DISTRIBUTION AND ABUNDANCE OF BROWSING MAMMALS IN WESTLAND NATIONAL PARK IN 1978, AND SOME OBSERVATIONS ON THEIR IMPACT ON THE VEGETATION

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ABSTRACT

The high country forests and scrublands of Westland National Park were surveyed by means of pellet lines during the 1977-78 summer to determine the distribution and abundance of the larger introduced mammals. The extent of canopy defoliation in the upper montane forest zone of the Park was also assessed.

Brush-tailed possums (**Trichosurus vulpecula** Kerr) were present throughout the Park with the exception of the headwaters of the Karangarua, Douglas, and Regina catchments. Highest pellet densities were recorded in the mid and upper montane forests and in the northern and southern portions of the Park (in the lower reaches of the Callery and Karangarua catchments). Possums were still in the process of colonising the lower southern bank of the Copland catchment and the upper half and lower northern bank of the Karangarua catchment. Red deer (**Cervus elaphus** L.) pellet densities were highest in the forested zone of the lower Karangarua catchment and decreasd towards its headwaters and northwards. Numbers in the Cook catchment were low and no deer pellets were recorded in the study area north of this catchment. Chamois (**Rupicapra rupicapra** L.) pellets were recorded throughout the Park with highest densities around timberline in the upper forest and scrub zones. Highest pellet densities were recorded in the headwaters and lower northern bank of the Karangarua catchment and in the Callery catchment. Relatively low densities were measured in the forests between the Cook and Callery catchments. Goat (**Capra hircus** L.) pellets were recorded only north of the Karangarua River in the vicinity of Havelock Creek, where highest numbers occurred in the lower forest zone.

Over half the montane forests showed some canopy defoliation, the degree of which appeared to be related to the length of occupation by possums and their density. The lower reaches of the Karangarua, Copland, and Callery catchments showed the most striking canopy defoliation and contained the highest possum densities. The collective browsing pressure from high densities of possums, chamois, and deer was affecting all stages of forest structure and composition in the lower Karangarua catchment.

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INTRODUCTION

The Forest Research Institute surveyed Westland National Park, South Westland, during the 1977–78 summer season to determine the distribution and relative density of brush-tailed possums, red deer, chamois, and goats, and the degree and spread of canopy defoliation.

The area surveyed (Fig. 1) is bounded in the north by the Callery catchment and in the south by the Karangarua catchment. Eastern and western limits are formed by the Main Divide and by the Alpine Fault which closely parallels the main West Coast Road (State Highway 6). The north-western part of the study area is relatively low-lying, while to the south-west of the Alpine Fault the country rises abruptly to the Main Divide. The topography, geology, vegetation, and climate of Westland National Park have been described by Wardle (1979).

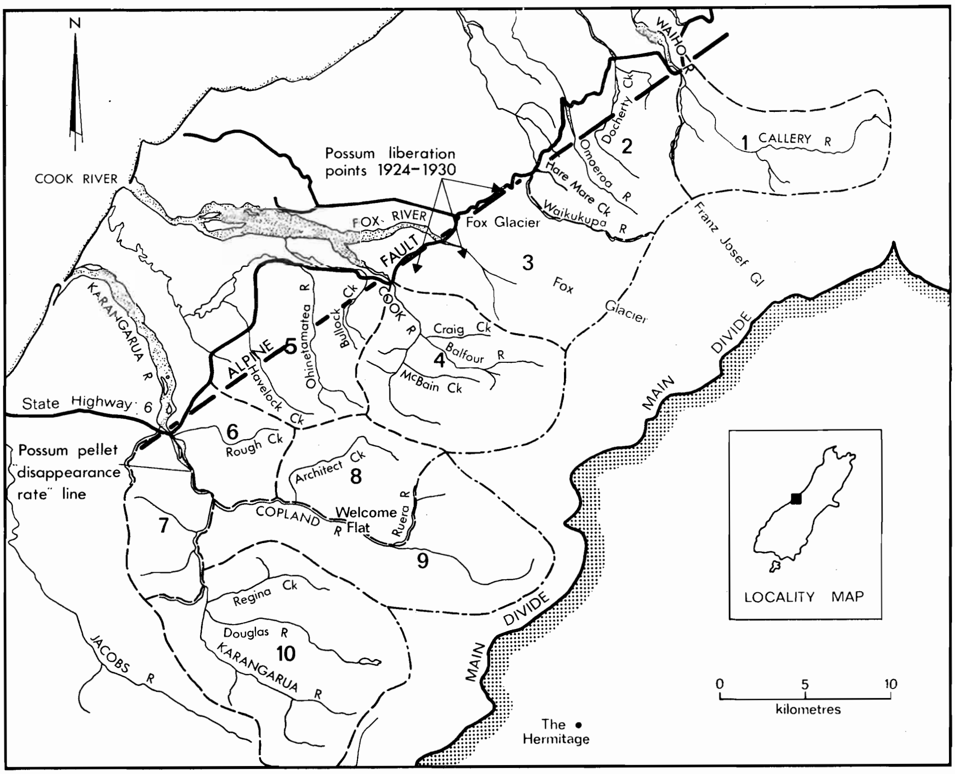

FIG. 1—The survey area, showing the block numbers and boundaries.

HISTORY OF MAMMALS IN THE PARK

Possums

At least 54 possums were liberated in Westland National Park between 1924 and 1930 (Pracy 1974). In 1949–50, L. Pracy (Department of Internal Affairs, pers. comm.) surveyed the possum populations within the park and observed that "severe and striking vegetation damage" was evident around the Fox and Waikukupa Rivers. Pracy reported that there were dense populations of possums between the southern side of the Waikukupa River and the northern side of the Cook River up to Craig Creek. No possum sign was seen in the Callery catchment or above the road bridge in the Waiho catchment during this early survey (Fig. 2a). In 1960, Pracy (pers. comm.) resurveyed the area and reported high population densities in the Cook and the lower reaches of the Omoeroa catchments (Fig. 2b). Severe canopy defoliation was noted throughout most of the Cook catchment, excluding the lower northern frontal faces from the Balfour River confluence to the main road bridge where the vegetation seemed to be recovering.

No Government control operations have been carried out in the Park against possums before this survey, and commercial hunting for pelts up to the winter of 1977 is considered to have had little effect on the spread or build-up of populations.

