SOME EMPIRICAL INFORMATION CONCERNING THE DIET OF MOAS

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SUMMARY: The paper summarizes information on the identity of plant fragments from 14 moa gizzard contents samples and outlines some features of moa diet, feeding habits and habitat which may be inferred from the investigation of these samples. Most of the moa specimens (possibly all of them) were from the genus *Dinornis*. Twigs of shrubs and trees, which were sheared off, formed the predominant part of the diet of the birds just before their death, but seeds, fruits. and leaves were also present. These moas were browsing animals and probably also penetrated the forest.

INTRODUCTION

I have investigated the fossil gizzard contents of 14 moas (Table I) to identify the plant species represented and to try to deduce as much as possible about the diet and feeding habits of the birds. This article summarizes and discusses the information about quantity and quality of diet, and feeding habits, which can be discovered by the analysis of gizzard contents. A brief account of analysis of one gizzard contents sample is given in Burrows (1980) and a full account of the investigation of organic contents and stones in such samples, including the methods used and full numerical data on the plant fragments identified, is given by Burrows, McCulloch and Trotter (in press).

METHODS AND MATERIALS

Many dozen samples of moa gizzard contents have been found during excavations from 1939 onward at Pyramid Valley swamp, North Canterbury (Duff, 1941; Falla, 1941; Gregg, 1972; R. Scarlett, pers. comm.; M. Trotter, pers. comm.). Several samples were also found in an exposure of peat at Scaifes Lagoon, Lake Wanaka, Otago in 1965 (Trotter, 1970). Unfortunately, few of the Pyramid Valley samples were retained and some of those which were kept, at the Canterbury Museum or National Museum, are badly preserved or badly labelled. Table 1 includes some details of the specimens which it has been possible to find. Only generic names of moas are used in the text below because moa taxonomy is in need of revision. Specimen 122B is the complete contents of a *Dinornis* gizzard with a volume of about 6500 cm^3 (2200 cm^3 of gizzard stones). Specimens 760, 89B, XA, 1210 and the Scaifes Lagoon samples are probably almost complete.

The better preserved specimens were sorted very fully and the potentially identifiable items of plant material separated out. A more rapid search of the less-well preserved specimens was made. Identifications of plant fragments were made using the reference collection of seeds, and other plant fragments, of the Botany Department, University of Canterbury. The various items except twigs were counted and all are labelled and stored in the Canterbury Museum or National Museum. Observations of the nature and condition of items such as twigs and leaves and some measurements were made to try to determine the feeding mode of the moas.

RESULTS

Table 2 includes summarized data for the plant taxa which have so far been identified from the moa gizzard content samples. In all instances the dominant material in the samples (usually about 30% of the volume of organic contents) consisted of short pieces of twig, 1.5-6 mm or more wide and commonly 1-3 cm long, but with many up to 4 cm and some up to 6 cm or longer. Twigs of *Olearia virgata, Rubus* spp., and *Plagianthus betulinus* are present but there are many unidentified twigs of which some have anatomy consistent with those of *Coprosma* spp. Although many twigs are partially disintegrated the ends of many of the fresher ones are clean-cut, which indicates that they have been sheared. A few bear old scars, indicating former injury. Many of the twigs are thin enogh to have been young and soft; many others are thick, old, fibrous and tough.

In only a few samples are leaves a prominent part of the volume (up to 10%) and in these instances almost all are from *Rubus* spp. *Myrsine divaricata* and *Podocarpus spicatus* leaves are

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TABLE 1. *Moa gizzard contents samples investigated.*

