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ERUPTION, DETERIORATION AND DECLINE OF THE NELSON RED DEER HERD

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ABSTRACT

Data are presented on population increase, physical deterioration and decline of red deer during the period 1900-1960, throughout the northern South Island region. Densities are mapped at decade intervals between 1910 and 1950. Population numbers increased rapidly after liberation in 1861; highest densities occurred between 1925 and 1940. Population peaks varied from 3-13 years in duration 10-30 years after colonisation and were primarily influenced by food supplies and speed of population increase in the different regions. Depletion of food supplies by deer is proposed as the reason for general physical deterioration of populations during the peak eruptive period. Decline of food supplies and associated population stress, coupled with harsh winter weather (especially in 1928-31 and 1939-42) resulted in overall herd decline.

INTRODUCTION

The liberations and dispersal of red deer (*Cervus elaphus* L.) throughout the northern South Island have been described in earlier papers (Clarke, 1971, 1973). In this paper patterns of increase, physical deterioration and decline of red deer populations during the period 1900-1960 are examined throughout the northern South Island districts.

Although several brief accounts of the Nelson red deer herd were published during the 1920's (Thomson, 1922; Forbes, 1924; Donne, 1924), the only recent papers are

those of the author. Information for the present study was collected between 1963 and 1973 from 134 people with local knowledge of red deer*. This information was used only when it was substantiated by data from two or more other sources. Other useful sources of information included Acclimatisation Society notes and records, government departmental files, newspaper articles, books and little known museum collections*. The study region and place names mentioned in the text are shown in Fig. 1.

Historical

Red deer liberated at Nelson in 1861 were legally protected until 1882 when licences for the shooting of stags during a limited season were issued by Acclimatisation Societies. Protection was removed from deer after 1923 in the Nelson district, south of an east-west line through Ben Nevis and Mt Owen to the boundaries of the district; Marlborough, except the Sounds; and the North Canterbury areas included in this study (Fig. 1). Protection was removed in 1927 in the remaining areas of Marlborough, North and West Nelson, and in the Grey and Buller districts in 1930 (Wodzicki, 1950). Deer shooting was encouraged by payment of bounties and provision of free ammunition. In 1927 the State Forest Service began limited culling operations in the Hanmer and South Nelson regions. Large scale deer destruction campaigns were organised in 1931 by the Internal Affairs Department and bounty payments were discontinued. Subsequently an alternative scheme for departmental marketing of deerskins led to the overall intensification of the private hunting effort. These activities together with official operations declined on the outbreak of World War II. Particularly high prices paid for skins at the end of the war presented an additional inducement for people to shoot deer. In 1956 responsibility for deer control passed to the N.Z. Forest Service. Since 1960 added commercial value of venison and deer by-products has intensified hunting, including extensive operations by helicopter.

Pre-eruptive Conditions of Deer and Habitat

The Nelson Thorndon strain red deer are described in early publications (Thomson 1922; Donne, 1924) as inferior to other strains liberated in New Zealand because of their smaller body size and small antlers. Nonetheless, in earlier years, weights of mature stags ranged from 135-185 kg and heads of 12 or more points were not uncommon (Adams, 1906). Considerably larger animals occurred on the periphery of the herd and in other places providing abundant forage. The antlers of these deer were especially robust, and noted for their prominent beading and palmation. In addition, deer occupying limestone areas were generally much above average size, whereas those in the volcanic regions, e.g. Red Hills, were quite small.

The habitats encountered by red deer during colonisation varied extensively in terms of terrain, vegetation and climate, and also in extent of modification by man and other animals. Prior to 1900, and before the influx of deer, many areas of forest and alpine meadow were substantially undisturbed. Early descriptions of the vegetation (von Haast, 1861; Anon, 1895), suggest that the vegetation was formerly more luxuriant. Contributors to this study tell of an abundance and diversity of species prior to the arrival of deer; masses of *Ranunculus insignis* (mountain buttercup) up to 1 m high in gullies on Mt Owen; alpine slopes covered with *Gingidium montanum* (aniseed) and *Anisotome*

* Undated citations in text refer to these sources, **see** Appendix.

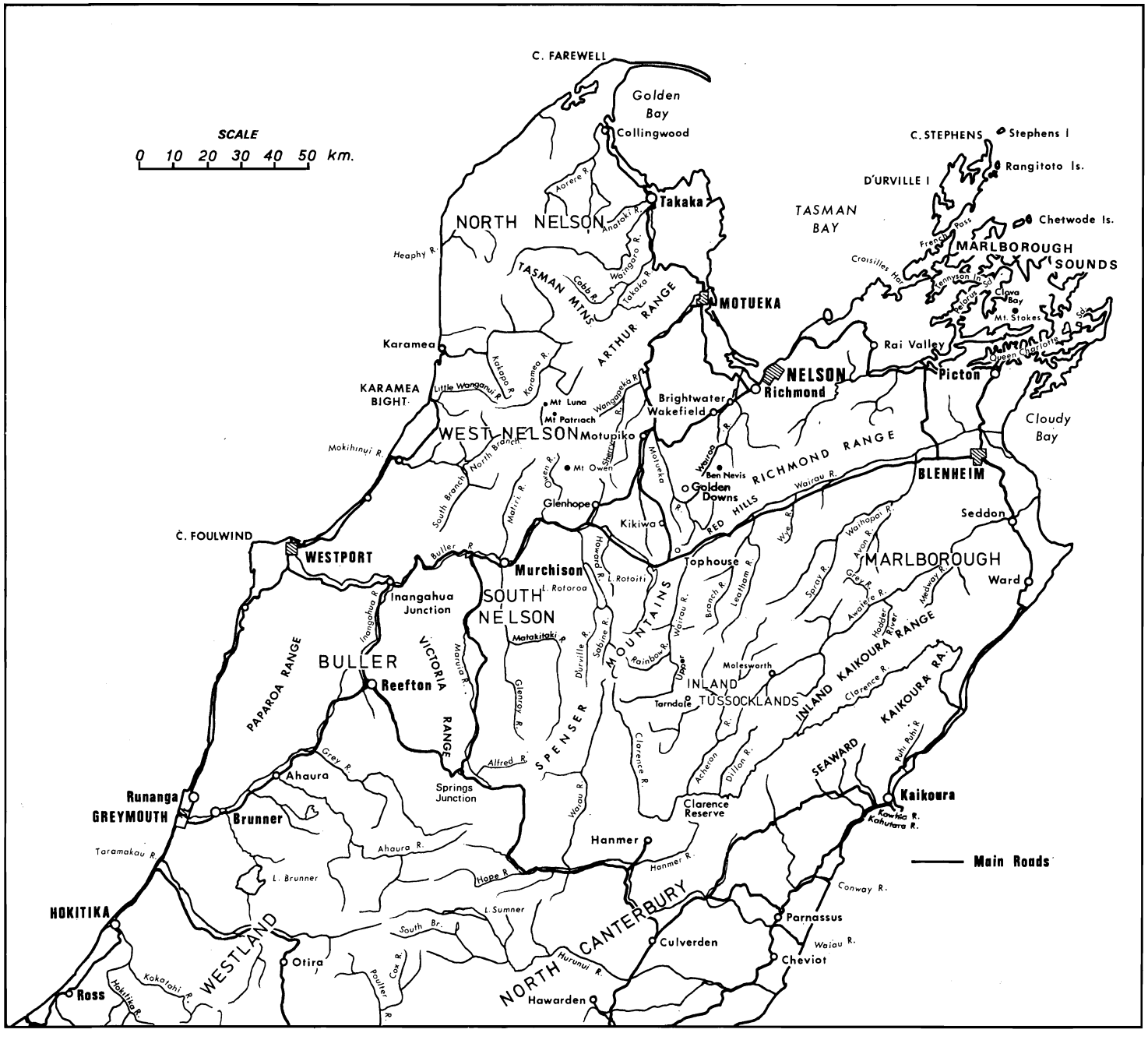

FIG. 1—The study region showing place names and areas mentioned in the text.

