Forestry Research Centre, FRI, ILAM, Christchurch

# MOA BROWSING AND VEGETATION FORMATIONS, WITH PARTICULAR REFERENCE TO DECIDUOUS AND POISONOUS PLANTS

**Summary**: Reconstruction of a generalised biology of moas suggests they would have been most abundant in grassland and scrubland, especially near forest margins and at lower altitudes. Their numbers would have been limited by the abundance of food and, on easier low altitude country, their feeding pressure would have been equivalent to that exerted by the introduced mammals. Steep and rough ground, dense sub-alpine scrub, and the risks to incubation and chick-rearing of summer snows, would have severely limited the extent to which moas could have used montane and alpine country.

As has been observed for divaricating shrubs, most deciduous and poisonous plants in New Zealand are low statured. They often dominate early in successions, forest canopy gaps, forest margins, open scrubland and grassland. Their general ecology is consistent with the hypothesis that browsing by moas was a significant selection force.

## Introduction

For the past 60 years, research on the evolution of New Zealand plant formations has dealt almost exclusively with four main topics: the predominance of tropical elements in the flora (Cockayne, 1928; Rattenbury, 1962); the gradual shift from equable Cretaceous climates to the harsher, oscillating climates of the Pleistocene (e.g. Diels, 1897; Cockayne, 1928; Axelrod, 1966; Dumbleton, 1967; McGlone and Webb, 1981; McGlone, 1985); the emergence of the present mountainous islands from a low-relief archipelago during the Kaikoura orogeny (Wardle, 1963; Fleming, 1979) and; fluctuations of Holocene climate (Holloway, 1954; Molloy *et al.,* 1963; Robbins, 1962). The possible significance of browsing by moas was consistently ignored.

Of course, everyone acquainted with the vegetation was aware that many native plants are seldom browsed by introduced mammals (e.g. *Knightia, Leptospermum, Kunzia, Dacrydium, Dracophyllum, Gaultheria, Pseudowintera, Phyllocladus,* some species of *Celmisia, Festuca, Juncus, Carex, Typha, Hypolepis, Histiopteris).* Some plants assume a compactly hedged form (e.g. some species of *Olearia, Senecio, Coprosma, Pittosporum, Nothofagus, Weinmannia),* and eventually break away into a free-growing form after they exceed the height or distance a browsing animal can reach. Some are highly toxic. Others form epicormic shoots, or coppice vigorously from the roots after browsing. The divaricating habit, spines, and mimicry protect plants from large herbivores (Greenwood and Atkinson, 1977).

The idea that browsing and grazing by moas had been a significant selection force obviously occurred to R.A. Falla, who, in Duff's words (1952), after "watching the massive beak of *Notornis* shearing clumps of snowgrass" perceived that "in ancient New Zealand the place of the hoofed mammals was taken by certain flightless birds". It smouldered as a heresy among the wildlife research and deerstalking fraternities during the 1950s - 1960s. It was mentioned by Simmons (1968), Carlquist (1974), and Taylor (1975). But Greenwood and Atkinson (1977) were the first authors to systematically analyse the biology of a particular quality - the divaricating habit - against the hypothesis that it evolved *primarily* as a defense against moa browsing.

Greenwood and Atkinson's hypothesis has been seen by some observers as a scholarly cold douche upon the law and reputations of people involved in managing deer and mountain lands. They (me included) had worked for decades on the premise that, because "no grazing mammals had ever been present to molest (the plants), they possessed no structures that could claim to be defensive (Cockayne, 1928, p426)". If that premise was wrong, then Cockayne's perception of "natural" vegetation as characterised by masses of such splendid plants as large-leaved Coprosmas, Araliads, Umbellifers, Ranunculas, *Todea* and *Asplenium,* would crumble. So too would the implied validity of the Reserves, National Parks and Animal Control Statutes which were, in part, designed to protect the "natural" plant formations and soil. Caughley (1983) has discussed this topic in some detail.

