
The Effects of Introduced Wild Animals on New Zealand Forests

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Abstract. Although New Zealand lacks native terrestrial mammals (except for two species of bats), more than 50 species of mammals have been introduced by human beings and have become established since the late eighteenth century. The impact of introduced browsing and grazing mammals on the vegetation of New Zealand is widely perceived as an ecological disaster involving severe depletion of the plant cover and widespread accelerated erosion. Although there is no doubt that introduced mammals have had profound and pervasive effects, determination of the magnitudes of these effects on the native forests is surprisingly difficult. For example, red deer (*Cervus elaphus*) are known to cause important shifts in understory species composition in beech (*Nothofagus*) forests but their long-term effects on the regeneration of the dominant tree species are not clear. Similarly, apparently excessive tree mortality in conifer-broadleaved forests has often been attributed to browsing by the Australian brush-tailed opossum (*Trichosurus vulpecula*), but natural stand dynamic processes also may contribute significantly to this mortality. Consideration of the effects of red deer and opossums on the native forests of New Zealand illustrates the difficulties in distinguishing animal-induced changes from other types of vegetation change.

Key Words: deer, disturbance, forest, herbivore impact, introduced animals, *Nothofagus*, opossum.

THE consequences of deliberate or accidental human introduction of plants and animals into areas outside their natural ranges are important research themes in both geography and ecology. Ecologists have been particularly concerned with the ecological impact of aliens upon native vegetation and animal populations, whereas geographers have tended to emphasize the cultural significance of and landscape modifications resulting from introductions. In most cases, however, research on this theme has been multidisciplinary in scope. The ecological and geographical literature on the impact of introduced plants and animals forms a common body of knowledge, which has recently been reviewed by Jarvis (1979). Attention should be drawn to a considerable body of pertinent geographical literature omitted by Jarvis, such as Street (1962) and McKnight (1971, 1976) on the distribution, ecological impact, and economic significance of es-

caped domestic animals; also omitted were the studies by Harris (1965), Watts (1970), Frenkel (1970), Kellman and Adams (1970), Parsons (1972), and Byrne (1980) on the impacts of plants introduced to the Americas deliberately or accidentally, by human beings.

One of the most notorious examples of the unforeseen ecological consequences resulting from human introductions of wild and domesticated animals is the so-called "noxious-animal" problem of New Zealand, which is often summarized as follows:

- (1) The absence of native terrestrial mammalian herbivores permitted evolution of a flora highly vulnerable to damage from browsing and grazing.
- (2) The populations of wild animals (especially deer) that were introduced mainly during the latter half of the nineteenth century grew explosively because of the lack of competitors and predators.
- (3) Browsing and grazing by the intro-

duced wild animals have had a devastating impact on the native vegetation, often resulting in severe depletion of the plant cover and accelerated erosion.

For example, Walter Howard (1965, pp. 464–65), a well-known American animal ecologist who spent 1962–63 surveying big-game problems in New Zealand at the request of the government, describes the situation as follows:

Since this vegetation must have evolved without the presence of browsing or grazing mammals, natural selection did not have the opportunity either to eliminate the highly palatable plants that could withstand the heavy selective feeding pressure of the introduced mammals or to favor those species that were browse-resistant or unpalatable to browsing animals (Holloway 1960). . . . These introduced mammals [several species of wild ungulates, European hare, European rabbit, feral goat, and feral pig] have upset the natural stability of the habitats over vast areas by destroying vegetation, thus also causing extensive erosion. The ecological impact of these introduced mammals must be seen to be believed.

Similarly, in a discussion of the effects of introduced animals in New Zealand in his biogeography text, Pierre Dansereau (1957, p. 282) comments:

There is not a single grazing or browsing mammal in the native fauna (Thomson 1922), i.e., if one excepts the recently extinct moa (*Dinornis* spp.), a bird of the ostrich group. The introduction of the red deer (*Cervus elaphus*) has proven catastrophic to the beech (*Nothofagus*) forests: in some stands, not a single seedling or sapling is to be seen for acres.

Similar interpretations of the effects of introduced wild mammals in New Zealand are given in the well-known works of Clark (1949) and Elton (1958).

Although there is no doubt that introduced wild mammals have had a profound and pervasive influence on the present structure and species composition of New Zealand's native forests, the influences of introduced animals are much more complex than the above generalizations suggest. In the present paper we illustrate some of the difficulties inherent in demonstrating these influences, with particular emphasis on the problem of distinguishing natural from animal-induced changes. Following a summary of the historical background of the present noxious-animal problem, two of the major introduced ani-

mal problems are discussed: red deer (*Cervus elaphus*) in beech (*Nothofagus* species) forests and Australian brush-tailed opossums (*Trichosurus vulpecula*) in conifer-broad-leaved forests.

The Historical Background

Prior to the settlement of New Zealand by Polynesians toward the end of the first millennium A.D., no terrestrial mammals were present except for two species of bats (Bull and Whittaker 1975). However, the absence of nonvolant native terrestrial mammals does not necessarily imply that the native flora lacks adaptive strategies to withstand browsing. The native fauna included at least 16 and perhaps as many as 24 species of the now extinct moas (order Dinornithormes). Moas were abundant on both the North and South Islands and some of these large flightless birds were up to 3 m tall (Bull and Whittaker 1975). The habitat of some moa species (as well as many other species of herbivorous birds) was forest, which covered about three-fourths of New Zealand prior to the arrival of human beings (Greenwood and Atkinson 1977; Nicholls 1980). A recent study of the contents of fossilized gizzards indicates that twigs of many shrub and tree species formed the major part of the diet of at least some moa species (Burrows 1980). The likelihood that moa browsing exerted some selective pressures on the flora has not been fully appreciated with regard to the presumed vulnerability of the New Zealand flora to browsing. It has even been suggested that the divaricating habit (i.e., closely interlaced branches) and tough stems of many New Zealand woody plants have evolved in response to browsing by moas (Greenwood and Atkinson 1977). The presence of toxic or distasteful secondary compounds in the leaves of some New Zealand plants may also be adaptations to moa browsing. Alternatively, presence of these toxic secondary compounds may have evolved in response to phytophagous insects and the divaricating habit may be related to formerly drier climates (Greenwood and Atkinson 1977). Despite the uncertainty of the evolutionary impact of moas on the flora of New Zealand, it is clear that prior to the introduction of browsing mammals the flora was subjected to considerable browsing pressure

by moas and that the flora is not uniformly palatable.

There has been considerable speculation about the cause or causes of the pre-European demise of the moas. Some authors favor mainly natural extinctions resulting from Holocene climatic fluctuations with only a minor role assigned to human activities (Oliver 1949; Williams 1962). However, because moas survived more drastic climatic fluctuations during the Pleistocene, it is more likely that hunting by Polynesians was largely responsible for their extinction (Fleming 1962). In addition to all the moa species, 21 other avian species were extinct by 1800 A.D.; the bones of 34 of these 45 species have been found in association with Polynesian middens (Kinsky 1970). Extensive burning of the vegetation by Polynesians is also likely to have contributed to the extinction of the moas and other birds. Long before the beginning of organized European settlement in 1840, burning by Polynesians vastly reduced the total forested land surface—perhaps by as much as one-third to one-half (Cumberland 1962; Molloy et al. 1963; Nicholls 1980). Furthermore, the Polynesian dog (*Canis familiaris*) and the Polynesian rat (*Rattus exulans*), both introduced by Polynesians, may too have contributed to the massive bird extinctions (Thomson 1922; Wodzicki 1950; Fleming 1969).

Thus, by the time of European contact in the latter half of the eighteenth century, Polynesians had already wrought significant changes in New Zealand wildlife and vegetation. At the time of the second (1774) and third (1779) voyages of Captain Cook, the domestic animals familiar to Europeans were introduced. Pigs and goats were the first to be liberated, primarily to provide emergency food for castaways and, at least in the case of pigs, to provide livestock for the Maoris (Thomson 1922). Many pigs and goats were liberated by sealing and whaling parties near the end of the eighteenth century on small islands where they had a devastating impact on the vegetation (Turbott 1963). Although the earliest recorded introductions of cattle, horses, and sheep were in the 1820s, it is likely that these animals were also introduced earlier by sealers and whalers (Thomson 1922; Wodzicki 1950). All of these domesticated animals became feral, forming large populations on the North and South Islands

during the nineteenth century. Wild goats and pigs are still numerous while only small populations of feral horses, cattle, and sheep survive (Wodzicki 1961). Goats have been repeatedly liberated, even in the past ten years, to impede the spread of blackberry (*Rubus* spp.) and other weeds and to help clear woody growth to facilitate sheep grazing. Owing to the tendency for herds to remain in restricted areas for lengthy periods, where goats are numerous they seriously deplete the vegetation (Atkinson 1964).