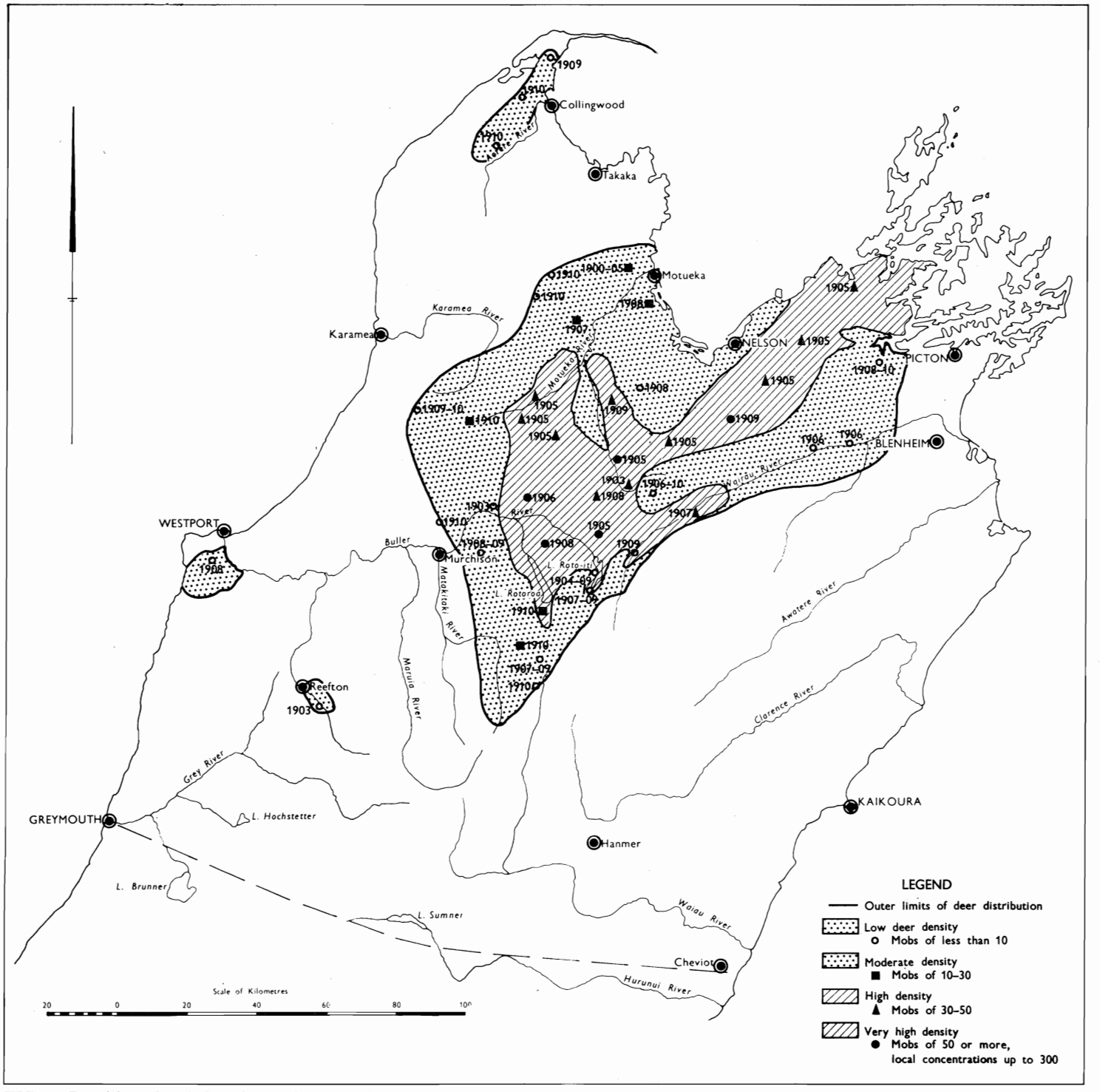

FIG. 2—Densities of red deer in northern South Island districts at 1910. Low and moderate densities, and high and very high densities are shown in two aggregate classes.

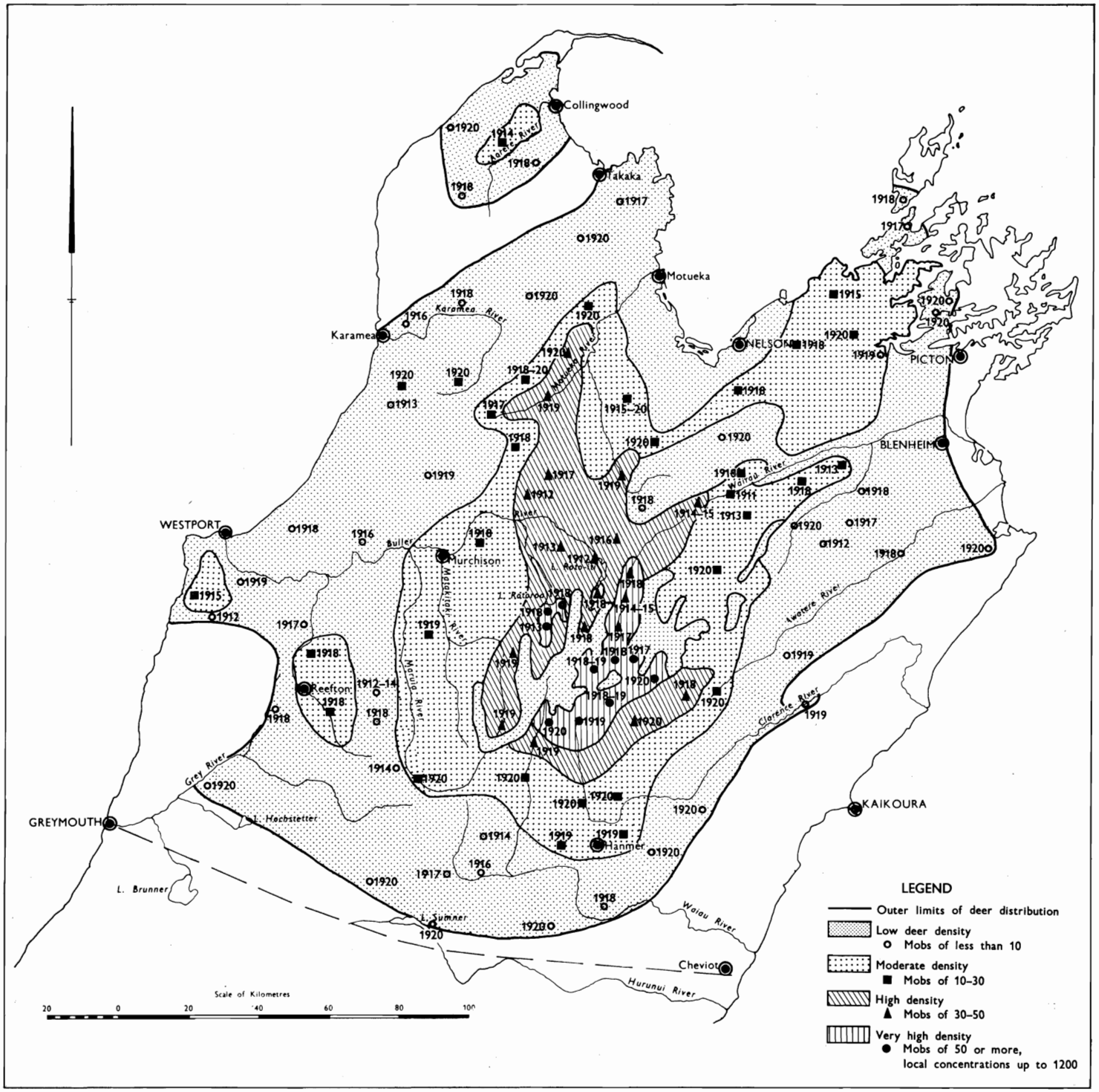

FIG. 3—Densities of red deer in northern South Island districts at 1920. Densities occurring outside of the main distribution indicate areas of separate liberation (see Clarke, 1971). Areas of low density within moderate and high density zones indicate alpine regions only recently colonised.

