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FOOTPRINT PRESSURES AND LOCOMOTION OF MOAS AND UNGULATES AND THEIR EFFECTS ON THE NEW ZEALAND INDIGENOUS BIOTA THROUGH TRAMPLING

Summary: Foot area and structure, body weight and locomotion are compared in moas and ungulates to give estimates of pressure and edge loading when standing and moving. Moa foot pressures ranged from 0.15 kg/cm^2 to 0.19 kg/cm^2 which is very similar to those of emu feet. Red deer foot pressures were 0.395 kg/cm^2, goat 0.430 kg/cm^2, and tahr 0.35 kg/cm^2. The differences in edge loadings were not so marked. During locomotion over soft ground, the ungulate hoof acts like a chisel, and as the toes splay out, the hoof edge shears the substratum. In contrast, the ratite foot is more flexible, and rolls off the ground causing little or no cutting damage with the edge. The action of the ungulate hoof is quantitatively and qualitatively different from that of moas in affecting the integrity of plants, animals, and substratum.

Keywords: Moa, footprint pressures, ungulates, deer, goat, tahr, trampling damage, *Euryapteryx, Pachyornis, Dinornis, Dromaius novaehollandiae, Cervus elephas, Capra hircus, Hemitragus jemlahicus*.

Introduction

The deleterious effects of introduced mammals on New Zealand's native biota have received considerable attention (e.g., Wodzicki, 1950; King, 1985). Predation, herbivory, competition, disease, and enrichment by faeces and urine have all been implicated.

By contrast, little attention has yet been paid to the effects of trampling by these mammals, yet much research overseas has shown that it is important. In agricultural areas and in forests, trampling can determine community composition, regeneration success, productivity, and soil characteristics. Trampling damage has been reported in agricultural systems (Horb, 1984; Richards *et al.,* 1976; Mullen *et al.,* 1977; Laycock *et al.,* 1972); tree plantations (Eissenstat *et al.,* 1982; Gotoh *et al.,* 1980; Leninger, 1984; Lewis, 1980; Schwenke, 1986; Schwab, 1979); native plant associations (Runge, 1984; Grulih, 1979; Laycock and Harniss, 1974); and soils (Reid and Parkinson, 1984; Scholesfield *et al.,* 1985; and Mullen *et al.,* 1977).

Trampling damage can be more important than damage from any other source. Trampling by cattle caused the most obvious and persistent damage to plants in a shrub-steppe community (Rickard, 1985). Damage to seedlings by cattle in a regenerating conifer forest was a result of repeated trampling rather than browsing (McLean and Clark, 1980).

The effects of trampling by large mammals was well known to the early European settlers in New Zealand who compacted dirt roads by driving sheep flocks up and down them. Indeed, the first mechanical rollers were called sheepfoot rollers.

The biota of the New Zealand forest floor evolved in the absence of ungulate trampling. Particularly vulnerable elements of that biota would have been: the mesic vegetation which was probably characterised by shallow feeding roots near the surface; especially low growing vegetation and seedlings; large-bodied animals such as frogs, lizards, and the larger insects; and soils which were probably open and uncompacted, with a high organic content. Trampling damage to anyone of these elements would have contributed to the massive changes wrought by man and the agents he introduced.

In comparing the effects of moas and ungulates, we examine two hypotheses:

a) the weight/unit area of moa feet was lower than for ungulates;

b) the bipedal locomotion and foot action of moas disturbed the substratum less than did the quadrupedal ungulates.

Methods

The dimensions of the skeletal elements of the feet of mounted moas of the genera *Euryapteryx, Pachyornis,* and *Dinornis* were measured and used to estimate the projected foot area. The body weights were estimated from the allometric relationships, derived from limb bone measurements, given by Alexander (1983).

Pad impressions, and hoof impressions, were taken in sand and mud for live emu *(Dromaius novaehollandiae),* red deer *(Cervus elephas),* domestic goat *(Capra hircus),* and tahr *(Hemitragus jemlahicus)* of known body weights.

The projected area of the skeletal elements of the feet of moa and emu, the length of the perimeter of the projected area, and the area and edge length of the ungulate footprints were measured using a digitizing tablet connected to a computer. Video recordings and still photographs of live emu, red deer, goat and tahr were analysed to see how their feet made contact with the substratum, and how they moved.

