tion in New Zealand. Rawlings (1953) noted sporadic outbreaks of the buprestid beetle, *Nascioides enysi* Sharp in *Nothofagus* forest. These outbreaks were attributed primarily to debility in the host trees due to overcrowding, root injury due to animal trampling, fungal attack on trees, the activities of man and changes in the general ecological conditions from natural causes including earthquakes. Once the beetles were present in large numbers even healthy trees succumbed to attack.

For many years concern has been expressed about death of rata *(Metrosideros)* in protection forest on the steep western slopes of the Southern Alps. As long ago as 1925 (Miller 1925) death of tree rata in this area was attributed to the presence, in large numbers, of an indigenous coccid, *Anoplaspis metrosideri* Mask. In 1955 a group of scientists made a preliminary survey of the situation in Westland. This group included foresters, animal ecologists, pedologists and entomologists. On the basis of this survey Hoy (1958) concluded that insects were not a primary cause of mortality but that a number of indigenous coccid species could possibly be implicated in the death of individual trees which had been weakened by other causes. As in the case of attack on *Nothofagus* by *Nascioides enysi*, these other causes included effects from ground feeding animals; also damage by opossums, overmaturity of trees and earth movements due to the steepness of the slopes involved. It is possible that this 1955 survey was conducted too late to detect the presence of an outbreak of *Anoplaspis metrosideri* since there was a marked disparity between the number of coccids collected and the evidence on the trees of their former presence, many branches being heavily coated with sooty moulds even though few insects could be recovered.

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MODIFICATION OF NEW ZEALAND'S FLORA BY INTRODUCED MAMMALS*

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An undisturbed environment evolved over a long period and composed only of native plants and animals has a well-established stability that is *not* delicately balanced. A change in the density of any one native species of mammal, either by man or some catastrophe, usually does *not* set off a dramatic chain reaction of responses by the other plant and animal components of the community. Even though the balance of nature is dynamic and not static, a fairly stable plant and animal equilibrium exists where man has not disturbed this environment.

Although natural environments are so stable, man can disrupt the animal-plant relationships by introducing exotic plants or by altering the native vegetation through farming, grazing,

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logging, or fire. A marked chain reaction of other responses may then be initiated. McNeil (1964) has shown how such man-made modifications of the environment in the state of Michigan resulted in an overpopulation of native white-tailed deer which did great destruction to their own habitat by eating out the native browse in their winter range. Sometimes such modification is irreversible, or nearly so, but often the habitat will eventually recover if the density of ungulates is kept in check.

Man can also disrupt the natural stability of a biome by introducing alien animals. New Zealand has no native land mammals. When herbivorous mammals were introduced, especially the red deer and the opossum, they greatly modified the composition of certain types of vegetation. Whenever similar introductions of mammals have been made in other countries, where related species were already present, the effect on the vegetation has been less than in New Zealand.

Important questions to be discussed here are when and how do the successfully adapted introduced animals modify the habitat? In New Zealand man disturbed the ecological equilibrium of the biome by exposing native plants to alien animals; some of the indigenous plants apparently could not withstand the heavy browsing from these animals.

Many of the same principles also apply to other animals. Hoy (1964) has shown how an exotic insect, the Australian scale (*Eriococcus orariensis* Hoy), continues to prevent a native plant, manuka (*Leptospermum scoparium* Forst), from being as aggressive as it formerly was, even though the scale's natural parasite (*Myriangium thwaitesii* Petch) has also arrived in New Zealand. A new ecological equilibrium has been established and the initially dramatic impact of the scale on manuka will probably never occur again. Hoy also mentioned how indigenous insects can affect native vegetation once some other factor has modified the environment. Beveridge (1964) reported some intriguing ecological investigations to determine the importance of seed-eating birds and small mammals in modifying existing patterns of native vegetation in North Island podocarp forests. This is a complicated field of research and I predict that for some time the more data he collects the more complex the ecological picture will become.

Domestic animals allowed either to roam too freely or to overgraze their habitat, especially if they became truly feral, have seriously modified native vegetation in many parts of the world. Atkinson (1964) has described how feral goats have modified the vegetation in several New Zealand localities. Feral goats are notorious throughout the world, and especially on islands, for their damage to vegetation. Cattle are not important now in New Zealand but, in earlier times, both domestic and feral cattle penetrated far into native bush; they are one of the most aggressive of all the introduced mammals in ability to open up indigenous forests. Feral pigs, and especially feral goats, are still modifying the vegetation in many parts of the country. Holloway (1964) has graphically described the general trends in forest modification resulting from introduced animals.

Wraight (1964) and Christie (1964) also indicated how deer, chamois, thar, hare and other grazing mammals have altered the original alpine vegetation. One effect has been a change from an herbaceous-dominant formation to one with grasses dominant, because of the greater susceptibility of herbaceous plants to grazing.

