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Aspects of the Biology of Two Moa Species (Aves: Dinornithiformes)

T. H. Worthy

43 The Ridgeway, Nelson

ABSTRACT

Both *Euryapteryx geranoides* and *Pachyornis elephantopus* seem to have inhabited lowland forest margins or shrublands in dry areas. Although these species were broadly sympatric, several contrasting skeletal features suggest that they exploited very different niches. The preliminary observations noted here show that *P. elephantopus* had relatively larger olfactory chambers than *E. geranoides*, suggesting a better sense of smell. In contrast, the relative size of eye orbits suggests similar visual acuity. The weakly constructed mandible and reduced temporal fossae of *E. geranoides* are associated with a gizzard of small volume that contains small stones. The form of an extensive tracheal loop within the body cavity of *E. geranoides* is described. Such a structure appears to have been present only in members of *Emeinae* and suggests that birds of this subfamily could make louder calls than other moa. A comparison of femur morphology suggests that *P. elephantopus* walked by placing its feet one in front of the other while *E. geranoides* probably waddled from side to side.

Keywords: MOA, *Pachyornis elephantopus*, *Euryapteryx geranoides*, SKELETAL DIFFERENCES, ECOLOGY, OLFACTORY ABILITY, DIET, TRACHEAL LOOP.

INTRODUCTION

This paper briefly presents some observations that contribute to a greater understanding of the biology of two moa species, *Pachyornis elephantopus* (Owen) and *Euryapteryx geranoides* (Owen). Since I follow the taxonomy advocated by Worthy (1988), *Euryapteryx gravis* (Owen) of many previous authors is here referred to as *E. geranoides* (Owen). I continue to use the common names advocated by Worthy (1988) for each species of moa.

I have chosen to discuss *Pachyornis elephantopus* (Owen) (or Heavy-footed moa) and *Euryapteryx geranoides* (Stout-legged moa) because although their bones are superficially similar, detailed comparison reveals that there were probably marked biological differences in these birds. Both were very squat, about one metre high at their backs, with short stout legs and a broad pelvis. There is a broad overlap in size between them, and with body weight estimates of up to 140 kg for *E. geranoides* and up to 247 kg for *P. elephantopus* (Atkinson and Greenwood 1989) they were among the avian heavyweights of the world.

An understanding of the biology of *P. elephantopus* and *E. geranoides* is important because these species, especially the latter, formed a significant portion of the diet of early Maori people in the eastern South Island (Trotter and McCulloch 1984; Anderson 1984).

This paper is not an in-depth study of moa biology but rather, a contribution aimed at

revealing some of the differences between these two species and the bearing these differences may have had on their ecology. Virtually no ecological data have been presented on *P. elephantopus* and only some very limited observations on the diet of *E. geranoides*. It is hoped this preliminary study may stimulate further research in one or other of the topics addressed.

OBSERVATIONS ABOUT THE BIOLOGY OF *Pachyornis elephantopus* AND *Euryapteryx geranoides*

CRANIAL REGION

Skulls of these two species have long been recognised as being fundamentally different (see, for example, Archey 1941; Atkinson and Greenwood 1989). *P. elephantopus* has a sharp pointed bill, *E. geranoides* has a short, blunt bill. Associated with this, the sharp billed *P. elephantopus* has a very robust mandible and extensive temporal fossae, indicative of greater strength (which may equate to shearing power of the bill), while the blunt bill of *E. geranoides*, especially the mandible, is weakly constructed, and the temporal fossae are very reduced. Possibly the blunt billed *E. geranoides* only 'plucked', rather than sheared, its food from trees and shrubs.

The olfactory chambers in each species of *Pachyornis* are much larger than those in *Euryapteryx* species of comparable size. The crania of *P. elephantopus* and *E. geranoides* are shown in Figure 1. The size of the olfactory chamber is probably directly related to that of the olfactory bulb which is housed by it. Bang (1971) described the anatomy of the olfactory system in 23 orders of birds, measuring relative olfactory mass as the ratio of olfactory bulb diameter to the largest diameter of the cerebral hemisphere. There was striking variation, ranging from 37 percent to 3 percent. The kiwi (*Apteryx* spp.) was ranked in second place with 34 percent. Kiwis are nocturnal and can locate food using olfactory cues alone (Wenzel 1968), and probably burrow location is also effected by smell.

