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RELATIONSHIPS BETWEEN MOAS AND PLANTS

Summary: Moas were common and widespread in pre-Polynesian New Zealand. They were most concentrated in the lowlands but ranged into the mountains with *Megalapteryx didinus* reaching at least 1800 m. This contribution examines niche separation between species of moa, the evolutionary effects of moas on plant species, and the effects of mammals and moas on New Zealand vegetation. The aim is to establish the extent to which mammals are ecologically equivalent to moas.

Within forest there was a high degree of coexistence between different species of moa. Their niches were separated by differences in feeding height, in bill shape, in gizzard development, and by other differences correlated with size. Femur circumference, as an index of weight, shows that moas were mostly in the range 20 to 200 kg.

It is suggested that herbivory by moas is responsible for the evolution of at least 11 kinds of growth characteristics seen in indigenous plants. Four of these, namely spiny tussocks, mimicry, reduced visual apparency, and divarication are discussed and suggestions are made on how hypotheses for such adaptations can be tested. These plant responses, together with adaptive responses among moas, are considered as an example of coevolution. Possible adaptive responses in moas are increase in the cutting power of the bill, increasing development of head and neck muscles, increasing development of the gizzard, and increase in height. Many other New Zealand plants have growth features including chemical characteristics which, although not originating as adaptations to moa browsing, nevertheless make them unpalatable to, if not ignored by, introduced browsing mammals.

There are both qualitative and quantitative differences in the feeding behaviours of mammals and moas. The ecological (and evolutionary) consequence of these is that selection pressures exerted on New Zealand plants by browsing mammals are not the same as those formerly exerted by moas. The preliminary conclusion reached is that mammals are equivalent to moas only in a limited site-specific sense, in particular, on lowland high-fertility sites such as river terraces. Elsewhere the effects of introduced mammals are either relatively minor or, in the montane and subalpine zones, are a major new effect on the vegetation, which is now much depleted from its pre-Polynesian state.

Keywords: *Aciphylla,* apparency, coevolution, divaricating plants, ecological equivalence, herbivory, mimicry, moa bills, moa gizzard stones, moa heights, moa niches, moa weights.

Introduction

Discussions of the effects of introduced browsing mammals on New Zealand plants and vegetation have sometimes included the suggestion that they are not fundamentally different from those formerly exerted by moas (e.g. Caughley 1983). This suggestion is treated here as a null hypothesis and tested by some comparisons between moas and mammals. The comparison is based on a preliminary consideration of three connected aspects of moa-plant relationships: niche separation between the various moa species; evolutionary effects of moas on plant species; and the ecological effects of moas on vegetation. From these comparisons it is possible to draw preliminary conclusions about the extent to which mammals are ecologically equivalent to moas.

Niche Separation Between Species Of Moa

Taxonomy of moas

Cracraft (l976a) recognised 13 species of moas, since reduced to 12 by Millener (1982). Size varied greatly, even within accepted species. South Island forms were usually larger and more robust than their closest relatives in the North Island, and there may have been a north-south clinal variation in conformity with Bergman's rule (Caughley 1977, Dr P. Millener, pers. comm.). In addition, there were size differences between sexes in some species (with the female apparently larger in at least one case) and at least one species became smaller between the last glacial and Holocene periods (Worthy 1987).

To elucidate the minimum number of niche differences that must be sought between moa species, we have grouped 6 of Cracraft's species into 3 North Island/South Island pairs, excluding *Megalapteryx benhami* known at present from only a few bones. The resulting arrangment (Table 1) allows niche comparisons between 6 North Island species and between 8 South Island species. More systematic work is needed before species limits in the moas are properly understood (Caughley 1977, Worthy 1987.)

Table 1: *Arrangement of moa species for comparisons of ecological niches.*

Subfamily and Species	Distribution
Anomalopteryginae	
1. *Megalapteryx didinus*	South Island only (incl. D'Urville I.)
2. *Anomalopteryx didiformis*	Both islands
3. *Emeus crassus*	South Island only
4. *Euryapteryx curtus/geranoides.*	Both islands; Stewart I.
5. *Pachyornis mappini/elephantopus.*	Both islands; Stewart I.
Dinornithinae	
6. *Dinornis struthoides/ torosus.*	Both islands
7. *D. novaezealandiae*	Both islands (incl. D'Urville I.)
8. *D. giganteus*	Both islands

*North Island member of species pair is listed first.

Weights of moas

Very few estimates of moa weights have been published and, with the exception of Caughley's data (this volume), they relate to six species only: *Megalapteryx didinus, Anomalopteryx didiformis, Euryapteryx geranoides, Pachyornis elephantopus, Dinornis torosus* and *D. giganteus* (Amadon 1947, Alexander 1983, Smith in Anderson 1984).

The present weight estimates, largely of South Island birds, are based on femur circumferences of 119 individuals in 8 species. These were obtained from sagittal diameters, measured to within 0.1 mm, midway between proximal and distal ends of the bone using vernier calipers. Because right and left femurs can be of different size, particularly in *Dinornis giganteus,* both bones were measured whenever possible (40 of the total of 119 individuals measured, including all ten *D. giganteus)*. Details are given in Appendix 1.

The allometric equation: $W = 1.08 \, C_f^{2.28\pm0.1}$ was used to calculate body weight, where femur circumference (mm) and the exponent gives the mean and 950/0 confidence interval (Anderson *et al.,* 1985). The equation was derived from the relationship between femur circumference and body weight in 72 species of flying birds. Both the exponent and the proportionality constant are similar to those found for running birds (Maloiy *et al.,* 1979).

The results (Table 2, Fig. 1) suggest an overall range of body weight in these 8 spp of 20 to 200 kg. It should be noted that although most if not all of these bones are considered to be from the Holocene, they are uncontrolled for time within this period (e.g. bones from different times in different swamps) and, with the exception of *M. didinus,* include individuals of a species from more than one locality. Thus although these estimates indicate the approximate relative weights of 8 South Island species, they do not estimate mean body weights of individual species populations.

Table 2: *Estimated body weights (kg) of species of moas using femoral circumference measurements and methods of Anderson et al., (1985). Confidence intervals are shown in Fig 1. and details of samples are given in Appendix 1.*

Species	n	mean	min.	max.
Megalapteryx didinus	10	23.7	16.9	34.3
Anomalopteryx Didiformis	16	41.3	31.7	58.7
Emeus crassus	24	74.9	45.6	120.1
Euryapteryx geranoides	19	95.7	48.7	139.9
Pachyornis Elephantopus	20	146.0	96.7	247.4
Dinornis torosus	12	96.2	82.0	114.8
D. novaezealandiae	8	143.7	100.0	199.7
D. giganteus	10	177.9	133.6	272.7

Distribution

Evidence of the former distribution of moas comes from moa-hunter middens, alkaline mire deposits, caves and sink-holes. Many moa bones found at midden sites are leg bones evidently carried there after the remainder of the bird had been discarded at the kill site (Anderson 1983a). The more complete the skeleton the greater the chance that the bird was killed nearby. It appears that in southern New Zealand most moas were killed at distances less than 40 km from the oven sites where they were cooked (Anderson 1984). These oven sites are not all of the same age but many moa-hunter sites have yet to be investigated and many more have been lost through erosion. For example, midden sites may survive on a stable or prograding shoreline but will disappear from retrograding
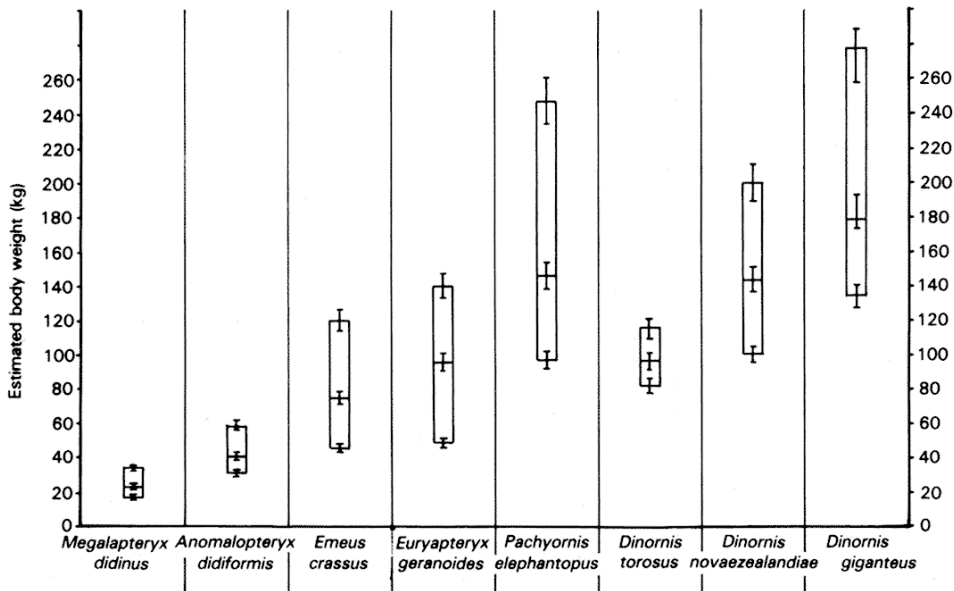
Figure 1: *Mean, minimum and maximum body weights with 950/0 confidence intervals estimated for* 8 *species of moa from femoral circumferences and method of Anderson et al., (/985). Further details of samples given in Table* 2 *and Appendix* 1.

shorelines or from flood-prone riverbeds. Other sites have been destroyed during recent development or digging for artifacts (Trotter and McCulloch 1984). In spite of these losses, coastal oven sites are in places very close together so that, here at least, moas were probably killed at distances much less than 40 km away. Thus regional distribution of moa species, although not the specific habitats in which they lived, can be inferred from bones identified in midden remains.

It is usual to assume that bones in mires, caves or sink-holes represent birds that were living in the immediate area. However, even if humans played no part in the deaths or transport of remains, this kind of evidence is still subject to bias. Alkaline mires, where moa bones can be preserved, are much more frequent in the lowlands, whereas the mires of montane districts are usually acid bogs that do not preserve bones. Caves and sink-holes are much more frequent in limestone rocks than elsewhere. With these various limitations in mind, some statements about the distribution of the different moa species are possible (see also Table I).

Megalapteryx didinus was apparently confined to the South Island. Although bones have been recovered from a few coastal sites, including D'Urville Island (Scarlett 1974), most are from inland South Island including Central Otago and Northwest Nelson. This moa reached at least 1800 m a.s.l. because its bones were found on Mt Owen in 1987 by T.H. Worthy (pers. comm.). It appears that this species could make greater use of shrubland and more open habitats than other moa species.

Anomalopteryx didiformis occurred throughout both islands, including the West Coast. It ranged from sea level to at least 750 m in the North Island (Yaldwyn 1956), and to at least 1225 m (Mt Arthur) in the South Island (Oliver 1949). However its bones are rare in mires of the eastern South Island.

Emeus crassus was confined to the South Island, predominantly the eastern part, and mainly in the lowlands. The highest altitude record known to us is at 760 m near Lake Tekapo. This distribution could imply that *E. crassus* used non-forest habitats as fires destroying forest are likely to have been more frequent in the drier eastern South Island than elsewhere long before the Polynesians arrived. However, the contents of the only gizzard examined contained mainly the fruit, seeds and leaves of forest plants (Mason in Gregg 1972).

Euryapteryx curtus and *E. geranoides* were widespread though mainly coastal and lowland birds, the former restricted to the North Island. Bones of *Euryapteryx* have been identified from caves in central North Island at 960 m a.s.l. (R.A.L. Batley, pers. comm.) and from as high as 1100 m in the South Island (Oliver 1949). *E. geranoides* predominates in South Island archaeological sites containing moa bones (Scarlett 1974). Bones of *E. curtus* have been found in natural dune deposits on Great Barrier Island by T.H. Worthy (pers. comm.). There are sufficient remains to confirm that *E. geranoides* lived on Stewart Island.

Pachyornis mappini and *P. elephantopus* were very widespread in North and South Islands, respectively. *P. mappini* occurred from sea level to at least 750 m in the North Island (Yaldwyn 1956) and *P. elephantopus* from sea level to about 1100 m in the South Island (Oliver 1949).

Dinornis struthoides and *D. torosus* appear to have been widespread in North and South Islands respectively but there are far fewer records of them than for the widespread species already discussed. *D. struthoides* reached at least 900 m in the North Island (T.H. Worthy, pers. comm.) and at least 1100 m in the South Island (Oliver 1949).

Dinornis novaezealandiae occurred up to at least 900 m in the North Island (Oliver 1949) and at least 1300 m in the South Island (Bell and Bell 1971). It was widespread in both islands, extending to D'Urville Island (Scarlett 1974) and several localities along the west coast of the South Island.

Dinornis giganteus was apparently a lowland species and, although occurring in both islands, it seems to have been more common in southern South Island than elsewhere. The highest altitude where remains have been found in the North Island is 520 m, and for the South Island, 535 m (Oliver 1949).