Thus for practical and academic reasons, it is of seminal importance to understand what the vegetation and moa populations looked like before the moas disappeared. Conveying an outline of that understanding is the purpose of this paper. However, before considering the general scenario on how many moas there might have been, and their likely effects on the vegetation, I summarise available information on the ecology of New Zealand deciduous woody dicotyledons and poisonous plants. The number of species of these plants is small. But because they are so often dominant in places where mammals usually choose to live, one must examine the possibility that these plants and moas had a pervasive influence on the lives of each other.

Table 1: *List of deciduous plants of New Zealand. Figures in brackets adjacent to generic names are number of deciduous species and total in the genus according to Dumbleton (/967). Initialled references in brackets are: KP - Mr K.H. Platt (pers. comm.); IA - Dr I.A.E. Atkinson (pers. comm.); L&B - Laing and Blackwell (/949); M&I - Moore and Irwin (/978); W - Wardle (/963); C - Cockayne (1919.* 1928 *and cited by Dumbleton* 1967),

| | | | |
|---|---|---|---|
| *Senecio* | (1/40) | *Olearia* (4/32) | |
| *hectori* | (KP, L&B) | *virgata* & allies | (C) |
| *Fuchsia* | (3/4) | *colensoi* | ( L & B ) |
| *excorticata* | (M&I) | *fragrantissima* | (L&B) |
| *perscandens* | (KP) | *hectori* | (KP) |
| *procumbem* | (KP) | *odorata* | (KP) |
| *colensui* | (KP) | *Carmichae/ia* | (4/38) |
| *Aristotelia* | (1/2) | *odorata* | (KP) |
| *serrata* | (L&B) | *angustata* | ( K P ) |
| *Muehlenbeckia* | (2/5) | *grandi/lora* | ( K P ) |
| *astoni* | (M&I) | *glabrata* | (KP) |
| *australis* | (IA) | *Hoheria* | ( 2 / 5 ) |
| *Discaria* | (1/1) | *lyallii* | ( C . L & B ) |
| *toumatou* | (W,C) | *glabrata* | (W,C) |
| *Plagianthus* | (1/2) | *Sophora* | |
| *betulinus* | M&I. L&B) | "the species of kowhai" | (C) |

## Deciduous and Poisonous Plants

### Deciduous woody plants

Altogether, 23 species or species complexes have been described as deciduous in the literature (Table 1). Dumbleton (1967), quoting Cockayne (1919, 1928), stated there are 19 typically winter-deciduous species in 10 genera. Neither author systematically listed them beyond generic level.

Five of these species or species complexes must be considered doubtful or inadmissable. *Senecio hectorii*

is not deciduous (I.A.E. Atkinson, pers. comm.). *Olearia colensoi,* listed by Laing and Blackwell (1949), and O. *virgata,* usually show some thinning of the crown in winter, but are not fully deciduous. *Fuchsia colensoi* is a hybrid *(F. excorticata* x *perscandens). F. procumbens* is apparently not deciduous in the field (I.A.E. Atkinson, pers. comm.). Neither *Sophora tetraptera* or S. *microphylla* are typically winter-deciduous. They lose their leaves just before the onset of spring flowering and bud-break. Among the 38 species of *Carmichaelia,* Dumbleton considered four to be deciduous. K. Platt (pers. comm.) suggests these can only be *odorata, angustata, grandiflora* and *glabrata,* which carry leaves during the early part of the growing season. Most *Carmichaelia spp.* are entirely leafless, or tend to become so with increasing maturity. *Discaria* is summer-deciduous (Wardle, 1963), losing its leaves at the onset of summer drought and remaining leafless until bud-break in the following spring (Cockayne *In* Laing and Blackwell, 1949). *Hoheria lyallii* and *H. glabrata* are probably one species (Moore and Irwin, 1978).

Taking these qualifications into account, my synopsis is: there are 17 deciduous species in the New Zealand flora; 10 are winter-deciduous; five are summer-deciduous; two are briefly spring-deciduous. They are small totals, as has been recognised by many botanists.