Two other groups of birds have notably enlarged olfactory bulbs: the procellariiforms (petrels, albatrosses, shearwaters) and vultures (Cathartidae). Most petrels, shearwaters and storm petrels are burrow nesters and visit land primarily at night. Wenzel (1980) documented laboratory and field observations that showed smell was instrumental in burrow and food location. Vultures are carrion feeders and observations recorded by Sells and Owen (1837) suggest that their sense of smell is important in food location.

As it is not possible to measure in moas the same structures measured in other birds by Bang (1971), I have attempted to relate measurements of bony structures to Bang's data (Table 1). I have measured the width of the olfactory chambers and the width between the temporal fossae and assumed that these measurements have a direct relationship to the width of the olfactory bulbs and cerebellum respectively. I have chosen *Apteryx australis*, *Puffinus gravis*, *Diomedea nigripes* and *Pagodroma nivia* for comparison with the moa species discussed here because some skeletal material was available for these species and they were among the 10 species that had the relatively largest olfactory bulbs of 120 species investigated (Bang 1971). Table 1 shows that measurements of the skull may be able to be correlated with soft part measurements and that the relative development of the olfactory chamber in moas can be quantified and compared to that of extant birds. As noted by Owen (1879) for *Dinornis* species, *E. geranoides* and *P. elephantopus* have well developed olfactory structures compared with those of other birds. The relative size of the olfactory

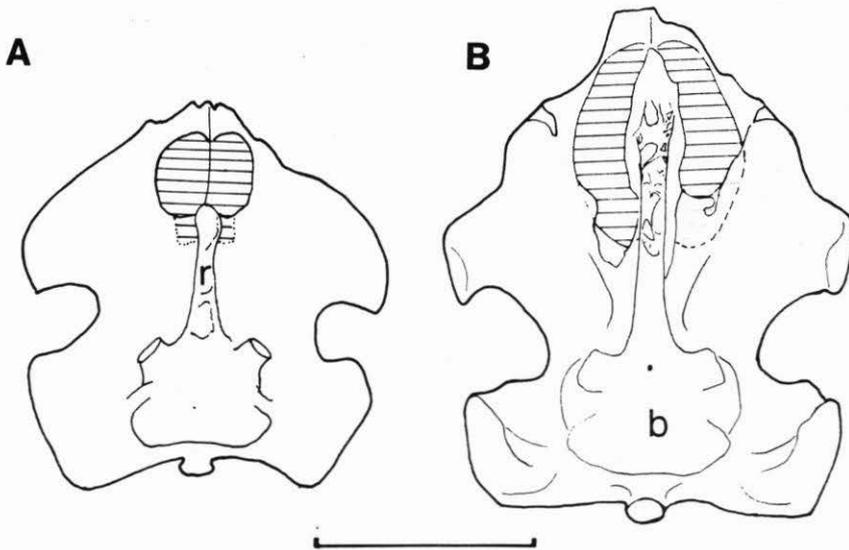


Figure 1: Ventral views of like sized crania of (A) *Euryapteryx geranoides* (NMNZ S139); (B) *Pachyornis elephantopus* (NMNZ S454). Shaded areas are the olfactory chambers, which in *Pachyornis* is seen to extend posteriorly beneath the rostrum (r) nearly to the basisphenoid (b). Scale bar is 50 mm.

chambers in *Pachyornis* exceeds that of the two species previously recorded as having the greatest development — *Pagodroma nivia*, and *Apteryx australis*.

This brief discussion shows that larger olfactory chamber size in birds is associated with an enhanced sense of smell. Thus, as suggested by Owen (1879: 117, 207) for *Dinornis*, these moas had a development of the sense of smell approaching or bettering that of kiwis. However, the fact that *Pachyornis* has markedly greater development of the olfactory chamber than *Euryapteryx* suggests these genera may have had similar differences in the use of olfactory cues in their ecology.

In contrast, the eye orbits of these two moa species are roughly similar in size, which suggests that their visual acuity was similar. The size of their olfactory chambers is positively correlated with development of their maxillary antra: in *Euryapteryx* they are totally collapsed, but in *Pachyornis* they are inflated so that a considerable space is enclosed.

In cassowaries the antrum is large, but in emus, rheas and ostriches the antrum is very reduced (Pycraft 1900). In these large ratites the presence of the antrum is correlated with a forest habitat (cassowary) and its absence with open savannah plains type habitat (rhea, emu, ostrich). If moas follow this pattern then *Euryapteryx* may have preferred more open habitat than *Pachyornis*.