Although there is no evidence that any of these species was restricted to tussock-grassland, there is still debate over their dependence on forest, and particularly their use of forest interiors as opposed to forest margins and shrubland. Moa bone deposits in eastern South Island are found mainly in areas that were forested until well into the early Polynesian era (Anderson 1983a). Analysis of the timing of deforestation (McGlone 1983) suggests that much of the burning came after the most intensive moa hunting (Anderson 1984). There is further evidence from mires for associating moas with forest and other forest birds (Simmons 1968). There is no physical reason why even the largest species *(D. giganteus)* could not have

moved through forest. With the head stretched forward, the resulting wedge-shape of head, neck and body would have been less prone to tangling with undergrowth than, say, a deer with antlers.

During interglacial periods and through most of the Holocene, New Zealand was apparently covered largely in forest. Consequently all moa species were probably adapted to feeding in forest and scrub even if a few were specialised to make greater use of more open habitats. The only living diurnal ratite that inhabits forest is the cassowary *(Casuarius casuarius)*. If moa species were usually territorial and diurnal, as are cassowaries (Chrome 1976), then the balance of use of forest, scrub, tussock-shrubland, etc., would have depended largely on the nutritional value of what was available in each at the time.

A second question concerns use of vegetation above treeline. The presence on Mt Owen of *Megalapteryx didinus* bones at 1800 m and of three species of moa in subalpine tussock grassland at 1305 m (Bell and Bell 1971, T.H. Worthy, pers. comm.) demonstrate that subalpine scrub was not an impenetrable barrier. The bones at 1305 m were in a cave, and associated with plant remmains that suggested the vegetation had been consistently subalpine to alpine during the period of deposition. The present vegetation at the site is a tussockland dominated by *Chionochloa* sp. ("*C. flavescens*" of South Island authors) on soils of high or very high base status (Taylor and Pohlen 1962, Bell 1973, A.P. Druce, pers. comm.).

The distribution of moa gizzard stones throughout New Zealand suggests that, whether moas were above or below the treeline, they were not restricted to vegetation on fertile soils. In 1986 A.P. Druce (pers. comm.) found a rounded quartz pebble of c.15 mm diam. c. 1380 m on Karamea granite in the Scarlett Range, North West Nelson, in tussock-shrubland 90 m above the treeline. It lay on top of a steep, narrow, ridge where there was no alluvium or evidence of other sediments overlying the granite so that it was most probably a gizzard-stone. On metavolcanic and metasedimentary rocks in southern Fiordland, Dr C.M. Ward (pers. comm.) has seen rounded quartz pebbles, 8-12 mm diam., at 1160 m on Mt Edgecumbe, Dusky South (300 m above treeline) and at the head of Long Sound, Preservation Inlet (c. 1000 m). Writing of these localities he states: "in the Dusky Sound area of southern Fiordland I have seen rounded quartz pebbles on glaciated inland ridge crests above the level of any former ice-marginal streams, and on bedrock hillocks on glacial valley

floors, where a Holocene (or very late Pleistocene) age is certain, a marine origin is impossible and a fluvial origin highly implausible, but a moa origin is reasonable" (Ward 1987). Bull and Cooper (1986) and other earth scientists have interpreted widespread but thinly scattered, rounded quartz pebbles at altitudes up to 1700 m on the ridges SE of the Alpine Fault in Westland as tectonically uplifted beach gravels on marine terraces. However, Ward (1988) demonstrates on geomorphic evidence that many if not all the surfaces on which the quartz pebbles are found cannot be marine terraces. The pebbles are very likely to be moa gizzard stones.

Small groups of rounded pebbles or even single pebbles sometimes occur in surficial peat or mineral soil horizons. If they are not washed in from sedimentary deposits at a higher level, they are likely to have originated from moas and thus indicate that moas used these areas. The widespread occurrence of moa gizzard stones in gumland scrub communities of Northland, noticed by pioneer farmers and gumdiggers, indicates that kauri forest (or possibly gumland scrub) was used by moas despite the generally low nutritional value of such vegetation. Stratigraphic analysis to determine the origin of moa gizzard stones at Kawerua, Northland, provides further evidence that moas used kauri forest (Hayward 1978).

Anderson (1983b) concluded that permanent watercourses near the base of the ranges were prime moa habitat in central Otago. Insofar as stream and river alluviums have enhanced nutrient status and plant productivity this is very likely (cf. Greenwood and Atkinson 1977). He further suggested that inland beech forests were generally avoided and that forests in the higher parts of the lower hill country were poor habitats. In view of the increasing amount of information indicating that moas ranged very widely, we must withhold judgement on these suggestions.

This widespread and varied information on moa distribution leads to the conclusion that moas of different species were at their highest density in the lowland zone. Some species also used the montane zone and, with the possible exceptions of *Emeus crassus* and *Dinornis giganteus,* visited the subalpine and alpine zones, presumably in summer when food was most abundant there.

Coexistence of moa species

In both natural and cultural sites, one can often find remains of more than one species of moa indicating overlapping distributions. Even taking a conservative approach to moa species (as here in which no more than 6 species in the North Island and 8 in the South are recognised) it is common to find 5 or more species at one site. Among cultural sites in the North Island, this is the case at Tairua (Davidson 1979), Waingongoro (Buist and Yaldwyn 1960) and Paremata (Scarlett 1974). In natural deposits of moa bone in sand dunes at Tom Bowling Bay there were at least 5 species including all three *Dinornis* species (Millener 1981). Two natural deposits in a cave near Waitomo both contained at least 5 species of moa together with forest birds and waterbirds (Worthy 1984). Worthy concluded from macro- and micro flora data that, during the period of deposition, a small wetland had drained into the cave which was surrounded by podocarp forest dominated by rimu *(Dacrydium cupressinum).*

Among cultural sites of the South Island coast, 5 or more species are represented at Redcliffs, Sumner (Scarlett 1974), Waitaki Mouth, Shag Mouth, Seacliff, Little Papanui, Pounawea, Papatowai (where 8 species are represented) and Tautuku (Anderson 1984). In the inland cultural sites of Hawksburn and Earnscleugh Cave, there were 7 and 5 moa species respectively (Anderson loco cit.). Five or more species of moa are commonly represented in bones dug from natural mire deposits of the eastern South Island (data from Canterbury Museum collection). At the Honeycomb Hill cave, Karamea, Millener (1984) recorded at least 7 species of moa. Though the bones were deposited over a long period, the close association of *Pachyornis, Euryapteryx, Anomalopteryx* and *Megalapteryx* bones clearly indicated coexistence of the species in these genera.

Within the limits imposed by North and South Island distributions, it appears that anyone species of moa can be associated with any other. Accepting that at some sites species have been misidentified, different species are frequently mixed together in the same layer; similar sized species occur together; larger species occur with smaller; and all three species of *Dinornis* atre somethimes found together. Even allowing that *Emeus crassus* and *Megalapteryx didinus* made more use of open habitats (see earlier), the conclusion seems inescapable that the different species of moa often lived together in the same forest habitat and maintained ecological separation by partitioning the available food in some way. This may have been achieved by feeding at different heights, having bills of different shapes and cutting power, or using the habitat at different times.

Table 3: *Relative heights (m) of Anomalopterygine moas.*

North Island/South Island species	Estimated heights and S.D. (sample n for tibiotarsus, tarsometatarsus)[1]	
	North Island	South Island
Megalapteryx didinus	—	1.34 ± 0.07 (15, 18)
Anomalopteryx didiformis	1.32 ± 0.09 (39, 43)[2]	1.32 ± 0.09 (39, 43)[2]
Emeus crassus	—	1.52 ± 0.14 (32, 32)
Euryapteryx curtus/geranoides	1.02 ± 0.12 (37,34)	1.52 ± 0.17 (17, 22)
Pachyornis mappini/elephantopus	1.11 ± 0.14 (24, 17)	1.83 ± 0.13 (27, 29)

[1]Data on bone lengths from Cracraft (l976a)
[2]Mean of sample from both islands.

Feeding heights of moas

The head heights of moas in a normal standing position have probably been overestimated in the past because in skeletal reconstructions the vertebral column has been tilted too far above horizontal or the femurs incorrectly tilted. On the other hand, there is no reason to think that moas drew in the neck to adopt the hunched stance of a kiwi, which is adapted for probing into the ground if not feeding on the surface. It is more likely that moas took much of their food from well above ground level with a body position resembling that of the forest-dwelling cassowary. However, even this analogy may not be close because cassowaries depend on fallen fruit (Stocker and Irvine 1983). The exact heights to which each species of moa could stretch during feeding will not be resolvable without careful anatomical study.

In this paper differences in head heights between moa species are assumed to be related to leg length. The estimator used was the combined length of tibiotarsus and tarsometatarsus using the mean lengths given by Cracraft (l976a). Cracraft (1980) estimated that *Pachyornis elephantopus* stood between 1.5 and 2.1 m high. We have chosen a mid-point of 1.8 m for this species to scale the heights of all remaining members of the subfamily Anomalopteryginae using the appropriate leg bone lengths (Table 3).

The remaining subfamily, *Dinornithinae,* contains only the genus *Dinornis*. It differs substantially from the *Anomalopteryginae* in having proportionally thinner leg bones than might be expected from body size (Cracraft 1976b). Following the conclusion that *D. giganteus* grew to between 2.7 and 3.0 m (Cracraft 1980), we applied a mid-point of 2.8 m to the South Island sample to scale all other *Dinornis* heights (Table 4). Again it must be emphasised that these figures indicate possible height *differences* between species in a standing position rather than the heights moas could stretch to reach food.

P. elephantopus may have had a height advantage over all other members of its subfamily (the Anomalopteryginae). Smaller members appear to have been about the same height, particularly the pairings of *Euryapteryx geranoides* and *Emeus crassus, Anomalopteryx* and *Megalapteryx* in the South Island, and *Euryapteryx* and *Pachyornis* in the North.

Table 4: *Relative heights (m) of Dinornithine moos.*

Species	Estimated heights and S.D. (sample n for tibiotarsus, tarsometatasus)[1]	Height differences between species (m)
North Island		
Dinornis struthoides	1.72 ±0 .01 (9, 15)	
		0.57
D. novaezealandiae	2.29 ± 0.16 (21, 13)	
		0.65
D. giganteus	2.92 ± 0.21 (10, 10)	
South Island		
D. torosus	1.91 ± 0.13 (14, 16)	
		0.45
D. novaezealandiae	2.36 ± 0.09 (15, 14)	
		0.49
D. giganteus	2.85 ± 0.18 (32, 29)	

[1]Data on bone lengths from Cracraft (1976a)

The *Dinornis* group shows a greater range of height than other moas but even the smallest *Dinornis* species in either the North or South Islands may have been taller than species of any other genera. The 4 size ratios that can be derived from comparing the heights of *D. giganteus* with *D. novaezealandiae* and *D. struthoides/torosus* with *D. novaezealandiae* in North and South Islands all fall between 1.21 and 1.33, thus com forming with Hutchinson's (1959) rule concerning size ratios of sympatric, congeneric species. However, of greater interest is the height difference between one species and its nearest neighbour in size: 45-65 cm (Table 4). This may suggest that access to vegetation 50 cm or more above that reachable by one's closest competitor is sufficient to allow coexistence of two closely related moa species.

