks. In the year cited, hunters on foot seldom hunted west of the main

divide. The nine accessible blocks east of the main divide were requested, on average, 35 times each. Similarly accessible blocks outside the Wapiti Area were requested 27.5 times ($n = 28$), indicating a slightly higher demand for blocks in the Wapiti Area.

Discussion

The three surveys between 1969 and 1984 showed a dramatic overall decrease of 81 % in deer densities. Because non-commercial hunting on foot before 1969 had had insignificant effects on deer densities (Smith, 1974), we attribute this reduction almost entirely to commercial airborne hunting. This confirms other studies (Challies, 1977, 1985; Clarke, 1985). However our study is the first with an objective estimate of deer density before commercial hunting began, which permits a more accurate assessment of the impact of airborne hunting.

Although Smith (1974) believed airborne hunting would have a significant impact only above or near timberline, our data show significant decreases at all altitudes within the forest by 1975. Initially, most deer were taken above timberline (C. Challies, pers. comm.), suggesting that at least some deer using the low altitude forest also ranged up to timberline and beyond. Since 1975, a greater proportion of deer have been taken from within the forest (R. Hayes, pers. comm.). The decrease in deer density at low altitude since 1975, without a corresponding mid-altitude decrease, is consistent with this, and suggests most of the within-forest harvest occurs on or near the valley floor. The changes in deer distribution appear to have

resulted mainly from selective removal from some areas or strata, as there is no evidence of any increases in density in 'safe' localities. The Catseye data suggest that a near complete forest cover severely limits the effectiveness of airborne hunters, as densities remained relatively high there in 1984, even though the area had been hunted for nearly a decade.

Airborne hunting has resulted in relatively low densities of deer in areas near timberline, with animals concentrated at low altitudes and in the lower reaches of catchments. Within these forests, deer density is determined primarily by slope, terrain, and vegetation type. Altitude or height above the valley had little direct effect on deer use, but distinct altitudinal distributions arose with different combinations of controlling factors (such as the presence or absence of a timberline, or the average slope of the mid-altitude forest). Deer preferred seral forest, presumably because of the many palatable plants (Wardle *et al.*, 1971). However the most important associations in terms of overall use were the extensive, low altitude, silver beech forests. The greater clumping of deer in small geographic areas, the greater relative use of the more preferred vegetation types, and the lesser use of steep areas in the low density sub-areas suggest that at low density the few remaining deer exist on the most preferred sites and seldom use sub-optimal habitats.

The decrease in deer density on these most preferred sites has probably been far less than the 81% overall decrease.

The reduction in deer density has resulted in an increase in the abundance of palatable plant species (Rose and Platt, 1987; Stewart, Wardle, and Burrows, 1987). Above timberline the greatest improvement in the vegetation occurred on the low altitude, high fertility sites in the alpine grassland (Rose and Platt, 1987), which are also the sites preferred by takahe (Mills *et al.*, 1984). In the forest, the recovery was most marked in the seral forests, which contain the fern *Hypolepis millefolium*. Takahe excavate this fern for its starchy rhizomes during winter (Mills *et al.*, 1980). Deer do not eat any part of this fern but Mills *et al.* (1980) suggested that deer browsing on other plants within the seral associations (e.g. *Polystichum vestitum* and *Griselinia littoralis*) allows the ground to freeze in winter, thus inhibiting the takahe's access to the rhizomes. Although plausible, we know of no evidence to support this theory, which now seems to have the status of fact (e.g. King, 1984). In reality, there is as yet little evidence that deer and takahe compete for food within the forest. The improvement in the alpine grasslands and the low deer densities

there in 1984 suggest that re-establishment of takahe should not fail because of competition from deer.

Our estimates of deer numbers include no allowance for error in the assumed defecation rate, or in the underlying model, and they may be slightly conservative, particularly for the more western catchments. In 1985 about 400 deer were taken from an estimated breeding population of 1600 red and hybrid deer (i.e. excluding the non-harvestable wapiti) in the survey area. This 25% yield is less than the annual harvest able increment expected for such a population (Challies, 1985) and suggests that further population reductions are unlikely under existing conditions. However, if hunting pressure continues to be concentrated in the Catseye sub-area there may be some reduction there. As the 1985 harvest was regulated primarily by the interaction of economic factors and deer density, any significant increase in hunting effort by recreational or official hunters may subtract from, rather than add to, the commercial harvest.