The second half of the nineteenth century was not only a period of rapid European settlement of New Zealand but was also the time of introduction of most of the wild animals. The European settlers found a land devoid of wild mammals (except for bats) but quickly sought to remedy the situation. Acclimatization societies were established throughout the country and vigorously set about the task of introducing plants and animals. In addition to the introduction of agricultural plants and livestock, the acclimatization societies introduced fur-bearing mammals to establish a skin trade, game animals for meat and recreation, and birds for hunting and for aesthetic reasons. The possibility of big-game hunting by the general population, in contrast to its restriction to the privileged few in England, was probably a major impetus for the introduction of deer (Thomson 1922). In addition to the acclimatization societies, private individuals and the New Zealand Department of Tourist and Health Resorts were responsible for many introductions. Twenty-two of the 54 species of introduced mammals and 90 of the 138 species of introduced birds arrived between 1860 and 1880; eventually, 33 species of mammals (Table 1) and 43 species of birds successfully became established (Wodzicki 1950, 1965). Among the introduced game animals that were established were the red deer (*Cervus elaphus*), sika deer (*C. nippon*), Javan rusa deer (*C. timorensis*), Sambar deer (*C. unicolor*), wapiti or Rocky Mountain elk (*C. elaphus nelsoni*), fallow deer (*Dama dama*), white-tailed deer (*Odocoileus virginianus*), chamois (*Rupicapra rupicapra*), and the Himalayan thar (*Hemitragus jemlahicus*) (Figure 1); of these species, the red deer is the most widespread and numerous (Figure 2). First introduced in 1861, red deer were liberated at least 220 more times at widely dispersed points throughout the

Table 1. Wild Exotic Mammals (Including Feral Domesticated Animals) Presently Found in New Zealand (after Thomson (1922) and Wodzicki (1950) and Modified in Accordance with Recent Changes in the Status of Some Species)

| Order Species | Date of Initial Establishment | Status |
|---|----------------------------------|---|
| <i>Marsupialia</i> | | |
| 1. Brush-tailed opossum (<i>Trichosurus vulpecula</i>) | 1837 | Widespread and abundant, North, South, and Stewart Islands |
| 2. Red-necked or bush wallaby (<i>Macropus rufogrisea</i>) | 1874 | Locally abundant, South Island |
| 3. Black-tailed or swamp wallaby (<i>M. bicolor</i>) | 1870 | Locally common, Kawau Island in Hauraki Gulf |
| 4. Black-striped wallaby (<i>M. dorsalis</i>) | 1870 | Local and rare, Kawau Island in Hauraki Gulf |
| 5. Dama wallaby (<i>M. eugenii</i>) | 1870 | Locally common, North Island and Kawau Island in Hauraki Gulf |
| 6. White-throated or parma wallaby (<i>M. parma</i>) | 1870 | Local and rare, Kawau Island in Hauraki Gulf |
| 7. Brush-tailed rock wallaby (<i>Petrogale penicillata</i>) | 1873 | Local and rare, several islands in Hauraki Gulf |
| <i>Insectivora</i> | | |
| 8. European hedgehog (<i>Erinaceus europaeus</i>) | 1892 | Widespread and abundant, North and South Islands |
| <i>Lagomorphora</i> | | |
| 9. European rabbit (<i>Oryctolagus cuniculus</i>) | 1838 | Widespread and abundant, North and South Islands |
| 10. European hare (<i>Lepus europaeus</i>) | 1851 | Widespread and abundant, North and South Islands |
| <i>Rodentia</i> | | |
| 11. Kiore or Polynesian rat (<i>Rattus exulans</i>) | Late in the first millenium | Local and rare, North and South Islands; locally abundant on offshore islands |
| 12. Black or ship rat (<i>R. rattus</i>) | Late 18th century | Widespread and abundant, North South, and Stewart Islands, and offshore islands |
| 13. Norway or brown rat (<i>R. norvegicus</i>) | Early 19th century | Widespread and abundant, North South, and Stewart Islands |
| 14. House mouse (<i>Mus musculus</i>) | Early 19th century | Widespread and abundant, North South, and Stewart Islands |
| <i>Carnivora</i> | | |
| 15. Stoat (<i>Mustela erminea</i>) | 1885 | Widespread and common, North and South Islands |
| 16. Weasel (<i>M. nivalis</i>) | 1885 | Restricted and rather rare, North and South Islands |
| 17. Ferret (<i>M. putorius</i>) | 1882 | Widespread and common, North and South Islands |
| 18. Feral cat (<i>Felis catus</i>) | Early 19th century | Widespread and common, North South, and Stewart Islands |
| <i>Perissodactyla</i> | | |
| 19. Feral horse (<i>Equus caballus</i>) | Early 19th century | Local and rare, North Island |
| <i>Artiodactyla</i> | | |
| 20. Red deer (<i>Cervus elaphus</i>) | 1861 | Widespread and abundant, North South, and Stewart Islands |
| 21. Sambar deer (<i>C. unicolor</i>) | 1875 | Restricted but common, North Island |
| 22. Javan rusa deer (<i>C. timorensis</i>) | 1907 | Restricted but common, North Island |
| 23. Wapiti or Rocky Mountain Elk (<i>C. elaphus nelsoni</i>) | 1905 | Locally common, Fiordland, South Island |
| 24. Sika deer (<i>C. nippon</i>) | 1885 | Restricted but common, North Island |
| 25. Fallow deer (<i>Dama dama</i>) | 1864 | Restricted but common, North and South Islands |

Table 1. Continued

| Order Species | Date of Initial Establishment | Status |
|--|----------------------------------|---|
| 26. White-tailed deer (<i>Odocoileus virginianus</i>) | 1901 | Restricted but common, South Island; abundant, Stewart Island |
| 27. Moose (<i>Alces americana</i>) | 1900 | Restricted and rare (possibly extinct), Fiordland, South Island |
| 28. Feral pig (<i>Sus scrofa</i>) | 1773 | Widespread and common, North and South Islands |
| 29. Feral cattle (<i>Bos taurus</i>) | Early 19th century | Local and rare, North and South Islands |
| 30. Feral sheep (<i>Ovis aries</i>) | Early 19th century | Local and rare, North, South, and Stewart Islands |
| 31. Feral goats (<i>Capra hircus</i>) | 1773 | Locally abundant, North and South Islands and off-shore islands |
| 32. Chamois (<i>Rupicapra rupicapra</i>) | 1907 | Restricted but common, South Island |
| 33. Himalayan thar (<i>Hemitragus jemlahicus</i>) | 1904 | Restricted but common, South Island |

country (Logan and Harris 1967). Repeated introductions of most of the wild animals led to their rapid spread and increase in numbers. In contrast, many of the animals that were liberated only once, such as the huemul (*Hippocamelus bisulcus*), zebra (*Equus zebra*), and alpaca (*Lama pacos*), failed to become established (Thomson 1922; Harris 1970). In most cases, rather than the lack of predators, the abundance of food as well as milder winter climates were probably the more important factors in the rapid increase in populations (Caughley 1970). Among the animals introduced to provide skins for export were the European rabbit (*Oryctolagus cuniculus*) and the Australian brush-tailed opossum (*Trichosurus vulpecula*), which were both introduced in the mid-nineteenth century.¹ The Australian brush-tailed opossum was liberated several hundred times (mostly between 1890 and 1940) at well over 100 locations and has successfully colonized nearly the entire range of native (and some exotic) forests on both the North and South Islands (Figure 3) (Pracy 1974).

Nearly all of the wild animals introduced to New Zealand have gradually come to be regarded as pests. For example, as early as the 1870s huge populations of European rabbits were believed to be lowering the carrying capacity of sheep pastures. Stoats (*Mustela erminea*), ferrets (*M. putorius*), and weasels (*M.*

nivalis) were introduced in the 1880s to control rabbit populations but were largely ineffective; in fact, they contributed to the depletion of native birds and also took many domestic fowl (Thomson 1922; Wodzicki 1950). Today rabbits are still considered to be major pests, especially on agricultural lands, and millions of dollars are spent annually on control operations (poisoning and hunting). Similarly, red deer and opossums, which are today considered the major problem animals in the native forests, were originally believed to be detrimental only to agricultural and pastoral activities. By the 1920s the New Zealand government became convinced that deer—especially red deer—were having detrimental economic effects through their depredations on crops and competition with sheep for pasture; during the 1920s there were also numerous reports of native forests being damaged by deer (Perham 1922; Cockayne 1926; Poppelwell 1929). Likewise, damage by opossums to orchards and crops was recognized in the 1920s, but it was not until the late 1940s and 1950s that a consensus developed that they were also significantly altering the native forests (Kirk 1920; Zotov 1949). Today, red deer and opossums are widespread in the native forests of New Zealand and are the objects of extensive control operations primarily because of the

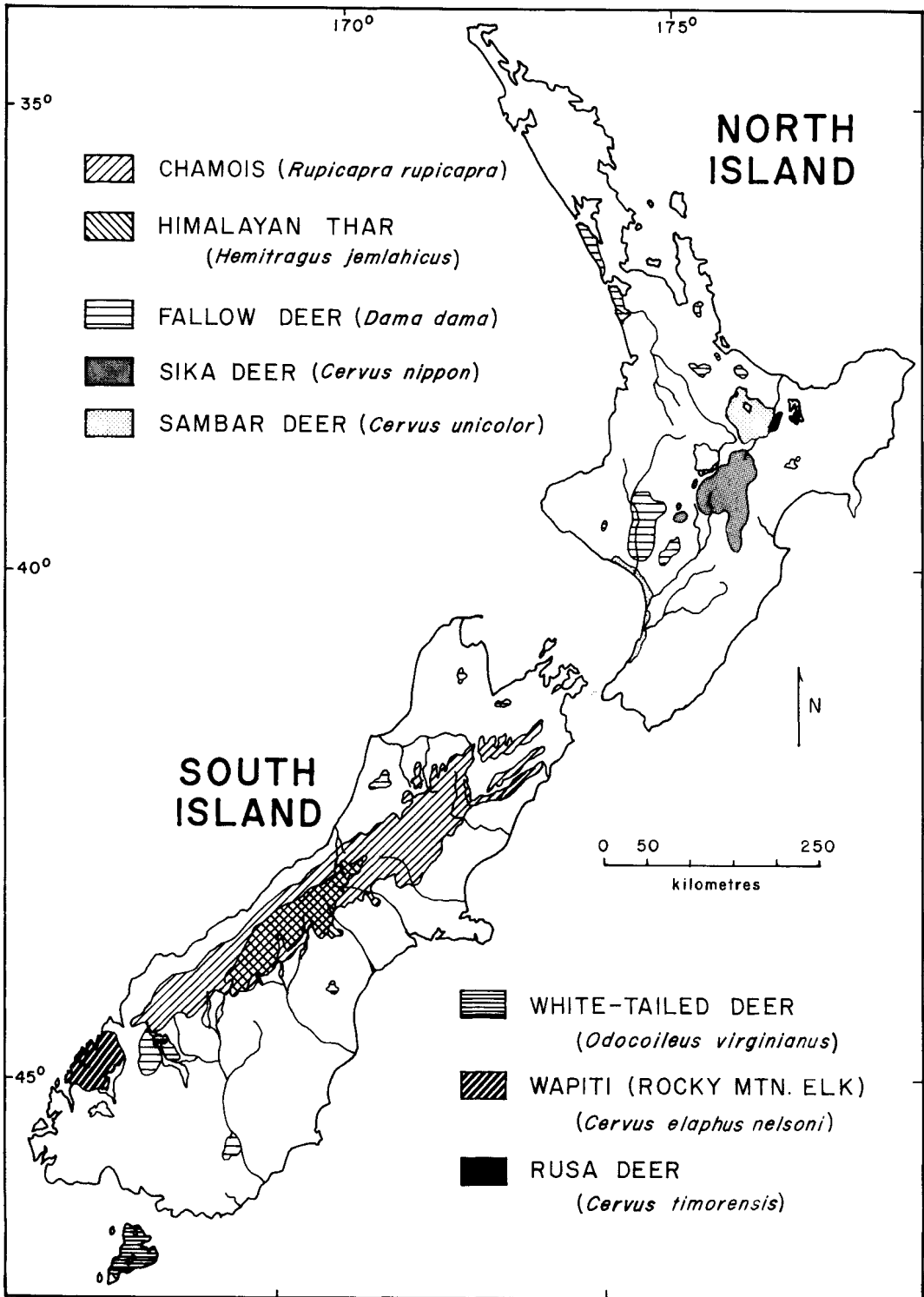


Figure 1. Distribution of major game animals other than red deer in New Zealand. After Wodzicki (1961).