Bill and gizzard differences in moas

Between species of moas, there are marked differences in either or both the size and shape of their bills (Figs. 2-4).
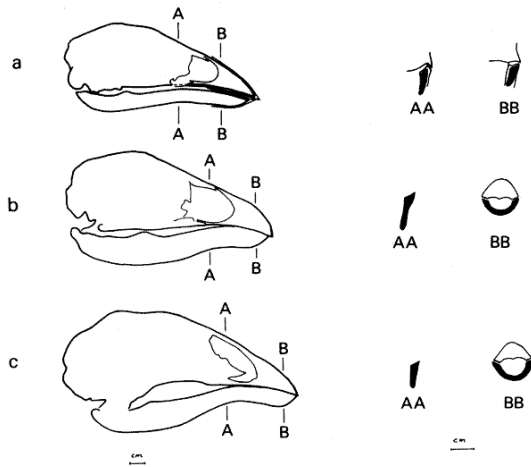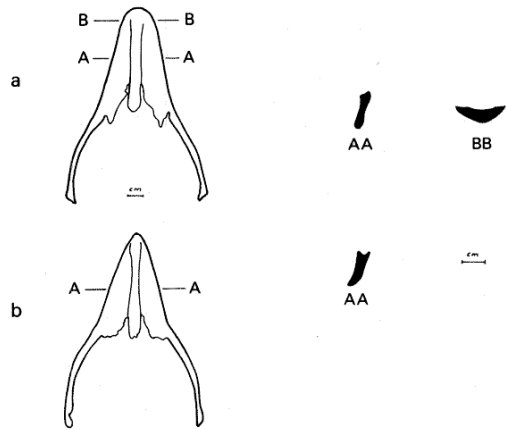

Figure 3: *Premaxillae of Euryapteryx* geranoides *(a) and* Pachynornis elephantopus *(b) together with cross-sections of mandibles drawn from specimens held at the Canterbury Museum, Christchurch.*

Figure 2: *Skulls of* Megalapteryx didinus *(a),* Anomalopteryx didiformis *(b) and* Emeus crassus *(c) (after Oliver 1949) with details of horny sheath of* M. didinus *drawn from the type specimen in the British Museum (Natural History) (BMNH A 16). Cross-sectional diagram of mandibles of* A. didiformis *and* E. crassus *drawn from specimens held at the Canterbury Museum, Christchurch.*
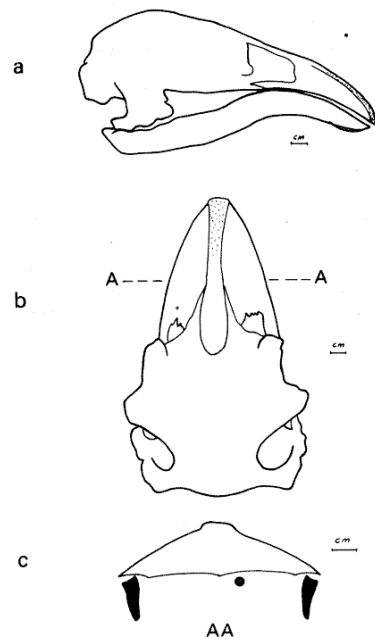

Figure 4: *Skull of* Dinornis giganteus *(after Oliver 1949) with cross section of mandible and premaxilla drawn from a specimen held at the National Museum, Wellington.*

Understanding the differences in the way different moas fed is hampered by the absence or poor preservation of the ramphotheca or horny sheath which covers premaxilla and mandible. This sheath does not always replicate the shape of the supporting bones (e.g. fig. 2a) so that, when it is missing, the degree to which the bill was adapted for cutting and/or pulling is difficult to determine. This constraint, together with film sequences showing the feeding of rheas in South America, led Greenwood and Atkinson (1977) to emphasize the clamping and pulling action of moa feeding. However, at least one species of moa (probably *D. giganteus)* could either cut or break off stems up to 6 mm in diameter (Burrows *et al*., 1981). Horny bill sheaths do not survive in the alkaline mire conditions that preserve bones, but they may survive in the acid peaty conditions that dissolve bones. They should be searched for wherever there are other signs of moas, such as gizzard stones in peat.

The best preserved bill sheath of a moa is that of the type specimen of *Megalapteryx didinus* in the British Museum (Natural History) which was examined by I.A.E.A. in 1982 (Fig. 2a and also Fig. 8 of Oliver 1949). Towards the gape, the mandibular sheath forms a sharp ridge that appears to fit into a groove formed by a sharp-edged downward projecting horny ridge on the premaxilla. Nearer the tip of the bill the horny cover is incomplete but the mandibular and premaxillary sheaths in this region appear to be shallowly grooved. An interpretation that can be drawn from this bill shape is that the distal portion was used for clamping and pulling and that a stem or leaf held near the tip could then have been slid towards the gape where mechanical advantage and interlocking cutting edges were best developed.

The distal portions (BB) of *Anomalopteryx didiformis* and *Emeus crassus* bills (Figs. 2b, c) both look suitable for clamping but, because the sheath is missing, we can only surmise that there was a powerful cutting capability near the gape in these species as well.

The incomplete cross-section of the *Euryapteryx* bill (Fig. 3a) shows an altogether heavier structure than in the smaller moas. Species of this genus are notable for the U-shape of the bill (rather than V-shape) when seen in plan view (Fig. 3a). This shape reaches extreme development in some forms of *Euryapteryx* recovered from southern New Zealand (Archey 1941) but we do not know its ecological significance.

The mandible of *Pachyornis* (Fig. 3b) is even more robust than that of *Euryapteryx* and, in contrast to all others examined, is strongly grooved near the gape. If this grooved bone supported a sharp-edged, double ridge in its horny sheath, the cutting power of the bill would have been greater than that of any other moa species.

Skulls of the three (or four) species of *Dinornis* appear to be similar in all respects except size. They are rather more dorsi ventrally flattened than those of other genera. A significant feature, not described before, is that in a fully articulated skull, the interior edges of the closed mandible meet the premaxilla in the centre of a shallow groove that runs the full length of the bill, although barely perceptible at the tip (Fig. 4c). Assuming the horny cover followed the cross-sectional shape of the supporting bones, a twig clamped by one side of the bill would be stressed at 3 points within a stem length of 10 mm. A stem clamped by this 3-point loading could have been held more firmly and may possibly have broken more easily than if only clamped at one point.

Substantial differences in either the cutting or gripping power of moa bills is suggested also by the minimum mandible depths measured close to AA in Figs. 2-4, (Table 5).

These differences in bill anatomy suggest that different moa species ate different kinds of plant food or fed in different ways. Cracraft (1980) mentions the

Table 5: *Depths of moa mandibles measured at minimum depths (AA of Figs. 2-4).*

Species	Sample n	Minimum depth (mm)	Range of depths (mm)
Megalapteryx didinus	10	7.9	7.1 - 9.3
Anomalopteryx didiformis	8	11.1	10.1 - 13.1
Emeus crassus	7	7.9	7.4 - 8.4
Euryapteryx geranoides	2	11.9	11.6 - 12.2
Pachyornis elephantopus	2	12.9	12.9 - 12.9
Dinornis torosus	7	14.5	13.4 - 16.5
D. novaezealandiae	16	15.9	14.3 - 16.8
D. giganteus	4	20.0	19.6 - 20.3

sizes of the mandible muscle scars in the decreasing sequence: *P. elephantopus, Euryapteryx geranoides* and *Emeus crassus*. He suggested that birds with the largest scars were capable of eating more "highly resistant foods" than those with the smallest.

Differences in gizzard size and musculature could be expected to correlate with feeding habits and bill shape. This is suggested by differences in total stone weights of gizzards. Gizzard stone weights from one individual each of *Euryapteryx geranoides* (253 g) and *Emeus crassus* (35.5 g) would not be anticipated from the difference in their body weights (Table 2), and suggest a large difference in gizzard development and diet between these species. If the *E. crassus* gizzard stone weight is representative, it is only one third the mean weight (of 97.5 g) for mineral matter found in a sample of 231 emu gizzards, a bird that eats relatively little foliage of woody plants (Davies 1978).

These gizzard-stone weights can be contrasted with that of 4.38 kg for a single gizzard of *Dinornis giganteus* (Gregg 1972). Other gizzard stone weights for individual moas found at Pyramid Valley exceeded 5 kg (Trotter and McCulloch 1984).

Careful anatomical study, identification of food remains in gizzards and faeces, and comparisons with living birds, are needed to understand the reasons for these gizzard differences and the way in which the different moa bills functioned.

Niche separation

The most fundamental difference between co-existing species of moa was probably size as indicated by body weight. With mammals, the main life history parameters, such as birth rate, growth rate, age at first reproduction, lifespan, etc., are scaled allometric ally to size (Western 1979). Table 2 shows differences in mean weight between Anomalopterygine moas of 19 to 46 kg; and differences between the three *Dinornis* species of 40 to 47 kg. Although *Euryapteryx geranoides* and *Dinornis torosus* appear to have comparable weights, as do *Pachyornis elephantopus* and *D. novaezealandiae,* both comparisons involve moas from different subfamilies so that other important differences can be expected. For example the moas within these two pairings were probably very different in height (Tables 3, 4).

Differences in feeding height between the *Dinornis* moas, and between them and the Anomalopterygine moas may not have been important until food became scarce because the tallest moa species could always feed throughout the height range available to its companion species. The ecological separation of browsing ungulates in Kenya involved no competition until food was in short supply (Leuthold 1978). In the wet season giraffes took 670/0 of their food within 2 m of the ground whereas in the dry season more than 60% came from above this level.

Moa populations, particularly those in the eastern part of the country, must at times have been severely stressed by food shortages resulting from summer droughts in the lowlands. This may sometimes have led to foraging at higher altitudes. Perhaps the reason why bones of so many moas are found in lowland swamps, is that during severe moisture stress. in the forest, when understorey plants were wilting, moas ventured further into swamps in order to reach foliage of higher moisture content.

Differences in body weight, height, bill size and shape, and gizzard development all appear likely, together with unknown behavioural differences, to have facilitated coexistence of moa species. This may have involved feeding on different plant species, different growth stages of the same species, or different parts of the same plant, not necessarily of the same nutritional quality.

This discussion emphasises interspecific partitioning of food resources within a particular habitat. However there were also substantial differences in size between sexes in some moa species (Cracraft 1976a, Worthy 1987) suggesting that food resources may have been partitioned at the infraspecific level as well.

Evolutionary Effects of Moas on Plant Species

Evolutionary consequences of herbivory for plants

Several distinct evolutionary consequences of herbivory associated with invertebrates, birds and mammals, have been identified among plants in other parts of the world (Table 6). They include the effects of various secondary compounds in making plants toxic or less palatable to invertebrate herbivores (Feeny 1976; Rhoades and Cates 1976); the production of silica bodies in leaves vulnerable to herbivores (McNaughton *et. al.,* 1985); spiny stems and prickly leaves (Cooper and Owen-Smith 1986); fruit dispersal mechanisms specialised to facilitate dispersal by birds or mammals (Snow 1981; Janzen and Martin 1982); and stinging hairs (Janzen 1975). It is difficult to conceive that any flora could evolve in the presence of herbivores without adaptations arising to reduce the

Table 6: *Some evolutionary consequences of herbivory.*

Evolutionary response	Herbivores involved	References
Chemical responses		
Production of secondary compounds, e.g., alkaloids, tannins, saponins, cyanogenic glycosides	invertebrates, vertebrates	Ehrlich and Raven 1964, Feeny 1976, Rhoades and Cates 1976.
Production of silica in leaves	mammals	McNaughton *et al.,* 1985
Morphological responses		
Spines, prickles	mammals	Cooper and Owen-Smith 1986
Cork	mammals	Janzen 1975
Tree habit (+ spines)	tortoises, land iguanas	Dawson 1966
Morpho-chemical responses		
Stinging hairs	mammals	Janzen 1975
Other responses		
Fruit dispersal mechanisms	bird, mammals	Snow 1981, Janzen and Martin 1982, Webb 1985

effects of herbivory. Even in the Galapagos Islands, which are unlikely to be more than 5 million years old (Simkin 1984), a close relationship has developed between the endemic prickly pear cacti *(Opuntia* spp.) and the islands' giant tortoises *(Geochelone elephant opus)*. Tortoises eat the fleshy cactus pads when they can reach them. Gigantic spiny arborescent species of *Opuntia* occur on islands which are, or were,occupied by tortoises. On islands such as Marchena or Genovesa which were never colonised by tortoises, there are small trunkless and decumbent, less spiny, forms of *Opuntia*. The tree habit in *Opuntia* appears to have arisen as a selective response to tortoise browsing (Stewart 1911, Dawson 1966) although cactus pads are also a major food of land iguanas *(Conolophus* spp.) which are absent from Marchena and Genovesa. Both these reptilian herbivores could have acted as selective agents.

New Zealand plants have evolved in the presence of two groups of moas as well as other vertebrate herbivores such as extinct geese *(Cnemiornis* spp.), the extinct swan *(Cygnus sumnerensis),* New Zealand pigeon *(Hemiphaga novaeseelandiae),* kokako *(Callaeas cinerea),* parakeets *(Cyanoramphus* spp.) and kakapo *(Strigops habroptilus)*. Although the geological age of these species may differ, there has been a long period of coexistence between plants and avian herbivores. It would be both surprising and puzzling if adaptations to reduce herbivory could not be found among the indigenous plants.

Because moas were so large, an individual of even one of the smaller species could have destroyed a juvenile woody plant in a single feeding if the plant was palatable. As several moa species occurred together, plants less than a metre high would often have been exposed to browsing by both juveniles and adults of several species of moa. Thus, on accessible fertile sites, there would have been great selection pressure on the juveniles of palatable species, particularly those less than a metre high. It is among plants of these sites and of this size, particularly the slower growing juveniles of woody plants, that one would look first to find adaptations that reduced the effects of moa browsing.

In this paper we have examined only the browsing effects of moas but this is not to imply that their trampling, manuring and seed dispersal effects were of no importance.

Tests of hypotheses

We focus here on four growth features or combinations of features exhibited by New Zealand plants that appear likely to have increased survival in the presence of moas and which, in our view, arose in response to past browsing pressure by moas. They are spiny tussocks, mimicry, reduced visual apparency, and divarication.

Although it is relatively easy to postulate that a particular growth feature in a plant population was once of adaptive significance in reducing browsing pressure from moas, it is not easy to devise satisfactory tests of such ideas. Even if we could now watch the browsing activity of moas, it would still be difficult to test hypotheses of adaptation, in common with many others relating to evolutionary change. We know that at least some moas ate divaricating plants (Greenwood and Atkinson 1977, Burrows *et al.,* 1981), but that does not prove that this peculiar growth form is a result of such herbivory. All that can be said is that if a large sample of moa gizzard contents or faecal remains failed to reveal foliage or twigs of divaricating plants, then the moa-browsing

hypothesis could not be sustained as an explanation for the origin of the growth form.