Locality	Code No. of Specimen	Taxon	Repository	Date of Excavation	Approx. Vol. (cm^3) Organic Sample Examined	Method of Preservation	Condition	Reference
PV	122B	*Dinornis*	CM	1973	*c.* 1500	deep frozen	excellent	Burrows, McCulloch and Trotter (1980)
PV	76D	*Dinornis*	CM	1941	$<$ 500	dried	poor	R. Duff field notes (1941)
		Dinornis	NM		$<$ 500	ethanol	good	
					c. 700	ethanol	excellent	
PV	76K	*Dinornis*	CM	1941	*c.* 800	ethanol	good	Falla (1941)
PV	76M	*Dinornis*	CM	1942	*c.* 800	ethanol	good	R. Duff field notes (1942)
PV	108D	*Dinornis*	CM	1956	$<$ 500	dried	poor	R. Duff field notes (1956)
PV	108E	*Dinornis*	CM	1956	$<$ 500	dried	poor	R. Duff field notes (1956)
PV	AA[1,2]	? *Dinornis*[3]	CM	?	$<$ 500	ethanol	moderately good	no record
PV	BB[2]	? *Dinornis*[3]	CM	?	$<$ 500	ethanol	moderately good	no record
PV	89B	*Dinornis*	NM	1940	*c.* 800	dried	moderately good	R. Falla field notes (1940)
PV	XA	*Dinornis*	NM	1939	*c.* 1000	ethanol	excellent	R. Duff field notes (1939)
PV	121D	*Dinornis*	CM	1965	*c.* 1000	dried	moderately good	Gregg (1972)
SL	I	probably[4] *Dinornis*	CM	1965	*c.* 800	dried	moderately good	Trotter (1970)
SL	II	probably[4] *Dinornis*	CM	1965	*c.* 800	dried	moderately good	Trotter (1970)
SL	III	*Dinornis*	CM	1965	*c.* 800	dried	moderately good	Trotter (1970)

PV = Pyramid Valley

SL = Scaifes Lagoon

CM = Canterbury Museum

NM = National Museum

[1] AA, BB are arbitrary code designations for unlabelled specimens.

[2] Calcareous matrix present strongly indicates recovery from Pyramid Valley.

[3] "?" indicates uncertain identity of the taxon, although *Dinornis* is likely.

[4] "probably" indicates strong probability that the genus represented is *Dinornis*, judged by large volume of sample, and/or size and number of gizzard stones.

TABLE 2. *Plant taxa identified from moa gizzard contents.*

Moa Specimen	Pyramid Valley 122B	76D	76K	76M	108D	108E	AA	BB	89B	XA	121D	Scaifes Lagoon I	II	III
TREES														
Carpodetus serratus													seed 1	
Cordyline australis	seed 1*									seed 1		seed 1	seed 1	seed 1
Elaeocarpus hookerianus										seed 1		seed 1		
Pennantia corymbosa	seed 1													
Plagianthus betulinus	seed 1									seed 1		seed 1		
	twig 2	twig 2	twig 3	twig 3			twig 1		twig 1	twig 3	twig 1			
	bark 1									bark 2				
Podocarpus spicatus	seed 1	seed 1	seed 1	leaf 1	leaf 1			leaf 1	seed 2	seed 1	seed 2	seed 1	sede 2	seed 1
	leaf 3	leaf 2	leaf 2							leaf 1	leaf 3			
P. dacrydioides													twig 1	
P. cf. *hallii*												leaf 1	leaf 1	
Pseudopanax ferox	seed 2									seed 1				
P. sp.	leaf 1					seed 1						seed 1		
SHRUBS														
Coprosma spp.	seed 3	seed 3	seed 3	seed 3	seed 3	seed 2		seed 2	seed 1	seed 3	seed 2	seed 3	seed 3	seed 3
Corokia cotoneaster			seed 2	seed 1	seed 2		seed 2			seed 3			seed 3	
Leptospermum scoparium	capsule 1						leaf 2			capsule 1				
										leaf 1				
Lophomyrtus obcordata	seed 1					seed 1								
Melicope simplex	seed 1			seed 1	seed 1	seed 1		seed 1		seed 1		seed 1	seed 1	seed 1
Myrsine divaricata		seed 1	seed 1	seed 1			seed 1	seed 1		seed 2				
	leaf 2	leaf 3	leaf 2	leaf 3			leaf 1	leaf 1	leaf 3	leaf 3	leaf 2			
Olearia virgata	twig 3	twig 2	twig 1	twig 1	twig 1	twig 1	twig 1	twig 1	twig 1	twig 2		twig 1	twig 2	twig 1
Pimelea sp.													seed 1	
Teucridium parvifolium			seed 2							seed 2				
Phyllocladus alpinus											cladode 1			
VINES														
Muehlenbeckia australis	seed 1	seed 1										seed 1	seed 1	seed 1
M. complexa	seed 1			seed 1				seed 1		seed 3				
	seed 2	seed 1		seed 2		seed 1			seed 1		seed 1	seed 3	seed 3	seed 2
Rubus spp.	leaf 3	leaf 3	leaf 1	leaf 2		leaf 2					leaf 3			
	twig 3	twig 3	twig 1		twig 1	petiole 2	twig 1	twig 3	twig 3	twig 1	twig 1	twig 3	twig 3	twig 3
Tetrapathaea tetrandra	seed 1													
Clematis sp.			seed 1											
HERBS														
Carex secta	seed 2	seed 1	seed 1	seed 1	seed 2		seed 1			seed 2		seed 3	seed 2	seed 1
Chenopodium cf. *allanii*	seed 2					seed 1						seed 1	seed 1	seed 1
Cyperaceae	seed 1				seed 1	seed 1				seed 1		seed 1	seed 3	seed 2
Phormium tenax		seed 1	seed 1							seed 2	seed 1	seed 2	seed 2	seed 2
												leaf 3	leaf 3	
Unidentified grass or sedge	leaf 1	leaf 1	leaf 1								leaf 1			