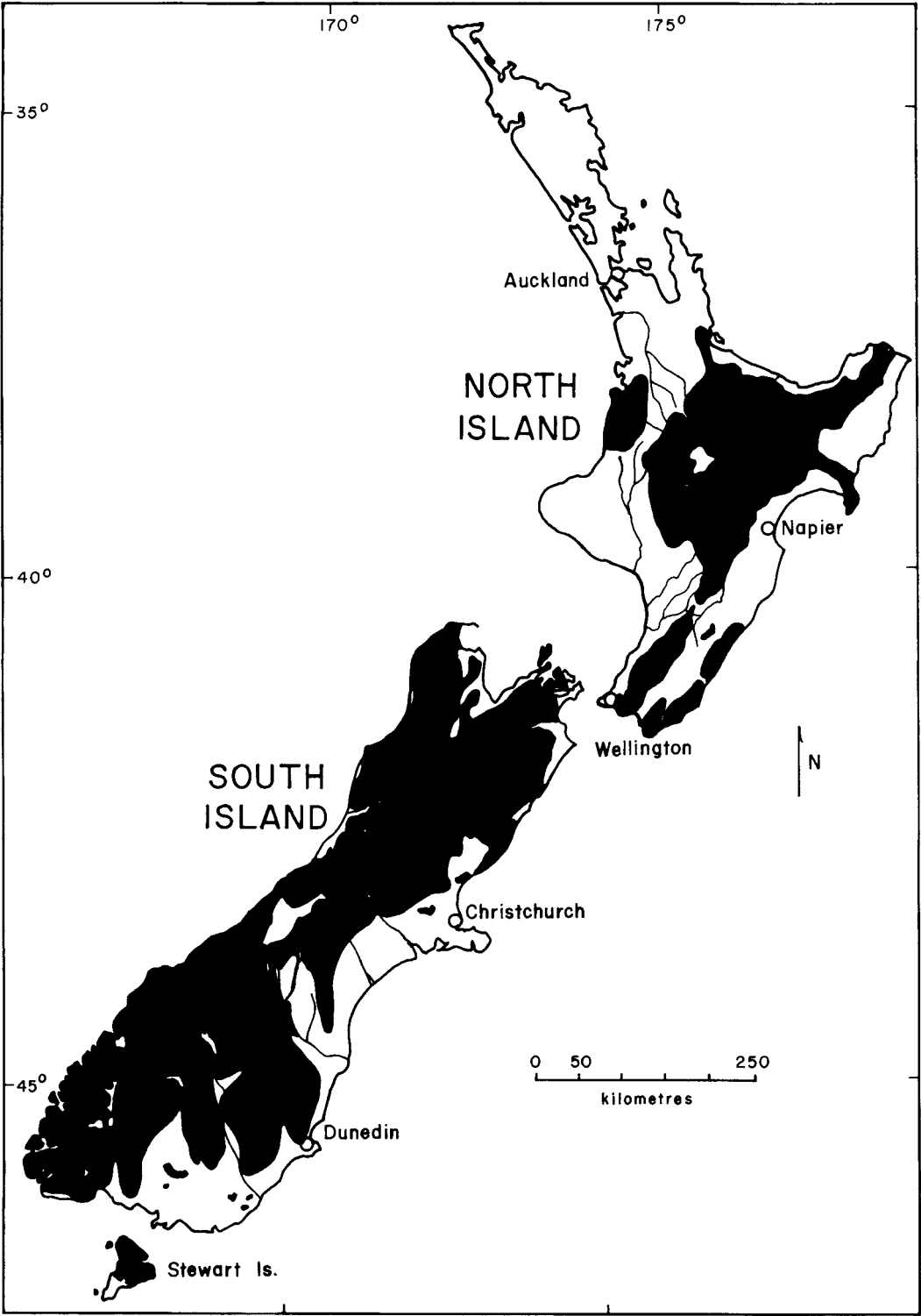


Figure 2. Distribution of red deer in New Zealand. After Wodzicki (1961).

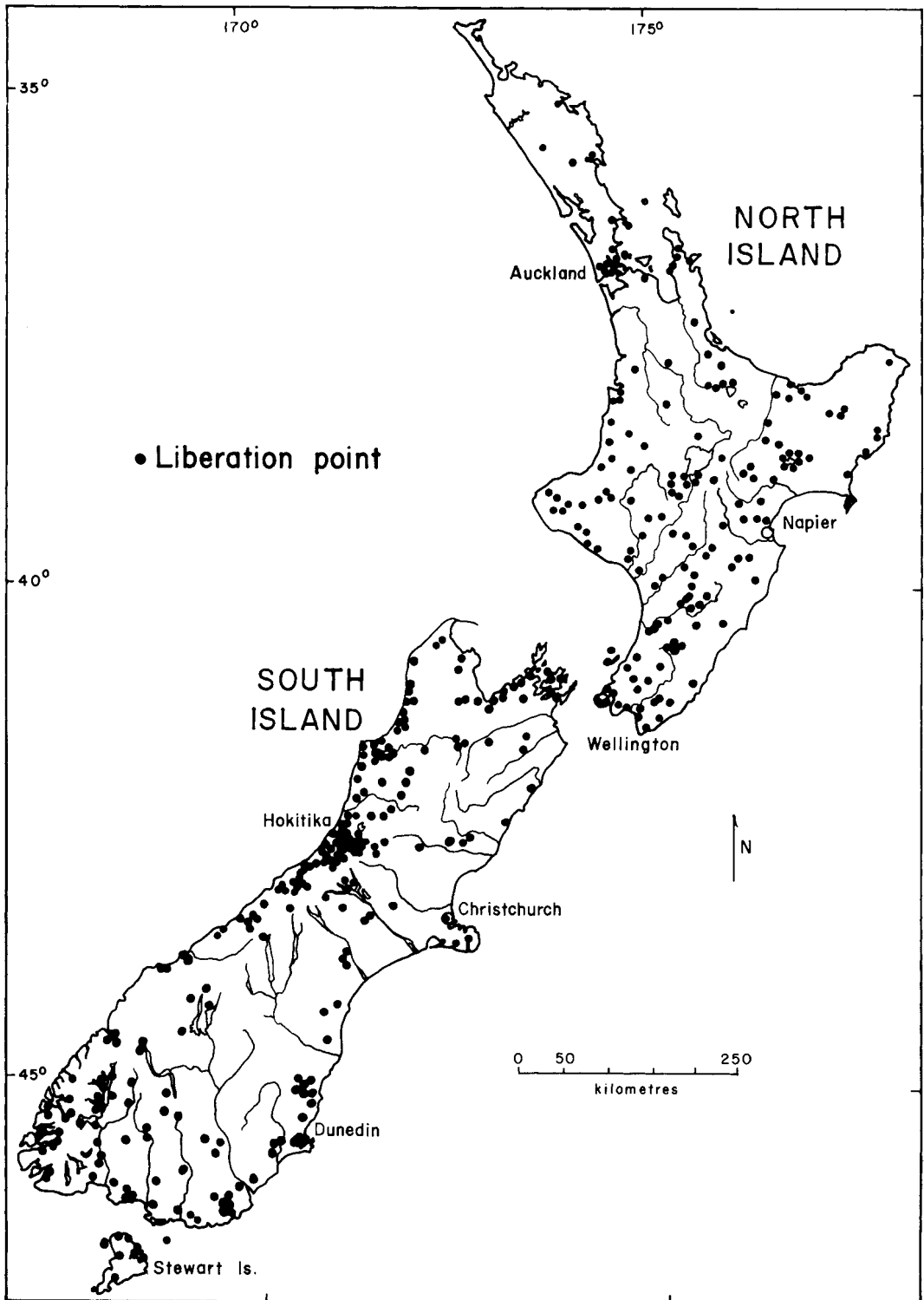


Figure 3. Liberation points of the Australian brush-tailed opossum in New Zealand. After Pracy (1974).

belief that they threaten to destroy the watershed-protection function of these forests. Another reason for controlling introduced wild animals in native forests is the preservation of the native flora and fauna. For example, in addition to their direct effects on the native flora, introduced browsing animals may alter habitats so that exotic bird species are favored at the expense of the native avifauna (Diamond and Veitch 1981). Opossums are also controlled because they are vectors for the spread of bovine tuberculosis. Since the mid-1960s most control operations have been commercial ventures financed by the sale of wild animal products such as venison and opossum skins. Although there is no doubt that red deer and opossums have had a significant impact on the native forests, the nature and magnitude of their effects are not easily determined, as illustrated by the following two examples.