Dumbleton classified his total of 19 deciduous species as: 5 trees with large and membranous leaves; 10 shrubs, several of which are divaricating; 4 lianoid. Those he classified as trees are (my interpretation): *Fuchsia excorticata, Aristotelia serrata* and *Hoheria.* However, at their largest, these species seldom exceed 5-6 m, and only *Plagianthus* typically has a single, erect trunk. I consider that, overall, the deciduous species are better categorised as much-branched shrubs or woody lianes *(Meuhlenbeckia),* of less than 3-4 m typical height. They are characteristic inhabitants of forest margins, forest canopy gaps, open places and bare ground. One-third of them typically form dense, short-lived stands early in successions. All except *Hoheria* are coastal *(Plagianthus divaricatus),* or lowland to lower montane species. They occupy relatively fertile sites. All appear to be preferred foods of the introduced mammals.

### Poisonous plants

Connor (1977) listed 32 indigenous plant species in 19 genera which are at least circumstantially known to be poisonous to livestock and people, and from most of which toxic compounds have been isolated (Table 2).

Table 2: *The poisonous plants of New Zealand, from Connor (1977). Heights given for dicots are from Allan (1961), Flora of New Zealand Vol. 1.*

| | | | |
|---|---|---|---|
| *Brachyglottis repanda* | 6 | *Myoporum laetum* | 10 |
| *Coriaria angustissima* | 0.5 | *Ranunculus hirtus* | 0.6 |
| *arborea* | 6 | *lappaceus* | 0.15 |
| *kingiana* | 0.4 | *rivularis* | 0.2 |
| *plumosa* | 0.4 | *Alectryon excelsus* | 10 |
| *pteridoides* | 0.6 | *Mimulus repens* | creeping |
| *sarmentosa* | 1 | *Solanum aviculare* | 3 |
| *pottsiana* | 0.4 | *amphitrichus* | 1 |
| *lurida?* | – | *laciniatum* | 3 |
| *Corynocarpus laevigatus* | 15 | *Pimelea prostrata* | prostrate |
| *Hypericum japonicum* | procumbent | *Centella uniflora* | creeping |
| *gramineum* | 0.25 | *Urtica ferox* | 2 |
| *Sophora spp* | 2-12 | *aspera* | 0.4 |
| *Astelia nervosa* | <2 | *Pseudowintera axillaris* | 8 |
| *Hedycarya arborea* | 12 | *Cheilanthes sieberi* | creeping |
| *Pteridium esculentum* | <2 | | |

Some species are seasonally palatable and relatively harmless to livestock (notably *Coriaria spp* and *Urtica*). Others, such as *Solanum,* are rarely eaten. In at least *Sophora* and *Corynocarpus,* the foliage and twigs are palatable and apparently harmless to mammals, whereas the flowers and fruits are mildly toxic.

Seven of Connor's 32 poisonous species exceed 10 m extreme height. Of these, *Brachyglottis* is usually less than 2-3 m tall, and usually occurs in dense, short-lived successional stands about forest margins, in canopy gaps, on old slip sites, and along stream banks. *Corynocarpus* usually regenerates in open forest understoreys. *Sophora* are tall shrubs to small trees, which typically occur on open ground, steep banks or cliffs. Only *Laurelia,* with toxic bark (and perhaps foliage, I.A.E. Atkinson, pers. comm.), is a co-dominant high forest tree, at more northern latitudes and low altitudes.

## Discussion

*Selection of the deciduous and poisonous habits*
Typically, as summarised in the preceding paragraphs, the deciduous and poisonous plants of New Zealand are low-statured. They are characteristic of open places, forest canopy gaps and margins, stream banks, and bare ground, particularly at lower altitudes. Some of the more conspicuous species (e.g. *Coriaria, Brachyglottis, Fuchsia excorticata, Aristotelia, Hoheria)* form the dominant early stands in successions which re-occupy bared ground (Batcheler, 1983).

Dumbleton (1967) suggested that deciduousness among New Zealand plants, being more common in the South Island and at higher altitudes (I consider the latter claim to be untenable), is primarily related to winter cold. However, Axelrod (1966) concluded that since evergreen and deciduous species all have a leaf abscission apparatus, winter deciduousness is clearly not an adaptation to cold as such. The habit is merely synchronized abscission of dead leaves long before the next growing season. Of its origins, he suggested that angiosperms evolved in tropical latitudes during the Cretaceous, and that the deciduous habit evolved in response to drought as they colonised arid sub-tropical regions. Then, as temperatures declined towards the Pleistocene period, drought-adapted deciduous plants had a competitive advantage over evergreens, particularly in the more continental climates of the Northern Hemisphere. Rattenbury (1962) and Raven *et al.,* (1982) similarly suggest that winter-deciduousness may be a response to physiological drought, not low temperatures, and be due to the failure of roots to absorb water from cold soils.