Any hypothesis relating a growth feature to herbivore selection must provide a mechanism that would reduce browsing pressure on the plant and hence give it greater survival value. It is important that this mechanism is clearly formulated. As experimental tests of the hypothesis will usually not be possible, comparative tests are the only option. These can be done by making predictions about the expected ecological and physiological response of these plants if the particular growth feature of interest did in fact originate as a selective response to browsing. We suggest that as many as possible of the following tests are applied:

1. The reason why moas would have browsed the plant in question should be identified and, if possible, measured, e.g. nutrient levels, chemical attractants ("nutritional test").
2. The growth feature of interest should reach maximal development during that part of the life cycle when the plant is most likely to have been browsed by moas. In woody plants this will usually be the juvenile. As a corollary, the growth feature should not be retained at stages of the life cycle that would have been out of reach of moas ("life-cycle test").
3. The plant species showing the adaptive growth feature should reach its greatest abundance on sites of higher fertility. These are the places where moas would have concentrated their browsing. One corollary of this is that the species should be unimportant on sites inaccessible to moas, or if present, should not retain the growth feature considered to have arisen from herbivory ("site-distribution test ").
4. The geographical distribution of the plant species and its associated growth feature of interest, together with the distribution of closely related species, with or without the growth feature, should be consistent with the known distribution of moas ("geographic distribution test").

Spiny tussocks

Spines are not common among New Zealand plants possibly because they would have been less effective against the horny bills of moas than the unprotected muzzles of mammals (Greenwood and Atkinson 1977). However the genus *Aciphylla* is exceptional in that at least 16 of its 30 or more species have leaves modified to form groups of rigid needle-sharp spines 0.4 to 1.5 m in length. The spines are dense and evenly spaced

to form a hemispherical tussock-like form. In addition the spiny leaves are very tough and fibrous. Those species with sharp spines also have spiny stipules which together form a collar of spines (of varying length depending on the species) around the base of the leaf rosette. Petioles are not evident in this genus, and the edges of the lamina have been rolled inwards towards the midrib so that the original adaxial surface has become reduced to a narrow longitudinal groove above the midrib (Dawson 1971, fig. 4). An intermediate leaf form showing partial rolling of the leaf edges towards a unifacial condition is illustrated by the natural hybrid *Aciphylla squarrosa x Gingidia montana* (Webb and Druce 1984). Those species having spiny leaves also have spiny bracts in the inflorescences.

The extent to which aciphylla-like growth forms occur in other parts of the world is not yet clear. Some members of the Agavaceae and Bromeliaceae have sharp teeth or spines along the edges of the leaves but the leaf itself is not modified to form a group of large spines. In the Andes of Central and South America, some species of *Eryngium* (Umbelliferae) produce large rosettes of leaves edged with spines as well as spiny inflorescence bracts (W. R. Sykes, pers. comm.). The genera *Nolina* and *Dasylirion* (Agavaceae), of Central America and California, may also share some similarities with *Aciphylla*. In New Zealand, *Chionochloa pungens,* an endemic tussock grass of Stewart Island, forms distinctly prickly tussocks which, however, are not spiny.

The possibility that the spiny leaves of *Aciphylla* are an adaptation to deter browsing moas has probably occurred independently to many observers. Wallace (1889) may have been one of the earliest to make the connection: "and may have gained their spines to preserve them from being trodden down by the Moas, which, for countless ages, took the place of mammals in New Zealand". Since then the idea has neither been developed nor evaluated apart from brief mentions by Greenwood and Atkinson (1977) and McGlone and Webb (1981).

The most important feature of the spiny aciphyllas, when considered as an adapatation against browsing, is that their hemispherical shape results in a surface of closely spaced sharp points that extends unbroken from the apex to the ground. Spiny bracts in the inflorescence may have some protective function but this has not been investigated.

Many of the spiny aciphyllas are very attractive to both mammals and birds. They are eaten by deer,

Table 7: *Distribution of Aciphylla spp. in relation to spinescence*. Compiled by I.A.E. Atkinson and A.P. Druce*

Species	Alt. range (m)	Geographical distribution	Vegetation and site distribution	Development of spines
I. *LARGE SPECIES*				
A. aurea	s.l.-1470	eastern S.I.	silver tussock land, subalpine tussockland and scrub; gentle slopes, rock outcrops, limestone cliffs	very spiny
A. colensoi (incl. *A. scott-thomsonii*)	600-1570	both islands; major ranges from Raukumara to Otago	subalpine tussock-shrubland and scrub, sometimes along water courses	very spiny
A. ferox	1000-1470	S.I.: NW Nelson, Richmond Ra	tussockland, tussock-shrubland; moderate slopes, cliffs, sometimes on calcareous rocks	very spiny
A. glaucescens	450-1470	S.I.: NW Nelson, Marlborough, inland Kaikoura Ra, W. Otago, Southland	tussockland and tussock-shrubland with *Chionochloa rigida;* often along water courses and on stream terraces; sometimes on calcareous rocks	spiny
A. horrida	1130-1300	S.I.: Westland, central and western Otago, Fiordland, Southland	tussockland and tussock-shrubland with *Chionochloa rigida*	very spiny with broad leaf segments
A. subflabellata	60-1070	eastern S.I. lowlands, from the Wairau V. southwards	fescue tussockland, silver tussock land, red tussock-fescue tussockland; often in stream courses or seepages; river terraces	fine spiny leaves
A. squarrosa s.s.	s.l.-1470	both islands; Rimutaka and Aorangi Ra., Cook Strait coast	coastal cliffs (incl. limestone); subalpine tussock-shrubland and scrub	very spiny
A. unnamed sp. (aff. *A. aurea*)	950-1200	S.I.: Otago	tussockland	very spiny with very broad leaf segments
A. unnamed sp. (aff. *A. aurea*)	1380-1530	S.I. Gordon Range	alpine tussockland	very spiny
A. unnamed sp. (aff. *A. squarrosa*)	850-1450	N.I. volcanic plateau, Mt Taranaki, Urewera Ra., Raukumara Ra.	*Chionochloa rubra* tussockland, tussock-shrubland; gullies, slopes, cliffs	spiny leaves
A. unnamed sp. (*A. squarrosa* var. *flaccida*)	1300-1400	N.I.: Ruahine Ra.	tussock-shrubland; steep wet flushes, ravine sides	flexible and lax spines
A. unnamed sp. (aff. *A. squarrosa*)	1150-1250	N.I.: Tararua Ra.	subalpine scrub, tussockland; well-drained sites on streambanks and cliffs	rather lax fine spines
A. unnamed sp. (aff. *A. glaucescens*)	1150-1300	S.I.: Mt Owen, Garibaladi Plateau	subalpine tussockland; steep slopes and cliffs	lax spines
A. dieffenbachii	10-250	Chatham Islands	coastal cliffs and steep detrital slopes	soft leaves
A. traversii	20-260	Chatham Islands	*Dracophyllum paludosum-Sporadanthus traversii* rushland; peat and sandy soils	coriaceous and non-spiny leaves
II. *SMALL SPINY OR PRICKLY SPECIES*				
A. cartilaginea	490-620	Stewart Island	subalpine herbfield, cushion field; bogs, wet peaty areas	short stiff sharply pointed leaves

Species	Altitude	Distribution	Habitat	Character
A. crenulata (incl. *A. anomala, A. stannensis, A trifoliolata*)	950-1840 (NW Nelson) 520-700 (Stewart I.)	S.I.: NW Nelson, Stewart I.	subalpine shrubland, tussockland and herbfield; rock debris and coarse scree, peaty flats	spiny or prickly
A. divisa	1100-1750	S.I.: Canterbury	subalpine and alpine tussocklands; rock outcrops, crevices in cliffs	prickly
A. hectorii	1070-1500	S.I.: Central and western Otago	open tussockland, bouldery herb field	prickly
A. hookeri (and *A. townsonil*)	580-1400	S.I.: NW Nelson, Westland	tussockland and cushionfield, red tussock land; wet poorly drained ground	spiny
A. kirkii	1680-1835	S.I.: central and western Otago	alpine herbfield	broad rigid leaves with sharp mucrons
A. lyallii	1130-1400	S.I.: Fiordland	snow tussock land, *Chionochloa crassiuscula* tussockland, herbfield; wet sites in stable debris	very narrow spiny leaves
A. montana (incl. *A. lecomtei*)	1300-1680	S.I.: Otago	snow tussock land, herbfield; rocky ground	short prickly leaves
A. multisecta	1300-1630	S.I.: Canterbury, Otago	*Chionochloa pallens* tussockland; sometimes near cliffs	prickly fern-like leaves
A. takahea	1000-1200	S.I.: Fiordland	subalpine scrub and tussockland	very spiny
A. dobsonii	1680-2140	S.I.: western Canterbury	herbfield; rock debris, ridge crests	cushion plant
A. simplex	1530-1840	S.I.: central and western Otago	rock outcrops and ledges	cushion plant

III. *SMALL NON-SPINY SPECIES*

Species	Altitude	Distribution	Habitat	Character
A. congesla	1220-1470	S.I.: western Otago, Fiordland	bouldery herbfield and cushionfield; screes, rock outcrops, old podzolised soils; peridotite	cushion plant
A. crosby-smithii	1200-1400	S.I.: western Otago, Fiordland	herbfield and tussockland; well drained colluvium and scree	cushion plant
A. monroi	1040-1780	S.I.: Canterbury	*Chionochloa australis* grassland, tussockland, herbfield; fine rock debris rock outcrops, screes	rhizomatous; fernlike grassy leaves
A. pinnatifida	1040-1530	S.I.: western Otago and Southland	*Chionochloa crassiuscula* tussockland, bogs and other wet sites	rhizomatous; bracken-like leaves with narrow points
A. polita (incl. *A. dissecta*)	1070-1780	both islands to c. lat. 420	alpine herb field and tussockland; rock crevices	fine fern-like leaves
A. similis	900-1600	S.I.: Canterbury, Otago, Southland	subalpine scrub and tussockland, *Chionochloa pallens/C. australis* grassland	small fern-like mucronate leaves
A. spedenii	1600-1700	S.I.: W. Otago	subalpine and alpine herbfield	small mucronate leaves
A. traillii	750-970	Stewart Island	subalpine scrub, shrublan, grassland and herb field	non-spiny mucronate leaves

*The classification of *Aciphylla* spp. used in this table follows that of Druce (1988). Other data are derived from field observations by the compilers of the table, herbarium records at the DSIR Herbarium, Christchurch; Allan (1961) and Dawson and Le Compte (1978).

chamois, rabbits and hares, though not by horses. The rootstocks are eaten by pigs (Richards 1947). Some species are eaten by keas (R.B. Morris, pers. comm.), and kakapo eat *A. takahea* (author's observations). Takahe eat both *A. takahea* and *A. lyallii* (Dr. J. Mills, pers. comm.). It seems likely that moas were attracted by concentrations of water-soluble sugars in the leaf bases which can sometimes exceed 20% of the dry weight (Dr J. Mills, pers. comm.). This is much higher than the sugar levels in the leaf bases of South Island tussock grasses such as *Chionochloa pallens* and C. *flavescens* (Williams *et al.,* 1976, Mills and Mark 1977).

As an aciphylla plant ages, some of the outer leaves deflex and open up gaps in the spiny crown. Mammals such as hares or rabbits use these gaps to gnaw their way towards the base of the plant. If moas attacked aciphyllas in the same way, perhaps by treading down the outer leaves, then the collar of stipular spines could well have functioned as a second line of protection for the sugar-rich base of the plant. To avoid impaling an eye on a spine during feeding, the birds would have needed a very precise mode of feeding. The end result would have been to reduce bite sizes and biting rates compared with those on unprotected plants in the same way as spines and hooks influence browsing ungulates (Cooper and Owen-Smith 1986).

Aciphylla seedlings are characterised by flaccid grass-like leaves which, if they were recognisable by moas, could have been browsed easily. However, in the spiny species, as the plant enlarges to a tussock form and becomes easily seen, the non-pungent juvenile leaves are usually quickly replaced by spiny leaves.

A site-distribution test can be applied to the browsing hypothesis by considering the data of Table 7. The first 10 of the large species all have long spines. Typically they are associated with water courses, stream terraces, seepages and rock outcrops where there are well-drained soils and where base status is higher than on surrounding soils. In dry lowland areas of the eastern South Island where *A. subflabellata* and *A. aurea* occur, reduced leaching has produced soils of generally higher nutrient status than those widespread in the wetter subalpine and alpine zones.

