On ratites and their interactions with plants*

Las rátidas y su interacción con las plantas

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RESUMEN

Se revisan las historias de los fósiles, patrones de distribución y preferencias de medio ambiente natural-hábitat, tanto de miembros extintos como sobrevivientes de las rátidas. Se pone especial énfasis en aquellas características físicas y anatómicas de las rátidas que tienen aparente significación desde el punto de vista de la dinámica vegetal, especialmente aquellos aspectos relacionados con la germinación de las semillas y establecimiento de los brotes. Aparte de los kiwis de Nueva Zelanda (Apteryx spp.), la característica principal que distingue a las rátidas de otras aves es su gran tamaño.

En tanto que las consecuencias evolutivas del gigantismo han resultado en la extinción comparativamente reciente de algunas especies, tales como, las moas (las Dinórnidas y Emeidas) de Nueva Zelanda y los pájaros elefantes (Aepornítidas) de Madagascar, el gran tamaño de las rátidas contemporáneas les confiere la capacidad de ingerir considerables cantidades de alimentos, como así también ítemes particulares como frutas y piedras demasiado grandes para otras aves, sin sufrir ningún menoscabo en el vuelo. Muchos de estos alimentos vegetales, especialmente frutas como las de los Lauranceae, pueden ser altamente nutritivos, pero las rátidas son omnívoras y pueden utilizar una gama de alternativas cuando es necesario. Es aún incierto si la selección de alimentos está relacionada directamente con la recompensa nutritiva; sin embargo, la estación de reproducción del casuario australiano (Casuarius casuarius johnsonii) está estrechamente ligada al período de máxima producción frutal de los árboles y arbustos en sus hábitat de selvas tropicales lluviosas.

Algunas rátidas extintas, tales como: las moas y los mihirungs (Dromornitidas) pueden haber también influenciado la selección de plantas y sucesión vegetal mediante su ingestión diferencial de especies y órganos fitógenos particulares. Existe un aparente mutualismo en lo que respecta a los beneficios sobre la población vegetal, consiguientes a la ingestión de los propágulos por parte de las rátidas. En ciertas situaciones, las semillas de las plantas germinan satisfactoriamente solamente después que la semilla ha pasado a través de los intestinos de las rátidas. Se postula que muchas de las diásporas de frutos grandes que comen las rátidas sólo germinan rápidamente en micrositos fecales, confiriendo por lo tanto considerables beneficios ecológicos al promover una importante, y dispersa, caída de semillas. En suelos de textura pasada, el arbusto semiárido Nitraria billardieri solamente se establece en abundancia una vez que el fruto suculento que madura durante el verano ha sido comido por los emus (Dromaius novaehollandiae). En sustratos arenosos de las áreas costeras donde la fruta caída es cubierta rápidamente por la arena llevada por el viento, la especie germina prontamente en ausencia de la ingestión aviaria.

ABSTRACT

The fossil histories, distribution patterns and habitat preferences of both extinct and extant members of the Ratitae are reviewed. Particular emphasis is directed towards those physical and anatomical features of ratites which have apparent significance in terms of vegetation dynamics, especially those aspects relating to seed germination and seedling establishment. Apart from the New Zealands kiwis (Apteryx spp.), the principal feature distinguishing the ratites from other birds is their large size.

Whilst the evolutionary consequences of gigantism have resulted in the comparatively recent extinction of some species such as the moas (the Dinornithidae and Emeidae) of New Zealand and the elephant birds (Aepyornithidae) of Madagascar, the large size of contemporary ratites confers an ability to ingest considerable quantities of food, as well as particular items such as fruits and stones too large for other birds, without having to suffer any impairment of flight. Many of these plant foods, especially fruits such as those of the Lauraceae, can be highly nutritious, but ratites are omnivorous and can utilize a range of alternatives when necessary. Whether prey selection is directly related to nutritional reward is uncertain however the breeding season of the Australian cassowary (Casuarius casuarius johnsonii) is closely linked to the period of maximum fruit production by trees and shrubs in their tropical rainforest habitatats.

Some ratites such as the moas and the mihirungs (Dromornithidae) may also have influenced plant selection and vegetation succession through their differential browsing of particular species and plant organs. There is some apparent mutualism in terms of benefits conferred on plant populations following propagule ingestion by ratites. In certain situations, seeds of plants germinate satisfactorily only after the seed has passed through the ratite gut. It is postulated that many of the large-fruited diaspores eaten by ratites will only germinate rapidly in faecal microsites thereby conferring considerable ecological benefits by promoting substantial, and dispersed, seedling recruitment. On heavy textured soils, the semi-arid shrub Nitraria billardieri, only establishes in abundance once the succulent fruit, which ripens during the summer, has been eaten by emus (Dromaius novaehollandiea). In the sandy substrates of coastal areas where fallen fruit is readily covered by windblown sand, the species germinates readily in the absence of avian ingestion.

INTRODUCTION

The term ratite, derived from the latin *ratis* or raft, refers to those flightless birds, some now extinct, whose skeletal structure is characterised by a raft-like breast-bone or sternum. To taxonomists and evolutionists however, they are a "truly confusing, vexacious group" (Rich & Balouet 1984). Much of the complexity inherent in their taxonomy and phylogeny results from the hypothesis that they are closely related to the "fowl-like" tinamous (Tinamiformes) of the South American Neotropics, both groups possessing a distinctive palate (Houde 1988) while differing in sternum structure. This relatively primitive, reptilian palate, described as palaeognathous or dromaeognathous, is a strong and rigid structure with individual parts either articulated along extended sutures or actually fused, in contrast with other birds (neognaths) whose palates are lighter and more flexible in construction (Bock 1963). Accordingly modern birds (subclass Neornithes) have been divided into two superorders. the Palaeognathae and Neognathae. An alternative classification divides the Neornithes into the Ratitae and Carinatae. Here the Carinates are distinguished by possessing keeled breastbones or carinate sterna to which are attached the powerful breast muscles required for flight (Houde 1988). Many extinct taxa such as the New Zealand moas (Dinornithidae and Emeidae), the mihirungs (Dromornithidae) of Australia, the elephant birds (Aepyornithidae) of Madagascar and the Eremopezidae of North Africa, have been tentatively included in the Ratitae pending conclusive palatal and other anatomical and biochemical evidence (Rich & Balouet 1984).

Phylogenetic relationships of ratites, as shown in Figs. 1 and 2, whilst understood at some levels and for some groups, are not clear for all. Together with other palaeontologists (e.g. de Beer 1956), Rich & Balouet (1984) claim that ratites evolved from flying ancestors and not independently from reptiles. With remarkable perception, Charles Darwin postulated that the wingless birds of New Zealand and other islands arrived by flight but their wings
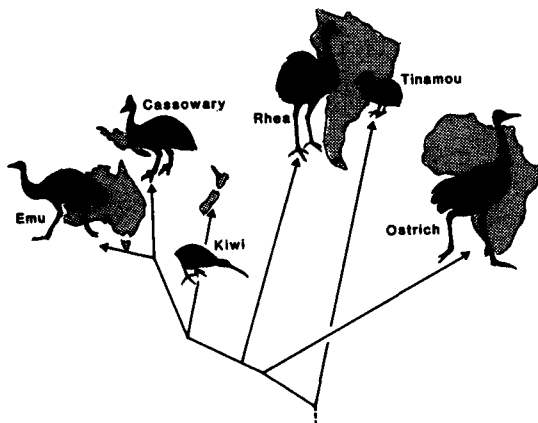

Fig. 1.: A phylogenetic scheme for ratites based on DNA x DNA hybridization data of Sibley and Ahlquist (1981).

Un esquema filogenético para las rátidas basado en los datos de hibridización DNA x DNA de Sibley y Ahlquist (1981).
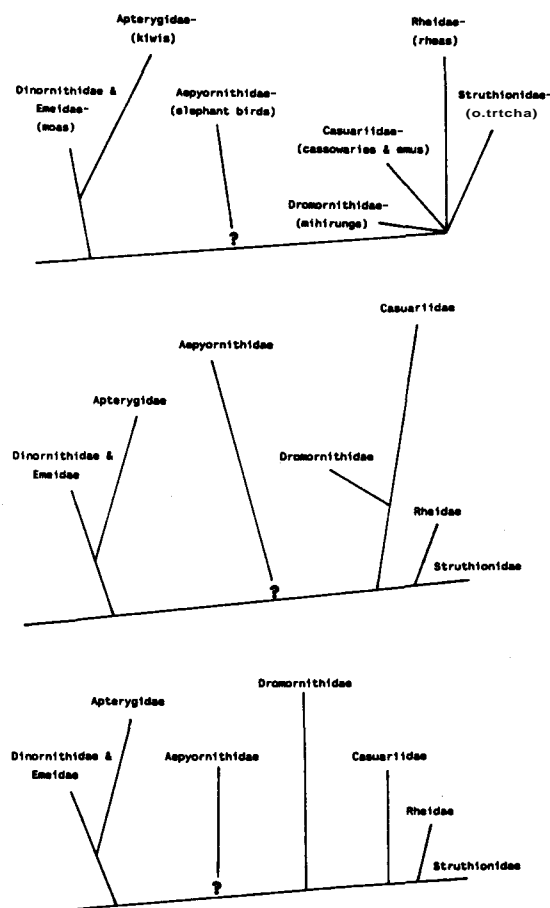

Fig. 2: Three phylogenetic trees for both extant and extinct ratites proposed by Rich (1979).