In considering the possible selective advantage of casting leaves to withstand drought (or cold), I am surprised to find no papers in the literature which correlate the more-or-less simulataneous evolution of the angiosperm plants and the homeothermic animals, from late Jurassic (Walton, 1940; Axelrod, 1966; Young, 1950), and of modern forms and families from the Eocene period. The point is of basic importance because, unlike the reptiles, most homeotherms remain active in winter, when food is very limited. In effect, with the evolution of homeotherms, there would be selective advantage to plants which, under the influence of triggers such as reducing day-length (Axelrod, 1966) or frost, cast their

leaves when photosynthetic gains are most likely to be exceeded by exploitation by herbivores. The amount of food and shelter available to herbivores is greatly reduced. This must limit the number of herbivores able to survive severe weather and, ultimately, reduce the amount of browse damage to dormant buds. In short, the ecology of the deciduous habit is easily explained by supposing that it is primarily an adaptation to browsing.

The synthesis of poisonous or distasteful compounds is an alternative strategy which is particularly relevant to defense against browsing during the growing season. Connor's list includes only the plants with toxins which are specially hazardous to mammals. Many New Zealand plants which are often browsed contain toxins (Cain *et al.,* 1961; Cambie *et al.,* 1961a; 1961b; Connor, 1977; Fitzgerald, 1978). Fitzgerald's (1978) observations in the field and from feeding trials with captive possums *(Trichosurus vulpecula)* show that of six food plants, those with lower concentrations of toxins *(Metrosideros robusta, M. fulgens, Weinmannia racemosa)* were preferred to those with higher concentrations *(Ripogonum scandens, Melicytus ramiflorus, Hedycarya arborea).* She suggested that the toxicity of the latter group "may make them very uneconomical foods".

Connor (1977) noted that all the indigenous angiosperms which are toxic to mammals have close relatives elsewhere. Greenwood and Atkinson (1977) and McGlone and Webb (1981) suggested that their poisonous habits may have evolved in response to moa browsing or phytophagous insects. If phytophagous insects are invoked as the cause, it makes no sense that the poisonous plants should be so conspicuous only within the range of terrestrial herbivores. Second, supposing a plant developed its toxic habit elsewhere, maintaining the investment in producing toxic compounds makes no sense without supposing that browsing by terrestrial herbivores was a significant selection force.

It is of interest to realise that the New Zealand ecological pattern of poisonous plants, is closely paralleled by North American rangeland vegetation and living mammals. Cronin *et al.,* (1978) recalled Stahl's (1888) hypothesis that "the ability to form secondary substances which are bitter, toxic or both . . . evolved. . . for defence against herbivores". Merrill and Schuster (1978) showed that, with few exceptions poisonous plants are not climax species. They are "invaders that increase with heavy grazing use". Cronin *et al.,* (1978) and Laycock (1978) also observed that poisonous plants tend to be colonizers.

Laycock (1978) suggested that "the effectiveness of (toxins) as defence mechanisms is clear (but) 'proof' that they evolved for that purpose is impossible". But, "since toxic compounds are structurally complex, the energy cost of producing and storing them is too high unless they have some function to increase fitness".

*Moa niches and habitat*

After their Cretaceous isolation from other ratites, Holocene moas had evolved by the upper Miocene (Simmons, 1968; but see Fleming, 1979 for the possibility that the deposit is Quaternary). Cracraft (1976) accepted I3 Holocene species. This is about equivalent to the fauna of large mammals which survived the Pleistocene in Europe. Their sizes ranged from the massive *Dinornis maxim us,* through *Pachyornis, Euryapteryx,* and *Emeus,* to the smaller *Anomalopteryx* and *Megalapteryx*. Their weights ranged from that of a large deer (about 200-300 kg or more) to a goat (about 10-20 kg) (see Atkinson and Caughley papers, this volume).