The next 3 species are large mainland forms with lax spines of reduced pungency which occur in the Ruahine Ra., Tararua Ra., Mt Owen and Garibaldi Plateau (Table 7). All four places have substantial areas of steep slopes or cliffs, which were both

inaccessible to moas and likely to have been unforested for long periods. If we assume these less pungent species originated from spiny forms, their partial loss of spinescence may have occurred on sites inaccessible to moas. The lax form of N.W. Nelson *(A.* sp. unnamed aff. *A. glaucescens)* can be found growing in some of the more gentle and accessible slopes of Mt Owen, which may indicate how few browsing vertebrates now use this area. It could have been more restricted to very steep slopes and cliffs when moas were present.

The small spiny or prickly species of *Aciphylla* grow at higher altitudes than the large species. Again there is a strong association with rock debris, cliff crevices and other microsites where base status is greater than in surrounding soils. A possible exception is *A. hookeri* which can also grow in poorly drained soils (Table 7).

The small non-spiny species occur most frequently in the alpine zone, often on cliffs, at altitudes up to 2140 m. Whatever the fertility of these sites, one would not expect moas to have used the alpine zone as frequently as zones where the larger spiny species predominate (Table 7, see earlier discussion on distribution).

Two geographic-distribution tests of the hypothesis are applied here, one relating to the Chatham Islands and the other to Australia. In the Chatham Islands. *A. dieffenbach;;* and *A. traversii* both lack spines (Table 7). The latter has narrow pointed leaves but they are not sharp and can be handled easily. The submergence of the Chatham Islands during the early Pleistocene (Mutch *In* Hay *et al.,* 1970) would have eliminated any ratite or other ground birds had they been present.

There are two species of *Aciphylla* in Australia in short alpine grassland (Dawson 1971). These plants either have short fern-like leaves *(A. glacia/is)* or stiff, spineless, grass-like leaves *(A. simp/icifo/ia)* (Personal obs, and N. Simpson, pers. comm.).

There are alternative explanations for the origin oflong spines in *Aciphylla*. Oliver (1956) suggested that it was an adaptation to "dry climatic conditions either on the eastern South Island lowlands or on the mountains where the species of this genus are mostly found". The distributions in Table 7 refute this argument. *A. aurea, A. glaucescens* and particularly *A. subflabellata* must be adapted to the drier conditions of the eastern South Island but the great majority of aciphyllas, whether spiny or not, are plants of the wet mountains. Most aciphyllas grow in moist or even saturated soils (Dawson 1971).

McGlone and Webb (1981) believed that "the spinescent habit in *Aciphylla* is correlated with exposure to damaging and drying winds". They cited the two leaf-forms of *A. hookeri* suggesting that the soft or weakly spinescent form grows in shelter while rigid pungent forms occupy exposed sites. Our observations of *A. hookeri* in the Glasgow Range, western Nelson, show that leaf form in the species is not related to exposure. The rigid spiny form occurs commonly in the sheltered inter-tussock spaces between *Chionochloa pallens* and *C. rubra* where the tips of the spines can be 20 cm or more below the canopy of surrounding tussocks. Both *A. horrida* and *A. takahea* grow among tussocks and shrubs in some of the most sheltered parts of the Milford catchment such as the Esperance Valley. Around the Cook Strait coast, the spiny *A. squarrosa* grows both in sheltered crevices at the base of wind-deflecting cliffs, and on exposed rocky spurs. Although the spinous leaves of aciphyllas may indeed give protection against drying winds as suggested by McGlone and Webb, there is at present no evidence to show that wind has been the primary selective force in their origin.

Mimicry

Birds and reptiles can probably distinguish between closely similar colours much more readily than most mammals (Loew and Lythgoe 1985). The majority of mammalian herbivores locate food by smell as well as sight. We can assume that moas, in common with other diurnal ratites, had acute vision and that they located their food by sight more than by smell. Consequently physical appearance (colour and form) may have been important in determining the relative frequency with which different plant species were eaten.

We use the term "mimicry" in the manner of Barlow and Wiens (1977): "any situation where resemblance to another object (animate or inanimate) confers upon that organism increased Darwinian fitness".

Empirical observations suggest that by mimicking other plants or non-living objects, some plant species palatable to moas would have reduced the frequency with which they were eaten and thus increased their rate of survival. It is convenient to separate mimicry of whole plants or their parts, from mimicry of non-living objects.

Mimicry of whole plants. The mimicy of *Pseudowintera colorata,* which is very unpalatable to ungulates, by *Alseuosmia pusilla,* which is readily eaten by ungulates, was commented on by Greenwood and Atkinson (19077). Often the two species cannot be distinguished unless the undersides of the leaves are examined. *A. pusilla* plants seldom grow taller than 1 m and throughout their life cycle would have been within reach of moas. This mimicry has been found widely in the montane zone of both North and South Islands although *A. pusilla* is not nearly as widespread as *P. colorata.* The species can grow together in the same forest on moderately to strongly leached soils.

Two species of the large genus *Celmisia,* C. *lyallii* and C. *petriei,* have long, stiff, pointed leaves making them look like aciphyllas. High levels of soluble sugars have been recorded from basal parts of C. *petriei* (Mills and Mark 1977) which may make it attractive to herbivores but, if mimicry is present in *Celmisia,* the reasons are unclear.

Mimicry may be present in the genus Aciphylla. *A. subflabellata* appears to mimic *Festuca novae-zelandiae* which is unpalatable to mammalian herbivores. *A. subflabellata* commonly grows in fescue tussockland and the two species have widely overlapping distributions in the eastern South Island lowlands.

Further examples of mimicry can be found among woody plants. *Pittosporum pimeleoides* is remarkably like *Leucopogon fasiculatus* (C.C. Ogle, pers. comm.). Both the soft young leafy shoots of *Podocarpus acutifolius* and the seedlings of *Pittosporum divaricatum* bear a remarkable resemblance to *Cyathodes juniperina,* a shrub that is very unpalatable to herbivores. In both species it is young foliage that is involved in the mimicry, growing at heights that make these leaves accessible to browsers.

Figure 5: Muehlenbeckia ephedroides *growing on beach at Rarangi, north-east of Blenheim. (Photo: I.A.E. Atkinson).*

Mimicry of dead twigs. Perhaps the most extraordinary example of this kind of growth is shown by *Muehlenbeckia ephedroides*. This grows on unconsolidated but otherwise stable medium-sized gravel of a few beaches, river beds and rock crevices in both central North Island and eastern South Island. The plant is prostrate, leafless and a dull grey colour above (though green beneath). Its closely spaced, trailing stems give every appearance of lifeless twigs unless inspected very closely (Fig. 5). A single feeding test made by I.A.E.A. showed that, in common with other species of muehlenbeckia, *M. ephedroides* is readily eaten by both cattle and goats.

Riverbeds are likely to have been regular routes for moas because they gave access to the nutrient-rich vegetation of the adjacent alluvial flats. Thus any palatable riverbed plant could have been subjected to intense browsing pressure.

Another riverbed plant that exhibits the "dead twigs" growth form is *Helichrysum depressum* which has a prostrate habit and trailing stems carrying small imbricate leaves covered with a greyish tomentum. It is distributed throughout river valleys of the eastern South Island as well as in rivers draining the Kaweka Range in the North Island.

The same growth feature is also present in some forest species. A common juvenile form of the vine *Parsonsia capsularis* has very narrow bronze or chocolate-coloured leaves with stems of a similar colour. The upper leaf surface is blotched with grey. When growing near the ground, whether among other vegetation or not, the plant is difficult to discern. When it is detected, the very straight linear shape of the leaves together with their spacing, the angle they make with the stem, and their dark greyish colour, give the appearance of fallen twigs. In young beech stands, where there are many fallen branches and twigs, as for example in the Hope Valley of North West Nelson, the plant is camouflaged to the human eye. With increasing height above the ground the proportion of dark coloured or greyish leaves decreases relative to the normal green leaves of the adult.

Reduced Visual Apparency

The concept of apparency was introduced by Feeny (1976) and Rhoades and Cates (1976) to explain differences in the susceptibility of individual plants to discovery by insect herbivores. Feeny distinguished 'apparent' plants, which by reason of their size, density, persistence, conspicuousness, etc., were "bound to be found", from 'unapparent' plants which for reasons of smaller size, low numbers, ephemeral life span, etc., are "hard to find". However, the concept included all the other non-visual cues that are used by animals, fungi and other pathogens to locate their host-plants (Feeny 1976:5). The difficulty of measuring variables that include an animal's perception, led Rhoades (1979) to separate 'ultimate apparency', - properties such as size, density, etc., from 'proximate apparency' which included the perceptual biases of animals (Courtney 1985) .

We use apparency here in the sense of 'ultimate apparency' but to clarify our meaning and separate out visual cues from chemical cues such as volatile terpenes, we use the term 'visual apparency'. The end result of a selective trend that reduces the visual apparency of a plant is camouflage, but fitness of individuals within a population may be increased long before they can be said to be camouflaged.

The eyes of three palaeognathous birds, the emu and two species of tinamou (related to the ratites), have identical oil globule systems, much simpler than those typical of neognathous birds (Sillman *et al.,* 1981). The difference is sufficiently large for them to conclude that emu and tinamous are not able to discriminate colours as well as neognathous birds.

The data of Sillman *et al.,* for the emu suggest that light absorbance was least at both the indigo-violet and the red ends of the spectrum (wavelengths of <450 and >650 nm respectively). If moas were similar in this respect, then foliage (or fruit) colours in these bands of wavelength would have been less apparent to them than blues, greens and yellows. Purplish-black or dark bronze (chocolate) colours are common among juveniles of woody plants in forests, e.g. in many populations of kahikatea *(Dacrycarpus dacrydioides),* matai *(Prummnopitys taxifolia),* lancewoods *(Pseudopanax crassifolius, P. ferox, P. lineare),* pokaka *(Elaeocarpus hookerianus)* and *Parsonsia capsularis*. This is surprising because most woody plants growing in shade become greener, presumably as a result of greater chloroplast density. It is not so surprising if it is a cryptic colouration developed in the juveniles of some plant species as a result of selective browsing by moas.

Cryptic colouration is not the only way in which visual aparency can be reduced. *Pittosporum patulum* is a small tree found locally in the South Island montane zone (Eagle 1982) where it grows in shaded beech forest understoreys, sometimes on colluvial deposits. Limited feeding trials with cattle and goats and field observations in the Cobb Valley show that it

is readily eaten by ungulates. In the field the plant is strongly monopodial in growth: a 1 m high plant in the Cobb Valley had been decapitated by browsing 4 times but had continued to grow monopodially. Leaves of juveniles less than 0.5 m high are narrow, short and toothed (7-14 x 2-4 mm) and of a deep purplish-bronze colour (Fig. 6). As the plant gets taller, the leaves lengthen to 60 mm or more but remain narrow and very dark in colour, projecting more or less at right angles from the stem. The adult leaves are green, 40-50 x 10-15 mm, and have either entire edges or just a few teeth.

In the shade of a beech forest, a juvenile *P.patulum* is hard to see because of the monopodial habit, and the shape, angle of presentation and colour of the leaves. We do not know the height range at which juvenile foliage is replaced with adult leaves but we suggest that this growth form is another case of reduced visual apparency that has arisen as a selective response to browsing by moas.

A second example is *Pittosporum obcordatum,* a small tree eaten by ungulates which is divaricate for most of its life but which has a very distinctive non-divaricate juvenile form when it is less than 0.5 m high. It has been found on alluvial flats in lowland
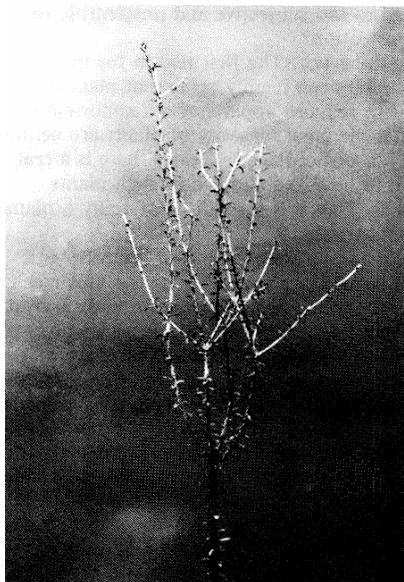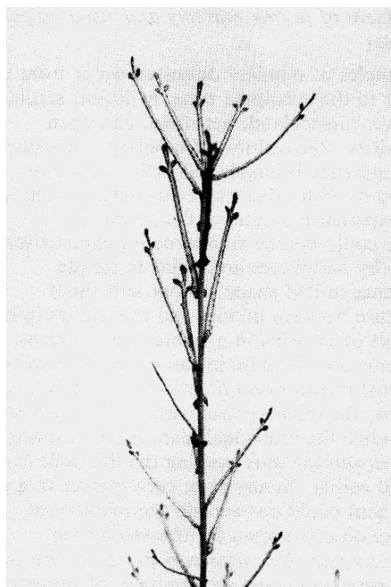

Figure 7: Pittosporum obcordatum. *Specimen from near Wairoa, North Island. (Photo: Q.R. Christie).*

forest near Wairoa, Hastings, and Masterton in the North Island (Eagle 1982) and at Akaroa and in Fiordland, in the South Island (Morrison 1982). It may well have been originally much more widespread. The leaves of the very young juveniles are narrow linear (20-45 x 1-1.5 mm) expanded towards the tip to a 3-lobed or irregular lobular shape. The leaf base is widened and partly envelops the stem. Leaf colour is dark bronze or chocolate (on the upper surface only) with a prominent whitish mark running along the upper surface of the midrib. Green tissue is restricted to the margins of the small lobes at the apex of the leaf (Fig. 7).