The skeletal outline of the foot of ratites is not the true outline of the surface presented to the substratum during locomotion because a horny pad extends well beyond the bone outline. It was impossible to measure this for moas but we measured the area of the skeleton outline for the emu to provide a scaling factor for the area of the moa foot. The static pressures and edge loadings exerted on the substratum by moa, emu, and the ungulates were then calculated.

Results

The static pressure exerted by each foot of a 40 kg emu during one step, neglecting dynamic forces, was 0.385 kg/cm'. Based on the skeleton outline of the foot the static pressure was 0.656 kg/cm^2. The edge loadings were: foot, 0.634 kg/cm; and skeletal outline of foot, 0.504 kg/cm. This gave correction factors of 0.59 for area and 1.26 for edge loadings to derive live loadings for moa (Table 1).

The edge loadings for the moas are estimated maxima because the outline of the digital pads within the sole was not included, whereas those of the ungulates are absolute values.

An important feature of the ungulate footstep is that when the animal presses its hoof on and into the substratum the front edges act as chisels. The chiselling effect spreads downwards and outwards as the foot presses into the soft substratum and the toes spread apart. Furthermore, the weight is applied suddenly.

In contrast, the emu's foot is applied gently to the substratum. *As* the animal steps forward, weight is smoothly and progressively applied to the forward foot until the hind foot 'rolls' off the substratum. *As* a result, the footprints were flat or planar without the deeper impressions which would have indicated pressure points.

Judging by the impressions in mud of moas feet reported and illustrated by Hill (1895), moa locomotion was very similar to that of the emu. There were no pressure points and no shearing action of the toes as the foot was applied or withdrawn. However, plaster casts of moa footprints held in the Manawatu Museum are not all flat and planar. The impressions of certain phalanges are a little deeper than others, but there is no indication that the edges of the foot cut the substratum since all the impressions are rounded, smooth, and shallow.

The impact of an animal's foot on the substratum increases with the speed of travel. Four authors have recorded moa tracks in sufficient detail to enable speed to be estimated from Alexander's (1977) equation.

Owen (1879: 451-453 and Plate CXVI) illustrates three series of tracks, but without scales. Elsewhere he gives the dimensions of a single foot which enables the scale to be established. Provided we have identified the correct foot in the tracks, we calculate the scale in his first series as 23.55:1; and his third series as 19.22:1. But he gives no information by which the scales can be established for his second series, and since there is clear evidence that the three series of

Table 1: *Corrected static foot pressures and edge loadings for an animal standing stationary on two feet (bird) or four feet (mammal).*

Species	Estimated or measured weight (kg)	Corrected static pressure kg/cm^2*	Corrected edge loadings kg/cm**
Euryapteryx gravis	98	0.191	0.55
E. gravis	97	0.184	0.55
Pachyornis elephantopus	129	0.176	0.64
P. elephantopus	88	0.178	0.55
Dinornis torosus	114	0.150	0.47
D. torosus	114	0.190	0.63
Dinornis sp.	198	0.185	0.83
Cervus elaphus	86	0.395 ± 0.11	0.56 ± 0.21
Capra hircus	33.5	0.430 ± 0.12	0.62 ± 0.05
Hemitragus jemlahicus	44	0.350 ± 0.06	0.65 ± 0.02

* 0.59 times skeletal area
** 1.26 times skeletal area

tracks were drawn to slightly different scales, it seems reasonable to assume that the scaling factor used in this drawing is the average of the other two. We calculate this to be 22.11: . The maximum error using this assumption is less than 8 %.

Williams (1872) reported a series of moa tracks found at Turangi, Bay of Plenty, with a mean foot length of 200 mm, and a mean step length of 507.09 mm. For a set of moa footprints in the bed of the Manawatu River (Hill, 1895) the mean footprint length is 381 mm, and the mean step length is 660.4 mm. For a set found at Turanganui, Poverty Bay, (Wilson, 1913) the foot length is 305 mm and the step length is 762 mm. The estimates of hip height based on these foot lengths are given in Table 2. In this table other estimates of hip height are given based on Owen's estimates and on measurements on, or photographs of articulated specimens.

By using Alexander's (1977) relationship between hip height and speed of locomotion, the gaits and speed of locomotion can be estimated (Table 2). In all instances the gait is a walk, and the speed of locomotion ranged from 2.54 to 6.16 km/h.