Given this diversity of species and the long period of species radiation, it can only be supposed that all available niches would have been occupied, with larger species predominant towards higher latitudes (Bergman's Rule), easier terrain and more open habitats (cf. *Rangifer, Cervus, Alces, Bison, Bos* among European ungulates), and smaller, more nimble species in forest or steeper country (cf. *Dama, Capreolus, Rupicapra).* Biomass would have been ultimately limited by the amount of food available.

It seems to be agreed that open grassland and scrubland formed a high proportion of the vegetation cover during the Pliocene and Pleistocene periods. However, the prevailing opinion is that, during the Holocene, lowland New Zealand has been mostly forested to at least 1000 A.D. (Molloy *et al.,* 1963; Burrows *et al.,* 1981; McGlone and Webb, 1981; McGlone, 1985).

Pollen profiles, buried tree trunks, charcoals and other remains show that forest was widespread (Simmons, 1968; Molloy, 1969; Burrows *et al.,* 1981; McGlone, 1985). Thus Molloy (1969) argues that any attempt to reconstruct large areas of primary grassland below timberline is faced with almost overwhelming evidence in favour of forest.

But it doesn't follow that the land was continuously under a high forest canopy. In the North Island, eruptions during at least the last 2 million years undoubtedly devastated the forests to much the same extent as near Mt. Tarawera and Lake Taupo during the last 2000 years. Storms also periodically

devastate the forest (Zotov *et al.,* 1938; Grant, 1963). Shaw (1983) observed that cyclone Bernie in 1982, which damaged 30% of the indigenous and exotic forests of the North Island, was at least the fifth storm which has flattened large areas of forest within the last 50 years. In the south, I interpret the gales of 1946, 1968 and 1975 (which flattened about 80070 of Canterbury's pine plantations) and lightning-induced fires (I can vouch for three in North Otago and Canterbury during my lifetime), as contemporary examples of ancient events which left wood charcoals and forest dimples (Molloy *et al.,* 1963) and large areas of grass- and scrubland in their wake. Some shallow, drier soils, may never have supported more than kanuka *(Kunzia)* scrub forest (Cox and Mead, 1963; Molloy and Cox, 1972), and were probably burned repeatedly. The imprint of these periodic catastrophes is undoubtedly a mosaic of grass, scrub and forest in various stages of succession. If so, open habitats have always been a prominent feature of the New Zealand landscape.

### The diet

Burrows *et al.,* (1981) found fragments of at least 23 woody species in *Dinornis* gizzards recovered from Pyramid Valley, North Canterbury, and Scaife's Lagoon, Central Otago. They concluded: "that the feeding effects of moas may not have been very different from those of browsing mammals"; "the study confirms beyond doubt that *Dinoris* inhabited forest or forest margins. . . and there is no evidence that they habitually lived in grasslands". This, Burrows claimed in 1980, "corrects the impression fostered by Duff (1941) and Falla (1941) that they were grazing animals, inhabiting open grasslands".

I submit that these are very dubious conclusions.

Reconstruction of a "normal" habitat or diet from swamp deposits is clearly prone to the objections that it is based on evidence from an atypically effective preservative medium for animal and plant remains, and deals only with those birds which happened to die while visiting a swamp. The miring of one moa per 2-4 years at Pyramid Valley (from about 2000 skeletons (Duff, 1952, 1955) accumulated during 3-4000 years (Duff, 196)) is scarcely proof that the swamp was preferred habitat. The preponderance of small seeds, mature leaves and woody stem tissue in the gizzards (Burrows *et al.,* 1981), if seen in the gut of a bogged deer or cow, would more likely be taken as evidence that the animal had ventured onto dangerous ground because of hunger, not preference.

The absence of chick skeletons at Pyramid Valley, and the discovery of only two eggs among 140 birds, all suggest that Pyramid Valley was part of the late summer - autumn range (Duff, 1952). Some had foundered in deep water (Eyles, 1955). More often, they became mired upright in the mud, with their heads in the air, and "would die with their long necks lying on the surface" (Duff, 1952). If so, we must suppose that some of them would have lived for several days after being mired. They would have struggled desperately (Duff, 1952; p.39) and eaten every plant scrap within reach until they died of exhaustion or drowning - as do mired mammals now. The *post mortem* remains would include the uncomminuted woody material recorded by Burrows *et al*.