Viewed aginst a dark background such as that of a forest understorey, very young *P. obcordatum* plants are difficult to see because their general appearance is that of small plants with many leafless twigs. The whitish mark along the midrib reflects light in such a way that the leaves look like small twigs or branches and this effect is enhanced by the leaf bases which widen gradually towards the main stem giving the appearance of a branch subtended by the stem. Insofar as this growth behaviour may mimic a dead plant, or at least a browsed one, *P. obcordatum* is showing both mimicry and reduced apparency.

Figure 6: Pittosporum patulum. *Specimen from Cobb Valley, Northwest Nelson. (Photo; Q.R. Christie).*

The problem of testing mimicry and visual apparency hypotheses

The examples of mimicry discussed occur from the shoreline to the subalpine zone, in forest, scrub, shrub land, tussockland, herb field, and open communities. Recognition of mimicry and reduced visual apparency is largely subjective although comparisons with other observers have shown that it is not an experience unique to the authors!

One could invoke an alternative explanation to selection by herbivores and point to simple convergence in leaf shape, colour and shoot architecture between mimics and the species imitated, as a result of growing in a similar environment. But this is untenable because in cases such as *Podocarpus acutifolius, Pittosporum divaricatum* and *Parsonsia capsularis,* the mimicry disappears at the next stage of growth while the individual plant is still growing *in the same environment* thus meeting the life-cycle test described earlier. In any case, convergence in a similar environment could not explain the mimicry of inanimate objects shown by *Muehlenbeckia ephedroides* and *Helichrysum depressum*. We suggest that the cases discussed are examples of protective mimicry resulting from natural selection by herbivores.

Apart from birds, herbivorous insects and perhaps some other invertebrates could be implicated in the development of protective mimicry in New Zealand. Most insects use chemical cues to locate their food plants (Barlow and Wiens 1977) thus giving the concealment of mimicry no advantage. Exceptions occur among butterflies (Gilbert 1975). At present it seems that birds, particularly moas, are the most likely selective agent for protective mimicry. As several extant species of ground bird eat *Aciphylla* (see earlier), selection by them as well as moas could be the reason why some aciphyllas mimic unpalatable tussock species.

An additional criterion for ascribing protective mimicry to a particular species is that it should be less common than the plant or other object mimicked, at least in the past if not today. If this were not the case, there would be a high chance of the herbivore learning to identify the food plant. After moas became extinct and were later replaced by herbivores which depended more on smell for locating food, there has probably been a much reduced selection pressure during the last 1000 years for both mimicry and reduced visual apparency.

Parsonsia capsularis and *Pittosporum obcordatum* demonstrate that there is no sharp distinction between mimicry and reduced visual apparency. The distinction is worth retaining, however, to help understand the diversity of plant form and colour shown among plants browsed by moas. Both hypotheses invoke cryptic behaviour that would have reduced the rates at which these plants were discovered and eaten.

Apparency in co-evolving relationships between insect herbivores and their host plants has been criticised as a largely untestable hypothesis. The 'apparency' of a plant cannot be objectively determined for a co-adapted herbivore that has evolved specific behaviour for locating its food plants (Fox 1981, Wasserman 1982). Exactly the same criticism can be levelled against both mimicry and reduced visual apparency as adaptations to reduce the intensity of moa browsing. Moas *may* have been better than humans at distinguishing plant species. We are unlikely to have identified all the visual (and non-visual) cues that moas used. The site-distribution and geographic-distribution tests offered above cannot always be applied to plant mimics and plants of reduced visual apparency; their present distributions may have been greatly reduced by introduced herbivores that use smell to locate their food. Does it follow then that the hypotheses of mimicry and visual apparency are unfalsifiable and should therefore be dismissed as too subjective and unscientific to warrant further attention?

We think not. The first reason for this view is that observers can readily agree that plant mimics and plants with reduced apparency are abnormal in the sense that the great majority of plants are neither mimics nor camouflaged. Clearly there is a real question to be asked about how such plants originated. That it is difficult to test any explanation is a separate issue.

A second reason is that both mimicry and reduced visual apparency offer reasonable mechanisms of origin based on natural selection and survival of the fittest variants. A third is that with woody plants that show these features, the loss of either mimicry or camouflage as adulthood is approached (life-cycle test) is entirely consistent with the postulated influence of ground herbivores such as moas. It is not consistent with selection by flying herbivores, either birds or insects. A fourth is that other parallels and additional ways of testing these hypotheses are likely to be found. And a fifth is that alternative hypotheses explaining the origin of mimicry and reduced visual apparency in New Zealand plants will often be testable. We find ourselves in complete agreement with Courtney's (1985) statement: "explanations based

on 'apparency' may be of considerable use as first hypotheses" .

Divaricating Plants

The hypothesis that divaricating plants owe their interlaced branching habit, reduction of the size and number of leaves on the outer branches, and tough stems to browsing by moas as a selective agent was developed by Greenwood and Atkinson (1977). The hypothesis was partly tested by use of the life-cycle, site distribution and geographic-distribution tests outlined above.

Earlier ideas to explain the origin of divaricating plants emphasised climatic adaptation. McGlone and Webb (1981) revived this idea suggesting that these plants originated "during the harsh, near-treeless glacial periods of the Pleistocene" and that their charactertistic growth features were an adaptation' 'to protect growing points and leaves from wind abrasion, desiccation and frost damage". They suggested that the small, well-separated leaves of divaricating plants would be less exposed to abrasion by neighbouring leaves and stems during windy conditions, that the uppermost interlaced branches act as a frost-screen for the interior leaves lower in the plant, and that the network of branches may act as a heat trap permitting higher rates of photosynthesis. This is the most
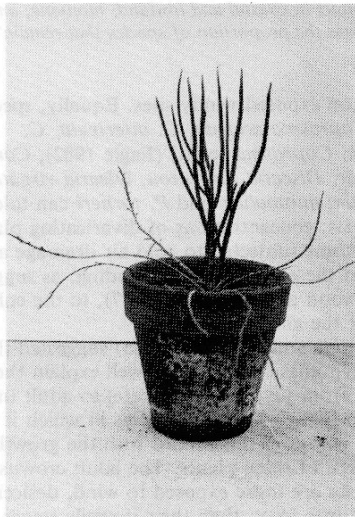

Figure 8: Carmichaelia arborea *var.* (C. petriei). *Specimen from L. Pukaki, South Island. (Photo: R.M. Greenwood).*

explicit statement of the climatic origin for divaricating plants and several aspects of it can be tested experimentally. However, in common with other climatic explanations, the hypothesis is flawed because of the exceptionally wide range of climatic and other habitat conditions in which divaricating species occur and in which they are likely to have evolved.

Of the 53 species of divaricating plants listed and defined by Atkinson and Druce (in Greenwood and Atkinson 1977), some forms are now recognised only at an infraspecific level while other species have been added (A.P. Druce, pers. comm.). The total remains at 53. Their known habitat distribution is summarised in Fig. 9. Half of these plants occur in lowland, montane or subalpine forest. Twenty-two *(*42% of all divaricating plants) are widespread and often abundant in forest even though many of them also occur in forest margins or scrub associated with past disturbance. The species are *Carpodetus serratus, Coprosma areolata,* c., *crassifolia,* C. *obconica,* C. *rhamnoides,* C. *rigida,* C. *rotundifolia,* C. *rubra,* C. *virescens, Coprosma* sp. (v) of Eagle (1982), *Elaeocarpus hookerianus, Melicytus micranthus, Myrsine divaricata, Pennantia corymbosa, Pittosporum divaricatum, P. obcordatum, P. rigidum, Plagianthus regius, Prumnopitys taxifolia, Pseudopanax anomalus, Melicope simplex* and *Streblus heterophyllus (Paratrophis microphylla).* Moreover, many of these species are strongly divaricate when growing in the shade. The last two are almost exclusively forest species and most if not all of the 22 appear to have evolved their divaricate habit within a forest environment; they are forest trees and shrubs. It is difficult to formulate any mechanism involving wind and/or frost as primary factors of selection in these plants which usually grow for much or all of their life in the shelter of a forest understorey.

Furthermore, 13 of these 22 species are strictly lowland plants (Greenwood and Atkinson 1977: Table 1) and thus are likely to be excluded from higher altitudes by low temperature. During a glacial period, rather than establishing in the open, these species would probably be even more restricted than now to the shelter of a forest or tall scrub community.

If drought and desiccation are invoked to explain the growth form, we have to explain how it is that 16 species (30%) are largely or wholly restricted to lowland, montane or subalpine habitats where either rainfall is high or where ground water is always adequate owing to site conditions. These species are
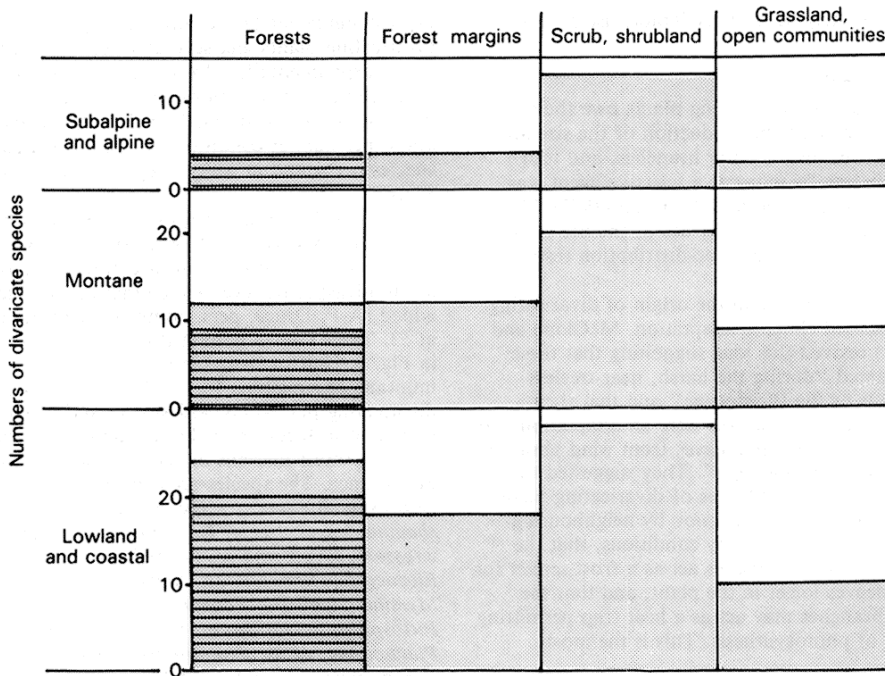
Figure 9: *Distribution of divaricating plant species (n = 50) in 4 kinds of habitats in coastal and lowland. montane, and subalpine and alpine zones. Horizontal hatching in the forests column indicates the proportion of species that remain markedly divaricate when growing in shade.*

Carpodetus serratus, Coprosma ciliata, C. *rugosa, Coprosma* spp. (p), (t) and (v) of Eagle (1982), *Hoheria angustifolia, Melicytus* sp. (a) (Eagle 1982), O. *virgata, Olearia* sp. (a) (Eagle 1982), *Myrsine divaricata, Plagianthus divaricatus, Pittosporum anomalum, P. rigidum* and *P. turneri*. In forest, some of the driest sites are those occupied by epiphytes but it is quite exceptional to find any divaricating species growing epiphytically notwithstanding the fact that related broader-leaved species are common epiphytes.

There is no doubt that some species of divaricating plants are tolerant of excessively dry conditions, strong winds, severe frosts, or combinations of these conditions. *Coprosma acerosa* and *Melicytus alpinus* grow in dry coastal sites, including dune sands and beach gravels. *Coprosma propinqua* tolerates the high wind runs of the Wellington coast and, in drier regions such as the McKenzie Basin, it occurs with *Coprosma crassifolia, Discaria toumatou, Melicytus alpinus* and *Sophora*

prostrata on exposed windy sites. Equally, species such as *Coprosma acerosa,* C. *intertexta,* C. *propinqua, Coprosma* sp. (t) (Eagle 1982), *Corokia cotoneaster, Discaria toumatou, Olearia virgata, Pittosporum anomalum* and *P. turneri* can tolerate severe frosts: concentrations of divaricating plants in valley bottoms subjected to cold air drainage are to be expected if these plants are responding, as suggested by Greenwood and Atkinson (1977), to the enhanced fertility of the alluvial terraces.