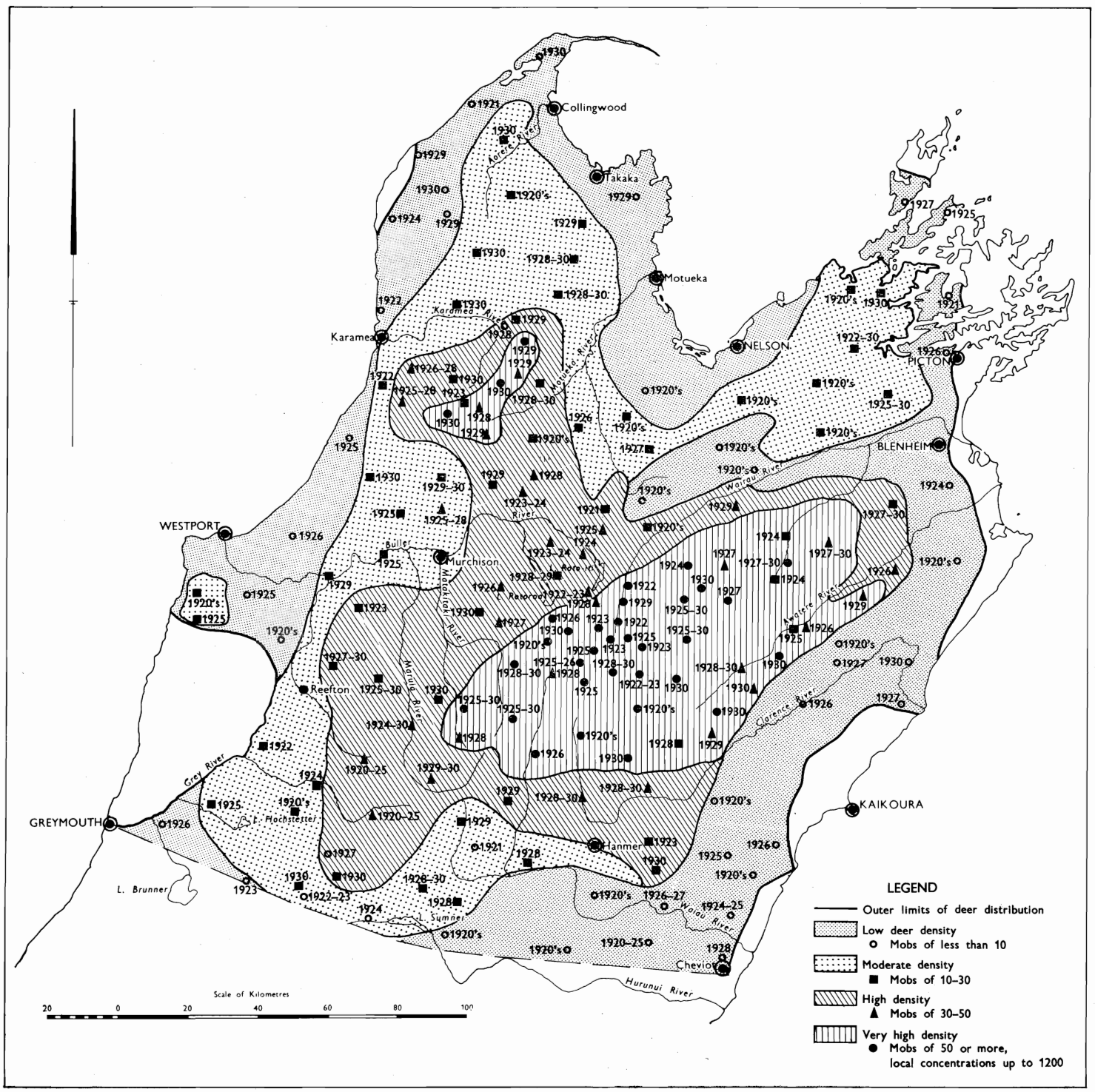

FIG. 4—Densities of red deer in northern South Island districts at 1930.

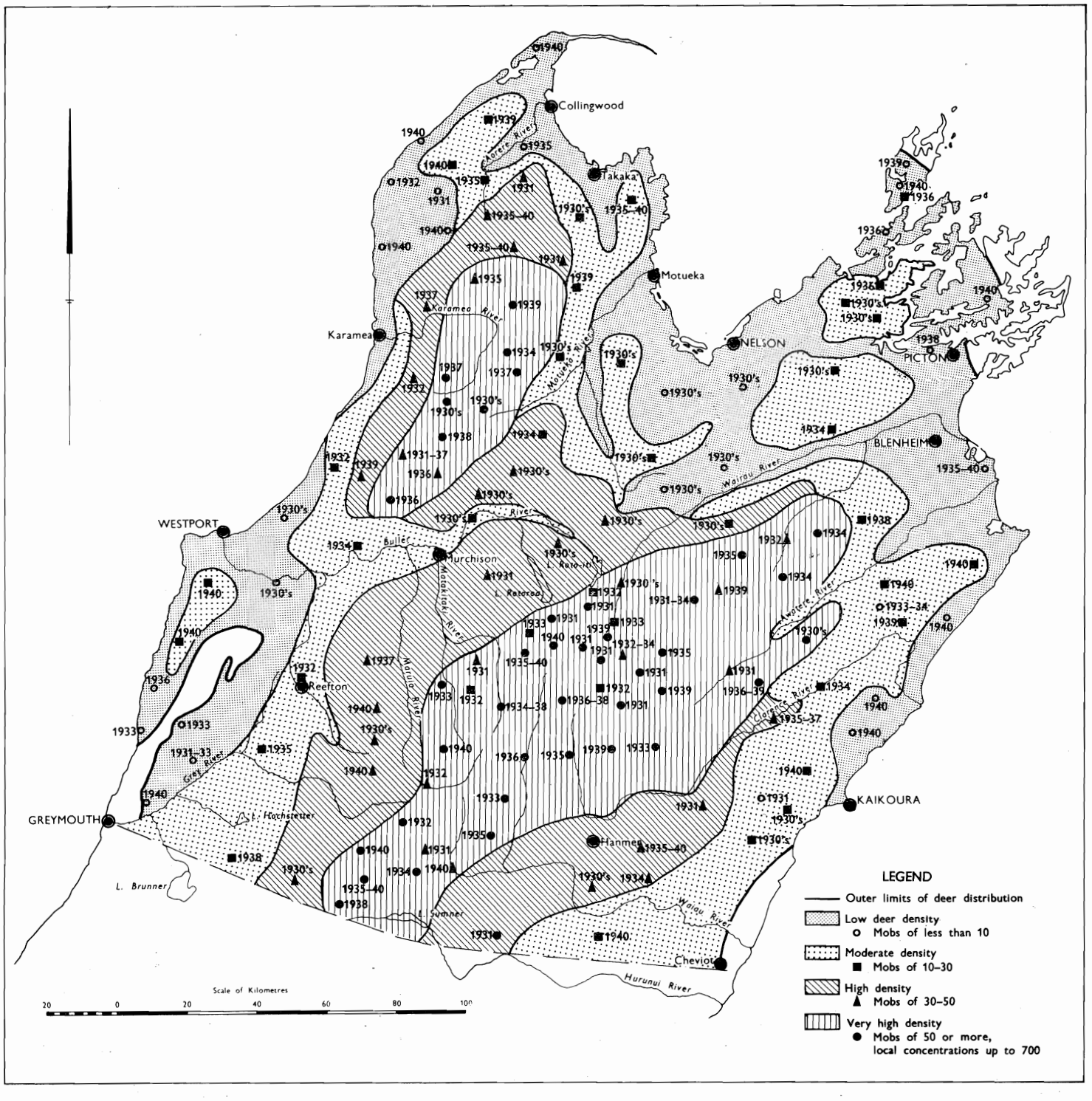

FIG. 5—Densities of red deer in northern South Island districts at 1940.