Red Deer

The red deer in Westland National Park are descended from animals liberated near Lake Hawea, West Otago, in 1871. Dispersal into Westland occurred via the Huxley, Hunter, and Landsborough catchments. By the mid 1930s, deer had become well established in the headwaters of the Karangarua catchment (Harrison 1967) where they were present in moderate numbers in 1948 (Hitchcock 1948). The lower Karangarua catchment was colonised by dispersing deer from the headwaters and/or by a northwards movement of deer from the Jacobs and Mahitahi catchments. The Copland catchment was colonised by an upstream movement from the Copland-Karangarua junction during the late-1940s/early-1950s. Deer first dispersed into the Cook catchment along the frontal country from the south in the early to mid 1950s, but breeding populations were probably not established until the 1960s. The central and northern high-country valleys of the Park are still largely free of deer.

After deer became established, numbers increased in the Karangarua catchment and Government deer control operations were undertaken from the late 1940s to the mid 1950s. Despite this, the population in the Karangarua catchment was at a high level and the Copland population had increased by the mid 1960s. After this time, numbers declined markedly with the increasing intensity and effectiveness of commercial aerial venison recovery (Challies 1974).

Chamois

The dispersal of chamois after their liberation in the Hooker catchment, Mt. Cook National Park, in 1907 and 1914 (Lambert & Bathgate 1977) is not well documented, but it seems likely that they had spread westward across the Main Divide into Westland National Park by the 1920s. By the mid 1950s, chamois were at moderate population levels in the Copland and Karangarua catchments while densities were high from the Cook catchment northwards, with hunters commonly seeing 100 or more chamois per day. Browse was extensive in parts of the scrub belt (L. Pacy, unpubl. data). Densities remained high through the 1960s when chamois carcass weights were light, pelts were in poor condition, and animals with horn loss and "scabby mouth" were common (Lambert & Bathgate 1977). Large-scale commercial hunting of chamois from helicopters began in the early 1970s and was still in progress at the time of the survey.

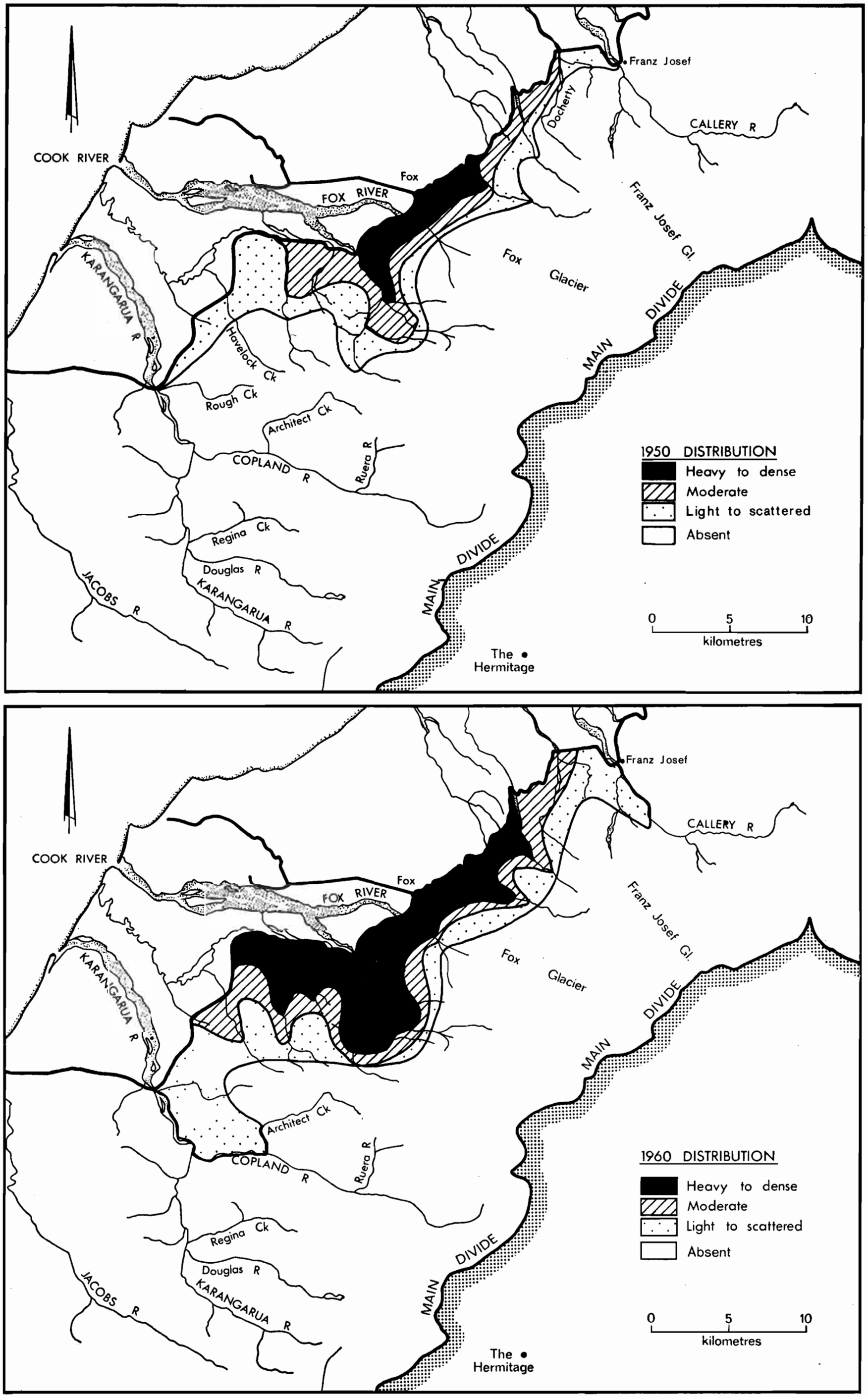

FIG. 2—Spread and build-up of brush-tailed possum populations in the Park from 1950 to 1960.

Goats

Goat populations within the Park boundaries are of unknown origin. They are one of several isolated populations occurring along the western flanks of the Main Divide in Westland which are all mainly confined to the lowland forests.

METHODS

The survey area was divided into 10 blocks (Fig. 1). In each block, possum pellet densities and ungulate pellet-group densities were recorded on transects running on a compass bearing from valley floor to alpine scrub or grassland. In total, 80 transects were sited by a restricted random process throughout the survey area. Plots were located at 20-m intervals except in the frontal country of the Karangarua catchment where transects started at much lower altitudes than those further up the valleys. On these longer transects, plots were located at 40-m intervals to enable a complete sampling of the forest and scrub habitats. Plots with radii of 200 cm were searched for pellet groups of deer, chamois, and goats; the same plot centres were used to search for single possum pellets but with a reduced radius of 114 cm. These different plot sizes were dictated by the different search entities, i.e., pellet groups for ungulates and one or more single pellets for possums. Point distance, nearest neighbour and second neighbour measurements were recorded along the slope of the land as described by Batcheler (1971, 1975)*.