Tres árboles filogenéticos, tanto para rátidas sobrevivientes como extintas propuesto por Rich (1979).

subsequently became atrophied from disuse in habitats devoid of predators. Studies by Houde (1986) conclude that the kiwis (*Apteryx* spp.) envolved directly from a Northern Hemisphere palaeognath that flew to New Zealand before losing its power of flight independently of other ratites. "In ostriches which inhabit continents and great islands, as we see that they can escape danger by their fleetness, and in close quarters by their dangerous kicks, quite as well as any quadruped, disuse together with the increasing weight of their bodies may well have rendered them incapable of flight" (Darwin in Stauffer 1975, p. 290).

The ratites generally have strong Gondwanan affinities even though ostriches were once present in Europe and Asia (Rich 1975). There may well have been strong coevolutionary links between the ratites and the primitive angiosperms, conifers and cycads of Gondwana (White 1986) however the precise details of such linkages remain in the realms of speculation.

This paper examines various aspects ot the ecology of extant members of the Ratitae, excluding the tinamous, with reference to extinct ratites where appropriate. After describing distribution patterns, habitat, preferences, fossil histories, and the interactions between ratites and man, the anatomical features of ratites in relation to their dietary preferences and subsequent influence on vegetation dynamics will be discussed in regard to plant-ratite mutualism.

SIZE CHARACTERISTICS

The continental ratites (ostriches, emus and rheas) have effectively substituted a rapid running (cursorial) capability for flight, decreasing wing size being inversely related to leg size. Not only is this an expedient defence mechanism from predators, but it also enables these birds to travel large distances seeking food during drought. Davies (1976) recorded tagged emus (*Dromaius novaehollandiae*) travelling as far as 500 km within 9 months of band-

ing. These birds are highly cursorial with the inside digit of the foot markedly reduced and the lengthened distal elements of the limbs enabling them to reach speeds up to 50 km/hr.

In terms of energy expenditure, flight is the most costly of all modes of locomotion and as size increases, so does the energetic cost (Carlquist 1974). As the weight of a bird is squared, the wing area must be cubed to support the increased weight (Davies 1976). The cursorial habit of continental ratites is not only economical of energy but also enables them to remain in close contact with their food crops on the ground, some of which are located in widely separated regions (Davies 1976). Consequently, there will be positive selection pressures for flightlessness whenever flight is unnecessary, and only small changes will push a bird over the threshold between flying and non-flying. Selection would be unlikely to eliminate wings entirely but rather to induce a reduction to small vestigial wings (Carlquist 1965). The moas are unique in this sense having lost all wing structures during their evolution (Oliver 1949).

The increasing cursoriality in continental ratites may have been a selection response to greater openness of the habitat as the temperate rainforests of the Tertiary decreased with drying of the climate around the Middle Miocene (15 m.y. BP) (Frakes *et al.* 1987). Many of the features of the extinct ratite *Emuarius gidju* (Boles 1991) indicate such an increase in cursoriality as the *Nothofagus*-dominant rainforests across much of the temperate Australia retreated. Nonetheless the cassowary is also cursorial despite its tropical rainforest habitat.

The large size of the continental ratites is correlated also with increased longevity (c. 15 years for emus in the wild), rapid growth rate and early maturity. Rheas may grow to one third their adult size in just two months (Bruning 1973), and all the large ratites lay eggs before they are two years old (Davies 1976). The incubation period though is quite long ranging from eight weeks to three months (Carlquist 1965).

TABLE 1

Physical dimensions of selected ratite species.

Dimensiones físicas de especies seleccionadas de rátidas.

Species	Weight (kg)	Toe Number	Clutch size	Egg size (mm)	Egg weight (g)	Relative egg weight (% bodyweight)	Reference
Giant Mihirung (*Dromornis stirtoni*)	500	3	n.a*	125 x 155	1,300	0.26	Rich & van Tets (1982) Rich & Balouet (1984)
Giant Moa (*Dinornis giganteus*)	250	4	1-2	178 x 253	7,000	2.80	Oliver (1949) Grzimek (1972)
Elephant Bird (*Aepyornis maximus*)	454	3	n.a	> 300 long. (c. 100 1 in volume).	n.a	n.a	Carlquist (1965) Grzimek (1972) Mahe (1972)
African Ostrich (*Struthio camelus*)	150	2	16-24	116 x 145	1,200	0.80	Grzimek (1972)
Emu (*Dromaius novaehollandiae*)	55	3	15-25	90 x 135	600	1.09	Davies (1967) Long (1965) Grzimek (1972) Noble (1975a)
Cassowary (*Casuarius casuarius*)	60	3	3-8	90 x 135	650	1.08	Grzimek (1972) Crome (1976)
Common Rhea (*Rhea americana*)	25	3	15-20	95 x 135	600	2.40	Grzimek (1972)
Brown Kiwi (*Apteryx australis*)	3	4	1	78 x 125	430	14.3	Grzimek (1972) Reid & Williams (1975) Reid (1981)

The egg dimensions for both extant and extinct ratites are shown in Table 1. In relative terms the elephant birds and the kiwis produced the largest eggs per unit bodyweight. The kiwi, according to Gould (1986), is a phyletic dwarf having evolved from much larger ancestors laying eggs appropriate to their size. Allometric relationships between egg and body weights (Rahn et al. 1975) suggest that while the kiwi body decreased greatly in bulk, egg size remained the same or was only slightly reduced. Carlquist (1965) has addressed the question of what is the largest egg size possible in terms of structural and physical considerations claiming maximum limits for egg size and body size in birds were attained by the elephant bird (*Aepyornis* sp.) whose 30 cm long egg with a shell several millimetres thick was first described in 1832 (Grzimek 1972).

Similar considerations apply to the largest fruit capable of ingestion and subsequent dispersal by ratites. Whilst the ecological ramifications of body size have been discussed by Peters (1983), certain questions relating to ratite size are germane to this paper. Does the large size of continental ratites enable them to eat certain plant foods unavailable to other birds, and has this been important in the evolutionary success of both predator and prey? Furthermore, does the gastrointestinal system of ratites bestow any benefits on dispersed plant propagules?

The potential ecological significance of this distinctive group of birds rests primarily on two fundamental characteristics; firstly, the fact that they are essentially terrestrial animals and secondly, their disproportionately large size when compared with other birds. It can be postulated that ratites have a significant influence on the seed dispersal and seedling establishment of some plant species through their ability to transport large quantities of diaspores and also their capacity to ingest fruit too large for other birds. Being terrestrial, their large size also implies some potential for physically modifying vegetation as they move through the landscape, particularly in groups. The male ostrich, standing up to

3 m in height and weighing more than 150 kg (Grzimek 1972), is the largest of the living ratites. As shown in Fig. 3, there is a linear progression in size from the kiwi, through the intermediate-sized rhea, cassowary and emu to the four largest ratites, three of which are now extinct.
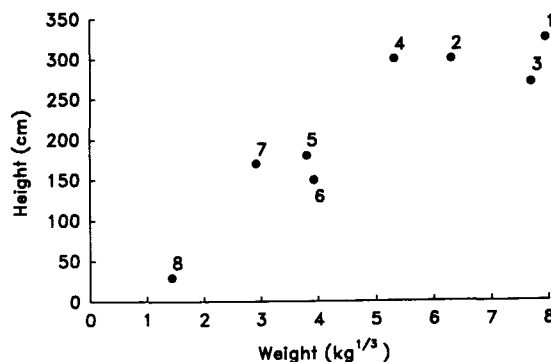

Fig. 3: The relationship between ratite height and cubed root of weight for selected species. Size specifications were obtained from a number of sources cited in Table 1.

1 = Giant Mihirung (*Dromornis stirtoni*)
2 = Giant Moa (*Dinornis giganteus*)
3 = Elephant Bird (*Aepyornis maximus*)
4 = African Ostrich (*Struthio camelus*)
5 = Emu (*Dromaius novaehollandiae*)
6 = Cassowary (*Casuarius casuarius*)
7 = Common Rhea (*Rhea americana*)
8 = Brown Kiwi (*Apteryx australis*)

La relación entre la altura de la rátida y la raíz cúbica del peso de especies seleccionadas. Las especificaciones de tamaño se obtuvieron de diversas fuentes citadas en la Tabla 1.

1 = Mihirung Gigante (*Dromornis stirtoni*)
2 = Moa Gigante (*Dinornis giganteus*)
3 = Pájaro Elefante (*Aepyormis maximus*)
4 = Avestruz Africana (*Struthio camelus*)
5 = Emu (*Dromaius novaehollandiae*)
6 = Casuario (*Casuarius casuarius*)
7 = Ñandú Común (*Rhea americana*)
8 = Kiwi Pardo (*Apteryx australis*)

DISTRIBUTION PATTERNS, FOSSIL RECORDS, HABITAT

Preferences and Sociability

The distributions of contemporary ratites, i.e. the rheas (*Rhea americana and Pterocnemia pennata*), the ostrich (*Struthio camelus*), the kiwis (*Apteryx australis, A. oweni* and *A. haasti*), the cassowaries

(*Casuarius unappendiculatus, C. casuarius* and *C. bennetti*) and the emu (*Dromaius novaehollandiae*), are shown in Figure 4. Australia is unique in being the only continent where birds from more than one ratite genus can still be found alive in contrasting habitats, i.e. cassowaries in tropical rainforest and emus primarily in semi-arid grassland/shrubland.