Extrapolating to the Wapiti Area as a whole, we estimate that about 3000 deer were present in 1984, of which about 600 were wapiti. Most of these were concentrated in the Catseye sub-area, and the George, Edith, Wapiti, and Glaisnock catchments. The proportion of the deer population classed as wapiti has declined considerably since 1930, and there are three possible explanations for this.

1. Wapiti may have been selectively harvested. This is unlikely as the proportion of wapiti was declining before 1969, when recreational hunters selectively culled red deer and some hybrids. Legal commercial harvests between 1971-1981 were also selective for red deer and hybrids (see Batcheler and McLennan, 1977). It is unlikely that illegal hunting would have been of a scale to counter this selectivity.
2. Wapiti may be interbreeding with red deer. There is no doubt that hybridisation occurs in Fiordland (Murie, 1966; Batcheler and McLennan, 1977) and although wapiti bulls may have initiated the hybridisation (Batcheler and McLennan, 1977) the present close similarity between some hybrids and wapiti makes it likely that wapiti females are now mating with stags with some red deer genes.
3. Red deer may have some competitive advantage as, although red deer colonised areas where wapiti were established (e.g., the George River), wapiti did not colonise red deer areas such as the Murchison Mountains (Parkes *et al.*, 1978). Red deer may also have a reproductive advantage, as

fewer hybrids than red deer were lactating in a sample of females shot in the south-west of the Wapiti Area in 1970 (C.N. Challies, 1970, unpubl.; wapiti were not sampled).

Some of the deer captured in 1982-83 and classed as wapiti have red deer genes (blood protein analysis, P. Dratch, pers. comm.). As these hybrids closely resemble wapiti, the selective culling of all hybrid deer in the field on the basis of external characters is impossible. The mating of such hybrids with the remaining pure wapiti (if any) is highly likely and the eventual disappearance of pure wapiti unavoidable, future liberations notwithstanding. Most of the decline in the proportion of wapiti seems to be the result of hybridisation, and possibly competition. Commercial hunting regimes selecting only non-wapiti-type deer might increase the proportion of wapiti-type animals remaining, but would be self-limiting in most areas; as the proportion of non-wapiti-type deer decreased so would the efficiency of the operator. It is therefore likely that continued selection against non-wapiti-type deer will result in a population of hybrid deer resembling wapiti, the degree of resemblance depending on the severity of the selection, and on the amount of further immigration by red deer.

Acknowledgements

We thank C.N. Challies, J.D. Coleman, and J. Orwin for commenting on early drafts of this paper, and C.N. Challies, R. Hayes, J. von Tunzelman and P. Dratch for unpublished information. We also thank those who helped in the field surveys.

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Appendix 1: Pellet group disappearance rate (DRs) and rainfall data.

A. Variation in pellet group disappearance rate between years

Location and Year	DR ± 95% C.L.	Sample size	Assessment period (days)
(a) Wapiti area east of main divide			
Worsley 1969	0.0085 ± 0.0025	146	330
Worsley 1975	0.0061 ± 0.0007	470	126
Glaisnock 1984	0.0090 ± 0.0012	414	92
(b) Wapiti area west of main divide ¹			
Windward 1969	0.0074 ± 0.0013	286	341
Windward 1975	0.0084 ± 0.0015	229	164

¹ A sample of groups marked in the George River in 1984 was biased by an over-representation of very old groups and so was disregarded.

B. Variation between major ground cover types in 1984

Ground cover type	DR ± 95% C.L.	Sample size
Open litter	0.0081 ± 0.0017	178
Fern	0.0113 ± 0.0033	84
Moss	0.0090 ± 0.0020	152

Assessment period = 92 days, $\chi^2 = 3.2$, $df = 2$, $0.25 > p > 0.10$

C. Variation in rainfall in the 6 months (Jul-Dec) preceding each survey

Year	Total Rainfall (mm)		Rain Days	
	East ¹	West ²	East	West
1969	790	3514	65	95
1975	511	3283	64	110
1984	666	3800	65	104

¹ Average for Te Anau and Te Anau Downs

² Milford