Discussion

The sample size of moas was small, but the body weights calculated for *Pachyornis* and *Euryapteryx* agree substantially with those given by Alexander (1983). Therefore, we are reasonably confident about the body weight and foot area estimates for these two genera. We have less confidence in the weight estimates for *Dinornis,* although the foot area estimates are probably reasonable, and the loadings obtained agree with those of other moa genera. Any errors in our body weight estimates for the moas are probably over-estimates, which would bias our conclusions conservatively in comparison with ungulates.

The area loadings for the ungulates were consistently 4 to 5 times those for the moas per foot, corrected for foot pad outline. Area loadings are more significant than the edge loadings as such because they indicate the penetrative power of the feet. It is the sharpness of the edge rather than the edge loading which is important in causing damage through shearing action. Although some ungulate hooves may become somewhat blunted and rounded through abrasion, the edge remains much sharper than that of a ratite's foot.

Ssemakula (1983), working on African ungulates, reported heavier loadings for goat (0.73 kg/cm^2) than we obtained. The other species he investigated - sheep, oryx, cattle, and eland - had mean footprint pressures of 0.69, 0.86, 0.98, and 1.09 kg/cm> respectively. These pressures are considered by Parker and Graham (1971) to significantly affect African rangeland at high population densities.

It should be emphasized that we calculate static loadings for an animal standing still in a normal resting posture. During locomotion, much greater forces are exerted because the body weight is carried by fewer feet over a smaller area of contact. These dynamic forces are usually far greater than static forces because of postural and momentum effects during locomotion. Furthermore, because of substratum irregularities the forces may not be applied evenly to the ground.

In contrast with ungulates, the toes of emus and moas have a rounded cross-section with no sharp edges, and they can both separate and flex vertically at the ends. When weight is applied it is taken by all three forward digits; there is little if any chiselling effect at the foot edge. On a soft substratum, these wide, flexible toes would have little shearing effect when they spread open. When the foot is lifted, the weight is removed progressively along the toe imprint,

Table 2: *Estimates of the speed of moos based on descriptions of tracks using Alexander's (1977) equation. The different speeds in the last column are based on the two estimates of hip height.*

Source	Stride length (mm)	Hip height from Alexander 1983[1]	Owen 1879	Present work[2]	Speed (km/h)
Williams (1872)	1014	686	–	704	4.47, 4.34
Owen (1879) Ser. 1	2250	–	–	1628	– 6.16
Owen (1879) Ser. 2	1700	–	1160	1116	5.73, 6.00
Owen (1879) Ser. 3	894	–	–	697	– 3.56
Hill (1895)	1320	1623	–	1094	2.54, 4.03
Wilson (1913)	762	–	–	–	– –

[1]Based on Alexander's allometric ratios of limb bones.
[2]Based on articulated specimens and illustrations of articulated specimens.

without tearing or other shearing damage. The foot is rolled off gradually without transient high pressure areas.

When a moa took a step, a single foot carried the whole body weight and the dynamic stresses of locomotion. Ungulates, being four-footed, might be thought to divide their body weight and locomotion stresses so that each foot would make proportionately less impression, but each forefoot in turn takes 60% of the body weight during any four-stroke cycle. Furthermore, during normal walking the hindfoot is often placed in the forefoot impression thus repeating the shearing action on the same piece of ground.

In prehistoric New Zealand, some large birds may have scratch-foraged and thereby turned over the top litter. Some moa taxa may have scratched, but the limited evidence from gizzard contents suggests that the birds browsed living vegetation or harvested fallen fruit from the forest floor. Chicks, and adults feeding chicks, may have scratched in the litter for invertebrates and small vertebrates. The effect would have been spread over a larger surface area and thus would have been less damaging than that caused by ungulates whose narrow foot tends to cut trenches rather than scrape the surface layer.

The reason for the profound difference between the footprint pressure of ratites and mammals is that they have fundamentally different modes of locomotion. Bipeds require large foot areas for stability, but quadrupeds do not (Charig, 1972). Thus mammals can have feet with small footprint surface areas which enables them to achieve rapid locomotion (Alexander, 1977).

The trampling damage caused by a large animal is a complex function of total footprint pressure, edge pressures, shape and flexibility of foot, impact frequency, population density, and its return time to a particular place. New Zealand's indigenous biota evolved in an environment where large animals were present, but they trod lightly. When it was exposed to trampling by the high pressure feet of mammals, it would have been damaged. This damage compounded the other damage inflicted by man and his introduced agents - habitat changes, predation, browsing, nutrient enrichment, competition, and disease - resulting in the profound changes to the indigenous biota which are such a feature of the natural history of New Zealand.

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