Details of habitat and social behaviour amongst ratites are summarised in Table 2. The emu, cassowary and kiwi are distinguished by the fact that for most of the year they are solitary or form breeding pairs. On certain occasions however, cassowaries (White 1913), kiwis (Reid *et al.* 1982) and emus (Noble 1985) may form flocks when feeding around fruiting shrubs and trees. The rhea and ostrich in contrast, may form large loose flocks, particularly during the breeding season.

One social feature common to all extant ratites is the degree to which the male bird is responsible for incubation. The male kiwi incubates the large, single egg for a period ranging from 85 to 92 days (McLennan 1988) and has ample fat reserves enabling him to survive fasts lasting up to 7 days. Both the rhea and the ostrich have shorter incubation periods of 35-42 days however while the male rhea incubates alone (Bruning 1974), incubation is shared by both the male and major female ostrich (Bertram 1980). The male emu has considerable fasting capacity and may incubate without eating or drinking for 56 days before leaving the nest with the chicks which hatch over a four day period (Davies 1976). The male cassowary also rears the chicks after an incubation period lasting from 47-53 days (Crome 1976).

EXTANT RATITE GENERA

Ostriches

There are currently five subspecies of ostriches surviving although a sixth, *Struthio camelus syriacus*, disappeared only recently in the 1920s from its range in Asia Minor and Arabia (Davies 1976). Grzimek (1972) refers to eight extinct species, all belonging to the genus *Struthio*. These birds were

well established in Africa by the mid-Tertiary and possibly much earlier, with ostrich-like birds found in the fossil records of Asia, Europe (Kurochkin & Lungu 1970) and Africa (Rich & Balouet 1984). Recent fossil studies (Houde 1986, Howgate 1986) indicate that the ancestors of ostriches evolved from a group of North American and European birds, the "Lithornis-cohort", that could fly.

Whilst the Lithornidae may have had a capacity for flight, they were found to possess a palaeognathous palate thereby extending the fossil record of palaeognathous birds back to the late Palaeocene (Houde 1988). *Palaeotis wigelti* was a crane-sized, flightless, palaeognathous ostrich from the Middle Eocene of Germany (Houde 1986). One biogeographical feature of the contemporary ostrich is its transtropical distribution, other ratites being restricted to the Southern Hemisphere. Ostriches generally inhabit the open savannas of Africa although they are extremely adaptable grazers, *S. c. molybdephanus* frequenting scrubland in Somaliland (Leuthold 1970).

Rheas

Within the ratites, the ostriches have been closely allied by taxonomists to the two species of South American rheas (Rich & Balouet 1984). Both are cursorial, inhabiting a similar range of habitats in opposing continents. *Rhea americana* (greater or common rhea) is regarded primarily as an inhabitant of the Pampas grasslands east of the Andes but in Brazil, where it was once common, its abundance has declined markedly (Davies 1976). *Pterocnemia pennata* is somewhat smaller than *R. americana*, occurring from Patagonia to the high plateaux of the Andes (Mayr & Cottrell 1979). Like the ostrich, the fossil record of the rhea extends back in the Cainozoic, and it was present in South America by the Pliocene (Brodkorb 1963).

Emus

The Australian emu (*Dromaius:* Dromaiinae) has a pan-continental distribution and is

1 Casuarius unappendiculatus

2 Casuarius casuarius

3 Casuarius bennetti

4 1:2:3

Dromaius
novaehollandiae

A Apteryx australis mantelli

B Apteryx a. australis

C Apteryx a. lawryi

D Apteryx oweni, A. haasti

Pterocnemia pennata pennata

Pterocnemia p. tarapacensis
Pterocnemia p. garleppi

Rhea americana americana

Rhea a. intermedia

Rhea a. nobilis

Rhea a. araneipes

Rhea a. albescens

Struthio camelus camelus

Struthio c. australis

Struthio c. molybdophanus
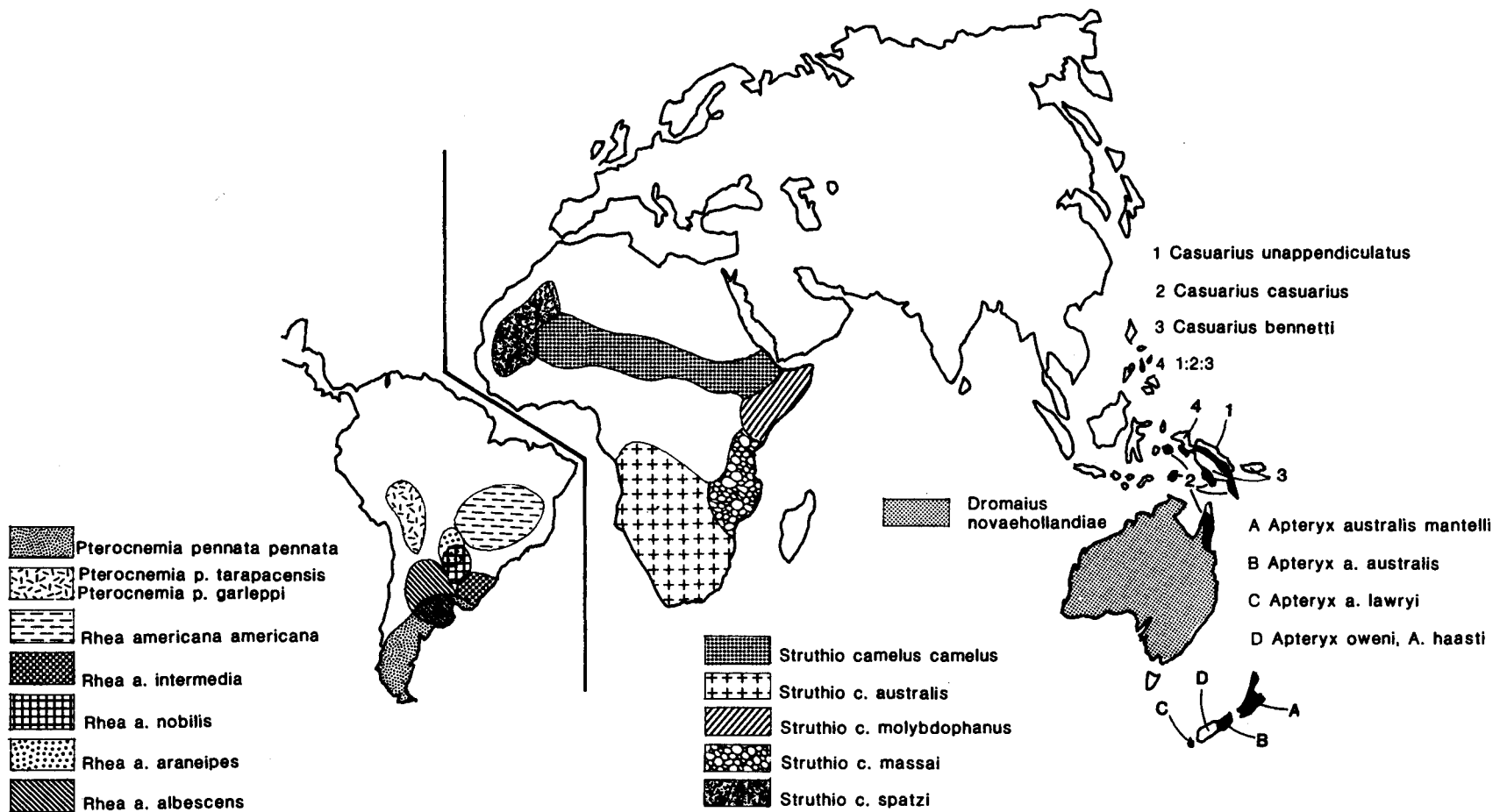
Struthio c. massai

Struthio c. spatzi

Fig. 4.: The world distribution of extant ratites (after Davies 1976).

La distribución mundial de las rátidas sobrevivientes (según Davies 1976).

TABLE 2

Habitat, social behaviour, diet and anatomical features of extant ratites.

Habitat, comportamiento social, dieta y características anatómicas de rátidas sobrevivientes.

Species	Habitat	Sociability	Diet	Gastro-Intestinal Tract	Reference
Rhea	Grass steppes of South American lowlands and plains up to 4,000 m in the Andes.	Loose flocks up to 50 females after breeding season. Polygamous.	Grasses and herbs (alfalfa, clover, serradella), fruit, insects and small animals.	Gut and particularly caeca very long. Urine stored in expansion of cloaca before elimination in liquid form.	Grzimek (1972) Bruning (1974) Davies (1976)
Ostrich	Open savanna in dry South African "bushveld", wide sandplains or desert or dense bush. Adaptable grazer and also found in steep rocky mountain country up to 3000 m in East Africa.	Often form peaceful aggregations up to 680 birds but individual flocks remain identifiable. Polygamous.	Supplement plant diet of various grasses, bushes and tree forage with invertebrates and small animals.	Three stomach segments with gut up to 14 m long. Rectum especially extended and caeca about 70 cm long. Urine concentrated in large cloaca but unlike other birds is secreted separately from faeces.	Grzimek (1972) Robinson & Seeley (1975) Davies (1976) Bertram (1980) Bakker (1987)
Emu	Grassland and savanna woodlands of semi-arid Australia primarily.	Solitary or breeding pairs for much of year except when feeding on specific diet when birds may form large flocks up to 80 in number. Monogamous.	Grasses and herbs, fruits from shrubs and trees and invertebrates.	Gut and caeca shorter than in rheas. Strongly developed gizzard musclature. Fermentation contained within the ileum.	Long (1965) Grzimek (1972) Dawson & Herd (1983) Herd & Dawson (1984) Noble (1985)
Cassowary	Tropical rainforests and fringes. Also woodland up to 3000 m altitude.	Solitary and only pair during breeding. Monogamous. Small flocks concentrated around fruiting trees.	Fallen fruit.	Gut and caeca shorter even than emus.	White (1913) Crome (1976) Davies (1976) Stocker & Irvine (1983)
Kiwi	Primarily subtropical and temperate rain-forest but also shrub, native grassland and even exotic forest. Sea level to alpine meadows.	Many form small flocks around fruiting trees. Solitary or as breeding pair. Monogamous. Nests underground.	Mainly invertebrates but vegetable matter including tree fruit commonly found in varying amounts.	Proventriculus small 75 x 55 mm, gizzard moderately muscular and 2 well developed caeca of equal length, each 19 cm long. Total length of alimentary canal 215-245 cm.	Oliver (1955) Watt (1971) Reid & Williams (1975) Reid et al. (1982) McLennan (1988)

traditionally associated with grassland and savanna formations where pastoralism is the dominant land use (Fig. 5). It can also be found in such extreme habitats as the Great Dividing Range in the east, even above the snow-line (Davies 1976), and dense mallee (*Eucalyptus* spp.) scrubland in southern Australia (Noble, pers. observ.). The word "emu" is derived from the Portugese "ema" meaning cranelike which itself is derived from the Arabic *"Naamah" (naema)* meaning ostrich (McDonald 1986).