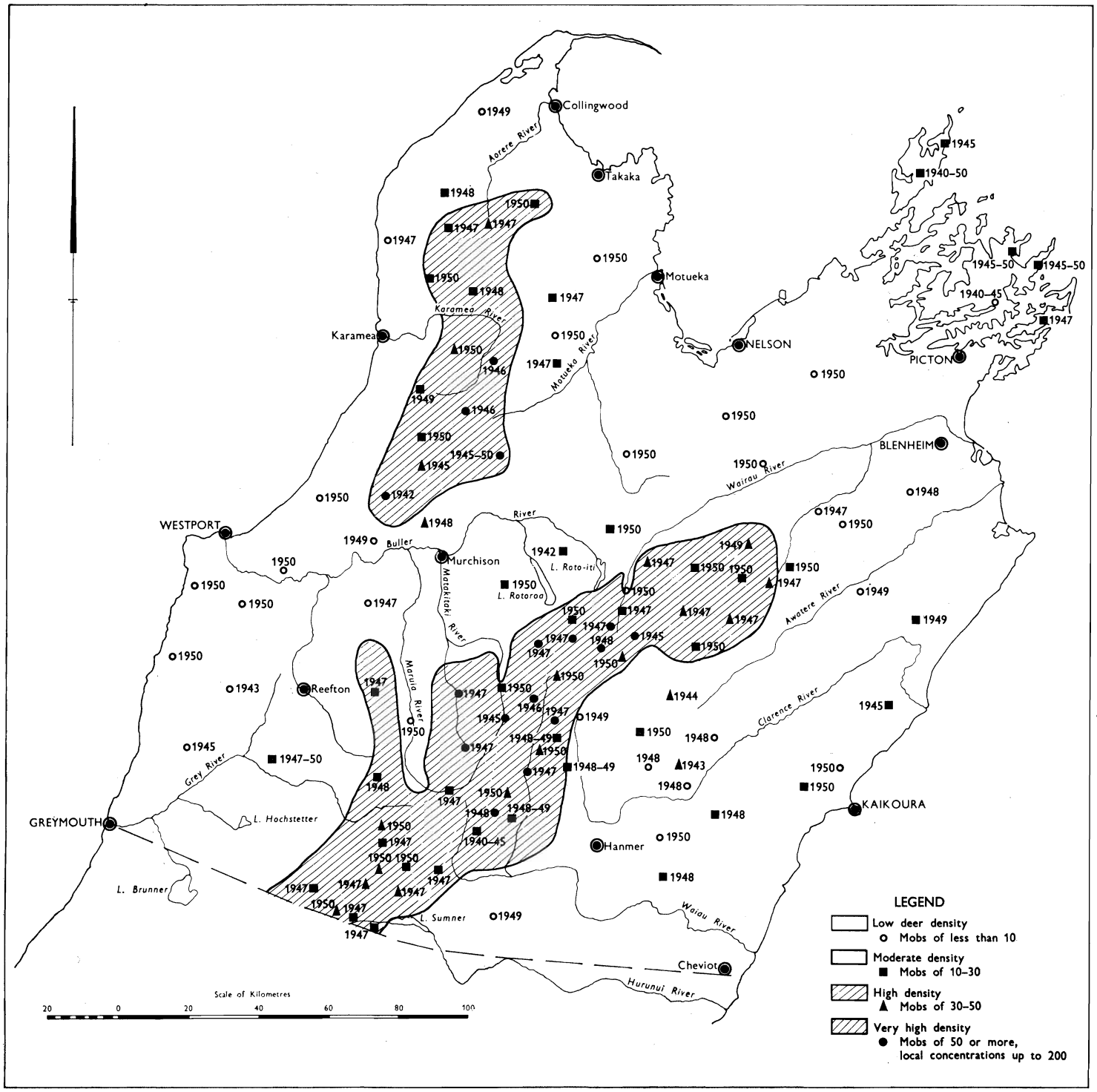

FIG. 6—Densities of red deer in northern South Island districts at 1950. Low and moderate densities, and high and very high densities are shown in two aggregate classes.

pilifera in the Spenser Mountains; and dense forest understoreys at Glenhope of *Griselinia littoralis* (broadleaf) *Coprosma foetidissima* (stinkwood) and *Neopanax colensoi* (three-finger) (L. Arnold; E. S. Griffith; D. W. Winn; N. McConachie). Animals feeding on these species were reported in excellent condition.

Burning, and grazing by domestic stock, profoundly influenced the vegetation in many areas prior to the influx of deer. In the inland tussocklands of Marlborough, sheep, rabbits, goats, and fire contributed heavily to their depletion (McIntosh, 1940; Tomlinson, 1968; McCaskill, 1969). Molesworth, Tarndale and the Rainbow run in particular were over-burdened with rabbits in the 19th century and high infestations persisted until the 1940s (McCaskill, 1969). To some degree, deer and rabbits did not compete, since rabbits occupied the river flats and lower slopes, and deer the higher montane areas for summer range. A rabbit proof fence between the Clarence and Waiau catchments was an important barrier to the westward dispersal of rabbits to the Waiau River (P. Newton). Despite the depletion of habitat east of the fence, grasslands in the Waiau valley were lush prior to the arrival of deer. Stock also occupied forests and formed many feral populations, some of which persisted until recent times (Tomlinson, 1968; McConachie, 1971; Clarke, 1972). In addition, accessible alpine grasslands were commonly used for summer pasturing of sheep and cattle between 1860 and 1920 (Clarke, 1972). In some areas, (e.g., Richmond Range and Clarence River) feral goats and pigs also competed with deer for range.

The impact of fire and other animals was not however, entirely unfavourable to deer; pasture establishment from burned forest benefited deer by improving access and providing lush new grass. Further, even in substantially modified areas, deer were able to exploit habitats unavailable to competitors. Unlike domestic stock, deer soon became distributed over a wide range of habitats, hence reducing their dependence on any single zone.

I ERUPTION

1. Eruptive Sequence

The densities of red deer, compiled from dated records of the numbers of deer seen and shot (Appendix) are mapped at decade intervals for the period 1910-1950 (Figs. 2-6). Mapped densities are defined from broad differences in population size and adjusted to coincide with known habitat limitations. The terms, mob and concentration, used in the text to describe population size, refer to deer in separate localised groups and regionally aggregated groups, respectively. Outer limits of deer distribution are from an earlier paper (Clarke, 1971).

The Nelson herd of red deer increased rapidly. By 1880 deer were plentiful in the ranges near Nelson city; then as the 1900's began deer spread out to the south and east, and densities in these areas rose accordingly (Fig. 2).

By 1920, high densities extended to Wangapeka River-Upper Buller River-Waiau River headwaters-Molesworth and to the Leatham River (Fig. 3). The largest numbers occurred along the Upper Wairau dispersal route (Clarke, 1971), and on the river flats of the D'Urville, Sabine and Travers River valleys where mobs of 30 or more and concentrations of 300-500 were commonly sighted (Fig. 3).

By 1930, the extent of high density populations, and overall herd size, had expanded enormously; mobs of 30-50 or more and concentrations of 600-1200 consolidated

throughout the Spenser Mountains and outlier ranges, Molesworth, Upper Awatere, south bank tributaries of the Wairau River and in the Arthur Range (Fig. 4).

Populations had further expanded by 1940, with high densities extending throughout the western and central montane regions (Fig. 5). In the Tasman Mountains and other more recently colonised areas the densities of deer continued to increase (Fig. 5). However, in the Spenser Mountains densities were generally lower at 1940 than those recorded earlier in the decade. Populations in the Upper Wairau-Tarndale region underwent a sharp decline in numbers during the early 1930's.

After 1945 many populations declined or did not increase further, and by 1950 few areas of very high density remained (Fig. 6). A few regions, for example, the outer Marlborough Sounds, Seaward Kaikoura Range, Paparoa Range and other more recently colonised areas experienced small rises in density and continued to do so into the 1950s. Thereafter however, densities generally declined.