TABLE 1: OLFACTORY MEASUREMENTS: COMPARISON OF MOA WITH KIWI AND PROCELLARIIFORMES.

Species	N	A	B	C	D
<i>E. geranoides</i>	9	25.4 (2.2)	50.1 (2.81)	50.8 (3.75)	-
<i>P. elephantopus</i>	5	39.5 (0.72)	54.4 (2.63)	72.7 (3.55)	-
<i>Apteryx australis</i>	12	19.9 (0.81)	31.2 (1.11)	63.9 (2.49)	34.0
<i>Pagodroma nivia</i>	4	16.9 (0.41)	24.8 (0.78)	67.6 (0.55)	37.0
<i>Puffinus gravis</i>	1	13.1	26.3	49.8	30.0
<i>Diomedea nigripes</i>	1	21.1	41.6	50.7	29.0

N = Number of specimens examined

A = width of olfactory chamber

B = width of cranium where cerebral hemisphere width is greatest (taken to be temporal fossa width in moa)

C = percent of temporal fossa width represented by olfactory chamber width

D = percent of largest diameter of cerebral hemisphere represented by diameter of olfactory bulb from Bang (1971)

Measurements in millimetres. Mean values are given first with standard deviations in brackets

Specimens examined: *Puffinus gravis* NMNZ 22144; *Pagodroma nivia* NMNZ 12036-37, 11946, 12461; *Diomedea nigripes* NMNZ 22146; *Apteryx australis* NMNZ 11243, 13588, 13590, 13591, 13700, 17205, 17209, 17332, 21035, 22074, 22114, 22115; *Euryapteryx geranoides* NMNZ S 1, 53, 55, 84, 134, 136, 139, 140, 310; *Pachyornis elephantopus* NMNZ S 56B, 56D, 409, 410, 454. The number of specimens was limited by the number of skeletons available in the National Museum of New Zealand.

GIZZARD STRUCTURE AND CONTENTS

Gizzard contents of *P. elephantopus* have not been described, but those of one *E. geranoides* (*Euryapteryx* 121A, Pyramid Valley) contained fruit and leaves of *Podocarpus spicatus*, seed of *Rubus* sp., fruit of *Muehlenbeckia australis* and leaf fragments probably of *Baumea* sp., and unidentifiable material (Gregg 1972). This sample contrasted markedly with contents of gizzards of *Dinornis giganteus* and *D. struthoides* in which twigs predominated (Burrows *et al.* 1981). The relative size of gizzards in *Euryapteryx* and *Pachyornis* is unknown.

The size of stones and volume of gizzards probably reflect diet preferences. The set of gizzard stones preserved with the gizzard from Pyramid Valley examined by Gregg (1972) weighed only 253 g, with the size of stones ranging from 2 to 28 mm. A set of gizzard stones preserved with a complete skeleton of *E. geranoides* from Honeycomb Hill Caves, Oparara, northwest Nelson (NMNZ S25656), which should have been complete because it lay undisturbed with the skeleton, weighed only c. 630 g. Small stones predominated and the largest stones were c. 15 mm for the lesser of the two greatest diameters (i.e., the diameter the bird had to be able to swallow; a long thin stone, if aligned along the long axis could probably have been swallowed easily). This was a large individual (Worthy 1988); the femur was 310 mm long and had a maximum diameter of 61.5 mm. The Model 1 algorithm of Alexander (1983) for femur diameter suggests that this specimen weighed between 112 and 155 kg in life. The set of gizzard stones associated with a skeleton of

another large *E. geranoides* which I collected from Kairuru Cave on Takaka Hill in November 1989, weighed only 330 g. Again, small stones predominated, and the largest stone's second greatest diameter was 19 mm. Another set of gizzard stones associated with a skeleton of a very small *E. geranoides* (tarsometatarsus length = 164 mm) collected at the same time and place, weighed only 92 g, with the second greatest diameter of the largest stone only 9.5 mm. Both the gizzard stone sets lay undisturbed in a discrete zone in sediment encompassing the skeletal remains, so I believe each is a complete set.