There were originally three other species living on coastal islands but these disappeared in the first 150 years following European settlement. The black emu (*Dromaius ater*, syn. *D. minor*), which was darker and smaller than *D. novaehollandiae*, was discovered in 1802 on King Island (Grzimek 1972, Boles 1991). Two birds were shipped to Paris in 1804 and kept in a private zoo by the Empress Josephine; the last died in 1822. The last known Tasmanian emu (*D. diemenianus*) survived until 1873 (Dove 1926, Boles 1991), while the species resident on Kangaroo Island (*D. baudinianus*) has only recently been recognised (Parker 1984).

The fossil record of the emus extends back to the mid-Tertiary in central Australia with one species (*D. ocypus*) collected from Pliocene sediments (Rich & Balouet 1984). More recently, another species (*D. gidju*) has been described from Oligocene/Miocene deposits in central Australia (Patterson & Rich 1987). Additional material of this small, gracile emu has been subsequently found from deposits of similar age in northwestern Queensland. This material prompted a systematic revision by Boles (1991) describing the new genus *Emuarius*, formed by combining "Emu" and "Casuarius", because many of its features are intermediate between both taxa.

Cassowaries

Although the emu and the cassowary are taxonomically allied (both belong to the Casuariidae: Casuariiformes), the three species of cassowary (*Casuarius:* Casua-

riinae), the single-wattled cassowary (*Casuarius unappendiculatus*), the double-wattled cassowary (*C. casuarius*) and the mountain or dwarf cassowary (*C. bennetti*), are quite distinct ecologically from the emu. The cassowaries inhabit dense tropical rainforest. In the rainforests of Cape York peninsula in Australia, only one subspecies (*C. casuarius johnsonii*) occurs (Crome 1976), whereas all three species can be found in New Guinea (Fig. 3). Diamond (1972) has referred to one subspecies of the dwarf cassowary (*C. bennetti shawmayeri*) resident in the Eastern Highlands of New Guinea. A large number of other subspecies have been superficially described for many island populations of cassowaries yet little is known about the influence of sexual dimorphism or age changes on diagnostic characters (Mayr & Cottrell 1979). Any simple geographical discrimination of subspecies is dubious because it is known that Melanesians take tame young cassowaries with them on canoe voyages between islands.

The birds are solitary in nature and are quite aggressive, being the only ratites with sharp claws (Majnep & Bulmer 1977). They develop a casque on the head (Crome & Moore 1988) which acts as a "crash helmet" protecting the eyes and cranium when moving through dense forest or when used defensively (Carlquist 1974). The fossil record of the cassowary is sparse with only a late-Pleistocene record of a pygmy cassowary (*Casuarius lydekkeri*) from New Guinea and an uncertain fossil from Australia (Rich 1975, Rich & van Tets 1982, Rich *et al.* 1988).

Kiwis

The kiwis (*Apteryx australis, A. oweni* and *A. haasti*) pose considerable systematic problems and some workers have suggested closer relationships to the cosmopolitan rails (Rallidae) and tinamous (see Rich & Balouet 1984) than to the ratites.

Based on the dates provided by the DNA-DNA hybridization clock of Sibley and Ahlquist (1981), Diamond (1983) postulated that the kiwi ancestor reached New Zealand from Australia via an island
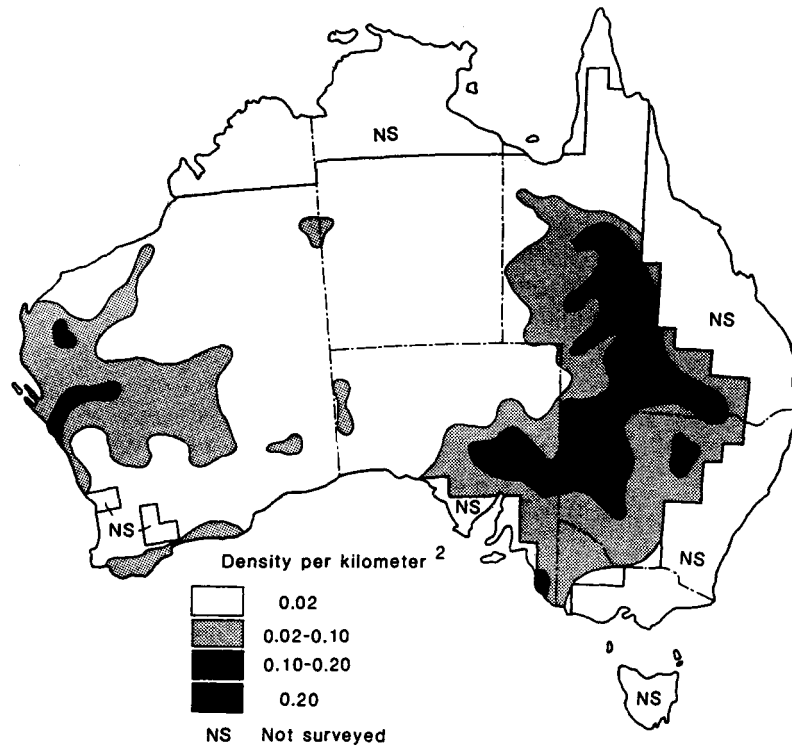
Fig. 5a: The distribution of emu-group density in the area surveyed by Grice *et al.* (1985).

La distribución de la densidad del grupo del emu en el área estudiada por Grice *et al.* (1985).
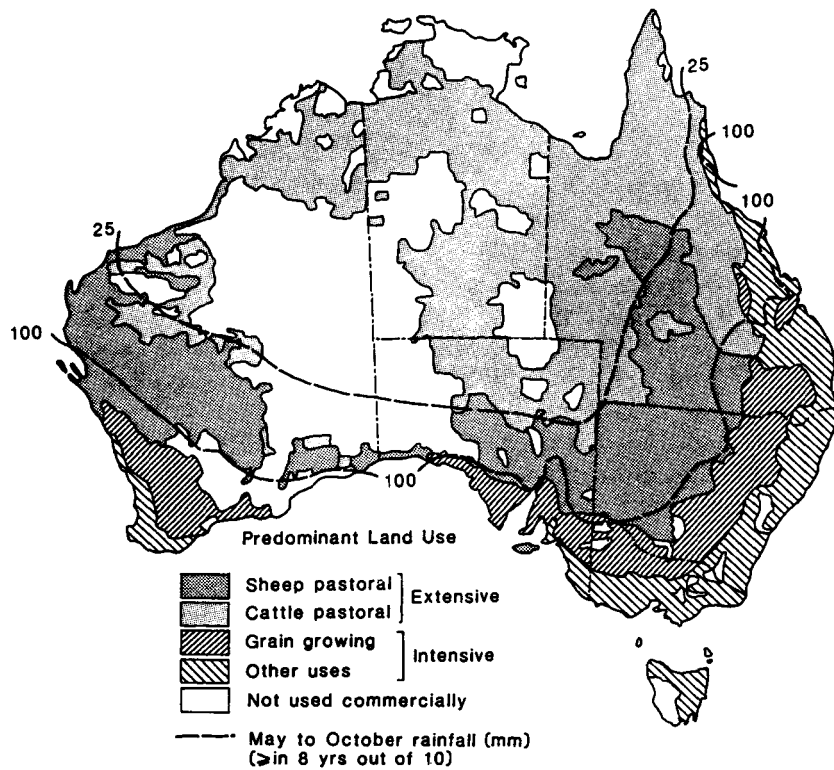
Fig. 5b: Land use zones in Australia (adapted from the Atlas of Australian Resources 1973).

Zonas de uso del terreno en Australia (adaptado del Atlas de Recursos Australianos 1973).

archipelago situated along the rises now bearing Norfolk and Lord Howe islands, with the three species of kiwis diverging within the last 10 Myr. Nevertheless, dates provided by this molecular clock still require futher calibration before they can be regarded as absolute (Howgate 1986).