Ungulate pellet-groups were defined as a minimum of six or more intact pellets belonging to any one defecation. A valid possum pellet was any single pellet that had retained its original pellet-like shape. Deer, chamois, and goat pellet-groups were differentiated by characteristics of size, shape, texture, and colour.

Possum and ungulate densities were examined in five altitudinal zones; lowland forest (LF = 0–400 m); mid montane forest (MF = >400–650 m); upper montane forest (UF = >650–850 m); subalpine scrub (>850–1050 m); and low alpine grassland (>1050 m).

Disappearance Rates

Disappearance rate estimates were used to correct the possum pellet density estimates. These were assessed on a "disappearance rate" line situated on the southern side of the lower Karangarua River (Fig. 1). Fifteen sample plots were sited on this line at 50-m vertical intervals within the forest zone, from the river flats at 50 m a.s.l. to just below the alpine-scrub/forest interface at 800 m a.s.l. Ten pellets were marked on each plot before and during the survey at 6- to 13-day intervals, giving a total of 16 assessments. These were tested by randomised block design analysis of variance for any significant variation in the disappearance rate of pellets. The mean rate of disappearance of possum pellets per day for the various assessment periods ranged from 0.03 to 0.17 and was highly significant ($p < 0.001$). Four rainfall-related variables obtained from the meteorological substation at Fox Glacier were tested by regression analysis (Table 1). Over-all moisture throughout each assessment period (i.e., number of raindays per assessment

* Distance measurements for possum pellets were made between single pellets; if pellets were touching, a nominal distance of 1 cm was recorded.

TABLE 1—Four rainfall-related variables linearly regressed against variation in disappearance rates of possum pellets

Independent variable/assessment period	Coeff. of determination (r^2) (%)	Error df	F
No. raindays/	63	14	23.6***
Millimetres of rain/day/	41	14	9.8**
No. raindays > 25 mm/day/	28	14	5.5*
Millimetres of rain/rainday/	13	14	2.1 ns

*** = significant at $p < 0.005$
** = significant at $p < 0.01$
* = significant at $p < 0.05$
ns = not significant

period and millimetres of rain per day per assessment period) appeared to have more effect on pellet disappearance rates than intensity of individual storms or raindays (i.e., number of raindays >25 mm/day/assessment period, and millimetres of rain per rainday per assessment period). There were no significant differences in disappearance rates between the three altitudinal forest zones ($p > 0.20$), so that differences in the density of pellets (expressed as recruitment rates) probably reflected differences in animal densities.

The disappearance rates of deer and chamois pellet-groups were assessed on six lines situated in Blocks 6 and 7 (Fig. 1). At the start of the survey, 727 deer and 85 chamois pellet-groups were located and marked with flags, and these groups were rechecked at the completion of the survey to determine the proportion that had disappeared. As disappearance rates of ungulate pellets in the forest showed little variation between altitudinal strata, estimates were calculated for the combined forest strata to give 0.00689 groups/group/day for deer and 0.00989 for chamois. Scrub and grassland strata were pooled to calculate a single scrub + grassland disappearance rate estimate of 0.00846 groups/group/day for deer and 0.01204 for chamois.

Possum pellet densities and deer and chamois pellet-group densities were transformed into recruitment rates (pellets or pellet groups per hectare per day) using methods given by Batcheler (1975). Corrections were made for changes over time in the disappearance rate of possum pellets on individual pellet lines; these were then grouped for blocks. Corrections were also made for differences in the disappearance rates of deer and chamois pellet-groups in forest and scrub + grassland zones. We assumed, however, that there were no significant differences in the disappearance rates of ungulate pellet-groups between blocks during the survey. The disappearance rate of goat pellet-groups was not assessed.

Canopy Defoliation

A visual estimate of the degree of canopy defoliation in the upper montane forests (approx. 600–900 m a.s.l.) throughout the Park was made from a helicopter in February 1978. The helicopter flight path fluctuated between the 950-m and 1200-m altitudinal contours (i.e., just above timberline). The unit areas surveyed contained discrete tracts of forest, geographically separated by secondary tributaries or large bluff systems containing stunted forest. Canopy defoliation in these swaths was scored on a five-point scale and natural-colour oblique aerial photographs were taken as representative examples of each of the various canopy condition classes:

(1) Conspicuous/Severe: Extensive areas of totally defoliated crowns merge with areas containing partially defoliated forest canopy; interspersed are smaller areas containing unaffected stands (>50% of the canopy totally defoliated, and <50% partially defoliated + intact).

(2) Moderate/Severe: Large tracts of forest containing partially defoliated crowns interspersed with many totally defoliated specimens merge with a mosaic of smaller apparently unaffected stands (>50% partially defoliated canopy and <50% totally defoliated + intact).

(3) Moderate: Large tracts of forest with distinctive "thin" grey-green tinted crowns (previously described as "pepper and salt" damage, L. Pracy unpubl. data) merge with totally defoliated crowns scattered throughout, singly or in small groups, and a mosaic of smaller apparently unaffected stands (*c.* 50% partially defoliated canopy, *c.* 25% totally defoliated + *c.* 25% intact).

(4) Moderate/Slight: Large tracts of apparently unaffected canopy merge with areas of "thin" grey-green tinted crowns (as above), with scattered defoliated crowns throughout, singly or in small groups (*c.* 50% intact canopy, and *c.* 50% partially + totally defoliated).

(5) Slight/Absent: Canopy appears to be in a healthy condition, isolated defoliated specimens show up as scattered individuals (90% of the canopy intact + 10% partially or totally defoliated).

The degree of canopy defoliation throughout the Park was mapped using these categories.

RESULTS

Possum Pellet Densities

The densities and distribution of possum faecal pellets (expressed as recruitment rates) for 1977–78 throughout the Park are shown in Fig. 3. Pellet densities for the scrub and grassland strata were too low for valid statistical analysis and comparison between blocks was made only for the forested strata. In the three high-density areas – the Callery catchment, the lower Karangarua catchment, and the lower northern part of the Copland catchment (Blocks 1, 6 + 8, and 7) – densities declined gradually upstream. The highest densities occurred on the lower northern side of the Copland catchment (Blocks 6 + 8); the lowest occurred upstream from Regina Creek, on both sides of the Karangarua catchment (Block 10).