In marked contrast, the stones in a *Dinornis giganteus* gizzard can weigh as much as 5600 g (Burrows *et al.* 1981). *D. giganteus* probably weighed about 240 kg (Alexander 1983) (about twice the weight of *E. geranoides* NMNZ S 25656), but its set of gizzard stones weighed nearly nine times as much. A complete gizzard of *Anomalopteryx didiformis*, in which the five largest stones are *c.* 20 mm in the lesser of the two greatest diameters, weighed *c.* 1105 grams (T. Worthy, unpublished data). I collected this gizzard with a skeleton of average dimensions from a cave in the Puketoi Range; it is now in the Manawatu Museum. Atkinson and Greenwood (1989) estimated the body weight of *A. didiformis* to range from 32 to 59 kg with a mean of 41 kg.

The above examples suggest that the sets of gizzard stones of *E. geranoides* are very small relative to the bird's body weight. If this is normal for this species, then the meagre set of gizzard stones when correlated with the weak musculature of the cranium suggests that this species usually ate soft or non-fibrous materials such as leaves and fruit. The one gizzard analysed so far supports this contention but further analysis of gizzard contents of *Euryapteryx* and other emeid genera is vital to a better understanding.

TRACHEA (WINDPIPE)

Pachyornis elephantopus, like most moa species, had a simple, straight trachea, but there was a long, yet apparently simple, tracheal loop in *E. geranoides* (Fig. 2). The existence of a tracheal loop has long been known (Archey 1941; Oliver 1949; Duff 1977) but its shape and extent within the body have never been described. The influence of a lengthened and looped tracheal tube on vocalization is not known (Nottebohm 1975) but many birds which are capable of loud calls, such as whooping cranes and trumpeter swans, have long tracheal loops. The loop is supposed to act as a resonating chamber. The tracheal loop in *E. geranoides* consists of a 1.2 m long series of relatively long (1 cm), closely applied (some are fused together), osseous rings. Near to the cervical vertebrae the rings are shorter (2–4 mm) and thin, as in all moas, so the trachea in this region has more cartilage per unit length. The long, more ossified, greater volume of the windpipe in the loop may have acted as a resonating chamber, perhaps allowing *E. geranoides* to make a loud, trumpeting call.

PELVIS AND LEG

Although both genera are characteristically squat and stout, they differ greatly in femur morphology. In *Euryapteryx*, the diameter of the femur shaft is usually greatest half way between the transverse (lateromedial) and the sagittal planes or in the transverse plane, but in *Pachyornis* it is greatest in the sagittal or dorsoventral plane (Fig. 3) (Worthy 1988). This reflects different stresses applied to this bone in the two taxa. In the tibiotarsus and tarsometatarsus the load is mainly parallel to the longitudinal axis of the bone, but the femur

of moas is under a bending load about the shaft, because this bone is normally aligned at 10-20° from the horizontal. A greatest diameter in the sagittal is usually associated with greatest loads in this plane. This would apply if the bird walked by placing one foot in front of the other, maintaining its balance with no load transfer from side to side. In *Pachyornis* this is aided by the medial inflexion of the distal tibiotarsus, which is a characteristic of the genus; but if, as in *Euryapteryx*, the femur diameter is usually greater lateromedially, then the greater loads must usually have been applied this way. Because the legs were widely splayed on a broad pelvis, and the tibiotarsi were straight, the feet were probably not placed one in front of the other when walking, necessitating the transfer of weight from side to side with each step to maintain balance. This would cause the sideways loadings suggested by the femur shaft shape.