The kiwis have been able to utilize a wide range of habitats including exotic pine forests and farm pasture, as well as rainforests and their margins. They are essentially nocturnal feeders. There are three subspecies of the brown kiwi, each based on geographical location, viz. North Island brown kiwi (*Apteryx australis mantelli*), South Island brown kiwi (*A. a. australis*) and Stewart Island brown kiwi (*A. a. lawryi*). The little spotted kiwi (*A. oweni*) was once widespread in both the North and South Islands but has not been recorded from the North Island for nearly a century (Reid & Williams 1975). The great spotted kiwi (*A. haasti*) is found only in the South Island west of the southern Alps.

EXTINCT RATITE GENERA

Moas

While the two groups of extinct moas (the Dinornithidae and the Emeidae) are closely related (Rich 1979), their relationship to the kiwis remains unclear. These relationships are unlikely to be refined through more detailed study of the fossil record since the oldest moa (*Anomalopteryx antiquus*) is late Pliocene and the oldest kiwi Pleistocene (Rich & Balouet 1984). The moas, endemic to both main islands of New Zealand, were classified by Oliver (1949) under the six genera *Anomalopteryx, Dinornis, Emeus, Eurapteryx, Megalapteryx* and *Pachyornis*. Oliver listed twenty-nine species, but this total was later reduced by Cracraft (1976) to thirteen species although neither classification has proved totally acceptable (e.g. Caughley 1977, Trotter & McCulloch 1984). Worthy (1988, 1990) has subsequently described eleven species, two of which (*Euryapteryx curtus* and *Pachyornis mappini*) were endemic to the

North Island, four (*Megalapteryx didinus, Emeus crassus, Pachyornis australis* and *P. elephantopus*) were endemic to the South Island, while five species (*Anomalopteryx didiformis, Euryapteryx geranoides, Dinornis struthoides, D. novaezealandiae* and *D. giganteus*) were common to both islands. The moas apparently inhabited primarily forests and their margins (Burrows *et al.* 1981, Anderson 1982) although evidence suggests they used shrublands and subalpine areas as well (Atkinson & Greenwood 1989, Worthy 1990).

Mihirungs

Accounts of the evolution, and ultimate demise, of the Dromornithidae in Australia provide fascinating reading (e.g. Rich 1979, Rich & van Tets 1982, Rich & Balouet 1984). While palatal evidence is still lacking, these birds may not have been ratites (P. Rich, pers. comm.). These flightless birds were endemic to this country being unique in possessing hoof-like, ungual phalanges. Their most distinctive feature was their size, some being truly gargantuan (Rich 1981) and they are probably the largest birds ever known standing more than 3 metres high and weighing more than 500 kilograms.

Taxonomic studies (Rich 1979) have at this point identified four genera and seven species present in the Miocene (*Barawertornis tedfordi; Bullockornis planei* and a second species of *Bullockornis* not yet named; *Dromornis australis, D. stirtoni; Ilbandornis woodburnei,* and *I. lawsoni*) with only the *Dromornis* species surviving into the Pliocene (Fig. 6). The only dromornithid present in the Pleistocene was *Genyornis newtoni* which survived up until at least 26,000 years B.P. (Rich 1981), thereby overlapping with colonisation by Aborigines.

Elephant Birds

Until the dromornithids had been adequately described, it was generally assumed that the elephant birds (Aepyornithidae) were the largest birds ever to have existed, some
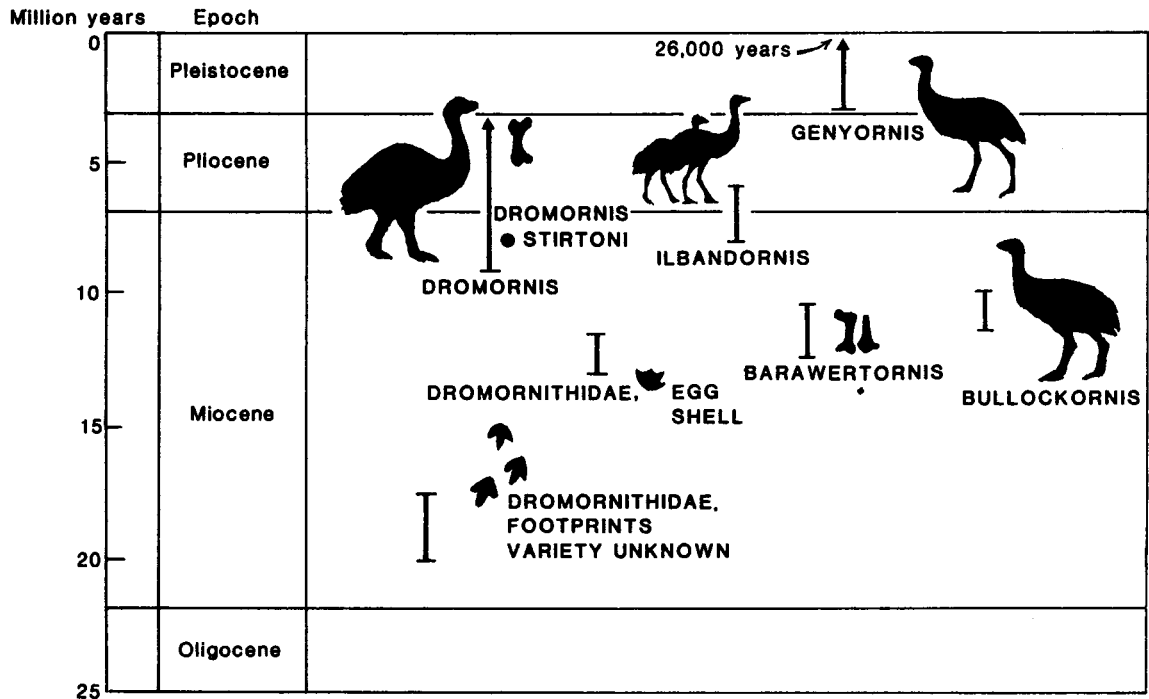
Million years   Epoch

		26,000 years
0	Pleistocene	
5	Pliocene	GENYORNIS
		DROMORNIS • STIRTONI ILBANDORNIS
10		DROMORNIS
15	Miocene	DROMORNITHIDAE, EGG SHELL BARAWERTORNIS BULLOCKORNIS
20		DROMORNITHIDAE, FOOTPRINTS VARIETY UNKNOWN
25	Oligocene	

Fig. 6: Stratigraphic distribution of the Dromornithidae in Australia (after Rich 1981).

Distribución estratigráfica de las Dromornitidas en Australia (según Rich 1981).

estimated to weigh from 450 kg (Amadon 1947, Carlquist 1965). These birds were unusual taxonomically in having no clear relationship with any other ratites, some features being common to ostriches-rheas and others similar to moas-kiwis (Rich & Balouet 1984). The meagre fossil record of both genera (*Aepyornis* and *Mullerornis*) suggests that *Aepyornis* at one stage inhabited the African continent at the beginning of the Tertiary (Mahe 1972). Like the moas, elephant birds survived the Pleistocene with *Aepyornis* surviving longer than *Mullerornis* (Carlquist 1965). The first French governor of Madagascar, Flacourt, initially described these "giant ostriches" with one particular bird called Vouron Patra, still frequenting the southern half of the island until the mid 17th century (Grzimek 1972).

EXTINCTION AND INTERACTION WITH MAN

The dromornithids apparently became extinct following habitat destruction through increasing aridity and the ever decreasing mesophytic forests covering much of Australia in the Tertiary (Martin 1982, Truswell & Harris 1982, Rich & Balouet 1984). Even though *Genyornis newtoni* overlapped with Aboriginal occupation, it is uncertain whether hunting was a significant factor in its ultimate disappearance (Rich 1981).

Extinction of the New Zealand moas however followed the arrival of Polynesian man around 1000 A.D. Not only did clearing and extensive use of fire result in a dramatic reduction of forests, but archaeological evidence from middens points to their use as a major source of food (Simmons 1968, Trotter & McCulloch 1984). Even the term moa, a Polynesian word for common fowl, denotes a culinary connection. Though some, like the *Dinornis* species, were probably capable of running (Cracraft 1976), the large size and reduced mobility of these graviportal (walking) species, must have made them easy prey. On the basis of moa-bone collagen and marine shell dating of moa-hunter sites, Caughley (1988) has calculated that moas and Polynesians coexisted in any single

district for only about one century. In any event, by 500 B.P. they were so scarce as to be rarely hunted (Anderson 1984).

The elephant bird was possibly the most recent ratite to become extinct. Like the moa, its ultimate demise has been attributed solely to human activities, including both direct predation and indirect destruction by burning of their forest habitat (Battistini & Verin 1972).

This lethal response to human activities has continued partially for the ostriches with their extermination by hunting from North Africa, Egypt, Iran and Arabia. Their future in southern Africa at least seems relatively secure following the establishment of conservation areas and ostrich farms. The latter were set up initially in South Africa as early as 1838 (Mosenthal & Harting 1877), and later in Algeria, Sicily, France and Florida (USA), to fill a fashion demand for hat feathers before later changing to leather production, 42,000 ostriches being kept for this purpose in South Africa as recently as 1970 (Grzimek 1972).

Ostrich farming was also attempted in Australia from the 1860s until 1914 (Rolls 1969). Commercial flocks were run on several properties in western New South Wales including some near Deniliquin (Eastman 1953) and north of Swan Hill in Victoria (Casey 1966), ostriches being fed mainly on irrigated alfalfa (*Medicago sativa*). The white wing feathers of the male bird, cut twice annually (1.4 kg/bird/cut), realized *c.* A$57-79 per kg at that time (*The Illustrated Australian News*, December 23, 1882). Commercial operations ceased in 1914 due to the outbreak of World War I, France and Germany hitherto being the best markets. The price for ostrich feathers by that time had fallen to 5 sovereigns per lb (*c.* A$30/lb or A$66/kg at current values).