By contrast, in a few regions (for example the eastern Marlborough Sounds, Red Hills and Paparoa Range) the eruptive cycle was poorly defined. Populations there increased slowly, fluctuated sporadically over several years, and then declined. These regions offer generally unfavourable habitat to red deer.

2. *Changes in Population Densities*

Figure 7 shows the area occupied by each of the four mapped density classes (Figs. 2-6) as percentages of total established range (Clarke 1971). Aggregate densities are shown for the decade periods ending 1910 and 1950, since not all classes can be delineated.

At 1910 the aggregated area occupied by high densities (i.e. high and very high classes, Fig. 2) totalled 39% of the established deer range (Fig. 7), then colonisation accelerated, and deer became more widely dispersed. Consequently by 1920 dense populations made up only 13% of the total range. As dispersal slowed and densities increased, the area occupied by high densities expanded to 39% by 1930, and later by 1940, to 47% of the total range colonised (Fig. 7). By 1950 however, the area occupied by high densities had fallen to 35%; for by then few areas remained uncolonised and the carrying capacity of much of the existing range had been heavily reduced.

3. *Patterns of Population Establishment*

The marked southerly-orientated dispersal of the herd was a topographically controlled feature (Clarke, 1971). Initially, and prior to 1920, deer moved along valley routes; alpine areas were utilised only after population pressure in the lower areas encouraged deer to exploit alternative habitats. Sites particularly favoured were newly burned forests, forest fringes, forest clearings and montane river flats.

After about 1920, as populations consolidated, deer collected in the preferred montane valleys in increased numbers (Fig. 3). The occupation of alpine areas then accelerated. Lapses of time of 4 and 6 years between occupation of river flats and alpine grasslands were recorded in the Travers and Upper Wairau valleys, respectively.

The montane and alpine grasslands of the Upper Wairau and Molesworth regions were especially favoured for summer range; large scale movements occurred between these areas and adjacent forest winter range in the Wairau, Waiau, Travers, Sabine, Leatham, Branch and Waihopai valleys. In summer, the numbers of deer in the Waihopai valley typically declined to a small fraction of those present in winter. Similarly, many

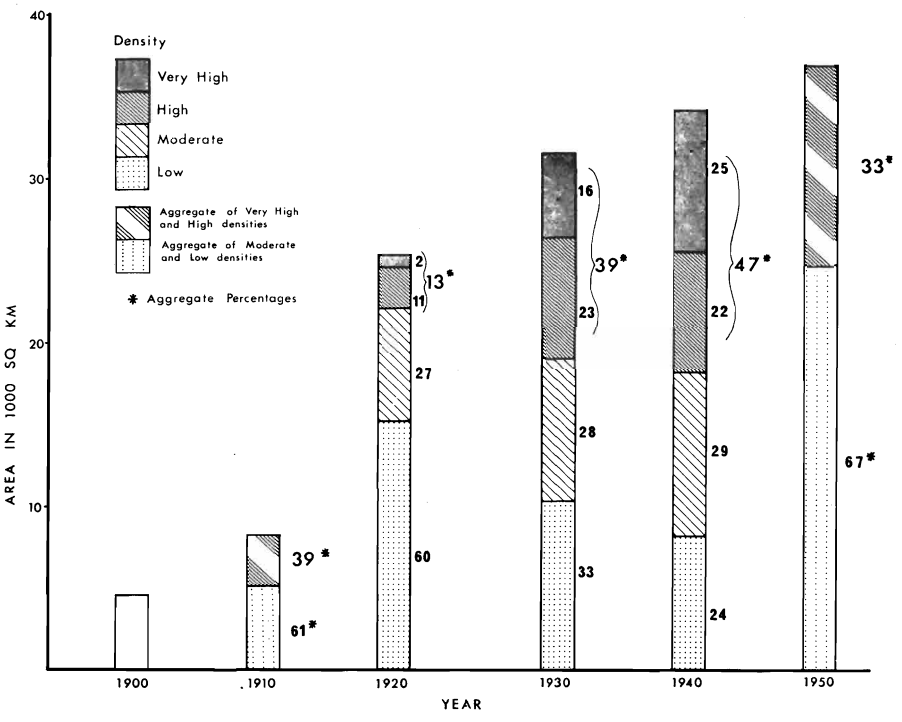

FIG. 7—Percentage area of range occupied by the different density classes at decade intervals from 1910 to 1950.

stags summering on Tarndale returned to the Rainbow River at the onset of the rut, considerably increasing the number of deer in that area.

The pattern of increase in North and West Nelson differed substantially to that in the Spenser Mountains and the other southern regions; fewer deer dispersed to North and West Nelson and increases there were accordingly much less rapid than in the southern districts. Also, the mode of dispersal was relatively uneven, accounting for subsequent irregularities in build-up in the different areas. The highest densities occurred initially on the river flats and clearings along the valley routes; deer and their sign were seldom seen far from open areas, since during this early period, the forest was dense and riverbeds and open streams provided the easier route of travel. However, the river flats were quickly depleted (Clarke, 1972) and after 1925 deer shifted increasingly to the alpine and upper forested zones. By 1928 mobs of 20-50 were commonly seen in the alpine basins of the Arthur Range (Fig. 4).

4. *Development and Maintenance of Peak Densities*

The approximate duration of peak densities of red deer in the different districts were as follows: Wairoa River, 1895-1905; Golden Downs, 1900-05; Tophouse, 1920-30; D'Urville-Sabine Rivers, 1925-31; Upper Wairau-Tarndale, 1927-31; Howard Valley, 1922-29; Wangapeka River, 1926-35; Rai Valley-Tennyson Inlet, 1920-30; Matakitaki River, 1926-31; Hanmer, 1929-31; Upper Maruia Valley, 1928-34; Upper Grey River,

1929-36; Branch River, 1929-33; Molesworth, 1930-33; Waihopai River, 1930-34; Middle Awatere Valley, 1930-34; Lake Rotoiti-Travers Valley, 1932-35; Hope-Waiau, 1932-35; Clarence Reserve, 1931-33; Cobb River, 1931-39; Conway River, 1932-37; Lake Summer, 1934-39; Victoria Range, 1933-39; Mokihinui River, 1933-43; Upper Karamea River, 1933-43; Anatoki River, 1933-43; Tasman Mountains, 1935-48; Lower Clarence Valley, 1939-45; Kowhai River, 1940-46; D'Urville Island, 1943-49. In Fig. 8 these data are summarised by region and related to the pattern of population growth. The times of initial antler deterioration shown in Fig. 8 are discussed in a later section. Records of initial occupation by deer and times when deer first become plentiful are derived from an earlier paper (Clarke, 1971).

Peak densities delineate for given areas the period of maximum population density, the actual value of which varied considerably. Where peak densities occur at separate times for different habitats within a catchment (e.g., river flats and alpine grasslands), only dates for the period of overall highest density are given. Peak densities cannot be delineated for populations in the Marlborough Sounds, Paparoa Range or Red Hills, where, as already mentioned, the eruptive cycle was poorly defined in all its phases.

Peak densities occurred more frequently during the period of the highest overall population from 1925 to 1940. In the inland tussocklands where dispersal and increase was rapid, peaks lasted 3-5 years (Fig. 8). Conversely, in western montane regions where the rate of increase was slow and forest food supplies initially abundant, peaks of 9-13 years were recorded.

The lapse of time between initial occupation and the date when the peak was reached similarly varied in different regions, but reflected the pattern evident in duration of the peaks. Hence, on such major dispersal routes as the Upper Wairau, populations reached a peak 15 years after initial colonisation, while further south at Clarence Reserve, the peak was reached after only 10 years (Fig. 8). By comparison 30 years elapsed before the peak was reached in the Upper Karamea River. Holloway (1950) and Riney *et al.* (1959) note a similar range of periods before populations peaked; these are for red deer in western Southland with peaks of 25-30 years and 14-19 years, respectively. A lapse of about 25 years before populations peaked in the Whitcombe River, Westland, is also noted by Pekelharing (1973).