Hercus (1964) has pointed out that the combined effects of man's use of sheep and fire on the tussock grasslands over many years have not eliminated many, if any, species of plants; but "have served to open up the plant community and allow the invasion of exotic species leading to a richer or more varied inter-tussock flora than the original." The effect of mammals on the indigenous forests has been different. For the most part it has largely been just a reduction in density either of certain age classes or of entire species of plants, since originally most of these forests were multi-layered with a spongy ground cover. In some South Island beech forests much of the ground cover and the lower tiers of vegetation have been destroyed. In others just the highly palatable plants that could not withstand heavy browsing are gone. The significant difference between this and the effect of sheep on tussock is that in most of the eaten-out indigenous forests where the original canopy still exists, few exotic plants have entered the community. Since adequate regeneration to replace the existing type of canopy is sometimes lacking, the future of such forest communities is uncertain.

It is convenient to describe the population cycle introduced mammals in New Zealand pass through as consisting of four stages, even though they are not really separate entities. Using red deer, the worst offender, as an example, Stage 1 commences with their liberation or immigration into a new area. Stage 1 continues until the maximum population density is attained, often 20 to 30 years with red deer.

Stage 2 is the dramatic one. It consists of an over-population of deer "eating out" their habitat. In Stage 2 deer eat plants and parts of plants normally ignored. Drastic winter losses do not reduce herds as in America, because New Zealand winters are mild and the broadleaved browse is evergreen. For these reasons, even though the animals will suffer from malnutrition and many other stresses, Stage 2 often persists for as long as from 5 to 10 years with red deer, resulting in severe destruction of the vegetation over much of their habitat.

Stage 3 starts when the initial peak density can no longer be maintained. It has a greater variation than Stages 1 and 2 in the time required for development in different localities and elevations. In Stage 3 the deer populations are lower and more nearly match the carrying capacity of their modified habitats. The significant point about Stage 3 is the gradual change occurring in the floral composition, although this also occurs to some extent in all four stages. The trend is for less palatable and more browse resistant plants to replace the accessible plants not resistant to heavy browsing. The ecosystem is modified and a new and more harmonious soil-plant-animal interrelationship is established. When erosion is acute or regeneration of browse-resistant vegetation slow, Stage 3 persists for a long time. The interval is often shortened when exotic vegetation can be introduced.

Stage 4 starts as soon as a greater degree of stability develops between deer and the vegetation-soil complex. Once Stage 4 is reached, deer numbers will tend to become regulated at a more satisfactory level or they can easily be controlled by moderate hunting pressure. During Stage 4 deer will continue to fluctuate in numbers but there appears no chance of the animals again depleting their habitat to the extent occurring in Stage 2. Introduced animals seldom attain peak density a second time, and food resources seem permanently reduced. Effective deer control is necessary in each locality until Stage 4 is reached. A realistic objective for deer control is the attainment of Stage 4 conditions; there is little need of trying to control all deer or to attempt to bring back the highly palatable plants. In many eroded localities the introduction of exotic vegetation is advisable to hasten and reduce the cost of attaining Stage 4.

To know to what exent and how permanently vegetation has been modifid by introduced mammals, it is necessary to distinguish their effects from those changes due to fire, domestic animals, wind-blown salt, and normal plant succession. This can be determined in many ways, for instance by exclosures excluding the animals in question from sample plots of various sizes. Vegetation can also be protected from animals by using chemical repellents or systemic insecticides. To make the best use of exclosures, more than just their construction is necessary: measurements can be taken outside and inside them recording differential growth rates of forage, survival of seedlings, density of individual species as a percentage of the total vegetation, species composition, and the total amount of vegetation and bare soil. To investigate the interactions of different mammals, such as deer and opossums, exclosures can be built to exclude some species of animals but not others. They can be used to protect only parts of one plant from certain animals. The amount of annual growth that takes place with different plants can be determined in exclosures.

To test hypotheses explaining the differences observed in and out of exclosures, further experimental alteration of the environment will be profitable. For instance: clear away the litter and expose bare soil; remove, ring bark or poison various percentages of the canopy trees to let in more light and to remove root competition; introduce exotic plants; to determine how browse-resistant various plants are, artificially simulate animal browsing by partially defoliating (clipping) different age-classes of plants; or, after varying periods of time, open up portions of exclosures to determine at what age plants are no longer damaged by the animals.

The following exciting and challenging fields of ecological research await further investigation in New Zealand. How irreversible are the mammal-caused modifications in the composition of the vegetation? What will be the plant succession on slips and screes in different areas? Has the riparian or early seral vegetation composed of highly palatable plants like konini *(Fuchsia excorticata)*, five-finger (*Nothopanax arboreum*), and wine-berry (*Aristotelia serrata*) been eliminated for ever from some habitats? Where unpalatable grasses like *Microlaena* and *Uncinia* appear, is this a permanent change from scrub to grass? What role will exotic trees and herbaceous plants play in indigenous forests? When opossums kill occasional canopy trees, will they be unable to replace themselves due to the canopy of less palatable but adjacent species closing the openings, hence allowing little light to reach the forest floor? What will result if new and unpalatable sub-climax trees, such as peppertree (*Pseudowintera*), become the principal canopy species? What will be the new mammal-influenced plant succession for different areas and how stable will the new plant climaxes be? From an ecological point of view, how can animal control and plant introductions best be handled to achieve Stage 4 mammal-vegetation-soil stability as soon as possible and most efficiently?

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