* summarised quantities of different items 1 uncommon or rare (1–9 items) 2 moderately abundant (10–49 items) 3 abundant (50 or more items)

common in some samples (but in all but one form only a small part of the volume). Some unidentifiable, much-disintegrated leaves occur in some samples. It seems unlikely that leaves formed larger proportions than 10 % of the organic contents of these specimens just before the death of the moas, because leaf cuticle (even in a very finely-divided state) is not abundant.

Seeds from a wide range of plant taxa are present but many are represented by only one or a few individual items. Some may be intrusive from the sediments in which the moas were trapped (especially those of aquatic plants like Cyperaceae), but it is assumed that if they are present in several to many gizzard contents samples they had been eaten. The materials in the gizzard contents are often wrapped into a bolus and thus it is likely that the great majority of items were eaten.

The seeds of *Coprosma* spp. *(C. rotundifolia, C. rhamnoides* and probably *C. microcarpa* and *C. robusta* are represented), *Podocarpus spicatus. Corokia cotoneaster, Melicope simplex, Myrsine divarica!a. Rubus* spp. *Muehlenbeckia* spp., *Carex secta. Chenopodium* c.f *allanii* and *Phormium tenax* are frequent and / or abundant in the samples examined. Very large numbers of *Coprosma* and *Corokia* seeds (> 1000) are present in some individuals. Only one sample (l21D) has many *Podocarpus spicatus* seeds-a total of 47-and this specimen also contains >3000 leaves of the same species.

DISCUSSION

Table 2 indicates plants (and particular items) which seem to be preferred foods of the *Dinornis* moas. The plant material present is overwhelmingly derived from woody plants; herbaceous plants are represented either only by seeds or, in two cases by *Phormium* leaves and in three cases by one or two leaves of a grass or sedge. These moas were browsing animals predominantly, but fed also on seeds and fruits. They sheared twigs off and ground them up in their large gizzards. Their feeding effects on plants may not have been very different from those of browsing mammals. It may be deduced that the birds had sharp-edged bills and strong facial musculature to enable them to cut through the tough, fibrous twigs on which they were feeding. Their gizzards too must have had strong musculature to enable them to grind up their woody food.

The list of plants indicates that the habitat of the birds just before their death included the edge of podocarp-mixed angiosperm forest round the margins of mires, or open forest of this type. It is not clear whether they ventured much into the depth of the forest (though *Melicope. Coprosma rotundifolia* and C. *rhamnoides* suggest that they did so). They probably traversed some open country and scrub-covered hillsides because their gizzards contain riverbed stones and *Corokia* seeds. All of the other plant taxa could have been obtained at forest margins beside mires.

Individual differences in the plant taxa represented in the gizzard contents may reflect vagaries related to feeding at different seasons and / or in different places, idiosyncracies of the moas concerned, or changes in habitat with time, or they may reflect differences in the food preferences of different species of moa. There is insufficient evidence on which to resolve this.