Lowry (1980) also seems to have found the woody plant diet hypothesis to be indigestible. He has suggested that, assuming the gut of moas was comparable with that of living ratites, they would have chosen foods which gave a greater yield of nutrients than is available from mature leaves and woody twigs. Davies (1976) described these as fruits, flowers, seeds, and the succulent green shoots and foliage of shrubs, creepers, forbs and grasses - representing "concentrated sources of nutrients when contrasted with the mature or dry grass and browse taken by many herbivores".

The final point regarding Burrows *et al. 's* hypothesis is surely that, if moas were specialised woody plant herbivores, what ate the more succulent plants which the introduced mammals found more attractive?

### Biomass of temperate herbivores

Caughley (this volume) has reviewed information which indicates that the biomass of mammal herbivores ranges from about 400-20000 kg/km$^2$. Dasmann (1964) gives 3,500 kg/km' biomass as the average for temperate mammal herbivores, with densities at and about forest/open land ecotones at least an order of magnitude greater than in dense forests.

Studies of the distribution of goats, deer and livestock have consistently shown the maximum use of grass and shrublands near forest margins and clearings (Riney, 1956; Riney and Caughley, 1959; Batcheler and Logan, 1963; Challies, 1977). Dasmann's average biomass figure is close to the 2,600 kg/km$^2$ average stocking rate of sheep and cattle in South Island high country (Kerr *et al.,* 1979). It is equivalent to about 0.5 red deer/ha – less than the numbers and biomass of

red deer *(Cervus elaphus)* taken out of some South Westland valleys by helicopters in about two years during the mid-1960s.

*The epiphytic habit*

Rattenbury (1962) and McGlone and Webb (1981), following Diels (1897) and Cockayne (1928), suggest that the gradient from large-leaved, open-growing species in warm, mesic habitats, to microphyllous and often-divaricating plants in colder, windier, more xeric habitats, is consistently explained in terms of adaptation to a colder and windier 'steppe' climate during the Pleistocene. That explanation is completely at odds with the fact that the common woody epiphytes - living in exceptionally xeric microsites - are highly palatable large-leaved "mesic" plants such as *Griselinia, Pseudopanax. Schefflera* and *Weinmannia*. Divaricating, deciduous, poisonous and spiny plants do not occur in such situations. Conversely, the epiphytic pattern of the 'mesophytes' is consistent with supposing that their epiphytic and bluff-dwelling habits (Greenwood and Atkinson, 1977) reflect adaptation to intense browsing by terrestrial herbivores.

*The regeneration gap*

Greenwood and Atkinson (1977), Wardle (1985) and Batcheler (1986) suggest that the regeneration gap of podocarps from about the 12th-14th centuries (Wardle, 1963) can also be explained without reference to supposed climate change (Holloway, 1954; Robbins, 1962), if it is assumed that their regeneration was swamped by palatable broad leaved plants as moas were wiped out by early Polynesians. The climate change hypothesis becomes superfluous.

*A synthesis for low altitudes*

The evidence leads to the following conclusions.

1.    In terms of species radiation, the moa fauna in ancient New Zealand was equivalent to the ruminant fauna which survived the Pleistocene in Europe.

2.    Low altitude grasslands and shrublands would have been the primary habitat of the larger moas, and forests and uplands would have been the population foci of smaller species.

3.    There were extensive areas of scrub/grassland communities throughout the Holocene period, even in regions of primary forest. These, plus climax grasslands in drier and montane areas, provided extensive suitable habitat for the moas.

4.    The biomass of moas would have averaged about 3500 kg/km$^2$ in lowland habitats except dense

forest, and populations would have been limited by food shortage. If the average weight of moas was 50-100 kg, and favourable habitat occurred over, say 50070 of the land surface, the population can conservatively be estimated at 6-12 million birds.

5.    Their grazing and browsing pressure at lower altitudes, being limited by availability of food, would have been as intensive as that experienced since the introduction of mammals. Plant successions would have been held in check for long periods. Browse-tolerant plants would have predominated, in the same pattern as has occurred since the introduction of mammals. Palatable species such as the Araliads, large-leaved Coprosmas and succulent ferns would have largely been confined to refuges such as bluffs, stream banks and epiphytic situations.