II DETERIORATION AND DECLINE

1. *Decline Sequence*

In accordance with described patterns of red deer eruption elsewhere in New Zealand (Holloway, 1950; McKelvey, 1959; Riney *et al.* 1959; Riney, 1964; Howard, 1964, 1965b) populations in Nelson increased rapidly, levelled out to a peak; and then declined. The early high rate of increase of the Nelson herd can be attributed to such favourable factors as unlimited food supplies, equitable climate and terrain, and the virtual absence of hunting and competition from other mammals. However, as the impetus of dispersal waned, densities built up to exceed the carrying capacity, and the decline in the general eruptive sequence is hypothesised to have followed the decline of food supplies.

In 1906, early indications of decline were seen in the recently deteriorated quality of antlers at Nelson (Adams, 1906). Then in subsequent years, the physical condition of red deer deteriorated rapidly. By 1920, wholesale physical deterioration was evident in all high density populations; during the 1930's heavy mortality of deer occurred and

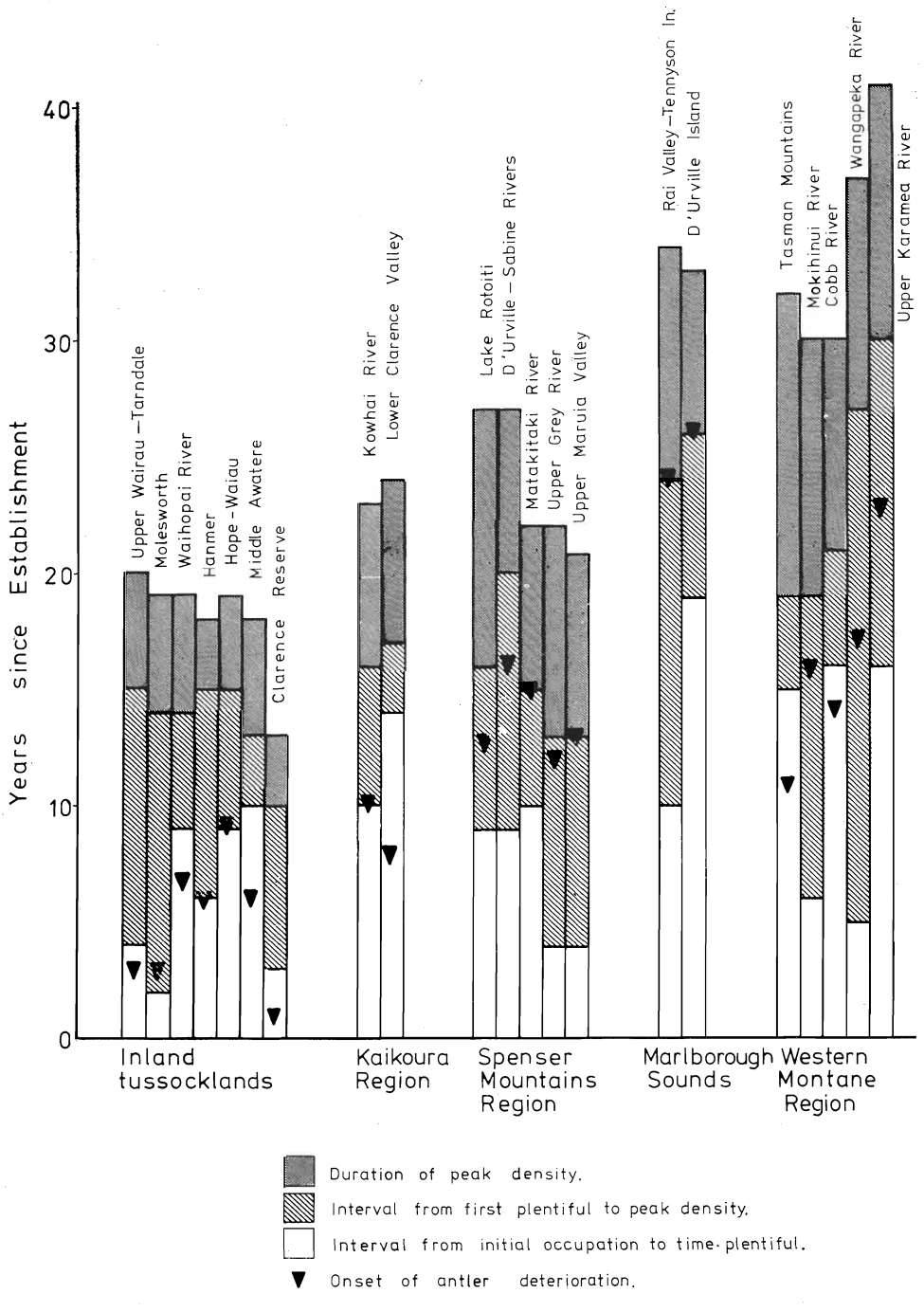

FIG. 8—Comparison of eruptive phases from establishment until end of peak for red deer populations in different regions.

many populations declined. Although numbers fluctuated considerably during the 1930's and 1940's the major pattern was one of general decline. By 1950 populations had levelled out at lower densities, and an improvement in physical condition (e.g., increases in fat reserves) followed as an apparent response.

2. *Decline of Food Resources*

Deer colonising, or moving through new areas, initially selected the most palatable species, for example, *Gingidium montanum, Anisotome pilifera, Ranunculus insignis, Neopanax colensoi.* The spectacular destruction of these species by deer has been previously described (Clarke, 1972). As these choice species were eliminated, or reduced in abundance, deer browsed a larger variety of less favoured plants. Many plant communities were in consequence drastically altered or destroyed. The well documented records of E. S. Griffith (Appendix) serve as an example. In 1917, on the slopes of Mt Patriach in the Arthur Range he noted the difficulty of passage to the alpine grasslands; bordering the timberline was a belt of alpine scrub (mainly *Hebe* spp.) some 3-4 m high and 70-130 m wide. Returning to this area over the years he subsequently witnessed increased tracking, browsing and bark stripping until in 1940 the scrubland had been completely replaced by alpine grassland.

Progressive depletion of food resources in most regions later resulted in formerly unfavoured species also being taken. Thus, forests in many drier valleys (e.g. Upper Wairau) were denuded of understorey vegetation and populations there became wholly dependent on the adjacent grasslands. These grasslands were not depleted nearly so rapidly as the forested habitat.

3. *Decline in Condition of Deer*

Indications of physical decline appeared among deer in the Nelson hills in 1906, concommitant with serious depletion of the habitat (Adams, 1906; McKinnon and Coughlan, 1960). Initially, it was noticed in antlers, i.e., smaller size, fewer points and an increased incidence of uneveness and malformation. In most instances, malformed antlers were aberrant in one or both beams. More rarely, the antlers were grossly deformed, or absent apart from a bulbous outgrowth from the pedicel.

Despite obvious deterioration of antler quality other facets appeared to remain unchanged for a further 3-4 years, after which average size was noticeably smaller, (D. J. Stringer; C. Gibbs).

Attempts to check this deterioration by culling and liberating other strains failed; poor conditioned deer with mediocre heads were recorded from a widening area: Red Hills 1913; Wairoa River 1914; Tophouse 1918; Upper Clarence River 1919; and Lakes Rotoiti and Rotoroa 1920 (Nelson Acclimatisation Society). In more recently colonised areas antler deterioration occurred later: Karamea 1931; Tennyson Inlet 1925-30; Upper Grey River 1928; Lewis Pass 1929; Kaikoura 1930-35; Clova Bay 1935-40; and D'Urville Island 1945-50. Whereas between 1910 and 1925 many good heads were obtained (Clarke, 1970), after 1925 the only comparable trophies secured were those of other strains recently dispersed to the study regions (Clarke, 1973), or Thorndon strain red deer from the periphery of the herd.