The altitudinal distributions of pellet densities for the highest-density populations (Blocks 1, 6 + 8, and 7) are shown in Fig. 4. These data were not converted into recruitment rates as no disappearance rate was available for the scrub belt. They

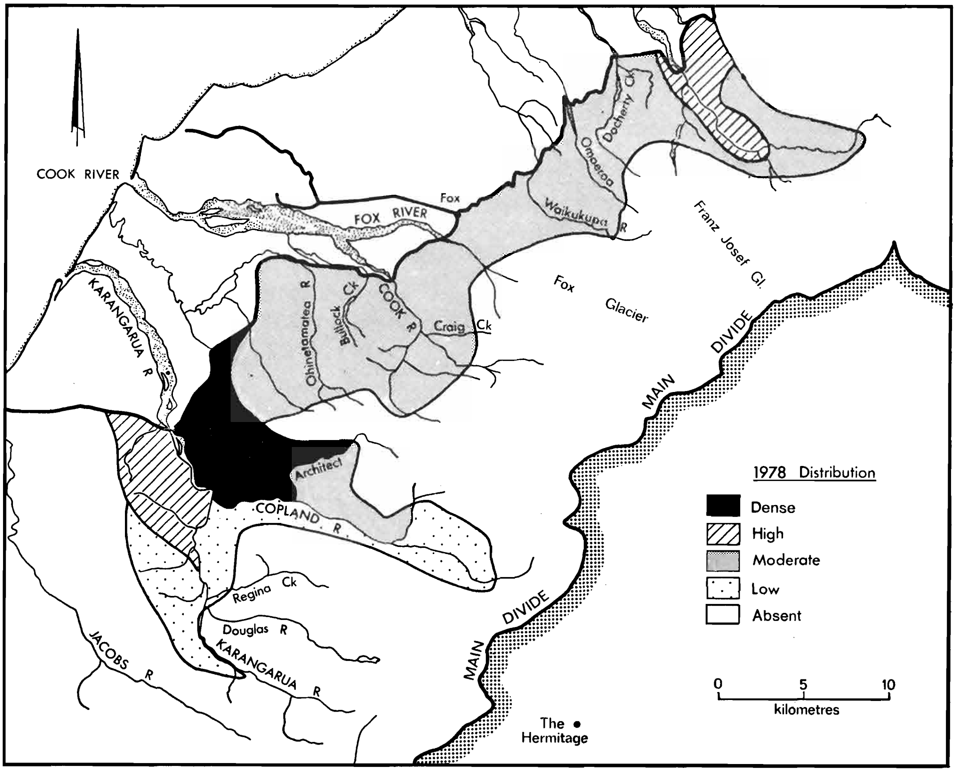

FIG. 3—Brush-tailed possum densities in the Park. For relative density estimates of population density classes refer to Fig. 5.

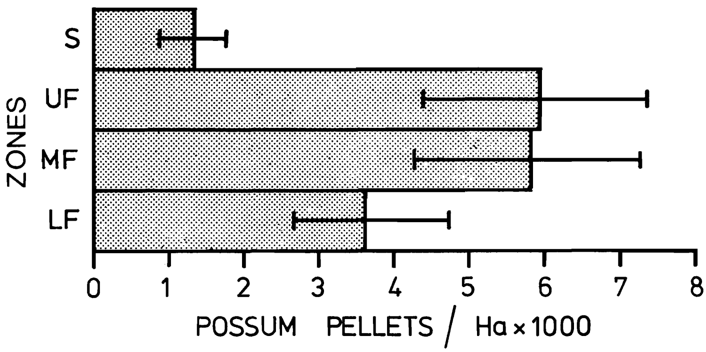

FIG. 4—Mean possum pellet densities per hectare for four altitudinal zones (Lower Forest, Mid Forest, Upper Forest, and Scrubland) in the highest-density areas, with 95% confidence limits.

indicate that pellet densities in the mid and upper montane forest zones were higher than in the lowland forest zone. The subalpine scrub belt had a significantly lower pellet density than any of the three forest zones.

Relative densities of possum pellets in the various blocks within the Park in 1977–78 are shown in Fig. 5. The blocks are geographically arranged along the Alpine Fault (i.e., the *X* axis) and conform to the layout of Fig. 1, 3, and 11. The distances on the *X* axis were calculated along the 500-m contour from the centre of each block around major rivers to the centre of the next adjoining block, and portray the nominal distance of assumed possum movement from the main liberation site in Block 3, the Fox region (Fig. 1).

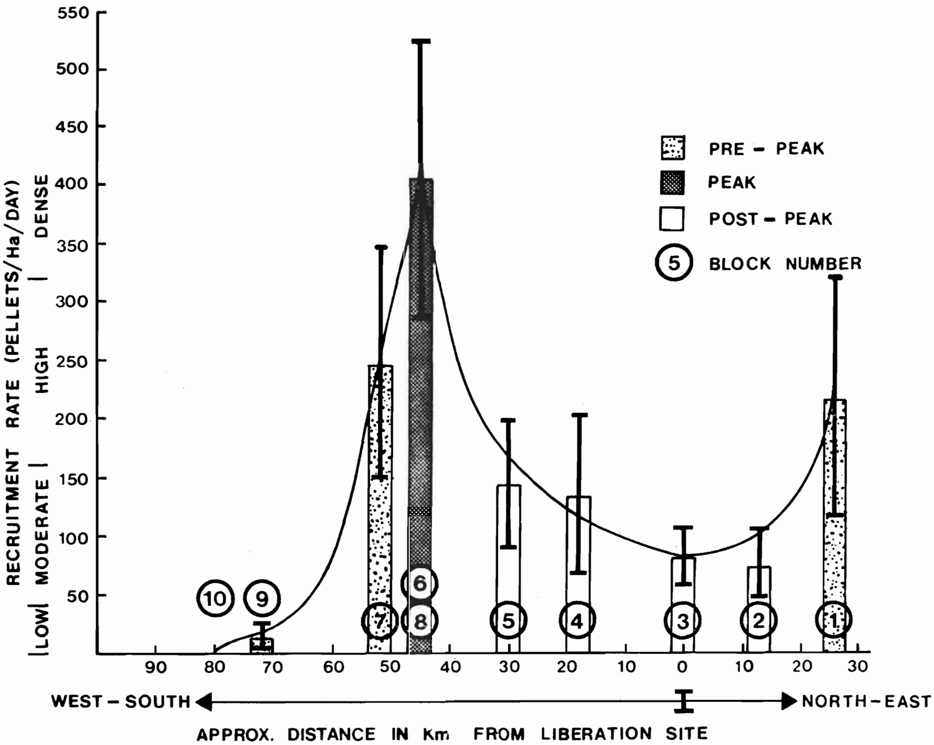

FIG. 5—Densities of possum pellets (expressed as recruitment rates/ha/day) shown for the various blocks, with their 95% confidence limits.