Size alone does not predicate the likelihood of extermination although the larger forms are obviously more vulnerable to hunting. Even the smallest ratite has been exploited in the past by humans. The Maoris did not regard kiwis as an important food source, although they did periodically hunt them using dogs and digging up their burrows (Oliver 1955). They prized their feathers for making the highly valued *Kahu-kiwi*, a feather cloak. Europeans also hunted kiwis extensively last century for their feathers which were used for feather muffs in Europe, one hunter killing more than 2000 birds in one season (Reid & Williams 1975) before they became fully protected.

Exotic predators introduced by Europeans have also imposed considerable depredations on kiwi populations, highlighting the vulnerability of these island species to such predatores as the fox (*Vulpes vulpes*), ferret (*Mustela putorius*), cat (*Felis catus*) and dog (*Canis familiaris*) (Diamond 1989). Taborsky (1988) documented the case where a single dog killed 13 North Island brown kiwis (*Apteryx australis mantelli*) out of a total of 23 carrying radio transmitters. The whole population may therefore have lost 500 out of 900 birds requiring 10-20 years of rigorous protection from predation for complete population recovery to occur.

The intermediate-sized rheas, cassowaries and emus have also been significantly affected by human activities. The rheas are possibly the most vulnerable of the three at the present time due to hunting for sport, loss of habitat by fencing, and replacement of native pastures with exotic species for cattle fodder (Bruning 1973). Unlike the rheas, whose meat is relatively unattractive and plumage of little value, the cassowaries are highly valued by Melanesians for eating, and their feathers are also utilized for headdress. There have been some attempts at domestication of cassowaries in the Highlands of New Guinea because of their trading value, a fully grown cassowary in 1973 fetching up to A$400, exceeding the price paid for a pig or cow (Majnep & Bulmer 1977).

The greatest threat to the Australian cassowary lies in the destruction of tropical rainforest habitat for agriculture although several conservation areas have been established in Cape York. Management problems in such reserves occur periodically following cyclone damage when much of the cassowaries' food supply, particularly in small rainforest remnants, is eliminated.

Because these have no natural corridors linking them with other less damaged reserves, conservation managers have to resort to supplementary feeding of cassowary populations until the rainforest regenerates (McKenzie 1986). Whilst the conservation status of cassowaries in New Guinea and other islands is unclear, Australian populations are relatively stable at densities of 1 bird to every 5 to 15 km² (Crome 1976).

The emu has long been an important food source for Aboriginals (McCarthy 1965) who used narcotics derived from plants such as pituri (*Duboisia hopwoodii*-Solanaceae) to drug water used by emus, thus enabling the semi-comatose birds to be easily trapped (Cunningham *et al.* 1981). Europeans arriving in the First Fleet in February 1788 first named the emu the New Holland cassowary (Stockdale 1789). Hotham provided the first scientific name of *Casuarius novaehollandiae* (Stanbury 1987). With the advent of Europeans, significant changes have occurred to emu populations (Grice *et al.* 1985). While numbers have undoubtedly declined in the more closely settled areas of the continent through loss of habitat, there are probably more emus present today than there were prior to European colonisation in 1788 (Davies 1976).

This increase can be primarily attributed to the additional watering facilities provided for sheep and cattle in the pastoral areas following closer settlement (Noble & Tongway 1986, Davies 1986). Emus require water daily, even in the winter except when the males are incubating. When transient water-holes in the desert dry out, the birds may migrate *en masse* towards permanent waters in settled areas. Protection from canine predators following wild-dog trapping and the construction of dingo (*Canis familiaris dingo*)-proof fencing, also contributed to increasing emu abundance in protected areas (Arnold 1941, Caughley *et al.* 1980).

The emu is now a protected species in eastern Australia. In the 1930s, it was regarded as a major pest in the wheatgrowing areas of Western Australia (Long 1965), despite the fact that, during the winter months, emus can consume significant quantities of pasture-eating caterpillars (Gooding & Long 1959). Large flocks of emus from the drought-stricken inland would periodically invade marginal cropping areas when cereal crops were ripening, resulting in one case in November 1932, of army personnel being employed with machine guns to shoot marauding flocks. In 1935, it was estimated that 86,000 had been killed in the Northampton district alone and as recently as 1970, the Western Australian government paid bounties on 24,479 emus (Riggert 1975). Landholders in Western Australia now have the right to destroy emus on their own properties but elsewhere they are protected under the Fauna Conservation Act. Since 1975, licences to farm emus have been granted at two locations in Western Australia for the commercial production of medicinal oil and leather for high fashion clothing.

DIET, INTERNAL ANATOMY AND GIZZARD STONES

The anatomy and physiology of the alimentary canal and digestive system in birds have been described by Worden (1964) and Ziswiler and Farner (1972). The gastric system in birds comprises two distinct chambers, an anterior glandular stomach or proventriculus and a posterior muscular stomach or gizzard. The proventriculus not only functions mainly as a site for the secretion of gastric juices but also as a storage area where limited peptide digestion occurs. The gizzard remains the primary site of digestion, both for mechanical digestion and also digestion by acid proteolysis whereby proteins are reduced to their constituent amino acids.

The emu and the ostrich differ from other ratites by having almost no crop, with only a slight swelling noticeable in the oesophagus (Davies 1978). The gizzard in these ratites is positioned so that the anterior entry in the left side and the posterior exit on the right side are both dorsal (Fig. 7). The dimensions of the gastrointestinal tract of the adult emu, and characteristics of gut contents after eating herbage, are shown in Table 3.
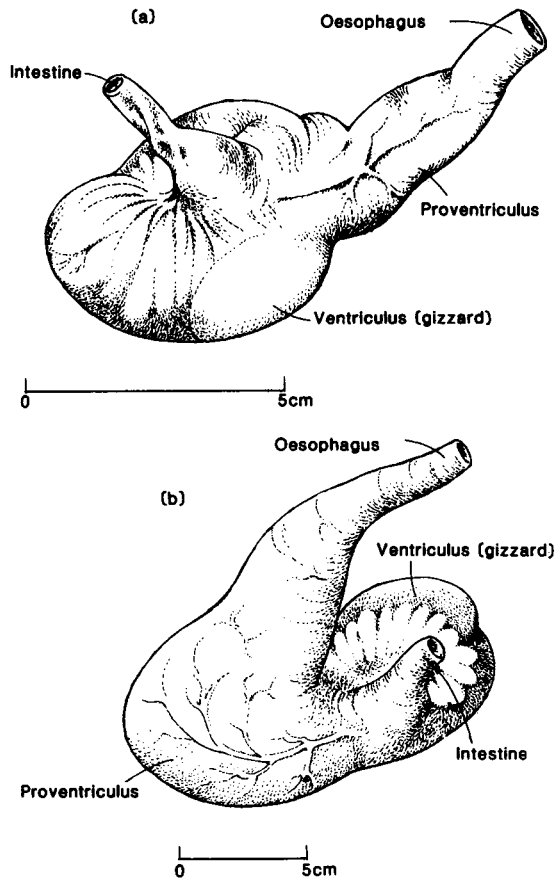
(a)

Oesophagus

Intestine

Proventriculus

Ventriculus (gizzard)

0   5cm

Oesophagus

(b)

Ventriculus (gizzard)

Intestine

Proventriculus

0   5cm

Fig. 7: Diagramas illustrating the gizzard region of (a) an emu chick about 2 weeks old and (b) an ostrich chick about 4 weeks old. Both organs are shown as if the birds were standing upright with the front of the bird facing the right hand margin (after Davies 1978).

Diagramas que ilustran la región de la molleja (a) un polluelo de emu de más o menos 2 semanas y (b) un polluelo de avestruz de más o menos 4 semanas. Se muestran ambos órganos como si las aves estuvieran paradas derechas con el frente del ave hacia el margen derecho (según Davies 1978).

A sophisticated digestive tract, based on fermentation in extremely long intestines, can provide processing systems that efficiently and rapidly reduce plant cellulose material. "Giant ground birds —rheas and ostriches— have tiny heads and no teeth whatever, yet these birds successfully employ rearward fermentation on a large scale" (Bakker 1987). The emu digests and metabolises plant fibre through fermentation within the ileum, the distal segment of the small intestine (Herd & Dawson 1984). It can compensate for the lack of

any specialised chambers in the gut for fermentative digestion because of its large body size and low metabolic rate (Calder & Dawson 1978, Dawson & Herd 1983).

The one internal organ likely to have the greatest impact in terms of plant-animal interactions, especially in relation to seed dispersal and germination, is the gizzard. In many birds, the muscular gizzard is regarded as the analogue of mammalian teeth. Mechanical grinding of food particles in ratite gizzards is often aided by stones collectively held as an accesory grinding device at certain times. Such gastroliths can be extremely useful in the field to palaeontologists searching for the remains of extinct forms (see Table 4). Rich (1981) described the piles of small, rounded stones on the otherwise featureless surface of salt lakes in arid Australia which commonly overlaid the remains of mihirungs trapped in unstable sediments around 35,000 years ago.

Gastroliths have also been conspicuous in preserved moa gizzards, individual stones measuring up to 9.6 cm in length with an entire stone collection from a single Dinornis weighing over five kilograms (Burrows et al. 1981). Rounded quartz stones, reputably moa gizzard stones, have been found overlying totally different parent rock material at altitudes up to 1700 m in the Westland of the South Island (Atkinson & Greenwood 1989). Widespread moa gastroliths were recorded last century in the scrublands of the North Island by pioneer farmers and gumdiggers searching for kauri (Agathis australis) gum.