Red Deer in South Island Beech Forests

Red deer are common to all forest types on both the North and South Islands; because significantly more information is available on red deer in the South Island beech forests, however, this discussion will deal mainly with these forests. The two broad forest formations of New Zealand are the conifer-broadleaved forests and the beech (*Nothofagus* species) forests (Cockayne 1928). The former are dominated by typically emergent conifers of the genera *Dacrydium*, *Podocarpus*, *Dacrycarpus*, and *Libocedrus*, and by numerous broadleaved genera of families such as Cunoniaceae, Myrtaceae, Elaeocarpaceae, and Escalloniaceae. North of latitude 38°S the giant conifer *Agathis australis*, the kauri, is often characteristic of the conifer-broadleaved forests, although logging has greatly reduced the extent of virgin stands containing this species. The beech forests that are dominated by one or more of the four *Nothofagus* species (*N. solandri*, *N. fusca*, *N. menziesii*, and *N. truncata*) are most typical of higher altitudes (commonly forming timberline) and higher latitudes (Figure 4). Relative to the conifer-broadleaved forests, beech forests tend to occur under less favorable temperature, moisture, or edaphic conditions. They range from extensive stands domi-

nated by a single *Nothofagus* species, through mixtures of two or three *Nothofagus* species, to mixtures that include components of the conifer-broadleaved forests. The present discussion is concerned mainly with the protection forests of the high country of the South Island, which are either pure stands of mountain (*N. solandri* var. *cliffortioides*) or silver (*N. menziesii*) beech or mixtures of red beech (*N. fusca*) with either silver or both silver and mountain beech.

In 1861 a red deer stag and two hinds were liberated in Nelson; their progeny increased and rapidly spread over an extensive area of the high country in the Nelson and Marlborough districts in the northern part of the South Island (Figure 5) (Clarke 1971). In 1871 the Otago Acclimatisation Society imported 15 red deer, of which 7 were liberated near Lake Hawea in the high country of the southern interior of the South Island. In 1897 the Canterbury Acclimatisation Society liberated 9 red deer in the gorge of the Rakaia River in the high country of the central part of the South Island. These earliest liberations were followed by many more in the late 1890s and early 1900s, particularly in the upper Waimakariri Valley and in Southland and Fiordland (Thomson 1922). Thus, populations were established in the northern, central, and southern districts of the South Island. These remained separated from each other by large tracts of deer-free country until about the late 1940s; although liberations ceased in 1924, it is likely that the dispersal and establishment of red deer into new areas ended only in the past one or two decades (Wodzicki 1961). Red deer thrive particularly where forest, scrub, and grassland lie in close proximity, which is characteristic of the high country of the South Island. In most parts of the South Island red deer populations were at their peak in the 1940s and 1950s. Since the development of an export market for venison and the widespread use of helicopters for hunting deer in the mid-1960s, populations have been drastically reduced.

In an early and influential paper on the beech forests of the western Southland district, John T. Holloway (1950) described red deer fluctuations and associated habitat changes. Although no census data were available, Holloway interpreted the general observations of deer abundances and the in-

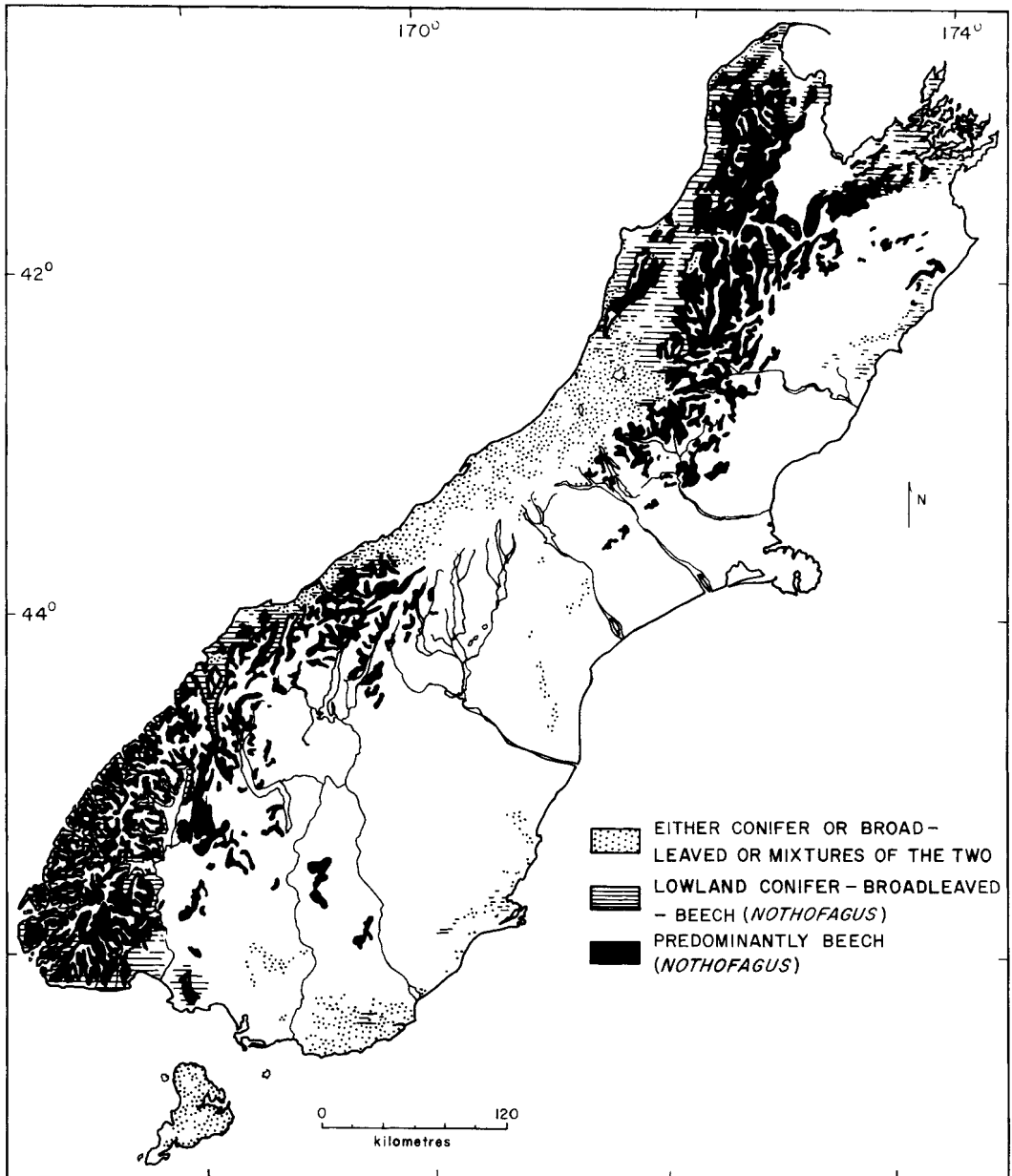


Figure 4. Major types of forest cover of the South Island, New Zealand. Broadleaved refers to angiosperm trees other than *Nothofagus*. The blank area includes mostly grassland, scrub, cultivated land, and plantations of exotic trees. After W. J. Wendelken (1976, p. 107).

direct evidence of the condition of the vegetation as reflecting irruptive fluctuations in the deer population involving the following stages:²

- (1) a period of rapid growth of approximately 25 to 30 years from liberation to initial peak;

- (2) a period of peak population lasting 5 to 10 years;

- (3) a period of declining population for 10 to 15 years; and

- (4) a final stage of relatively stable population.

During Stage 1 of rapid population increase,



Figure 5. Map of New Zealand showing place names mentioned in text.

browsing is highly selective and the preferred food plants are gradually depleted. During Stage 2, when the population is at its maximum, the food habits of the deer change rapidly and previously untouched species of plants are browsed. The deer show obvious signs of malnutrition and the population begins to decline in Stage 3. At Stage 4 Holloway believed that the deer population becomes more or less stable, with its size being determined by the renewal rate of the preferred species, the degree to which deer can utilize the less attractive plants in the forest, and the availability of alternative browse in adjacent habitats (i.e., scrub or grassland) (Holloway 1950). Several other authors have described irruptive fluctuations for many red deer populations in New Zealand, and in each case depletion of food supply is suspected as the cause of the population decline (Elder 1956; McKelvey 1959; Riney et al. 1959; Clarke 1976). The duration of the first three stages, however, varied widely; for example, in 21 herds studied in the Nelson area, Stage 1 varied from 10 to 30 years and Stage 2 from 3 to 13 years. Such variation is expected because of differences in climate, topography, food supply, competition from other animals (e.g., sheep and goats), and in some cases variation in hunting pressure (Clarke 1976).

Holloway derived his interpretations of deer effects on beech forests from an extensive firsthand knowledge of the forests of the South Island and from information pertaining to deer numbers and vegetation condition informally gathered from many people in the forestry sector. The vegetation changes he described for Stages 1 and 2 are congruent with the reports of observers who were familiar with New Zealand native forests before and soon after invasion by red deer (Cockayne 1926; Zotov 1938; Mark and Baylis 1975). There is no doubt that during Stages 1 and 2 red deer drastically deplete palatable understory herbaceous species and many shrub and small subcanopy tree species; they also browse seedlings and saplings of the main canopy beech species (although not preferentially). During Stage 2, extensive areas of relatively bare forest floor may occur or, in some cases, there may be an increase in the abundance of unpalatable understory species. Given the depleted food supplies characteristic of Stage 2, the red deer population declines in Stage 3. On the other hand,

in Stage 4 it is not clear to what degree a new stability will be attained or what the condition of the vegetation will be. Roy Nelson, a leading conservationist, has argued that deer have eliminated the forest cover from extensive areas, resulting in accelerated erosion in the high country of the South Island; by implication, at Stage 4 the deer induce a change from forest to scrub or grassland (Nelson 1979). However, high rates of natural erosion are expected in this recently uplifted mountainous land and can also be related to the shattered, easily eroded greywacke sandstone prevalent in the high country. Accelerated erosion may also be attributed to deforestation by Polynesians and Europeans and to overgrazing by millions of rabbits and sheep for several decades prior to the spread of deer into the high country (Howard 1966). No studies have demonstrated that red deer alone have eliminated the beech forest cover from any extensive area in New Zealand. It may be more reasonably argued that red deer may have reduced the extent of beech forest by impeding tree regeneration along forest margins and at other open sites. The magnitude of this type of reduction in forest area, however, has not been documented. On the other hand, many studies, including Holloway's, purport to show that for certain localities beech regeneration has been so impaired that the future persistence of a forest cover over extensive areas is threatened. Although deer-induced shifts in the species composition of the undergrowth of the beech forests are known to have occurred (and such shifts are not unimportant from a forest management point of view), the major objective of research on deer influences in beech forests is the assessment of browsing effects on the regeneration of the main canopy tree species. In other words, following the death of the main canopy trees, which attain ages of at least 300 years, do uncontrolled deer populations threaten to reduce significantly the present extent of forest cover?