The eye-fitted trend for 1977–78 shows in broad concept that the high possum numbers present in Block 3 in 1950 (Fig. 2a) had declined and dispersed to either side of the main liberation area, to Blocks 6 + 8 and the lower portion of Block 1 respectively. Differences between blocks in forest composition, topography, and the presence/absence of browsing ungulates probably account for local variations in possum density within the blocks, but these were apparently not large enough to obscure the eruptive oscillations implied in Fig. 5.

The shading within the blocks shows population trends estimated from past field surveys by Fraser (1979) and L. Pracy (unpubl. data) and from the results of this survey. Blocks 6 + 8, the highest density areas, were probably close to peak population density in 1978 (*see* Fraser 1979). Blocks 1 and 7 both contained high pre-peak population densities; Blocks 2, 3, 4, and 5 moderate post-peak populations; and Blocks 9 and 10 scattered to low pre-peak colonising populations.

Red Deer Pellet Densities

The relative densities of deer pellets (estimated from mean recruitment rate of pellet groups per hectare per day) are shown in Fig. 6. Data from the scrub and grassland zones were not included in the mean estimates as they consistently showed pellet densities much lower than those in the forest.

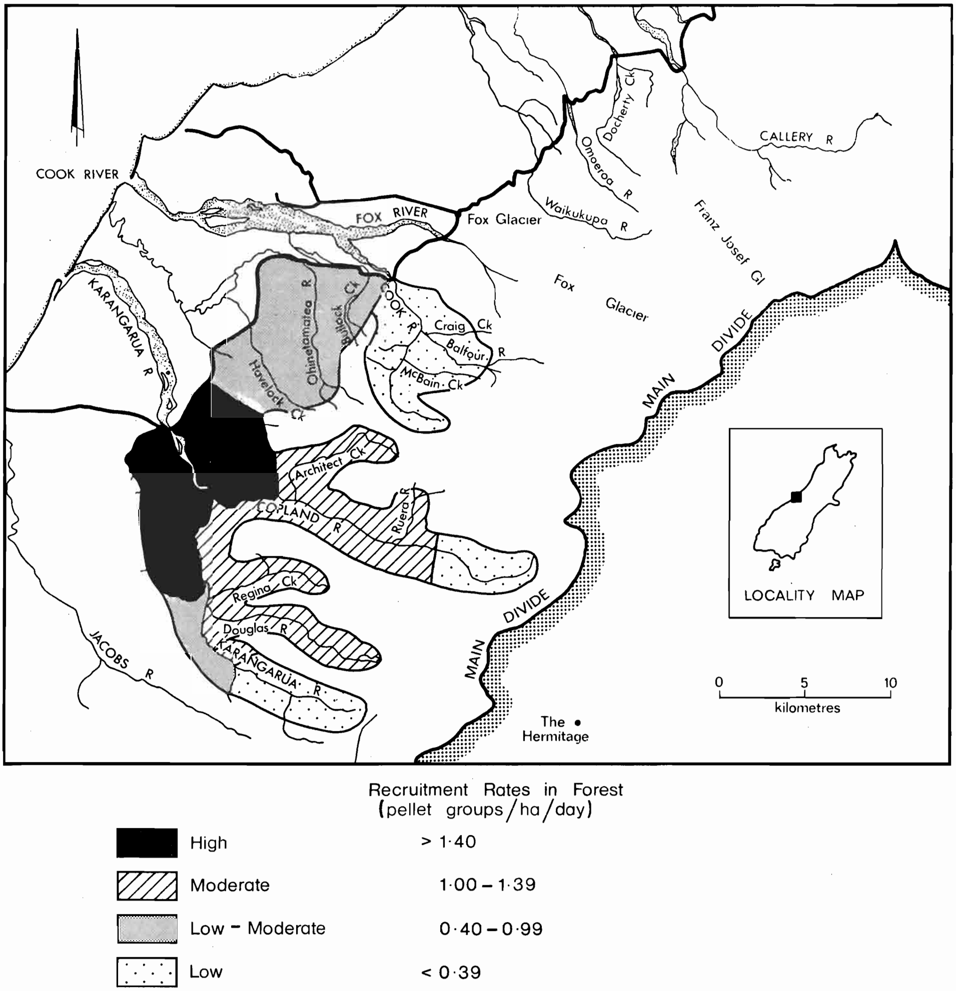

FIG. 6—Red deer pellet-group recruitment rates/ha/day in the Park (excluding scrub and grassland zones).

No pellets were recorded on any of the lines in Blocks 1, 2, and 3; however, a few deer have been seen in this area by commercial hunters operating from helicopters. Pellet densities were low throughout the forests of the Cook catchment (Block 4) and low to moderate in the Havelock Creek area (Block 5). The lower Karangarua catchment (Blocks 6 + 7) had the highest density recorded in any area of the Park. Pellet densities in the Copland catchment (Blocks 8 + 9) were moderate, with the terraces in the vicinity of Welcome Flat having higher localised densities. Densities upstream of Welcome Flat were low. In the upper Karangarua catchment (Block 10), pellet densities were at low to moderate levels over-all, with relatively higher densities in the Douglas and Regina catchments. Densities upstream of the gorge in the Karangarua headwater area were low.

When the pellet lines in Blocks 6 to 10 were pooled and re-sorted on the basis of altitude at their valley floor origin, a definite relationship between altitudinal depth of the forest and deer density was indicated. As the amount of forest decreased with the rise in altitude of the valley floor towards the Main Divide, deer densities also decreased.

The altitudinal distribution of deer in Blocks 5–10 (Fig. 7) showed no obvious preference for any particular forest zone. In the lower Karangarua catchment (Blocks 6 + 7, the highest-density area) field observations suggested that deer densities were relatively higher in the upper forest. Above timberline, in the scrub and grassland zones, deer densities were significantly lower than in the forest.

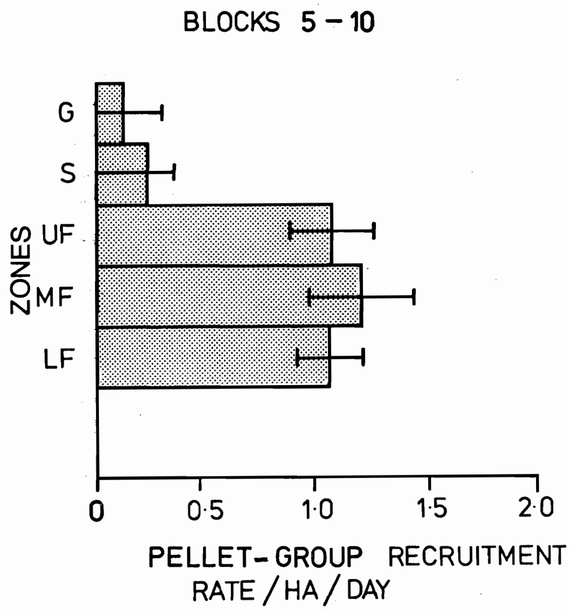

FIG. 7—Red deer pellet-group recruitment rates/ha/day for the five altitudinal zones for Blocks 5–10 (with 95% confidence limits of pellet-group densities).