The ability to carry such stone loads internally was obviously enhanced by the size of these birds and the fact that they were not required to fly. Other extinct flightless birds including the dodo (Raphus cucullatus) and the solitaire (Pezophaps solitarius) of the Mascarene Islands also possessed gizzard stones, one solitaire's gizzard containing a stone of "the size of a hen's egg" (Hachisuka 1953, p. 97). The dietary significance of gizzard stones is uncertain and the presence of stones does not necessarily imply, as Owen thought in the case of the dodo (Hachisuka 1953), that a bird is granivorous. The gizzards of

TABLE 3

Dimensions of the gastrointestinal tract of the emu and characteristics of gut contents
(after Herd & Dawson 1984)

Dimensiones del conducto gastrointestinal del emu y características del contenido del intestino
(según Herd & Dawson 1984)

| Region | Dimension[a] | | | | | Gut Contents[b] | |
	Length (m)	Total Length (%)	Weight (g)	Relative Weight (%)	Dry Matter (%)	Osmolality (mosm. kg^{-1})	pH[d]
Oesophagous	0.76	17.1	23	0.7	6.0	340	6.8
Proventriculus	0.14	3.1	86	2.6	16.6	328	2.8
Gizzard	0.11	2.5	1,306	39.7	27.3	290	2.5
Duodenum	0.50	11.2	446	13.6	14.8	681	6.7
Jejunum	1.23	27.6	446	13.6	14.8	681	6.7
Ileum	1.42	31.9	1,260	38.3	12.4	367	8.2
Caecum	0.12[e]	–	5	0.2	30.6	–	–
Rectum	0.29	6.5	165	5.0	16.8	323	7.2
TOTAL	4.45[f]	–	3,291				

a Body weight, 38.3 ± 2.2 kg (n = 3)   b Body weight, 35.3 ± 2.1 kg (n = 3)   c Plasma osmolality 309 mosm. kg^{-1} (Skadhauge 1974)   d pH values, after Davies (1978)   e One caecum   f Excluding caeca

Adelie penguins (*Pygoscelis adeliae*), whose diet is primarily marine, also contain stones (Emison 1968). Mineral grit can also be a significant component of gizzard contents in waterfowl (Norman & Brown 1985, Norman & Mumford 1985).

The ostrich, when eating coarse vegetable matter, may carry up to 907 g of pebbles in its stomach, some 2.5 cm in diameter (Thompson 1964). Stones have also been found in the proventriculus of emus (Noble 1975)a) intimating that some mechanical digestion may be occuring in this organ, although they may have been regurgitated from the gizzard when the birds were shot. Proventriculus samples were obtained from emus feeding in two contrasting habitats on the Riverine Plain of southeastern Australia (Leigh & Noble 1972), one a ripening wheat crop and the other a low shrubland dominated by fruiting nitre bush (*Nitraria billardieri-*Zygophyllaceae). Emus feeding on the wheat contained stones comprising up to 52% by weight of the total proventriculus contents whereas those feeding exclusively on drupes of the nitre bush contained no stones in December and January (Table 5). As the nitre bush component declined, so the stone content increased suggesting replacement of "vegetative stones" by "mineral stones".

A similar replacement phenomenon has been reported for the digestive system of the North Island brown kiwi. After examining the gizzard contents of 50 brown kiwis, Reid *et al.* (1982) found an inverse relationship between the number of seeds from drupes of the hinau tree (*Elaeocarpus dentatus-*Elaeocarpaceae) and the quantity or mineral grit (Figure 8).

Temporal variation in mineral matter content of emu gizzards in Western Australia has been studied over 12 months by Davies (1978). He found a trend for the stone and gravel content to be low in the cooler months and high in the warmer months (Fig. 9). The increase in gizzard mineral content in the summer period indicated a major shift in diet composition. Since seeds were more commonly eaten during this period, a positive correlation may exist between seed and mineral gizzard contents. Regression analysis however found only 41% of the variation in both variables could be attributed to this relationship (Fig. 10).

TABLE 4

Mineral matter recorded in either the ventriculus (gizzard) or proventriculus of different ratites.

Materia mineral registrada ya sea en el ventrículo (molleja) o proventrículo de diferentes rátidas.

Ratite	Max. stone weight per gizzard (g)	% stone (weight) per gizzard contents	% stone (weight) per proventriculus contents	Largest stone weight (g)	Maximum stone length (mm)	Geology	Reference
Emu	98	n.a.*	52	n.a	n.a	Claystone	Noble (1975a)
(*Dromaius novaehollandiae*)	76.3	n.a	45.8	36.4			Davies (1978)
				30.0			Herd & Dawson (1984)
North Island Brown Kiwi	20.2	n.a	n.a	8.8	n.a	n.a	Reid *et al.* (1982)
(*Apteryx australis mantelli*)							
Mihirung	400	n.a	n.a	n.a	n.a	Jasper, siliceous sandstone, claystone and quartz	Rich & Van Tets (1982)
(*Genyornis newtoni*)							
Moa	> 5,000	1.9	n.a	56	96	Quartz	Oliver (1949)
(*Dinornis, Emeus & Euryapteryx* spp.)	4,380						Gregg (1972)
							Burrows *et al.* (1981)
							Trotter & McCulloch (1984)
	24.2	4.81	n.a	n.a	15	Quartz	Eastman (1953)
Ostrich							Thompson (1964)
(*Struthio camelus*)	907				25		Robinson & Seely (19750
Mountain Cassowary	n.a	n.a	n.a	n.a	n.a	Quartz	Majnep & Bulmer (1977)
(*Casuarius bennetti*)							

* Not available.

TABLE 5

Emu diets (% dry weight of proventriculus contents) on two contrasting vegetation types (after Noble 1975a).

Dietas del emu (% de peso seco del contenido del proventrículo) en dos tipos contrastantes de vegetación (según Noble 1975a).

(a) *Nitre bush*

	December (n = 5)	January (n = 5)	February (n = 4)
Nitre bush fruit (seed & pericarp ± S.E.)	96.4 ± 1.5	94.8 ± 1.3	58.6 ± 20.5
Stones	0	0	3.1
Other	3.6	5.2	38.3

(b) *Wheat crop*

	December (n = 6)	January (n = 5)	Mean (± S.E.)
Wheat grain	15.2	16.8	16.2 ± 7.0
Wheat rachis	2.0	5.8	4.4 ± 2.0
Charcoal	7.4	15.5	12.6 ± 4.2
Stones	46.2	52.3	50.1 ± 8.0
Other	29.2	9.6	16.5 ± 4.0
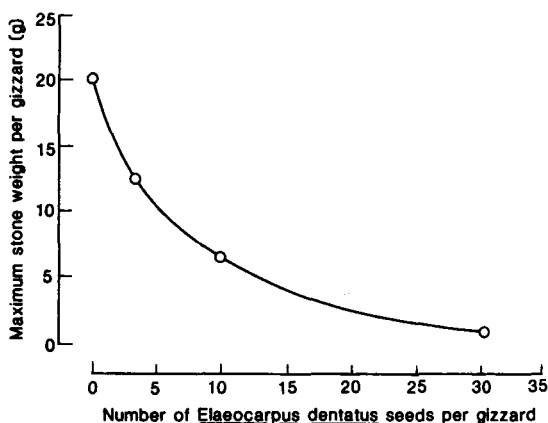
Fig. 8: The relationship between seed content of hinau (*Elaeocarpus dentatus*) and weight of grit in gizzards of the North Island brown kiwi (*Apteryx australis mantelli*). The exponential curve was fitted from data of Reid *et al.* (1982) and is defined as y = 19.58e − 0.11 x (r^2 = 0.99).

La relación entre el contenido de semilla de hinau (*Elaeocarpus dentatus*) y el peso de granos de arena en las mollejas de Kiwi Pardo de la Isla Norte (*Apteryx australis mantelli*). La curva exponencial fue ajustada según los datos de Reid *et al.* (1982) y se define como y = $19.58e^{-0.11x}$ (r^2 = 0.99).

The nature of the diet may also influence the distribution of food residues throughout the gastrointestinal tract. More than half the mass of gut contents resided in the gizzards of emus feeding primarily on *Nitraria* fruit (Table 6), even in February when *Nitraria* comprised only 59% of the diet (Noble 1975a), unlike those feeding solely on herbage when less than half the contents was held in this organ (Table 3).

Unfortunately there is a dearth of information detailing the internal anatomy of the rhea. There are few published reports, if any, of any rhea x plant interactions. Rheas apparently are not very efficient at digesting either grasses or seeds (D. Bruning, pers. comm.).