In order to demonstrate the response of the vegetation when freed from heavy browsing by wild game, numerous small (c. 200–400 m²) ungulate exclosures were established in beech forests on the North and South Islands, mostly during the 1950s and 1960s. Unfortunately, few of these exclosures have been maintained annually and treefalls have destroyed many. Also, in most cases failure to

measure the vegetation inside and outside the exclosures at the time of establishment has reduced their utility. Consequently, there is insufficient information available from long-term observations of exclosures to provide a clear indication of the response of beech seedlings (i.e., less than 1.35 m tall) released from red deer browsing pressure. For example, two exclosures installed in 1958 in mountain and red beech stands near the Tutaekuri River on the North Island and remeasured in 1964 show a marked increase in the frequency of mountain and red beech seedlings and saplings; however, in nearby permanent plots not protected from ungulate browsing, seedlings and saplings of these species also increased markedly from 1960 to 1965 (Wallis 1967). In exclosures established in 1951 and 1970 in black beech forest in the Aorangi Mountains on the North Island, the densities of black beech seedlings are less inside than outside the exclosures (Jane and Pracy 1974). In an exclosure of unspecified size installed in 1925 in red and silver beech forest in Nelson, "regeneration" of these two species was reported as noticeably greater beneath gaps within the exclosures than outside (Conway 1949). In contrast to the inconclusive pattern of beech seedling response to release from deer browsing in exclosures, there is a consistent pattern in terms of the response of many species other than the dominant beech species. Following elimination of deer browsing, the main vegetation response is a proliferation of palatable species, which include ferns as well as shrubs and subcanopy trees such as *Coprosma* species, *Pseudopanax* species, *Pittosporum eugenoides*, *Melicytus ramiflorus*, *Myrsine australis*, and *Schefflera digitata*. The vigorous response of the understory shrubs and small trees when released from deer browsing in some cases appears to inhibit the establishment and development of beech seedlings, thus sometimes resulting in lower densities of beech seedlings and saplings inside than outside the exclosures. Apparently, no exclosure data are available from the driest mountain beech forests where the general lack of competitive understory shrubs and trees would be expected to result in greater beech seedling densities inside exclosures. As discussed below, even in the absence of ungulates *Nothofagus* species gen-

erally do not regenerate (i.e., grow from seedling size to tree size) beneath closed forest canopies. Because most exclosures have been located beneath closed forest canopies, the absence of tall seedlings and saplings of *Nothofagus* species is expected regardless of the effects of deer. Thus, the often-published photographs of dense undergrowth in ungulate-exclosures surrounded by a relatively sparse forest understory illustrate deer effects on subcanopy species but do not necessarily imply that deer have impeded the regeneration of the main canopy *Nothofagus* species (Nelson 1979; Salmon 1975).

Only two quantitative comparative studies of beech forests on deer-free islands and adjacent deer-infested mainlands have been published. These studies fail to show a consistent pattern of inhibition of beech regeneration by deer. For example, at Lake Manapouri on the South Island red deer appear to have reduced the relative density of mountain beech stems in the 0.3 to 5 m height class but not in shorter or taller height classes; the author of the study, however, believes that a cause other than browsing ungulates (i.e., possible site differences) may be responsible for some of the differences in the forests of the two areas compared (Johnson 1972). At Lake Waikareiti on the North Island 12-to-46 cm-tall seedlings of both silver and red beech and saplings and small trees (taller than 1.5 m but less than 10 cm diameter-at-breast-height) of silver beech are significantly more abundant in the deer-infested mainland forest (James and Wallis 1969). In this case, if it was assumed that absence of browsing animals from the island site is the only difference from the mainland site, browsing would appear to have favored the regeneration of beech species. Both of these comparative studies show that the same shrub and small tree species that proliferate in exclosures are much more abundant in all height classes on the deer-free islands than in adjacent mainland forests (James and Wallis 1969; Johnson 1972). Reduction in density of these competing shrubs and small tree species owing to deer browsing is believed sometimes to promote an increase in the densities of beech seedlings and saplings (James and Wallis 1969).

The New Zealand Forest Service relies mainly on extensive vegetation surveys to assess both the long- and short-term effects of

red deer on beech forests. The five specific objectives of these surveys are the evaluation of (Wardle and James 1973):

- (1) susceptibility of the forests to animal damage;
- (2) the degree to which forests have been modified from their original condition;
- (3) the extent to which forests are being used by animals at the time of the survey;
- (4) the magnitude of the short-term changes in forests following animal control operations; and
- (5) the long-term changes (i.e., at least several decades in the future) in forest structure, composition, and regeneration potential.

Surveys are of both the reconnaissance type and the permanent-plot type.³ Permanent plots installed for 10 or more years have been remeasured in several areas of beech forest on both the North and South Islands, but no evaluations of the results have yet been published. The 10- to 12-year period since the installation of many of these plots is considered too short to provide the type of data for which they were primarily installed (Wardle and James 1973). Although the measurement of change over several decades is the main justification for the costly permanent-plot type surveys, the data obtained at the time of initial installation of the plots (often in combination with data from reconnaissance surveys) have served as the bases for numerous publications and unpublished reports on forest structure and composition and the effects of animals on the surveyed forests (e.g., Wardle 1970; Bathgate 1976; Wardle and Guest 1977). These publications and reports indicate that the vegetation surveys are reasonably effective in attaining three of the five previously listed survey objectives: evaluation of susceptibility of the forests to animal damage, indication of extent of present use by animals, and assessment of short-term changes following animal control operations. They are unlikely ever to satisfy the objective of evaluating the degree of modification from the pre-deer state of the forests because of the general lack of quantitative data on forest structure and composition prior to the introduction of deer.

From a management perspective, the fifth objective—assessment of the long-term

changes in forest structure, composition and regeneration potential—is by far the most important. Because of the immediate need to provide information for management decisions, predictions of future conditions of the forest must be made on the basis of the present forest structure and composition. Such predictions are based mainly on the analysis of the population structures of the dominant tree species as inferred from the frequency distribution of trees in diameter-at-breast height (dbh) size-classes. The use of size-class analysis as a time-specific method of assessing long-term forest dynamics requires that tree diameters be at least crude indicators of age. For New Zealand *Nothofagus* species, within the same forest stand and on homogeneous sites, tree age and dbh are generally positively related (Wardle 1970; Ogden 1978). Tree species represented in a given area by abundant small dbh trees as well as larger individuals are assumed to be regenerating vigorously and would be expected to continue to occupy the site. It is often assumed that for "stable" tree populations, the age-class or size-class structure should follow a reverse J curve, which may be described by either a negative exponential or power function (Leak 1975; Hett and Loucks 1976). For New Zealand *Nothofagus* species, especially mountain beech, a relatively small number of stems in the less than c. 5 cm dbh size range often results in a poor fit of the size-class distribution to a reverse J curve; this apparent underrepresentation of small stems has frequently been attributed to the effects of deer browsing (Wardle 1970; Burrows et al. 1976; Cuddihy and Ross 1979). However, similar size-class distributions occur in many Chilean subalpine *Nothofagus* forests where browsing mammals are not a significant factor (Figure 6) (Veblen et al. 1981). These distributions result from the tendency of many New Zealand and Chilean *Nothofagus* species to regenerate periodically in even-aged groups mainly following massive natural disturbances such as mass movements, extreme snow damage to forest canopies, snow avalanches, extensive windthrow, severe insect attack, flood deposition, volcanic ash deposition, and fire (Figure 7) (Wardle 1970; Ogden 1971; James 1974; Veblen, Schlegel, and Escobar 1980; Veblen et al. 1981). Even in the absence of browsing