Chamois Pellet Densities

Mean chamois pellet densities (assessed from recruitment rate of pellet groups), for the forest and scrub zones only, are shown in Fig. 8. The grassland was not included in the mean estimates as it was under-sampled in the majority of blocks.

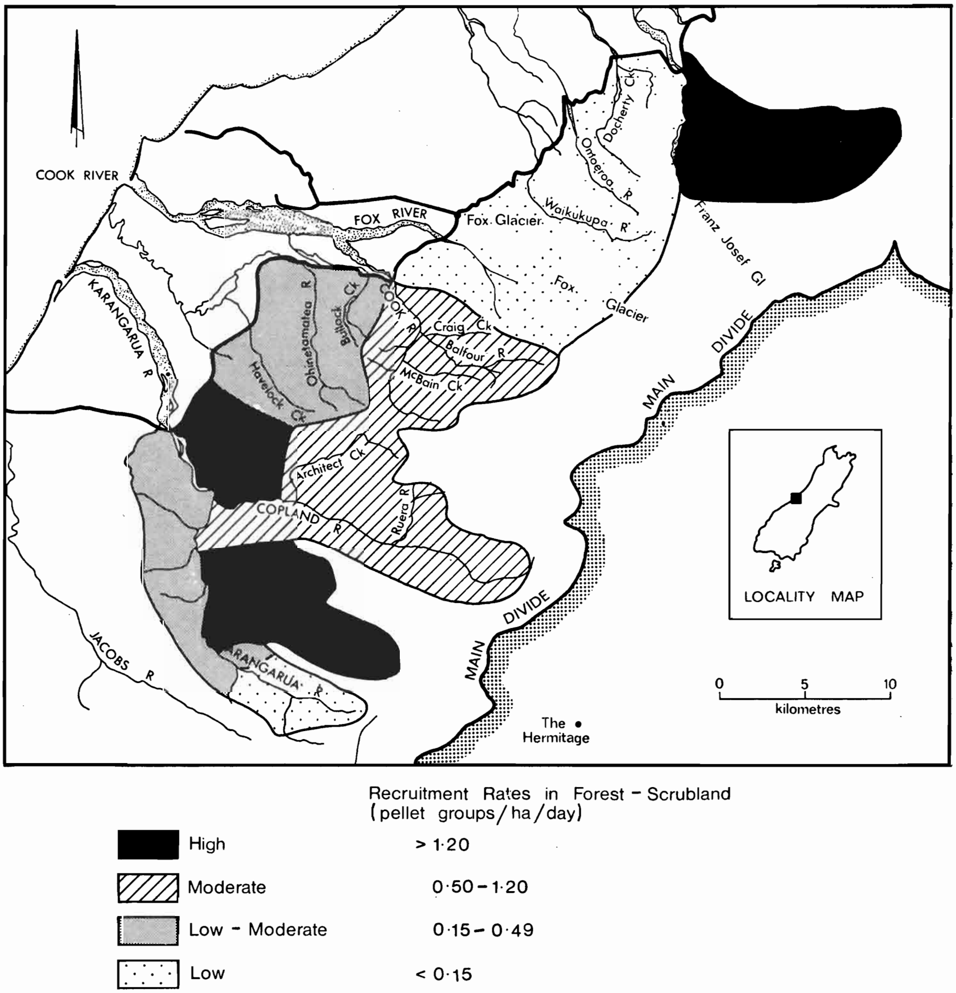

FIG. 8—Chamois pellet-group recruitment rates/ha/day in the Park.

The highest densities occurred in the Douglas and Regina catchments of Block 10. Densities were also high in the Callery catchment (Block 1), particularly in the upper forest, scrub, and grassland zones, and in the northern part of the lower Karangarua catchment (Block 6). The reason for the local abundance of chamois in Block 6 (the only high-density area along the frontal country) is not clear. Chamois densities were relatively low from the Franz to the Fox but increased in the Cook and Copland catchments. The lower densities in the Havelock catchment were similar to those in the lower southern part of the Karangarua catchment (Block 7). In the Karangarua headwaters, densities were much lower and no pellets were found upstream of the Douglas River confluence.

Densities for the whole survey area combined (Blocks 1–10, Fig. 9) progressively increased from the lower forest up to the scrubland before declining in the grassland. The alpine scrublands were subjected to the highest chamois densities.

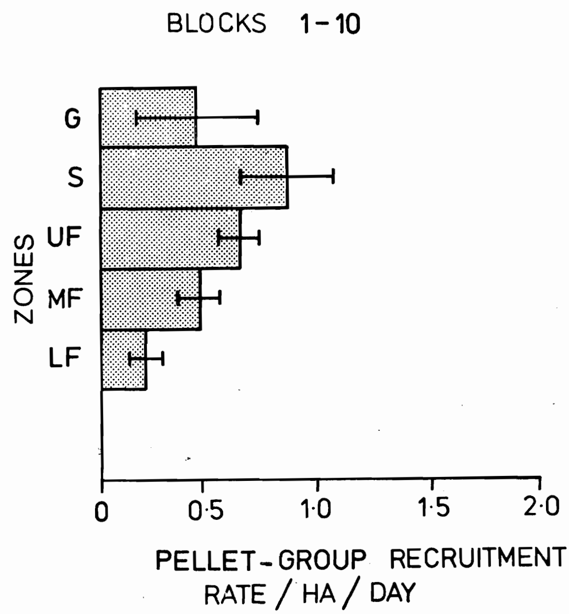

FIG. 9—Chamois pellet-group recruitment rates/ha/day within the five altitudinal zones (with 95% confidence limits of pellet-group densities).

Goat Pellet Densities

Block 5 (the Havelock area) was the only area in which goat pellets were recorded. A preference was shown for the low forest zone, where pellet-group density (not expressed as recruitment rates) was estimated at 371 ± 190 groups/ha (Fig. 10). Densities declined in the mid and upper forest strata. The grassland and scrub zones were not adequately sampled.