Further insight into the timing of antler deterioration is obtained by relating the times of initial antler deterioration in the different regions to the stage of population growth, and the years elapsed since occupation (Fig. 8). In the inland tussocklands and

Kaikoura regions, antler deterioration began 1-10 years after initial occupation, either prior to deer becoming plentiful or timed to that event. Its onset was later in the Spenser Mountains and western montane regions, timed just prior to the peak or soon after it commenced, 11 and 23 years respectively after colonisation. On D'Urville Island and at Rai Valley-Tennyson Inlet the onset of antler deterioration coincided with the peak, 24-26 years after initial occupation. These differences in timing of initial deterioration appear associated with the elimination of the favoured forest food in the different regions. A different pattern occurred at Hanmer and Clarence Reserve, where because of exceptionally rapid dispersal deteriorated stock were among the colonising animals. It is interesting to note that the times of initial antler deterioration in the Nelson, Rakaia and Otago herds are about the same; antler deterioration in the Nelson herd occurred 46 years after liberation whereas the appropriate periods for the Rakaia and Otago herds were 41 and 35 years, respectively (North Canterbury Acclimatisation Society; Wilson, 1963; Banwell, 1968).

Deterioration was rapid in the Upper Wairau. Heads of 12 or more points were commonly secured up to about 1920 (C. Gibbs), but were poor thereafter. In 1923 no better than 10-pointers were obtained from approximately 400 stags killed (C. Andrews). Similarly, two small 10-point heads were the best obtained from approximately 800 stags shot during the mid-1930s (A. Birkes). Records of a few "better than average heads" shot in the Upper Wairau-Rainbow River area between 1932 and 1934 relate to Warnham strain red deer recently dispersed from North Canterbury regions (Clarke, 1973).

The deterioration of antler and body condition among populations in North and West Nelson was equally dramatic. Before 1925 deer were in generally excellent condition and some very heavy trophy antlers were obtained. In about 1929 antler quality deteriorated, and by 1931 antler malformation was rife (E. S. Griffith). Many stags failed to produce antlers, or developed shortened beams on which the velvet was retained. Ingram (1934) reported that good heads could be obtained only in the more remote valleys north of Karamea; all other areas by then holding only "scrubby beasts with malformed antlers". Numerous hunter records of unthrifty animals in poor condition between 1934 and the 1950s suggest that the status of populations remained similar throughout that period. Of 27 stags shot by the author in the Upper Karamea River in 1959, 18 possessed aberrant antlers.

Soft, decalcified antlers were another characteristic of the poor state of the populations. These were seen in the Howard Valley in 1928-29 (A. H. McConachie) where palatable forest species had been eliminated and deer depended solely on limited grassland forage. A similar situation occurred in the nearby Sabine and D'Urville valleys where most stags failed to produce antlers in the 1934-35 season; those produced were seldom more than a few inches long (C. A. Flowers; J. A. Palmer). In other instances (e.g., Upper Karamea River 1933, Wangapeka River 1934) antlers were found to be soft and flexible (E. S. Griffith).

Palmated antlers were also commonly seen during these years in the D'Urville and Waiau Rivers in 1929, Clarence Reserve 1931, Branch and Leatham Rivers 1932, and Travers River 1932 (D. W. Winn; G. Lott; G. Andrews; M. R. Clarke). Palmated antlers were usually small, characteristically flattened over their entire length, and quite distinct from earlier palmation resulting from exuberant growth. Known occurrences are associated with harsh winters in the high country valleys.

4. Starvation and Winter Mortality

Although the lifting of protection in 1923 resulted in some reduction of numbers in lowland areas, populations in montane areas continued to increase. They were estimated at 3000 in the Rainbow River in 1919 (Nelson Acclimatisation Society), yet by 1925 at least that number were being shot there each year. In that year it became clear also that deer had drastically over-extended their winter food resource; Tomlinson (1968) reports general starvation, many being so weak that they fell down as they attempted to run away. Throughout, there were no epidemics observed, or evidence of deer dying of disease alone.

The Winters 1928-31

For the next 3 years (1925-28) the status of populations remained similar, with animals near starvation in the winter but recovering in the summer. Then from 1928 to 1931 a series of harsh winters struck the northern South Island high country (Newton, 1952; McCaskill, 1969). Heavy mortality occurred in all montane valleys from the Leatham River to the Lewis Pass, the one exception being the Waiau River where, as earlier described, the valley bottom habitat remained in good order. In the East Sabine valley, particularly large numbers of deer died from starvation, or were killed by avalanches in the winter of 1930 (McNair, 1971; J. McNair). Earlier in 1929 very heavy snow destroyed most populations of feral sheep and cattle in the Travers, Sabine and D'Urville valleys (Christie, 1964; D. W. Winn; D. W. Oxnam). The winter of 1931 was exceptionally severe, and was followed by a poor spring and summer. Speargrass (*Aciphylla colensoi*) flowered in early April, 8 weeks later than usual, and flowering of rata (*Metrosideros* spp) and mistletoe (*Eletranthe tetrapetala*) were similarly about 10 weeks late (C. F. Shuttleworth).

In the Upper Wairau-Tarndale region snow lay on the flats for 14 weeks and the spring thaw was about 6 weeks late (M. R. Clarke). Deer stripped the forests of forage (Clarke, 1972) and subsequently very large numbers died. Carcasses of deer were found littering the river flats and lower valley slopes in the spring (A. Birkes; H. Randerson). Many dead deer were found in the rivers and streams where they had died while seeking water. In the Rainbow River alone, 1132 tails from dead deer were recovered for bounty payment by one man from along the river flats (A. Birkes; H. Randerson). Many deer were also found hung by the neck or foreleg from the forks of trees, inescapably trapped whilst reaching for foliage.

By summer 1932, deer in the forested areas of the Upper Wairau had become infested with lice, probably *Damalinia longicornis* (Andrews, 1964), and their condition was extremely poor (M. R. Clarke). Infestations of lice and less commonly of the cattle ticks, *Haemaphysalis bispinosa,* were also reported from deer in the Leatham and Matakitaki Rivers and on Molesworth Station in that season (J. Fowler; D. W. Oxnam; W. Couper).

The status of the population in the Upper Wairau-Tarndale region between 1932 and 1934 is not altogether clear, but it appears that it quickly stabilised. The winter seasons from 1934-1938 were much less rigorous than in 1928-31 and no reports of die-off have been found.

By 1936 the numbers of deer in the Upper Wairau-Tarndale region had risen substantially, but a movement of deer away from the depleted forested areas resulted in the marked concentration of populations in the adjacent tussocklands. Both in the

Upper Wairau-Tarndale and other alpine regions deer spent the winter in the tussocklands instead of descending to the now-depleted forested valleys.

About this time (1936-37) hunting activities also began to disrupt populations. Both mob size and mob structure were profoundly influenced; mobs were broken-up and dispersed in alpine areas, but in the montane tussocklands deer gathered on the open plains where unseen approach by hunters was difficult. The movement of deer now became increasingly wide-ranging and nomadic. Despite the effect of shooting, numbers were not reduced. By spring 1938 deer had lost condition; in the Rainbow River and neighbouring valleys they were reported to be weak and gaunt (D. W. Oxnam; R. Voyce; G. Andrews). Hinds without fawns at foot were commonly seen in the Upper Wairau during summer 1939. Similarly, in the Travers valley stags retained their antler velvet until March, 2 months longer than usual (D. R. Cummings).

The Winters 1939-42

The winters from 1939 to 1942 were particlarly harsh. Their effect on domestic stock in the Molesworth-Upper Waiau region was catastrophic; upwards of 50,000 sheep died and as a result St James Station discontinued sheep farming (Newton, 1952; McCaskill, 1969). Heavy mortality of deer occurred in the Upper Wairau, Waiau, D'Urville, Sabine and Matakitaki valleys (D. W. Oxnam; C. A. Flowers; H. Melville). In spring 1940, in the Upper Matakitaki valley, groups of deer were found lying cast with the hair chewed from their backs (D. W. Oxnam). Similarly, in spring 1942, about 300 dead deer were found along a 4-km section of the river flats in the D'Urville River (C. A. Flowers). There, starving deer foraged alongside rotting carcasses in order to obtain food.