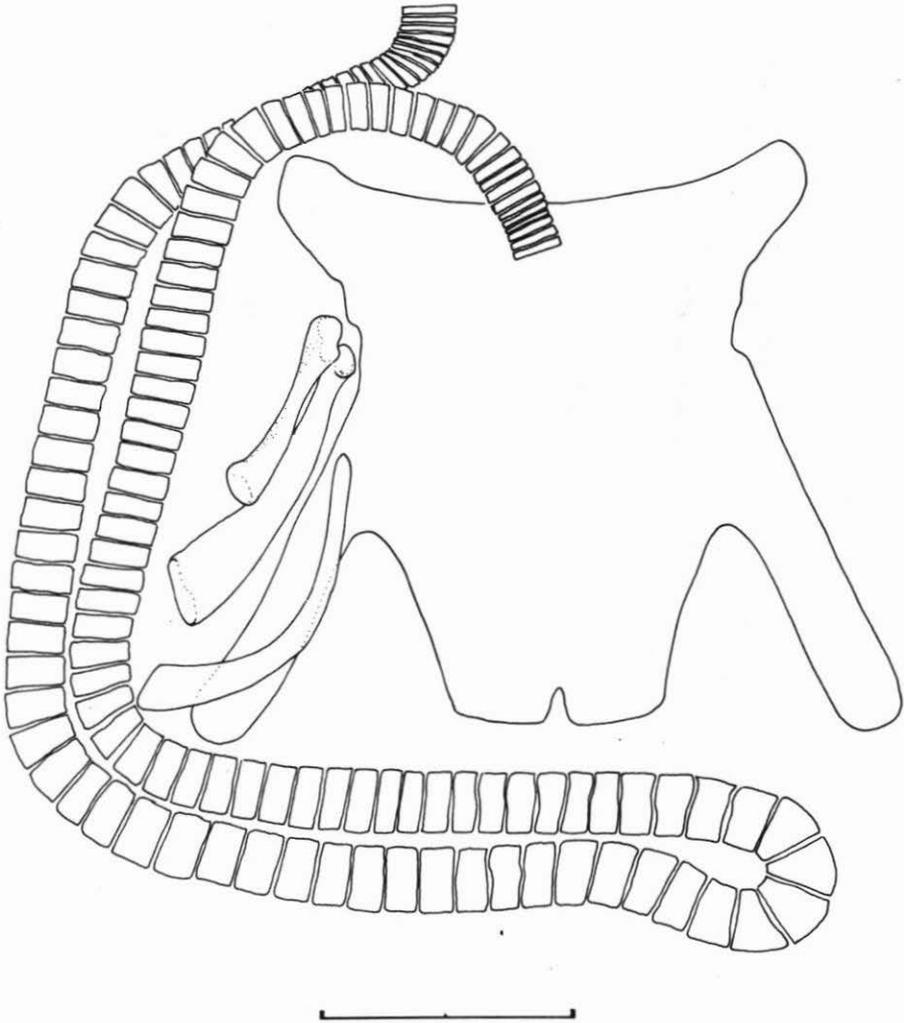


Figure 2: Dorsal view of sternum of *Euryapteryx geranoides* showing left sternal ribs and the relationship of the tracheal loop as revealed by excavation of NMNZ S25656. Scale bar is 100 mm.

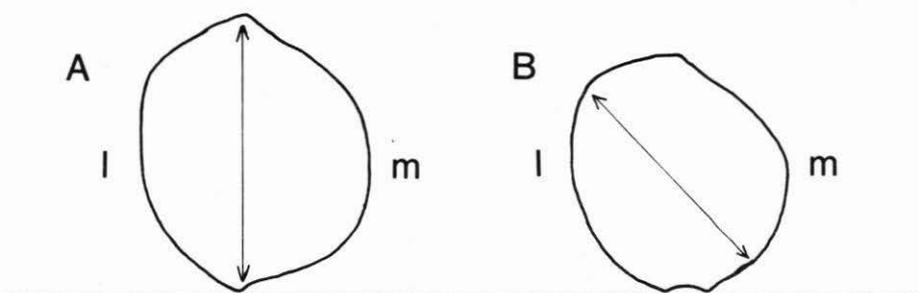


Figure 3: Femur cross-sections of (A) *Pachyornis elephantopus* (NMNZ S25868) and (B) *Euryapteryx geranoides* (NMNZ S471) showing axis of greatest diameter. l = lateral, m = medial.

A set of moa footprints at Turanganui, Poverty Bay (Williams 1872) shows large prints (probably made by a large *Dinornis* species because of their size) and smaller prints in which the lateral and medial toes are directed more forward. The smaller prints are similar to those expected from feet with the trochlear configuration of *Euryapteryx*; the prints are out of alignment, indicating a waddling gait.

DISTRIBUTION AND POSSIBLE ECOLOGY

Both *P. elephantopus* and *E. geranoides* inhabited lowland, eastern districts of the South Island during the Holocene (Worthy and Mildenhall 1989). Bones of these two species are not found or are very rare in fossil deposits laid down in a landscape dominated by dense, wet lowland forest, whereas other species are abundant within deposits from these conditions. However, they predominate in loess deposits which form under a dry scrubland or grassland. Their bones are also common in swamp deposits, especially in the Canterbury and Otago regions, and swamps provide an open or at best a forest margin habitat. They occurred in the Oparara Valley, near Karamea, during the Otira Glaciation (Worthy and Mildenhall 1989), but they disappeared when wet and dense continuous forest cover was established at the start of the Holocene. Although both species were relatively rare in the wet subalpine conditions of the Otiran Oparara, *Pachyornis australis* was quite common. It was only in the drier eastern lowland districts that they were very common, with *E. geranoides* often numerically dominating the moa fauna during the Holocene (Anderson 1989).