6.    The low stature of deciduous and toxic plants in New Zealand indicates that these attributes are adaptations to browsing and grazing by terrestrial herbivores. These habits can therefore be regarded as alternative defenses against moa browsing to the divaricating habit, spinescence, mimicry, heteroblasty, tough leaves, coppicing and epicormic shoots.

7.    It is likely that moas preferred to feed on the more nutritious plants, and would turn to less 'profitable' or less nutritious plants, or those growing in more dangerous places, in times of food shortage.

*Moas in the mountains*

Assessment of the degree of adaptation of moas to steep and alpine country has wide implications for the management of introduced mammals (e.g. see Greenwood and Atkinson, 1977; Caughley, 1983).

The abundance of bones in the McKenzie Basin and gizzard stones as high as 2100 m altitude, *Megalapteryx didinus* remains at high altitudes in Central Otago (Buick, 1931), and Takahe Valley, Fiordland (Duff, 1952), show that smaller moas ranged to high altitudes. Feather cladding from the base of the bill to the base of the toes of *Megalapteryx* (Oliver, 1949) suggests that it was adapted to cool conditions. Moa bones have been recovered from caves above timber-line (Bell and Bell, 1971).

However, opinions are sharply divided as to whether moas occupied the uplands to the same degree as have the hardier introduced mammals.

Caughley's (1983) narrative evokes the idea that moas would have been seen dotted around the alpine grasslands like grazing red deer. Bell and Bell (1971) suggested that moas "were far more agile and active in their penetration of mountain areas than has so far

been proposed". Greenwood and Atkinson (1977) suggest that, "excepting limestone areas, . . . moas were much less important than they were in the lowlands" .

Having worked on forest surveys in the mountains of both islands, with horses on rabbiting and sheep mustering blocks, and watched deer and chamois for many hundreds of hours, I believe that most of the steep main range country would have been extremely dangerous for moas. A heavy-bodied, three-toed, bipedal moa would have been at constant risk of serious falls and injuries on steep ground. Although it is an anthropomorphic comment, one cannot ignore the fact that moas didn't have studded boots, horseshoes, or a cutting-edge hoof. They would have had immense difficulty negotiating steep slopes, the sub-alpine scrub belt, boulder fields and tall tussock alpine grasslands. The ratites of other regions seem to avoid rough and steep ground (Davies, 1976).

Second, if the breeding biology of moas can be inferred from that of kiwis and other ratites, it would have involved an incubation period of at least 50-80 days (Falla *et al.,* 1979), and one or both parents committed to continuous sitting and turning the eggs (like emu; Davies, 1976). Their opportunities for emulating the intense feeding of the mammals from December through March, with a fawn at foot, would be seriously hampered. With a high likelihood ~f snow at any time of year (Morris and O'Loughlin, 1965; Coulter, 1967), the chances of successfully raising chicks would be low.

Accordingly, I conclude that moas were not habitual occupants of the alpine zone. This would be consistent with the abundance of many fleshy, palatable plants (e.g. *Gingidium, Ranunculus lyallii* and *R. insignis, Coprosma serrulata, Traversia baccharoides, Pseudopanax colensoi, Pittosporum patulum),* and with the scarcity of deciduous, poisonous and divaricating species.

## Conclusions

The principal conclusions are simple. The diversity of moas was equivalent to that of large herbivores in other temperate ecosystems. The abundance and biomass of moas would have been regulated by food. Browsing and grazing pressure would have been reflected in browse-resistant adaptations of the plants, successions, and structure of the vegetation. Although the moa browse hypothesis is unlikely to ever be "proved", it is consistent with the evidence from New Zealand and elsewhere and simply explains many vegetation attributes which otherwise require a

plethora of special case hypotheses and ecological principles which have no counterpart elsewhere in the world. The principles of Occam's razor and parsimony of hypotheses therefore suggest that the moa browse hypothesis is essential to interpreting the form of present-day New Zealand vegetation, and its responses to introduced mammals.

## Acknowledgements

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