The highest densities of goat pellets were present on the true left of Havelock Creek. Densities on the true right of Havelock Creek were lower and declined progressively in a northerly direction. Densities declined southwards to moderate levels, with low numbers of pellets in Rough Creek. No goats have been recorded further south in the Park (J. Dixon, J. Scott, pers. comm.). Bullock Creek was probably the northernmost catchment in which goats were present. No evidence of goats was found upstream of

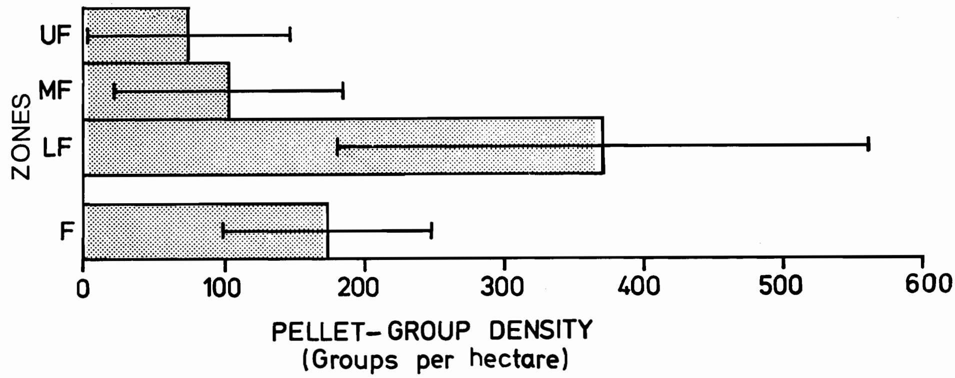

FIG. 10—Goat pellet-group densities per hectare in three altitudinal forest zones and in the combined forest (F) in Block 5 (with 95% confidence limits).

the Waikukupa River and Omoeroa River road bridges by survey parties. Goats reported seen in these areas in the past (J. Dixon, pers. comm.) do not appear to have established breeding populations.

Canopy Defoliation

Broad patterns of canopy defoliation recorded in the Park in 1978 are presented in Fig. 11 and show the variation in condition of the canopy of these forests.

The most conspicuous and widespread canopy defoliation was observed and photographed around the northern and southern boundaries of the Park and in the headwaters of the Cook catchment, around the lower portion of the Karangarua and northern side of the Copland catchments (Blocks 6 + 8 and 7), and in the lower reaches of the Callery catchment, especially on the southern side.

The central portion of the park and the headwaters of the Callery and Copland catchments showed moderate or moderate-to-slight canopy defoliation. No defoliation was observed on the lower southern side of the Copland catchment, or on the lower northern side of the Karangarua catchment upstream from the Copland River confluence. The headwaters of the Karangarua catchment were not surveyed.

DISCUSSION

Possums

High population numbers described in 1950 at the main liberation site in the Fox and Waikukupa River areas (L. Pracy unpubl. data) had declined by 1978. The centre of high numbers had moved north to the lower reaches of the Callery catchment (25 km in 28 years, 0.8 km/annum) and south to Architect Creek in the Copland catchment (45 km in 28 years, 1.6 km/annum). The slower rate of spread northwards could have been caused by the unmodified dense forest understorey in this area and the more dissected topography.

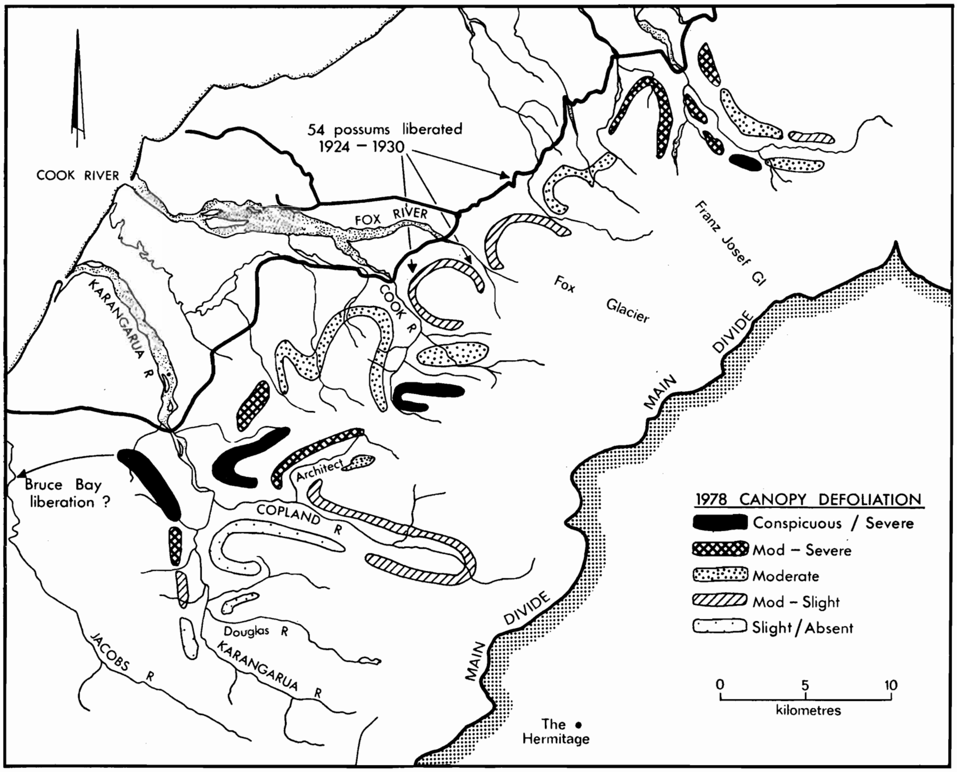

FIG. 11—Canopy defoliation patterns in the upper montane forests of the Park in February 1978. The swath widths shown are approximately 300 m wide and follow the flight path of the helicopter between the 950- to 1200-m contour lines (i.e., just above timberline).

Based on the results of this report, future broad trends in possum populations can be predicted. The current high densities on the lower northern bank of the Copland (Blocks 6 + 8) and lower reaches of the Callery (Block 1) catchments are likely to decline. Conversely, populations inhabiting the lower southern bank of the Karangarua catchment (Block 7) and the upper half of the Copland and Callery catchments are likely to increase in density, followed by an increase in density of the colonising populations in the upper half and on the lower northern bank of the Karangarua catchment.

A peak density population was not recorded between the post-peak population in Block 2 (Franz Josef, *see* Fig. 5) and the pre-peak population in Block 1 (the Callery catchment, including the northern bank of the Waiho catchment). We consider that this was an artifact of the relatively large size of Block 1 and its rugged topography, which was under-sampled. Pellet densities in the lower half of Block 1 were much higher than those in the upper half, although this could not be demonstrated statistically because of small sample sizes. It is probable that the lower half of Block 1 contained the "missing" peak population.