There are very few data available to enable vegetation reconstructions for the lowlands of the Canterbury Plains. Some data suggest that a mosaic of shrubland and forest existed around Pyramid Valley 3–4000 years ago (Moar 1970) and other data for sites in coastal Canterbury (Moar and Mildenhall 1988) reveal a Holocene history of swamp forests with nearby manuka stands. At Timaru a shrubland or low forest was present at 6730 B.P. (Moar 1971).

Lists of taxa in themselves are often not too revealing, as in New Zealand, the limited number of plant species results in the same species contributing to forests ranging from extremely wet to dry. It is often not the species composition but rather the structure of forests that exhibits the most striking changes. So whilst McGlone (in Stevens *et al.* 1988) maps the prehuman Holocene vegetation of the lowland Canterbury region as podocarp

forest with large areas of tall lowland scrub, bounded to the west by a dry inland forest, these forests must have differed markedly from those elsewhere in New Zealand. The low rainfall of the area, predictable summer drought and large 'wetland' areas, particularly riverine areas of the braided river channels, make it probable that the region was a mosaic of grassed river margins, shrublands and open forest. The very survival of *Euryapteryx geranoides* in the Canterbury region during the Holocene, when seen in relation to its absence from dense forest communities elsewhere but frequent occurrence in loess deposits, attests that the Holocene vegetation of Canterbury was characterised by dryness and openness. It is unlikely that the structure of the vegetation occurring throughout the later part of the Holocene was any different 1000 to 800 years ago when moahunting occurred. It may have been, if anything, more open as natural conflagrations destroyed the dry inland forests of Otago and the inland Canterbury region and probably other dry areas as well (Stevens *et al.* 1988).

Therefore, the preferred habitat of *P. elephantopus* and *E. geranoides* is inferred to be dry lowland mosaics of shrubland, grasslands and forests. Anderson (1989) tabulated the relative abundance of each of these species for natural swamp and archaeological sites in the South Island. *E. geranoides* is consistently the most commonly represented of these species in these sites and if frequency of occurrence is correlated with relative abundance, then *E. geranoides* was the more abundant bird.

SUMMARY

Although the stout-legged moa, *Euryapteryx geranoides*, and the heavy-footed moa, *Pachyornis elephantopus*, were sympatric, they were probably separated ecologically by diet. *E. geranoides* probably had a more succulent, less fibrous, diet than *P. elephantopus*. There is no evidence that the two genera differed in visual acuity but *Pachyornis* probably had a better sense of smell. An enhanced sense of smell in *Pachyornis* could have facilitated either food location, social contact, or orientation, as it does in other birds with well developed olfactory systems. Other evidence suggests that *Euryapteryx geranoides* ate predominantly soft foods such as fruit and leaves, and such foods are more likely to be aromatic than the coarser more fibrous foods here postulated to be favoured by *Pachyornis*. This combination of observations therefore leads me to suggest that *Pachyornis* may have been nocturnal in habit, or possibly the sense of smell played some part in social contact rather than in food location.

The relatively abundant *E. geranoides* could possibly make loud, perhaps trumpeting, calls. The social function of this ability is inferred to be communication and would facilitate group formation. The fossil distribution suggests that *E. geranoides* lived in relatively open areas such as open shrublands or forest margins. I suggest that its relative abundance combined with this habitat makes it likely that it moved about in small flocks. With loud calls revealing their presence, flocking behaviour, and a waddling (therefore slower and more cumbersome) gait, *E. geranoides* would have been the moa most easily located and killed. The relatively less numerous *P. elephantopus*, which probably had greater ability to make use of olfactory cues, was probably more difficult to hunt. With *E. geranoides* weighing between 100 and 150 kg, the meat weight return for effort would therefore have been most economical and would have compared very favourably with hunting the much smaller, forest-dwelling moas, such as *A. didiformis*, or the larger but presumably much less common *Dinornis* species, the two smaller of which were dense forest dwellers also. Therefore,

abundance, ecology, and relative size were probably the contributing factors leading to the dominance of *Euryapteryx* in the largest South Island moa hunter middens.

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