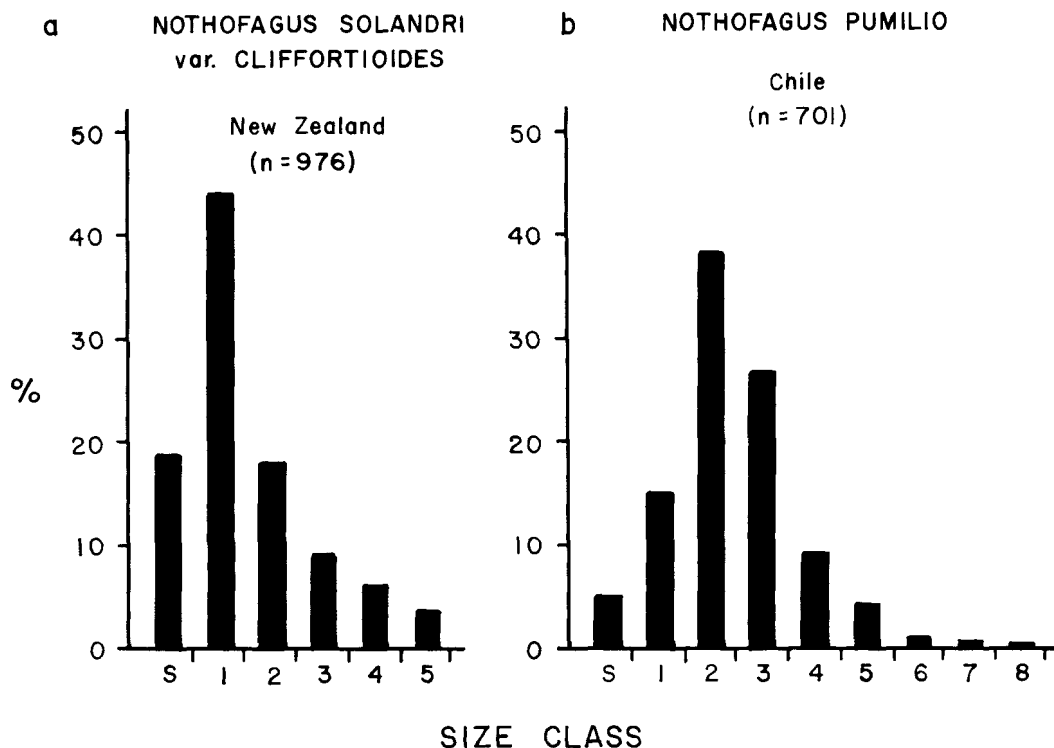


Figure 6. Percentage frequency distributions in size-classes of (a) *Nothofagus solandri* var. *cliffortioides* in pure subalpine stands in southern Fiordland, New Zealand (data from Bathgate 1976) and (b) *Nothofagus pumilio* in pure subalpine stands in the Chilean Lake District (data from Veblen et al. 1981). The total area sampled was 0.84 ha in (a) and 0.78 ha in (b); *n* indicates the total number of trees in each sample. The size-classes used are 1–8 for trees in 10 cm dbh classes from 5 to 85 cm dbh and S for saplings; in (a) saplings are trees 2–5 cm dbh and at least 1.3 m tall and in (b) saplings are trees <5 cm dbh but at least 2 m tall. These distributions are illustrative of size-class distributions found in many subalpine *Nothofagus* forests in New Zealand and Chile, although many other types of distributions also occur in subalpine *Nothofagus* forests in both countries.

mammals, where sites beneath closed forest canopies are sampled, an "underrepresentation" of stems in the small size-classes for most New Zealand *Nothofagus* species is expected because of the dependence of their regeneration on canopy openings. Deviations from theoretically expected size-class distributions may result from natural stand dynamics and are not necessarily the result of deer browsing.

Although there is abundant evidence that heavy browsing by red deer in beech forests can result in marked shifts in understory species composition (including, in some cases, reduction in beech seedling numbers), the long-term effects on the forest regeneration potential are still undetermined. Beech forest structures resulting at least partially

from natural stand dynamics have in the past been mistakenly related to the effects of deer browsing.⁴ Although it is known that after depleting the forest understory deer populations decrease drastically, it is not known whether at these lower population levels the deer will severely inhibit beech forest regeneration. The most certain means of determining the long-term effect would be through the monitoring of numerous exclosures installed over the full range of beech forest associations at sites where conditions are suitable for the development of beech regeneration. Whether the area of beech forest is being significantly reduced by deer may eventually be determined by concentrating monitoring activities on appropriate sites such as along forest margins, beneath



Figure 7. Extensive windthrow in mountain beech forest in the high country of Canterbury. Regeneration following such disturbances usually results in even-aged stands. Photo by J. Barran, New Zealand Forest Service, 1981.

canopy gaps and other areas of reduced canopy cover, and on other sites lacking a dense forest cover.

Tree Mortality and Opossums in Westland Rata-Kamahi Forests

In the highland conifer-broadleaved forests of Westland, known commonly as rata-kamahi (*Metrosideros umbellata*-*Weinmannia racemosa*) forests, large numbers of dead or dying standing trees are conspicuous (Figure 8). Since as early as the 1940s this extensive

tree mortality has caused considerable concern that these protection forests were deteriorating, with consequent accelerated erosion and increased flooding of the adjacent pastoral lowlands. Browsing of the foliage of the main canopy trees by the introduced Australian brush-tailed opossum (*Trichosurus vulpecula*) is commonly accepted (by both forest managers and the public) to be responsible for the widespread tree mortality. Consequently, trapping and poisoning of opossums is strongly encouraged by the New Zealand Forest Service and others to reduce opossum densities and thereby prevent

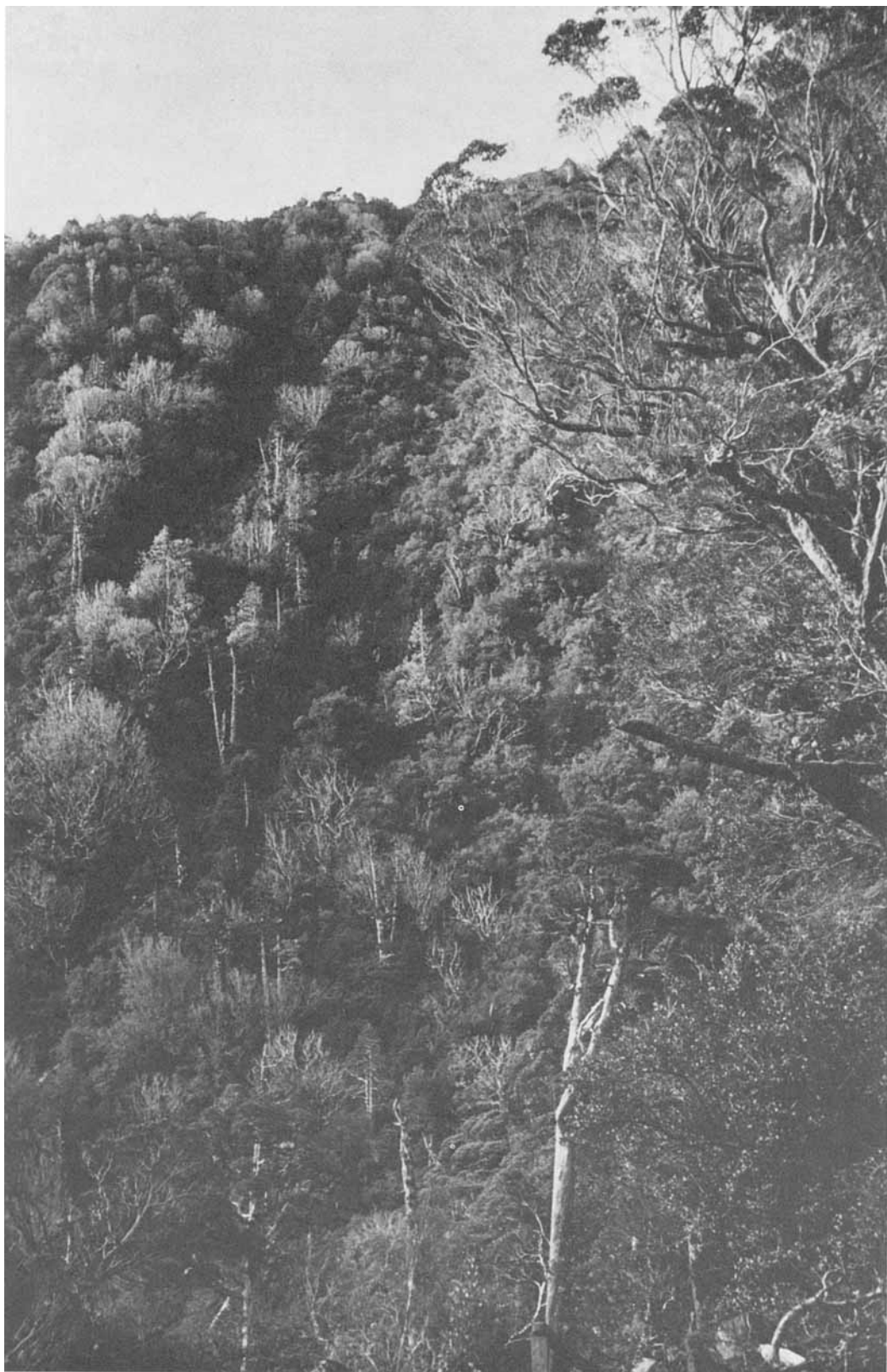


Figure 8. Conspicuous tree mortality in central Westland highland conifer-broadleaved forests. Photo by M. Clark, New Zealand Forest Service, 1980.

further deterioration of these and other protection forests (McCaskill 1973; Salmon 1975). Opossums are also controlled because they are pests in forest plantations and vectors for the spread of bovine tuberculosis.

Although opossums were locally abundant and widespread in New Zealand—from Auckland to Stewart Island—by the 1920s, they were not regarded as detrimental to the native forests until the 1940s. For example, in 1926 Leonard Cockayne (1926, Part 2, p. 11), the leading authority on the vegetation of New Zealand, wrote:

Were the opossums doing noticeable damage, the forests would unmistakably point to this in their dead trees. But the forests, so far as damage from opossums goes, are as they ever were. Nor do these animals affect the all-important floor covering or reduce the seed crop to any extent.

In a report on opossums commissioned by the government and based on inspections of many forests on the North and South Islands, H. B. Kirk (1920, p. 2) stated, "I have found no native tree that has in my opinion, been killed by the opossum." Kirk did, however, report many dead rata, kamahi, and *Fuchsia excorticata* on slopes near Lake Kaniere in Westland, but he could not find any evidence that their death was related to opossums. Similarly, in a report to the Forest Service A. N. Perham (1924) noted for the same area that there were many dead or dying specimens of rata and *F. excorticata* and that he also did not believe opossums were responsible. Even as early as the late nineteenth century, extensive areas of dead trees in central Westland were reported by the explorer and geologist, Charles Douglas (Holloway 1957); he described dead mountain cedar (*Libocedrus bidwillii*) as being so numerous that they gave a white tint to the landscape. Photographs taken between 1905 and 1907 of the Whitcombe, Mungo, and Toaroha Valleys, which are tributaries of the Hokitika River, also show extensive areas of dead trees (New Zealand Geological Survey Department 1907, photos facing pp. 12, 16; Morgan 1908, Plates VI, XXVIII, and XXIX). Some of these dead trees are conifers such as mountain cedar or Hall's totara (*Podocarpus hallii*), as indicated by their conical form. Many other dead trees, however, appear to have rounded crowns, which is suggestive of broadleaved species

such as rata. Furthermore, the extensive area of dead trees in these photos suggests that more than just the conifers must be involved. Thus, the presence of numerous dead rata and kamahi in Westland is documented as early as 1920, and perhaps as early as the late nineteenth century, even though it is generally believed that the exceptional mortality began to appear only in the 1940s (Gibb and Flux 1973). Because opossums did not occupy these valleys in large numbers prior to the 1920s, it is reasonable to question the conventional view that opossums are wholly responsible for the extensive tree mortality (Pracy 1974; James, Jane, and Barr 1973).