Ungulates

Deer densities in the headwaters of the Copland and Karangarua catchments were much lower in 1977–78 than they were in the mid 1960s because of intensive commercial harvesting with helicopters. As a result, the present populations were almost certainly better fed than in the 1960s. Challies (1978) described this phenomenon for red deer populations in the Arawata catchment, South Westland, which have also been intensively hunted both for control purposes and commercially. The distribution of the deer had also changed and they were now found mainly in the forest habitat (Fig. 7). Earlier reports (Batcheler 1968; Challies 1974, 1977) had indicated that, before intensive commercial harvesting, high densities of deer were present in the alpine grasslands of Westland. No deer were recorded north of the Cook catchment and the forests in this area had not been modified by their browsing.

Chamois numbers were high in the northern and southern regions of the Park, mainly in the headwaters of the Callery and Karangarua (i.e., Douglas River and Regina Creek) catchments. Numbers in these areas had also declined markedly since the late 1960s. Between 1971 and 1975 commercial recovery teams shot and recovered approximately 9000 chamois and thar from the Copland/Karangarua area alone (K. Tustin, pers. comm.).

The altitudinal distribution of chamois in 1978 showed highest densities in the upper montane forest and subalpine scrub belt (Fig. 9). This was above the altitudinal zone where the highest densities of deer were recorded (Fig. 7). Chamois did, however, use the forest at all altitudes and during the survey were sighted on seral slips and grassy flats along State Highway 6. Isolated sightings have been made in the forests west of this highway and even along the beach (P. Fullerton, pers. comm.).

Goats were recorded in a relatively small part of the survey area, where highest densities of pellets were found in the lower altitude forest (Fig. 10). However, as they occurred concurrently with deer and chamois, their effects on the forest understorey in combination with these two species should not be under-estimated.

Canopy Defoliation

High possum population densities recorded in 1978 in the northern and southern regions of the Park coincided with localities where widespread and conspicuous canopy defoliation was observed and photographed. "Severe" canopy defoliation recorded and photographed in the Fox and Waikukupa River areas in 1950 (C. G. R. Chavasse, unpubl. data) also coincided with regions of high possum density. Pekelharing (1979) showed a direct relationship between conspicuous and widespread canopy defoliation and high-density possum populations in the mixed rata/kamahi (*Metrosideros umbellata* Cav./*Weinmannia racemosa* L.f.) forests of the Taramakau catchment in central Westland. That the conspicuous canopy defoliation in these areas was a relatively recent event was demonstrated by a study of enlargements of historical aerial photographs. These showed no conspicuous defoliation in the northern and southern regions of the Park in 1965, nor in the Taramakau catchment in 1963 (Pekelharing 1979).

The "severe" canopy defoliation described and photographed in the possum liberation area at Fox in the early 1950s (Chavasse, unpubl. data) had recovered to some extent by 1978. Relatively few defoliated crowns were seen in these upper montane forests during our 1978 aerial survey. Allen & Rose (in press) have stated that recovery within the dieback stands in this area was caused in part by epicormic regeneration of previously defoliated kamahi crowns. Southern rata trees within the canopy had died, however, over a wide diameter range. The defoliation and mortality occurred synchronously and have not spread into new areas since.

Tentative predictions can be made about future trends of canopy defoliation in the montane forests of the Park, the extent and speed of which may be related to the extent and effectiveness of commercial possum-harvesting. They are based on the assumption that the degree of rata/kamahi canopy defoliation is directly related to the intensity and duration of possum browsing pressure:

pre-peak low-density populations = inconspicuous canopy defoliation;

peak high-density populations = conspicuous and widespread canopy defoliation;

post-peak moderate-density populations = widespread inconspicuous canopy defoliation and mortality (in the absence of understorey modification by ungulates) or widespread and conspicuous mortality (in combination with severe understorey modification by high densities of ungulates).

Stewart & Veblen (1982), in their work on tree population dynamics in forests elsewhere in Westland, and Veblen & Stewart (1982), in their discussion of the effects of introduced wild animals on New Zealand forests, pointed out some inconsistencies (including supposed instances of pre-possum canopy death) in the preceding basic assumption. They have proposed alternative explanations, i.e., that natural stand dynamics resulting in synchronous mortality of senescent even-aged stands can account for much of the larger-scale canopy dieback. However, Allen & Rose (in press) found that the patterns of canopy dieback in their study areas (which included part of Westland National Park) could not be explained by the process put forward by Stewart & Veblen (1982) alone, partly because the mortality occurred over so wide a diameter range. Batcheler (in press), in his review of the literature on rata/kamahi canopy dieback, concluded that the possum is responsible. Fitzgerald & Wardle (1979) showed in their study of possum diet in part of Westland National Park that possums have a clear preference for the leaves (which formed the bulk of their diet) of two major canopy species, southern rata and kamahi.

If our basic assumption is correct, an increasing trend of canopy defoliation is likely to occur within the next decade in the upper half of the Copland and Callery catchments. Canopy defoliation may be expected in the next two decades in the upper half of the Karangarua cacthment (Block 10). Some "recovery" of the canopy should in time become apparent along the frontal faces of Block 2. No deer were present in this area, chamois densities were low, and the understorey had remained largely intact.

Slight-to-moderate canopy defoliation was observed around Welcome Flat in the Copland catchment, where low densities of possums were recorded in 1978 and in the past. Most of the defoliated crowns in this area consisted of Hall's totara (*Podocarpus hallii* Kirk). Wardle (1978, 1979) discussed the mortality of mature stands of Hall's totara and suggested that it did not appear to be solely possum-induced. J. Coleman (pers. comm.), however, found that in the Haupiri catchment totara foliage was a favoured possum food.

Possum and Ungulate Interactions

The only area in Westland rata/kamahi forest where partial canopy-recovery has been documented (the Fox area north of the Cook catchment) coincides with the only area where browsing pressure from ungulates in the understorey tiers has been low or absent. In central Westland, however, where possum population peaks coincided with high deer numbers and a severely depleted open understorey, repeated canopy defoliation caused widespread mortality and forest modification (Coleman *et al.* 1980; I. L. James, unpubl. data). The containment of large-scale canopy mortality in Westland National Park, therefore, may hinge on maintaining an unmodified forest understorey concomitant with the lowest possible ungulate browsing pressure.

Although chamois in Westland National Park appear to be predominantly subalpine, they were the only ungulate recorded at high population levels in the Callery catchment (Fig. 8). Some modification of the forest understorey has presumably taken place in this area, especially in the upper montane forests. Possum densities were also high in this habitat, which may account for the conspicuous and widespread canopy defoliation.

The lower reaches of the Karangarua catchment contained high numbers of possum, deer, and chamois (Fig. 3, 6, and 8). The combined effects of these three species will undoubtedly influence the structure and composition of these forests in the future.

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