Further details of mortality during the 1939-42 period are incomplete. However, observations of many decayed carcasses and smaller numbers of deer in the spring and summer seasons following severe winters, indicate heavy mortality throughout the Spenser Mountains. Perhaps the most significant evidence for this was the heavily reduced grazing pressure exerted by deer on some farmlands, during the 1940-44 period. (H. Melville; D. W. Oxnam).

After 1945, there are no further reports of heavy winter die-off, despite greater public utilisation of the back-country and increased observation opportunities. Also, the winters after 1945 were generally less severe and the cumulative effects of several harsh seasons were not repeated. Records of mortality do exist, but they are insignificant when compared with data from earlier periods.

5. *Earthquake Mortality*

There is no evidence that deer died from starvation in North and West Nelson, despite abundant signs of poor nutrition. A series of severe earthquakes (known alternatively as the Murchison or West Nelson earthquakes) which struck on 17 June 1929, caused catastrophic damage throughout North and West Nelson and deer fatalities were exceptional in some areas (e.g., Mt Lunar slips). The numerous carcasses protruding from slips and prevalence of injured animals testified to the severity of the events (J. A. Palmer; F. A. K. Price; E. S. Griffith; L. Arnold). Of greater significance however, was the immediate loss of habitat and consequent disruption of populations. Some areas which had formerly held large numbers of deer were found deserted when visited 3 months after the earthquakes (J. A. Palmer). Later however, many slips and drained

lakes were revegetated and soon provided an abundance of food. Grasses colonised these new sites and the area of montane grasslands available to deer increased enormously. Moreover, slips opened up the streambeds and forested gullies, allowing freer movement between areas. These factors favoured red deer, and densities rose accordingly.

By 1934, however, this new flush of growth was depleted. Replacement of grasses by less palatable shrub and tree species (mainly *Coprosma* and *Nothofagus* spp) also reduced the area of grassland. Despite these changes, substantial areas of low altitude grasslands remained, providing a subsistence resource in winter months. This probably explains the absence of extensive winter mortality in North and West Nelson, and would be compatible with the recorded pattern of semi-starvation prolonged over many successive winters.

DISCUSSION

The Nelson red deer herd offers exceptional opportunities for the reconstruction of historical events relating to the rise and fall of animal numbers.

Figure 9 gives a schematic interpretation of the major eruptive patterns of the deer populations as they fluctuated from colonisation until post-peak times. Eruptive cycles are extrapolated from data given in Figures 2-8, and in the text, and further supplemented by unpublished details relating to the original records. While numerical accuracy is not explicit in these cycles, they show population size and events in relative orders of magnitude.

In outline, Figure 9 shows that populations followed a pattern of a single eruptive fluctuation (Caughley, 1970) marked by a slow and erratic decline. A notable exception

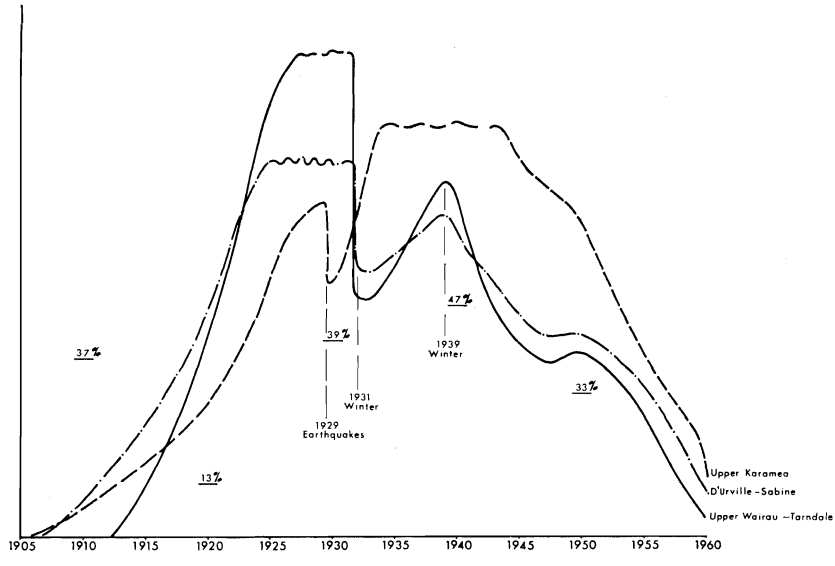

FIG. 9—Schematic representation of changes in red deer population size during eruptive fluctuation following establishment. Vertical axis is a scale of comparative magnitude and the separate cycles are featured relative to one another in size and time. Superimposed figures show percentage of high densities at decade intervals (Fig. 7).

occurred among populations in the Upper Karamea River (and other western regions) where the eruptive phase was clearly arrested, although only temporarily, by the 1929 earthquakes. Post-peak declines in the eruptive cycles of populations in the D'Urville-Sabine and Upper Wairau-Tarndale regions have been interpreted in terms of winter weather and starvation. Conversely, the periods of renewed rise in population or temporary arrest of decline (i.e. 1934-39; 1947-49, Fig. 9), resulted from improved weather conditions for deer during those periods.

The eruption of populations in the inland tussocklands and Spenser Mountains (Figs. 2-5) indicate that between 1910 and 1920 the rise in numbers only roughly kept pace with the spread into new areas (Clarke, 1971). Up to 1910 deer were concentrated in the Motupiko-Lake Rotoiti region (Fig. 2); then dispersal accelerated faster than the increase in numbers so that by 1930 these high densities had been dissipated over a substantially widened area (Fig. 3). By 1930 however, as the rate of spread declined, densities in the recently occupied areas increased, and the extent of high densities (Fig. 7) again came to reflect the increase in absolute herd size. The relevant values from Fig. 7 have been superimposed on Fig. 9 for each decade.

It is the patterns of decline, controlled primarily by natural factors which are of special interest. Natural factors transcended the effects of shooting, except in the Marlborough Sounds and on farm and station land where sustained hunting was, in part, successful. By the time official control programmes commenced in the early 1930's most high density populations were already in decline. During the late 1930's, when populations in the inland tussocklands and Spenser Mountains were again in ascendance (Fig. 9), an increased hunting effort had little apparent effect. However, as the overall numbers declined into the 1950's significantly greater proportions of populations were shot and effective reductions were at last achieved.

The patterns of decline in the D'Urville-Sabine and Upper Wairau-Tarndale regions (Fig. 9), are typical of those occurring in most montane valleys flanking the Spenser Mountains chain. Populations in these regions rapidly reached a peak; but by then they had drastically depleted food resources. This shortage of food interacting with harsh winter weather, especially in 1931 and 1939, precipitated the decline phase. It is significant that in 1918, population numbers were not stressing the food resource and were unaffected by the winter of that year, although it was easily the severest winter of the study period.

One feature of decline in the inland tussocklands and Spenser Mountains not evident elsewhere, was the fluctuation in numbers after the initial decline. Improved access to grasslands, due to milder winter weather is the reason postulated for this. The extensive tracts of montane and alpine grasslands were capable of supporting large deer populations for longer periods than they did; in fact heavy winter snowpacks in some years prevented deer from using these resources. The impression therefore, is of post-peak populations regulated primarily by a shortage of forage in forest and valley bottom habitats during winter months. Observations of deer concentrated in the grassland regions in the mild winters following their initial decline support this impression.

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APPENDIX — Sources of Data

Personal communications

Comprehensive records, based on interviews and correspondence, are retained on file. Names of 118 informants appeared in a previous paper (Clarke, 1971). To these are added the following: Messrs C. Andrews, Brightwater; G. Andrews, Levin; L. Arnold, Korere Valley; G. Atkinson, Richmond; A. Birkes, Christchurch; R. Dunphy, Nelson; G. Elliott, Nelson; H. Hodginson, Rangiora; R. Johnson, Richmond; (Mrs) S. Johnson, Richmond; R. McKay, Rangiora; J. McNair, Blenheim; H. Melville, Awatere Valley; P. Newton, Rangiora; H. Randerson, Auckland; R. Voyce, Wairau Valley.

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