In the 1940s apiarists complained of a decline in rata bloom as a main source of nectar in Westland because of opossum damage to rata, and they reported that rata and kamahi were dying extensively in central Westland (Wodzicki 1950; Gibb and Flux 1973). Concern over this widespread tree mortality led in 1955 to an inspection of the forests by an interdisciplinary team of ten scientists and land managers from several government departments and culminated in an extensive unpublished report (Chavassee 1955a). Although the team members did not totally agree on the cause (or causes) of the mortality, they did concur in their descriptions of the affected vegetation. The two most affected species were rata and kamahi, particularly on steep slopes between 330 and 1000 m elevation with the most severe mortality occurring on north-facing slopes and the most affected trees measuring more than 30 cm in diameter-at-breast-height. Opossums were present in areas of both high as well as low tree mortality, while red deer (and occasionally goats) were present in most of the affected forests (Tyndale-Biscoe 1955). The possible causes of the mortality considered by the inspection team included tree overmaturity, recent drought, long-term climatic change, insect attack, and the direct and indirect effects of browsing mammals. Although opinions varied as to the relative importance of the different factors, Chavassee summarized the consensus of the team as follows (Chavassee 1955a, pp. 2–3):

It was concluded that opossums are primarily responsible for major defoliation of the canopy trees; that ground-browsing animals [red deer and goats] are responsible for destruction of

shrub and ground layers, for trampling and destroying the duff layer, and for the complete inhibition of regeneration. Both are responsible for the alteration of the microclimate, possibly leading to damage by drought, and for the destruction of optimum conditions for insectivorous birds. These activities lead to insect damage to weakened trees, (and possibly to fungal attack at tree roots) causing death. Insects may also have been encouraged, particularly those feeding on stems and branches, by the reduction in species of birds brought about by introduced disease, cats, rats and mustelids.

The main evidence in support of the consensus view of the 1955 inspection team was the coincidence of apparently high opossum densities (estimated mainly from the presence of fecal pellets) with areas of defoliated trees and the association of sparse undergrowth with the presence of red deer or goats. One member of the team, Tyndale-Biscoe, though accepting that introduced animals were responsible for some of the changes in Westland forests, questioned the degree to which they were the sole agents of change. He noted that the consensus view did not explain why dead trees were found mainly on steep slopes rather than on summit ridges and gentle slopes, nor why some stands seemed unaffected despite opossum infestation (Tyndale-Biscoe 1955). Furthermore, today it is well known that many dead standing stems of conifers are also present at relatively high elevations in the rata-kamahi forest type. For example, mountain cedar and Hall's totara are often represented by many dead stems with basal areas per hectare in some stands exceeding that of the dead rata and kamahi (Coleman, Gillman, and Green 1980). Probably the most important conclusion of the 1955 report was that excessive tree mortality in Westland forests was the result of a complex interaction of several factors and that much further investigation would be required to assess the relative role of opossums (Chavasse 1955a, 1955b; Tyndale-Biscoe 1955).

Soon after the 1955 report, J. M. Hoy (a member of the 1955 inspection team) conducted a survey of coccids (scale insects) in relation to the mortality of rata and kamahi and found no significant difference between abundances of coccids in healthy stands versus stands with numerous dead or dying rata. He concluded that if coccids contribute to the mortality of rata, they are clearly a secondary factor; he also did not consider them to be

important in the death of kamahi. Hoy suggested that the mortality of rata and kamahi was probably due to a combination of factors such as senescence of old trees, loss of root hold on steep slopes, insect damage, and opossum browsing (Hoy 1958).

Following these early studies, which emphasized the multiplicity and probable interaction of factors in the mortality of rata and kamahi, most of the subsequent research has centered exclusively on the single mechanism of opossum browsing. Building on the early work of Kean and Pracy (1953), who listed 70 native tree species browsed by opossums, studies of fecal pellets and stomach contents have identified the diet of opossums in many districts of New Zealand (Mason 1958; Gilmore 1967; Fitzgerald 1978; Fitzgerald and Wardle 1979). These studies show that, when present, rata and kamahi leaves are among the major constituents of the opossum diet. The other major components of their diet in Westland include the small trees *Melicytus ramiflorus*, *Fuchsia excorticata*, *Schefflera digitata*, *Pseudopanax colensoi*, *Hoheria glabrata*, *Coprosma* species, and *Aristotelia serrata*, as well as numerous species of ferns. The order of preference for these species varies greatly from place to place as well as seasonally. Although rata and kamahi together often account for 30 to 40 percent of the opossum foliate diet, the amount of available foliage of these two large trees in well-developed rata-kamahi forest (i.e., the type of old-growth forest apparently threatened by opossums) would be several times greater than that of all the small trees combined. One of the most pertinent findings of these studies is that the opossum's diet is highly varied, and it has been suggested that opossums require a nutritionally balanced diet (Coleman, Gillman, and Green 1980).

The general coincidence of extensive tree mortality with high opossum densities in Westland forests and the fact that rata and kamahi are important in the diet of opossums have led most investigators to the conclusion that opossums are responsible for the mortality (James, Jane, and Barr 1973; Wardle 1974; Coleman, Gillman, and Green 1980). However, this explanation leaves several unanswered questions:

- (1) Why do many relatively young rata and kamahi appear totally healthy and vig-

- orous (even though some are browsed by opossums) in the midst of older dead or dying individuals of the same species?
- (2) Why, as observed by the 1955 inspection team (Tyndale-Biscoe 1955; Hoy 1958), are numerous dead rata found on steep slopes while adjacent ridge summit stands and gentle slopes generally show much less excessive mortality?
 - (3) Why are some rata-kamahi forests (such as in the Catlins area in south-eastern Southland) unaffected by the mortality despite a long history of occupation by large opossum populations?⁵
 - (4) Why in the Westland forests are many of the dead trees of species that are only lightly browsed (e.g., Hall's totara and mountain cedar) by opossums (James, Jane, and Barr 1973; Coleman, Gillman, and Green 1980)?

We propose that the above questions can be partially resolved by taking into account the natural stand dynamics of rata-kamahi forest in Westland. Synchronous massive establishment of rata and kamahi on sites where the previous vegetation has been devastated by a natural disturbance and the development of even-aged stands eventually result in the senescence of many trees at approximately the same time in a given area. In a senescent state the trees are more susceptible to lethal damage by any of several deleterious factors such as fungal pathogens or insects, droughts, severe frosts, or browsing by opossums. Mortality of the groups of senescent trees may be made more coincident over a shorter period due to opossum browsing even though the mortality would eventually occur in the absence of browsing mammals. In this explanation, senescence resulting from natural stand dynamic processes is an important contributory factor to the excessive tree mortality, although in many cases the immediate factor that hastens the death of the tree may be opossum browsing.⁶ There is no doubt that persistent browsing by opossums contributes to the death of individual old trees, as has been demonstrated experimentally for northern rata (*Metrosideros robusta*) on the North Island (Meads 1976). What is questioned, however, is the degree of mortality to expect even in the absence of opossums.

The hypothesis that much of the apparently

excessive tree mortality is related to natural stand dynamics is supported by the structural patterns characteristic of Westland rata-kamahi forests. The apparently even-aged structure of many stands reflects past periods of massive synchronous establishment (Wardle 1966, 1971; Stewart and Veblen 1982). In the 1955 report Chavassee (1955b, p. 5) described and interpreted these stands as follows:

As can be observed throughout Westland, at some time in the past regeneration of strips and patches has taken place in the rata/kamahi forest. These patches appear to be even-aged, whether rata, kamahi, or a mixture of these two species. Throughout the areas inspected these young stands appeared to be the same age, whether forming thin strips down ridges or in broader patches on country of relatively smooth contour. . . . They form a pattern similar, in some places, to the present mortality pattern. . . . The most probable explanation is that they originated after a major earthquake.

Generally in Westland the major areas of rata and kamahi mortality are found in strips down steep ridges and on steep spurs, while on other ridges and spurs relatively young, vigorous stands often occur. As Chavassee (1955c, p. 7) observed, this pattern "suggests that there might be periodic or cyclic disturbance of some sort leading to excessive mortality in the older, and probably relatively even-aged stands." In the late nineteenth century Charles Douglas (Holloway 1957, pp. 35–36) also described, as a general feature of Westland, even-aged stands on sites previously devastated by mass movements; he noted that "up every river there is evidence of whole hillsides having come down . . . as if some exceptional commotion had taken place along the [West] coast, perhaps a very wet season combined with an earthquake at the right moment did the business." Recently Wardle (1980) has suggested that many of the prominent even-aged rata-kamahi stands on steep slopes in southern Westland became established following a major earthquake about 1730–40 A.D., which triggered massive landslides. Mass movements, whether triggered by earthquakes or by periods of prolonged heavy rainfall, are abundant on the steep slopes of Westland. When seed is available, rata and kamahi are often the principal colonizing species of the devastated sites (Wardle 1966, 1971; Wardle and Hayward

1970; Stewart and Veblen 1982). Windthrow is another important type of disturbance affecting the forests of Westland, sometimes resulting in even-aged patches of rata and/or kamahi (Coleman, Gillman, and Green 1980; Veblen and Stewart 1982).