Only five fossil moa gizzard contents samples have previously been investigated (two *Dinornis.* two *Emeus,* one *Euryapteryx),* by R. Mason (Falla, 1941; Gregg, 1972). The two *Dinornis* specimens were subsamples from 76D and 121D. The *Emeus* and *Euryapteryx* specimens yielded a smaller range of plant taxa than those described above (Table 2), but included seeds of *Rubus* sp., *Coprosma* spp., *Podocarpus spicatus, Muehlenbeckia* sp. as well as a few other genera not recorded by me. Twigs were prominent in all. Unfortunately, we have no empirical information whatsoever about the diet of *Pachyornis. Anomalopteryx* and *Megalapteryx.* We will understand better the niche differentiation of moas with respect to diet when more gizzard contents samples have been examined. Size differences alone would create some such differentiation, but *Emeus* and *Euryapteryx* may have relied more on seeds and leaves than did *Dinornis.* One *Emeus* sample contained 58 seeds of *Podocarpus spicatus* (Falla, 1941). Bill shape differences are apparent in the moas (d. figures in Oliver, 1949) also suggesting that there were different feeding niches.

Evidence that *Dinornis* (and, on the basis of the meagre information, also *Euryapteryx* and *Emeus)* were browsing animals living in forests or at forest margins was presented by R. Mason (Gregg, 1972) and this is amply confirmed for *Dinornis* by the present study. This corrects the impression fostered by Duff (1941), Falla (1941) and the captions to the moa display in the Canterbury Museum, that these large moas were grazing animals, inhabiting open grasslands. In fact such grassland was not widespread in the lowlands of New Zealand during most of the Holocene, till the era of Polynesian burning of forests, within the present millenium (Molloy *et al.,* 1963).

The diet of living ratite birds sheds a little light on the apparently unusual diet of moas. In the wild all of the living species of ratite feed predominantly on plants. Emus *(Dromaius),* ostriches *(Struthio)* and rheas *(Rhea, Pterocnemia)* inhabit open grassland country or savanna and also open forest. They eat a wide range of items, including foliage of grass, seeds, buds, leaves and occasionally twigs of trees and shrubs and some animal material (Davies, 1976; Robinson and Seely, 1975; Nayman, 1972). Cassowaries *(Casuarius)* are more specialized forest animals, feeding on many kinds of fruit which fall to the forest floor (Hyass, 1963). The large moas *(Dinornis)* were also specialized compared with emus, ostriches and rheas, but they followed the common trend in the ratites; they fed on a wide range of items including seeds and leaves, while specializing, particularly, on twigs.

Greenwood and Atkinson (1977) outlined an hypothesis that moa browsing had been responsible for the evolution of the divaricate form of many New Zealand shrubs and the heteroblastic habit of trees with divaricate juvenile and non-divaricate adult form, as well as for the evolution of microphylly and toughness of stems of these shrubs and trees. The evidence outlined above shows that many microphyllous divaricate shrubs, or heteroblastic trees with divaricate juvenile form, were attractive to *Dinornis*. The twigs of some of them were undoubtedly eaten, so the divaricate form did not prevent or discourage browsing, which would seem to be one of the functions of evolution in this direction. The development of microphylly, with most of the leaves held inside a more or less tight network of branches, would, however, be a means of preventing too much loss of foliage on plants which were heavily browsed. The twigs of these plants are photosynthetic and contain storage tissue. This may have enhanced the nutritive value to the animals of a diet of their twigs. I suggest that the divaricating plants are able to cope with browsing in a way that evergreen plants with simpler branch form and larger leaves cannot. There is good evidence, however, of feeding by *Dinornis* on twigs and/ or leaves of non-divaricate plants, especially *Rubus* and to a lesser extent *Phormium*. Some of the divaricate plants which I have examined respond to browsing by abundant coppicing and regenerated branches are often straight and elongated (e.g. on *Olearia virgata, Coprosma propinqua Hymenanthera alpina)*.

In contrast to Greenwood and Atkinson's (1977) suggestion (p. 24) that twigs would be broken off the plants by moas, the direct evidence is that they were cut off; the bill served as a kind of "hedge-clipper". The plants being browsed would be hedged and, in response to this some, at least, would undergo coppicing, producing young branches which would be more easily browsed by the next moa to feed on the plant. That the birds would have to shear off the twigs which formed so much of their diet could be deduced from the strength and fibrous tissue of twigs of plants such as *Plagianthus betulinus*. *Olearia virgata* and *Rubus* spp. These twigs are quite difficult to break off the plants unless they are very young. Larger, mature twigs of all were eaten.

The evidence from the moa gizzard contents generally supports the hypothesis that moas are likely to have played an important part in the evolution of the divaricate form in plants in New Zealand, but some of the speculative details outlined by Greenwood and Atkinson (1977) are shown not to hold.

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