McGlone and Webb (1981:25) suggested that a climatic hypothesis can equally well explain the transition from juvenile (divaricate) to adult (non-divaricate) foliage for the 9 species in which it occurs; but in no way does this accord with the growth development of these plants. The adult crowns of all these species are more exposed to wind, desiccation and sometimes frost, than their juvenile stages growing in forest or scrub understoreys. Matai *(Prumnopitys taxifolia)* is particularly tolerant of

frosty valley-bottom sites, and in the central North Island the crown foliage is exposed to heavy frosts long beyond the juvenile divaricate stage.

Divaricating plants tolerate other environmental extremes: *Melicytus alpinus* and *Pittosporum anomalum* grow in the alpine zone; *P. rigidum* can sometimes occur on strongly leached stony soils; *Plagianthus divaricatus* is found in coastal saline swamps; and *Coprosma* sp. (v) (Eagle 1982) tolerates high winter water tables. In almost all mainland environments where woody plants can grow, from the North Cape to Stewart Island, at least some divaricating species are likely to be present. This basic fact negates any explanation of their selection and origin in terms of past or present climate, or edaphic factors. To account for the occurrence of this growth form in such a diversity of environments requires a selective factor capable of influencing plants growing in this wide range of latitude, altitude, topographic and geologic conditions. Moas meet this criterion of wide distribution and provide the most satisfactory selective factor that can explain the characteristics of divaricating plants, namely, multiple growing points, interlaced branching, tough stems and the reduced size and number of leaves on the exterior of the plant.

Much work remains to be done on this interesting group of plants. Since 1976 we have become aware that divaricating species are browsed by introduced mammals to a far greater extent than we realised earlier. Lee and Johnson (1984) found that, among 10 species of *Coprosma*, foliar concentrations of N. P and Na were higher in divaricating than in non-divaricating species. This provides some support for our (1977) assumption that divaricating plants have a higher nutrient content than their non-divaricate relatives. It is also consistent with the interest shown in divaricating plants by introduced herbivores such as deer, goats, hares or possums.

The main restriction to mammalian browsing of divaricating plants appears to be mechanical. In a feeding trial of 3 replicates I.A.E.A. offered fresh leafy branches of *Pseudopanax anomalus,* to 3 cattle and 3 goats, all pasture-fed animals. In all cases the branches were briefly sniffed and then either nibbled sparingly or ignored. After removing all the leaves from these branches, and offering them again to the goats, they were rapidly consumed (leaving none for trials with the cattle!). The same thing happened in an idential trial with *Coprosma rigida* and the semi-divaricate C. *parviflora* (s.s.). *Pseudopanax anomalus* plants are frequently seen to be browsed in the wild but, like many other browsed divaricating plants, they survive.

The mechanical restriction presented by the interlaced branches and small inaccessible leaves would have reduced the bite size and the biting rate of moas, no matter what their particular mode of feeding. More energy would have been required for a given food intake when feeding on a divaricating plant than on many non-divaricate plants. A parallel is seen in a study of the effects of plant spines on browsing by ungulates (Cooper and Owen-Smith 1986).

Dr W. Harris (pers. comm.) has suggested two further ways in which divaricate plants may have exerted a mechanical restriction on browsing by moas. First is the very springy nature of some of these plants which, after compaction or stretching, spring back to their original shape when the pressure or tension is released. Second is the possibility that larger divaricate plants, particularly if growing as a stand, are likely to have impeded the progress of large birds which, unlike mammals, are dependent on two feet only for balance.

The effect of the divaricate growth form in increasing the energy expenditure of feeding moas was emphasised by Greenwood and Atkinson (1977:25) and by Lowry (1980). However Lowry interpreted the 1977 hypothesis to mean that the divaricate growth form was "an effective defence against moa browsing" although "defence" was never suggested in the 1977 paper (Atkinson and Greenwood 1980). This led McGlone and Webb (1981:25) to conclude there were two hypotheses: one arguing for divarication as an effective defence, and the other advocating divarication as a means of increasing survival although not preventing browsing.

In terms of natural selection only the second hypothesis is possible. Moas and divaricating plants evolved together and we know that these plants were eaten by moas (Burrows *et al.,* 1981). There is likely to have been a co-evolutionary relationship, involving changes in both plants and moas. If at any stage the growth form became an "effective defence" against moa browsing, then further selection and development of the growth form would have ceased. Selection acts on organisms only when they are stressed (Berry 1985). We cannot now accept the suggestion we made in 1977 that the primary focus of feeding gradually shifted from divaricating plants to others because we do not yet know what the primary focus of feeding was for the different species of moa. The only reasonable conclusion is that for some plants there was a selective advantage, in terms of survival and/or reproduction, in developing a divaricate habit (Atkinson and Greenwood 1980). Any protection it

gave against browsing would at best have been a partial protection.

Shoot tips and developing leaves may have been important in meeting the nutritional requirements of birds such as moas whose ability to digest cellulose may have been limited (Lowry 1980). There are certainly indications that this was the case but, as young growth was not available for much of the year, the birds would have had to feed on mature foliage (Atkinson and Greenwood 1980). The massive gizzard in some moa species (relative to other ratites) is difficult to explain unless seen as an adaptation for crushing plant fibrous material.

Other growth responses in New Zealand plants that relate to moas

In addition to spiny tussocks, mimicry, reduced visual apparency and divarication, New Zealand plants show several other growth responses that we consider are adaptations to moa browsing. We include here spine-tipped leaves such as those of *Podocarpus hallii, P. totara* and *P. acutifolius;* small-leaved non-divaricate juveniles of species such as *Hoheria sextylosa* and severallianes; reduced leaf area as in juvenile *Rubus squarrosus;* leaf loss as in *Clematis afoliata* and many species of *Carmichaelia;* close interlacing of tough-stemmed vines such as *Muehlenbeckia complexa;* fibrous leaves of great tensile strength that can resist pulling even if not cutting action as exemplified by *Phormium tenax* and *Cordyline australis* (Greenwood and Atkinson 1977); and the linear and fibrous juvenile leaves of low nutrient value of *Pseudopanax crassifolius* (Greenwood and Atkinson 1977, Mitchell 1980). Although stinging hairs are a feature of overseas species of *Urtica,* the large brittle-pointed stinging hairs of *U. ferox* may have been enhanced by moa browsing. Each of these putative adaptations deserves study and testing.

Divarication may differ from other growth responses in that it results from a combination of several growth characteristics: loss of apical dominance, wide-angle branching, continued rebranching and growth to form re-entrant branches that interlace, fewer or smaller leaves on the outside of the plant, and increased stem toughness. Different species vary in the degree to which each individual characteristic is expressed.

A different combination of characteristics related to moa browsing appears in the genus *Carmichaelia*. For example, *Carmichaelia arborea* var *(C. petriei)* belongs to a group of plants commonly eaten by introduced vertebrate herbivores and which may well

have been eaten by moas also. This *Carmichaelia* grows in open tussockland where it is fully exposed to browsing animals. As a seedling, it has prostrate trailing stems with very small leaves and the dark chocolate-bronze colour of the whole plant makes it inconspicuous when growing among other plants. This form is followed abruptly by an upright leafless stem which is easily seen but which is very difficult to break because it is very fibrous. This combination of characteristics may well have contributed to reduced browsing pressure on this species in the past.

A number of New Zealand plants have characteristics including toxic or distasteful chemical constituents, and very low nutrient contents, that make them unpalatable to mammalian herbivores. There is no evidence that these characteristics originated as adaptations to moa browsing, but it is possible that the levels of some constituents may have been enhanced by that browsing pressure. For example, some podocarps such as *Halocarpus bidwillii, H. biformis, Lagarostrobos colensoi, Lepidothamnus intermedius* and *L. laxifolius* are not eaten by ungulates, presumably because of their high content of gums, resins and tannins. Other plants such as both species of *Pseudowintera, Cassinia leptophylla, Olearia solandri, Leptospermum scoparium, Kunzea ericoides* and *Pteridium esculentum* may be avoided because of their content of essential oils, cyanogenic glycosides or other compounds that are distasteful. Whether moas avoided these plants is not yet known but the low nutritive quality, if not toxic properties, of many New Zealand plants, including some of those above, is likely to have greatly restricted the amount of browsing they sustained from moas.

Several studies (e.g. Owen-Smith and Cooper 1987) have suggested that plants with structural adaptations against browsing grow on fertile soils whereas those with chemical adaptations are commonest on infertile soils. Plants with structural adaptations such as divarication, spines, and fibrous leaves of high tensile strength do seem to grow mostly on soils of higher fertility in New Zealand but more work is needed to sustain this as a general principle.

When all these kinds of evidence are considered it is possible to see how New Zealand plants could have co-existed and co-evolved wtih large herbivores for millions of years. It is apparent that the established view that New Zealand plants and vegetation evolved in the absence of browsing animals is wrong. This view also obscures the extent to which the growth characteristics of many New Zealand plants allow

them to either avoid or tolerate browsing by introduced mammals.

Coevolution of plants with moas

In presenting these hypotheses of growth characteristics as responses to moa browsing, we have not labelled them "defence strategies" even though we acknowledge that they must have had deterrent value. Notwithstanding the widespread use of such terms as "chemical defence" in the overseas literature on plant-animal interactions, we consider that the term "defence" when applied to plant populations, obscures the co-evolutionary nature of the interaction between plants and their herbivores. We use the term coevolution to mean the changes that result from the interaction between two species when "each exerts selective pressures affecting the other's gene pool". It implies an "ongoing stepwise evolution within both populations, with the properties of first one and then the other continuing to evolve in response to specific changes in properties of the other species" (Fox 1981).

Some possible growth responses shown by plants in this coevolutionary relationship have been identified. Matching the parallel adaptive responses of the moas, especially behavioural responses, to identified growth responses of plants is difficult. However, in contrast with living ratites, we can discern at least 3 trends of adaptive change in the moas, most probably related to the importance of fibrous foliage and twigs in the diet:

(a) Increase in the cutting power of the bill to allow feeding on stems and leaves of increasing toughness and tensile strength

(b) increased development of head and neck muscles (associated with increase in size) for pulling leaves and stems which are becoming more strongly attached to the plant

(c) increased development of the gizzard to grind plant material of increasing fibre content.

The size differences within the genus *Dinornis,* as well as the possibility that ancestral moas were smaller than those discussed here, suggest a fourth adaptive trend:

(d) increase in height in order to reach plant food that was previously too high to reach

Circumstantial evidence for these trends comes from two sources. First, the above characteristics vary greatly between species of moas in their degree of development. Second, growth characteristics such as the toughness of stems and leaves, and the force required to remove them from the plant, are well developed in plant species, particularly the juvenile

stages, that are likely to have been browsed by moas. Other adaptations shown by moas as a result of their feeding habits will probably be identified when the appropriate studies are made.

Ecological Influence of Mammals on Vegetation Compared with Moas

Differences between mammals and moas in feeding behaviour

Qualitative differences. It is unlikely that moas bit and stripped bark from stems, in the way that deer and goats bark *Pseudopanax* spp. and some podocarps. It is also hard to imagine them ploughing the soil and destroying roots in the way that pigs do even though they may have scratched and torn at the ground with their feet. Moas were presumably not capable of climbing trees, so there would be no parallel with the arboreal feeding of brush-tailed possums *(Trichosurus vulpecula)*.

In common with other ratites but in contrast to ungulate herbivores, moas are likely to have fed opportunistically on small animals such as beetles, wetas, landsnails, skinks and geckos. There is at present, however, no evidence for this behaviour from the contents of the few gizzards examined.

Mimicry and reduced visual apparency may well have reduced the browsing effects of moas. But mammals can locate plants with these features by smell so that such plants are now likely to be browsed more frequently.

The influence of browsing mammals extends from sea-level to the alpine zone. Forest understoreys in the montane and subalpine zones have been depleted greatly since they were introduced. By contrast, the greatest influence of moas appears to have been in the lowlands although montane and higher zones were also extensively used. The subalpine and alpine zones were probably used seasonally and no one species of moa seems to have been adapted exclusively to them. In marked contrast, breeding populations of chamois *(Rupicapra rupicapra)* and tahr *(Hemitragus jemlahicus),* are highly adapted to, and indeed self-restricted to, subalpine and alpine habitats.

It is possible that a few plant species that were browsed preferentially by moas are not preferred by ungulates. Although a great deal is now known about the browsing preferences of ungulates in different parts of the country, too little is known of moa diets to make the necessary comparisons.

Quantitative differences. In common with all birds and almost all living reptiles, the moas had an

isognathic jaw frame and simple adductor muscles. This means they could bite food only with a scissor action and swallow it without chewing. They had no teeth nor a prehensile tongue which were further restrictions on feeding efficiency. Crushing and grinding of food was done in the gizzard. In contrast, mammalian herbivores have an anisognathic jaw system. This can produce a transverse power stroke by the rotary action of the lower jaw which cuts plant tissues and crushes them between rasp-like teeth (Norman and Weishampel 1985, 1987).