The numerous apparently even-aged rata-kamahi stands in Westland are easily attributable to natural disturbances. Synchronous senescence of trees that became established at approximately the same time probably accounts for the excessive tree mortality apparent in photographs of central Westland rata-kamahi forests taken prior to the presence of large populations of opossums (Morgan 1908). The general coincidence of the tree mortality with high opossum densities today may be both cause and effect. As previously indicated, the diet of the opossum is highly varied, and areas of greater tree and shrub diversity are believed to be more attractive to opossums (Coleman, Gillman, and Green 1980). Relatively young even-aged rata and kamahi stands are often dominated exclusively by these two species, and because of their dense, homogeneous canopy the development of understory shrubs and small trees is sparse. However, as these stands age there is a marked increase in diversity of understory species—including ferns, shrubs, and small trees (Stewart and Veblen 1982). Areas of forest with extensive mortality of the main canopy trees are characterized by greater abundances of several species of relatively small trees such as *Pseudopanax* species, *Griselinia littoralis*, *Carpodetus serratus*, *Aristotelia serrata*, *Fuchsia excorticata*, *Schefflera digitata*, and *Melicytus ramiflorus* (James, Jane, and Barr 1973). This greater diversity of diet may permit the attainment of higher opossum densities and may partially account for the general coincidence of extensive mortality of main canopy trees with high densities of opossums.⁷

Conclusions

Both red deer and opossums have undoubtedly altered the native forests of New Zealand. However, the magnitude of changes in forest composition and structure that can be attributed to these introduced species is not at all clear. Browsing by red deer has

caused drastic shifts in the species composition of the understories of many beech forests (and in many conifer-broadleaved forests), as has been suggested by the changes observed in deer exclosures. However, the long-term effects of deer on the maintenance of a beech forest type of cover are not known. As an agent of forest elimination and accelerated erosion, browsing by red deer has clearly been less important than extensive burning in both pre- and post-European times. In some instances, red deer may have inhibited tree regeneration following burning, but, in general, overgrazing by sheep and rabbits has been far more destructive of soil and vegetation resources. Similarly, although canopy browsing by opossums is certain to have caused some shifts in the relative abundances of some tree species, demonstration of the magnitude of such shifts has proved intractable. In central Westland rata-kamahi forests, it is not clear the degree to which the excessive tree mortality should be attributed to opossum browsing as opposed to natural stand dynamics. Given that introduced wild animals have been present for more than a century and have had a pervasive influence on the vegetation of nearly the entire country, it is a daunting task to separate natural from animal-induced change. However, there is ample evidence relating the more dramatic changes in the forests of the South Island to natural geologic and meteorological events or to direct human activities such as burning (Molloy 1969; Mosley 1978; Nicholls 1980).

In New Zealand, where noticeable changes in forest composition or structure have occurred in the absence of other obvious causes, there has been a tendency to associate the changes with the introduced wild animals. More than half a century ago A. N. Perham (1924) suggested that many people, upon seeing an area with dead or dying trees and an abundant opossum population, jump to a conclusion of cause and effect without further evidence. The tendency uncritically to blame introduced animals for dramatic vegetation changes is illustrated more recently by the example of extensive mortality in the coastal forests of Stewart Island. Dead patches of trees of several different species in lowland conifer-broadleaved forests along the coast of Stewart Island were first noticed in the 1950s and were assumed to be due to

the effects of either white-tailed deer or opossums (Purey-Cust and McClymont 1979). However, highly similar mortality patterns in the same forest type on nearby Bench Island, where no browsing mammals occur, clearly indicate that introduced animals cannot be assumed to be the cause of the mortality. The most likely explanation for the mortality in the coastal forests of both islands is storm damage (Veblen and Stewart 1980).⁸

Although the introduction of wild animals to New Zealand is presented in the international ecological and geographical literature as an unmitigated ecological disaster, this is not a universally accepted point of view within New Zealand. The perception of introduced wild animals as solely detrimental is appropriate only where the primary objective of land management is strict preservation of the native flora and fauna, such as in National Parks and Nature Reserves. However, of the four-million-hectare area covered by native forest in New Zealand (23 percent of the entire land surface) only one and a half million hectares are in National Parks and allied reserves (Nicholls 1980). Most of the native forest land is State Forest, where multiple use is the accepted land-management objective. In these State Forests the presence of introduced wild animals certainly has enhanced recreational values from the point of view of the thousands of deer hunters. It may also be argued that the wild animals have enhanced aesthetic values. With the value of exports of wild animal products (mostly opossum skins and venison) exceeding thirty million U.S. dollars in 1980, the economic value of wild animals is also far from insignificant (New Zealand Forest Service 1980). The enhancement of the recreational, aesthetic, and economic values of native forest lands owing to the presence of introduced wild animals must be considered in the light of losses in values such as watershed protection and native flora and fauna preservation. There is no doubt that such losses have occurred nor that wild-animal control policies are necessary; however, before the magnitude of the effects of introduced mammals on the forests of New Zealand can be assessed, much further investigation is required.

Given the recency of the occupation of New Zealand by human beings, the magnitude of their impact (either direct or via introduced

animals) on the native vegetation should be easily determined. However, though the effects of forest clearance and burning are fairly evident, the degree to which native forest structure and composition have been altered by introduced mammals is far less apparent. The challenge, in New Zealand as well as in the many other parts of the world where exotic wild mammals have been liberated, is to separate natural from animal-induced changes in the vegetation. In assessing the impact of human beings and introduced animals on native vegetation, it is particularly important to recognize fully the dynamic nature of vegetation as influenced by numerous types of natural disturbances. Studies from many parts of the world have demonstrated that frequent natural disturbances often prevent the development of expected equilibrium vegetation types (White 1979; Oliver 1981). Consequently, older ecological models of vegetation change (i.e., climax theory), which emphasize progressive change toward a stable endpoint, are being abandoned in favor of more dynamic or kinetic models that accept, as normal, instability of the vegetation (Drury and Nisbet 1971). In investigating the influences of human beings and introduced animals on vegetation, it must not be assumed that in the absence of human influences, vegetation will be in an equilibrium condition.

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Notes

1. The name "opossum" properly applies to the true American opossum of the family Didelphidae, whereas *Trichosurus vulpecula* belongs to the family Phalangeridae in a different suborder of marsupials. In Australia *T. vulpecula* is known as a "possum" whereas in New Zealand the term "opossum" is commonly

used. In this paper, "opossum" is used to refer to *T. vulpecula*.

2. The sequence of changes described generally by Holloway were later categorized into stages by Howard (1966).
3. In the reconnaissance-type survey, at observation points systematically located along transects, presence of all vascular species is recorded in five height classes and site characteristics (e.g., altitude, aspect, soil parent material, drainage status) are noted. For an example of a mainly reconnaissance-type survey in mostly beech forest, see Wardle, Hayward, and Herbert (1971). Although no area is delimited, in practice the observations refer to an area of c. 500 m². In addition to the recording of subjective ratings of the degree of browse on each species, presence of fecal pellets is recorded (in some cases, actual counts are made) to assess the present relative densities of deer populations. Such surveys allow data on forests extending over tens of thousands of hectares to be gathered at relatively low cost; they permit the classification of the forests into floristically defined associations and provide rough indications of the intensity of animal use. An evaluation of the susceptibility of major plant species to deer browse is attempted by comparing the frequency of each species in the height class that is most accessible to deer (31 to 183 cm) with its frequency in the other height classes. Indicator species are used to compare the degree of vegetation modification by deer in different forest associations and areas.

In the permanent-plot type of survey 20-by-20 m permanent plots are systematically located along transects, and general observations are made as in the reconnaissance surveys (including presence of deer pellets) (Allen and McLennan 1978). In each plot the diameters-at-breast-height (dbh) of all trees and shrubs greater than 2 cm dbh are measured and permanently tagged to facilitate remeasurement, usually at five- to ten-year intervals. Stems less than 2 cm dbh but at least 1.35 m tall (i.e., breast height) are counted but not tagged. Within each 20-by-20 m plot, presence of all vascular plant species and the numbers of seedlings of tree and shrub species are recorded in height classes in 24 systematically located circular plots of 0.49 m radius.

4. It should be mentioned that beech forest structures previously attributed to deer browsing are now recognized in New Zealand by at least some forest ecologists as being unrelated to herbivore influences (Wardle and Guest 1977).
5. Opossums were introduced to the Catlins area in 1894, and as many as 60,000 opossum skins were taken out of the area in 1912, but today rata is both abundant and healthy (Thomson 1922; Wardle 1973; New Zealand Forest Service 1979).
6. A highly similar canopy mortality to that described for rata-kamahi forests also occurs in

Ohia (*Metrosideros polymorpha*) forests in Hawaii. Extensive dieback of *Metrosideros* has occurred in Hawaii in the absence of opossums or any other mammalian canopy folivore. It has not been possible to relate the dieback of Ohia to either insect infestation or fungal pathogens (Papp et al. 1979), and it has been suggested that the dieback is a totally natural phenomenon (Mueller-Dombois 1980). Adee and Wood (unpublished manuscript) have recently related the Ohia dieback to the senescence of even-aged stands that establish following volcanic disturbance. Thus, explanations (arrived at independently) for the remarkably similar patterns of *Metrosideros* dieback in Hawaii and New Zealand both stress the importance of natural stand dynamic processes.

7. Extensive mortality of northern rata (*Metrosideros robusta*) and kamahi also is typical of some North Island forests, but in contrast to Westland is not limited mainly to steep slopes (Hoy 1958). The mortality on the North Island may also be related to synchronous senescence of large proportions of the tree populations but, compared to Westland, fire and perhaps wind damage may be more important as disturbance agents relative to mass movements (Thomson 1936; Elder 1965).
8. It should be noted, however, that on Stewart Island white-tailed deer have dramatically depleted the forest undergrowth and impede regeneration of numerous tree and shrub species beneath open canopies, such as the coastal dieback strip (Veblen and Stewart 1980).

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