Moas probably lacked a cellulose-digesting system as efficient as that of ruminants (Lowry 1980). Consequently the daily intake of plant food may have been greater than that of a ruminant of comparable body weight. But the less efficient pulling and cutting action of the moa bill may have been compensated for by a greater amount of time spent in feeding. Thus although herbivorous mammals have a more efficient feeding mechanism and can probably browse thicker and more fibrous stems than could moas, an individual deer or goat would not necessarily have had a greater impact on its food plants than a moa of similar weight.

It would not be surprising if moas were more selective feeders for plant parts than mammals especially if young shoots and leaves were of critical importance (Lowry 1980). Selection of particular plant parts for their nutrient content implies a probing and pecking capability that is extraordinarily precise, as can be seen in the feeding of takahe, geese and pigeons (Dr. W. Harris, pers. comm.).

A crucial question relevant to quantitative differences is whether or not moas moved in herds when foraging. Herd (or flocking) behaviour has been suggested from time to time, possibly influenced by the early interpretation of moas as birds of tussock grassland (Archey 1941, Duff 1977). We are not aware of any firm evidence of herd behaviour in moas. Cassowaries and kiwis, the only living forest-dwelling ratites, are either territorial or at least maintain exclusive ranges (Chrome 1976, McLennan *et al.,* 1987). We are inclined to the view that moas foraged singly or in small family groups. With the immense forest eagle *Harpagornis moorei* functioning as a major predator (Braithwaite and Holdaway 1987), moas would have been less conspicuous moving singly than in large groups.

Foraging singly, or in twos and threes, would contrast greatly with the herd behaviour of many introduced ungulates. One reason why mammals can deplete vegetation so greatly is that they feed and trample in herds that sometimes remain in restricted areas for lengthy periods (Atkinson 1964).

Ecological consequences of differences in feeding behaviour

Many plant species have been subjected to major changes in browsing pressure (and therefore selection pressure) since the advent of herbivorous mammals in New Zealand. These changes arise from the greater range of plant parts (such as bark, roots, arboreal foliage, flowers and fruit) that can be eaten by mammals; from the ability of mammals to locate plants by smell as well as sight; and the greater concentrations of mammals at higher altitudes. Differences in the mode of feeding are also likely to have changed the kind of selection pressure to which plants in New Zealand are now subjected but these differences are difficult to evaluate.

Most New Zealand plants must have evolved in the presence of moas except those restricted to islands or those adapted to cliffs or epiphytic positions out of reach. Many evolved adaptive responses to reduce moa browsing but others show no obvious protective features. At present we do not know enough about food preferences and behaviour of moas to understand how these plants maintained adequate populations in the presence of moas., In particular, trees such as the fivefingers *(Pseudopanax arboreus, P. colensoi, P.* sp. unnamed), broadleaf *(Griselinia littoralis), Brachyglottis rotundifolia,* wineberry *(Aristotelia serrata)* and *Fuchsia excorticata* could not have evolved on cliffs; yet neither could they have evolved within a browsing regime comparable to that operating at present. Their greatly depleted populations on sites accessible to browsing mammals has resulted in significant decreases in habitat range and density since the moa period.

A number of other species, particularly those of the montane and subalpine zones, are severely browsed by introduced mammals, e.g. some species of *Astelia* and, locally, *Hoheria lyallii*. Browsing mammals have caused significant reductions in population density and habitat distribution of many of the plant species they eat and this provides some of the strongest evidence that the effects of mammal browsing are often both qualitatively and quantitatively greater than those of the moas they have replaced.

Degree of ecological equivalence between mammals and moas

The browsing effects of mammals and moas on vegetation can be compared within different

Table 8: *Browsing effects of mammals and moas on vegetation*.

Altitudinal zone	Nutrient status of soils	Differences between mammals and moas m their effects on vegetation
ALPINE	High nutrients	*Major difference from moa period*. Widespread effects by deer, chamois, tahr, goats and hares, including depletion of larger herbs and some tussock grasses.
	Low nutrients	*No significant difference* between mammals and moas in many widespread communities. Local major effects by tahr, goats, not comparable to moa effects.
Treeline		
SUBALPINE AND MONTANE	High or low nutrients	*Major difference from moa period*. Widespread depletion of forest understoreys by deer and goats on soils of high and low nutrient status, e.g., barking and death of mountain fivefinger, decrease of broadleaf, stinkwood, astelias. Increase in pepperwood, divaricating plants, some tree ferns.
Altitudinal limit of rimu		
LOWLAND	High nutrients	*Partial equivalence of mammals and moas*. Many forest, scrub and swamp plants tolerate moderate browsing by mammals.
	Low nutrients	*Some difference from moa period*. Greater depletion of vegetation by mammals than by moas related to feeding differences. No significant difference in vegetation associated with very infertile soils.

altitudinal zones and with reference to soils of low and relatively high nutrient status (Table 8).

Alpine Zone. On calcareous soils and others of high nutrient status, vegetation receives concentrated browsing by deer and sometimes goats and, in the South Island, chamois and tahr. These last two species, together with hares, feed in the zone throughout the year. Larger herbs such as *Celmisia* spp., *Gentiana* spp., *Dolichoglottis* spp. and *Ranunculus* spp. have been depleted as well as some tussock grasses, in particular, *Chionochloa* sp. (*C. flavescens* of South Island authors). In contrast, moas were probably at lower density and therefore had a smaller impact.

Soils of low nutrient status are widespread throughout the mountains and we would generally expect little difference in the effects of mammals and moas on their vegetation. Vegetation dominated by species such as carpet grass (*Chionochloa australis*), *C. acicularis* and red tussock (c. *rubra),* or species of low growing *Dracophyllum,* cannot support large herbivores in significant numbers.

Where tahr, goats and chamois occur in this zone, they are often able to climb up to plants on cliff sites many of which are fertile but which would have been inaccessible to moas.

Subalpine and montane zones. On soils of both high and low nutrient status below the treeline, forest understoreys have been depleted throughout the country by deer and goats. It has resulted in widespread decreases of mountain fivefingers (*Pseudopanax colensoi, P.* sp. unnamed) and broadleaf (*Griselinia littoralis),* and less widespread decreases of stinkwood (*Coprosma joetidissima), Pseudopanax simplex, Hoheria lyallii* and astelias. Related to these decreases have been increases in mountain horopito (*Pseudowintera colorata*), toru (*Myrsine salicina),* some tree ferns and probably some divaricating plants. We conclude that the present condition of montane and subalpine forest understoreys in New Zealand is substantially different from that in the moa period. Many of the species affected were coevolved with moas and so their present low numbers cannot be taken as indicative of population sizes during the moa period.

Lowland zone. This zone is defined here as land below the altitudinal limit of rimu (*Dacrydium cupressinum)*. On soils of relatively high nutrient status, such as those derived from river alluvium, there are many indigenous forest, scrub and swamp plants that can tolerate light to moderate browsing by deer, sheep or cattle, particularly if it is intermittent. These include many divaricate species, *Rubus* spp., *Muehlenbeckia* spp., some *Metrosideros* vine species, *Pittosporum tenuifolium,* totara (*Podocarpus totara),* cabbage tree (*Cordyline australis)* and flax (*Phormium tenax)*. In addition to these partly browse-tolerant species there are others, such as kanuka (*Kunzea ericoides),* rewarewa (*Knightia excelsa),* pukatea (*Laurelia novae-zelandiae),* kahikatea (*Dacrycarpus*

dacrydioides), and rimu that are often ignored by browsing mammals. To the extent that such browse-tolerant or browse-resistant plants can regenerate and dominate in the presence of browsing mammals, the composition of the community that develops may partly replicate that likely to have been present when moas were the major herbivores. Regeneration and survival of these plants is very dependent on the frequency with which they are browsed. However it appears reasonable to conceive of a partial equivalence of mammals with moas on these high-fertility sites in the lowlands.

On soils of low nutrient status in the lowlands, mammals have probably had greater ecological effects on the vegetation than did moas although not to the extremes found in the montane and subalpine zones. This supposition can be related to the diversity of mammalian herbivores now present in the lowlands and the variety of food preferences they have. However, it is doubtful whether the effects of mammals are any greater than those of moas on the vegetation of exceptionally infertile soils. Any large herbivore would have difficulty maintaining itself on such vegetation.

A question not explicitly answered by the model of Table 8 is whether the regeneration and thus the distributional ranges of the major forest trees such as kauri *(Agathis australis),* podocarps, *Libocedrus* spp., *Weinmannia racemosa, Beilschmiedia* spp., *Metrosideros robusta, M. umbellata,* were in any way determined by moa browsing. Present information suggests that this is unlikely. Most if not all of these trees appear to have features of growth or reproductive behaviour by which they could have adequately regenerated in the presence of moas. The canopy trees of some mature kauri, podocarp and *Libocedrus* forests are, in places, old enough to have established when moas were still present. Thus there appears to be no strong argument for believing that extinction of the moas produced sudden changes in canopy composition of New Zealand forests. The understorey changes that followed this event, however, are a different matter. One can expect that loss of all large herbivores led to significant changes in the proportions of different species in both forest understoreys and non-forest woody vegetation. It has been suggested by Wellman in Fleming (1977) that these changes resulted in less regeneration of some major forest trees, particularly the podocarps at low altitudes, and this possibility deserves further study. However, where the browsing of deer, goats, possums or other introduced mammals is now curtailing the

regeneration of any of the major trees mentioned, we are almost certainly looking at a new effect that did not operate in pre-Polynesian New Zealand.

Conclusion

The mammal/moa comparison advanced here is only a first approximation towards a more precise comparison. We have concentrated solely on browsing effects ignoring trampling, manuring and translocation of nutrients, and seed dispersal in our comparison. Even if they were included, we doubt if it would affect our general conclusion that the mammals have not been simply a substitute for moas, except in a limited site-specific sense. For the most part, introduced browsing mammals are acting as a new influence on vegetation and, in many places, are depleting its structure and composition compared with that of pre-Polynesian New Zealand.

Acknowledgements

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Appendix I. *Details of moa femurs measured.*
Megalapteryx didinus (n = 10) National Museum specimens judged to be femurs from 10 individuals from Takahe Valley, Fiordland and numbered DM 445, 472 or unnumbered.

	Mean	Max.	Min.
Femur circum. (mm):	79.9	98	69

Anomalopteryx didiformis (n = 16) National Museum specimens. North Island (n = 12): Te Aute (DM 49), Makirikiri (3 specimens numbered DM 152 and 7 unnumbered). Wanganui (unnumbered). South Island (n = 4): Broken River (DM 202, 202A), East Winton swamp (S 23330), Takaka Hill (DM 415).

	Mean	Max.	Min.
Femur circum. (mm):	103.7	116	92

Emeus crassus (n = 24) Canterbury Museum specimens from Pyramid V. (AV 8300,8302,8304,8305,8307,8308,8310, 8312,8321, 15,032). National Museum specimens from unknown locality (DM 64, 65, 141), Herbert (DM 344A, 349), Wakapatu (DM 455), Broken River (DM 172A, 179A-E, 179FG), Pyramid Valley (DM 469).

	Mean	Max.	Min.
Femur circum. (mm):	127	145	112

Euryapteryx geranoides (n = 19) Canterbury Museum specimens from Waipara (A V 22427, 33187, 33252, 33885), Rakaia R. (A V 34582), Molesworth (A V 16216), Waimate (A V 8948), Cashmere (AV 22408), Albury Park (AV 31328), 'Canterbury' (A V 30493). National Museum specimens from Tarakohe (DM 427), Pyramid Valley (A V 8370), Herbert (DM 369, 378, 379), Broken R. (3 specimens all labelled DM 192), Waitaki R. mouth (DM 321).

	Mean	Max.	Min.
Femur circum. (mm):	143.7	165	119

Pachyornis elephantopus (n = 20). Canterbury Museum specimens from Glenmark (unnumbered), Kapua (A V 8928, 8937,8938,9170-9173), Banks Peninsula (AV 25568). National Museum specimens from Tarakohe (DM 401, 406 A-F), Takaka Hill (DM 417), Herbert (DM 352, 359), Bannockburn, Otago (DM 30).

	Mean	Max.	Min.
Femur circum. (mm):	172.6	200	154

Dinornis torosus (n = 12). Canterbury Museum specimens from Molesworth Station (A V 16211, 2 individuals), Pyramid Valley (A V 8415), Enfield (AV 8807, 9018, 9031), Kapua (A V 8806, 8871, 9026, 9040, 9043), Glenmark (A V 9019).

	Mean	Max.	Min.
Femur circum. (mm):	141.4	148	130

D. novaezealandiae (n = 8). Canterbury Museum specimens from Molesworth Station (A V 16214), Enfield (A V 9034, 9035), Kapua (A V 9010, 9011), Glenmark (A V 9016), Hamilton's swamp (A V 36159), Roxburgh Gorge (A V 8579).

	Mean	Max.	Min.
Femur circum. (mm):	171.2-	193	157

D. giganteus (n = 10). Canterbury Museum specimens from Pyramid Valley (A V 8478, 8480, 8482, 8486, 8488, 8491, 15026,20117), Glenmark (AV 9511, 9531).

	Mean	Max.	Min.
Femur circum. (mm):	192	217	167