SEED GERMINATION FOLLOWING DISPERSAL

BY RATITES

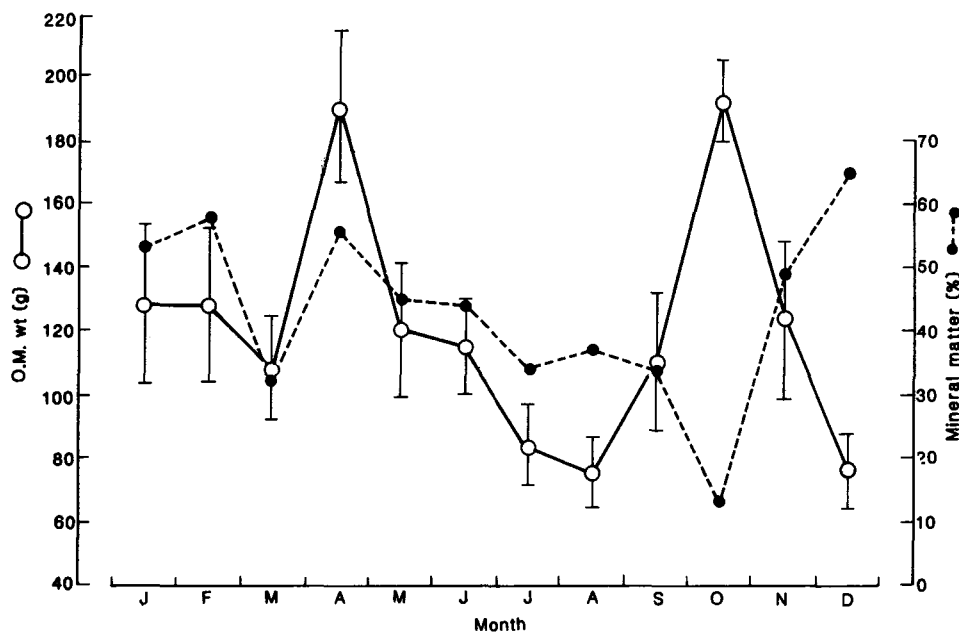In any plant's life history, the germination and seedling establishment phase (ecesis)

Fig. 9: Mean monthly weight of organic fraction (± S.E.) and percentage mineral fraction in gizzards of emus (*Dromaius novaehollandiae*) (after Davies 1978).

Peso mensual medio de la fracción orgánica (± S.E.) y el porcentaje de fracción mineral en mollejas de emus (*Dromaius novaehollandiae*) (según Davies 1978).
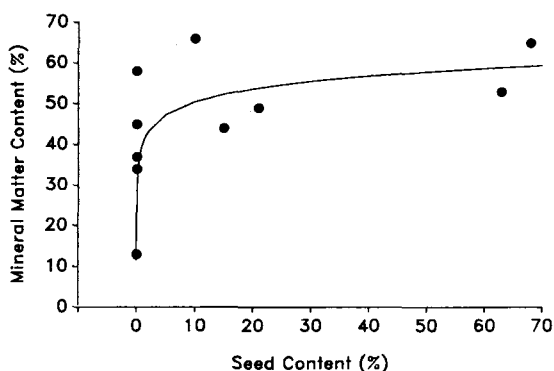

Fig. 10: The relationship between seed and mineral contents of emu gizzards. The logarithmic curve was derived from data of Davies (1978) and defined as: $y = 39.92 + 4.58 \ln x$ ($r^2 = 0.41$).

La relación entre el contenido de semilla y el mineral en mollejas de emu. La curva logarítmica fue derivada de datos de Davies (1978) y definida como: $y = 39.92 + 4.58 \ln x$ ($r^2 = 0.41$).

is critical. The most hazardous period of seedling life occurs at this transition between dependence on seed reserves and independent assimilation (Harper 1977). Seed development and dispersal, and the establishment of seedlings, must all be studied before valid conclusions can be drawn about any "adaptive" significance of plant x animal interactions (Howe & Smallwood 1982).

Ratites, like many granivorous and frugivorous birds, are important seed dispersal agents (Table 7). Unlike many other birds however, they add a further dimension to seed dispersal. Not only can they carry large internal seed loads over considerable distances but they may also confer some selective advantage on the diaspore that is dispersed by enhancing germination in "safe sites" (Harper 1965).

A series of germination experiments conducted with both emu-ingested and non-ingested seed of nitre bush indicated such selective advantege through emu dispersal (Noble 1975b, Noble & Whalley 1978b). Germination was significantly increased by emu ingestion (67% compared with only 17% of hand-collected seed after 24 days) while germination was also much quicker (50% vs. 3% in four days). This improved germination was attributed primarily to removal of the epicarp and mesocarp of the nitre bush drupe during

TABLE 6

Internal partitioning of *Nitraria* fruit and endocarp in emu guts (n = 6)
over one fruiting season (after Noble 1975a)

División interna del fruto y endocarpio del *Nitraria* en los intestinos del emu (n = 6)
durante una estación frutal (según Noble 1975a).

	Oesophagous and Proventriculus		Gizzard		Intestine		Total
	Weight (g)	%	Weight (g)	%	Weight (g)	%	Weight (g)
December	87.9	32.3	173.4	63.6	11.2	4.1	272.5
January	102.1	28.0	169.0	46.4	93.1	25.6	364.2
February	11.0	21.2	39.1	75.2	1.9	3.7	52.0
Mean	67.0	29.2	127.2	55.4	35.4	15.4	229.6

digestion by the emu, chemical analysis of this tissue indicating high concentrations of both sodium (0.4%) and chloride (3.5%).

The osmotic potential created by pericarp residues on non-ingested seed creates major germination problems, demonstrated by soaking hand-collected seed in distilled water and then using the leachate as a moisture source for seed germinating in petri dishes. This leachate contained 416 ppm sodium and 756 ppm chloride and severely depressed germination of emu-ingested seed (Figure 11).

Improved germination may also result from grinding of the nitre bush endocarp in the gizzard, thereby increasing permeability and subsequent imbibition by the embryo. To determine whether such scarification occurred only in the gizzard, the germination of nitre bush propagules collected from different organs in the emu's alimentary tract was compared with faecal and hand-collected controls. After 21 days, there was no significant difference in germination of seed collected from either the proventriculus (5.0%), gizzard (4.5%) or intestine (0.5%); in fact, there was a decline in germination of seed taken from the emu gut, though non-significant, when compared with the hand-collected seed (13.5%).

Davies (1978) found the proventriculus and gizzard of the emu to be acid (pH 2.5-3.2) whereas the intestine and colon were neutral to alkaline (pH 6.7-7.2). Such variations in acidity/alkalinity cannot be easily related to any changes in germination behaviour. The marked improvement in nitre bush seed germination following defaecation by the emu also was partly attributed to the removal of autotoxic residues, as yet unidentified, in the endocarp following diurnal variations of temperature and moisture content in the emu dropping (Noble 1975b).

Numerous, often subtle, factors interact to determine whether a site is suitable for germination. The potential values to plants of having only few seed dispersers depend on both the treatment of the seeds and how they are deposited (Wheelwright & Orians 1982). Faecal deposition of seeds by ratite dispersers such as the emu and the cassowary enhances germination by providing a relatively large and homogeneous microenvironment. When large seeds are not dispersed by suitable agents, they may have difficulty imbibing sufficient water for germination due to the low ratio of seed surface to volume (Harper *et al.* 1970). The quantity of material voided by a ratite in one dropping is sufficient to provide an organic matrix enveloping the dispersed seed thereby optimising seed imbibition, particularly in exposed sites, once this matrix has been saturated by rainfall.

TABLE 7

Plant species whose propagules are dispersed by ratites.

Especies de plantas cuyos reproductores son dispersados por las rátidas.

| Ratite	Plant species	Family	Life Form	Fruit type	Fruit diam. (mm)	Seed weight (g)	Content weight of fully distended gizzard (g)	Reference
Cassowary	Beilschmiedia sp.	Lauraceae	Tree	Berry	60	52	n.a*	Stocker & Irvine (1983)
	Elaeocarpus angustifoluis	Elaeocarpaceae	Tree	Drupe	45	n.a.	n.a.	Stocker & Irvine (1983)
	E. bancroftii	Elaeocarpaceae	Tree	Drupe	45	n.a.	n.a.	Stocker & Irvine (1983)
Emu	Nitraria billardieri	Zygophyllaceae	Shrub	Drupe	5	0.05	280	Noble (1975b)
	Santalum acuminatum	Santalaceae	Tree	Drupe	25	2.3	n.a.	Noble (unpubl. data)
	S. spicatum	Santalaceae	Tree	Drupe	25	2.3	n.a.	Davies (1978)
	Eremophila longifolia	Myoporaceae	Shrub	Drupe	8	n.a.	n.a.	Cunningham et al. (1981)
	Petalostigma pubescens	Euphorbiaceae	Shrub	Drupe	25	5.0	n.a.	Clifford & Monteith (1989)
Kiwi	Elaeocarpus dentatus	Elaeocarpaceae	Tree	Drupe	15	1	49	Reid et al. (1982)
	E. hookerianus	Elaeocarpaceae	Tree	Drupe	n.a.	n.a.	n.a.	Reid et al. (1982)
	Podocarpus dacrydioides	Podocarpaceae	Tree	Nut	n.a.	n.a.	n.a.	Reid et al. (1982)
	P. totara	Podocarpaceae	Tree	Nut	n.a.	n.a.	n.a.	Reid et al. (1982)
	Dacrydium cupressinum	Podocarpaceae	Tree	Nut	n.a.	n.a.	n.a.	Colbourne & Powesland (1988)
	Pentachondra pumila	Epacridaceae	Shrub	Nut	n.a.	n.a.	n.a.	Colbourne & Powesland (1988)
Moa	Podocarpus spicatus	Podocarpaceae	Tree	Nut	n.a.	n.a.	n.a.	Burrows et al. (1981)
	P. dacrydioides	Podocarpaceae	Tree	Nut	n.a.	n.a.	n.a.	Burrows et al. (1981)
	Elaeocarpus hookerianus	Elaeocarpaceae	Tree	Drupe	n.a.	n.a.	n.a.	Burrows et al. (1981)

* Not available.
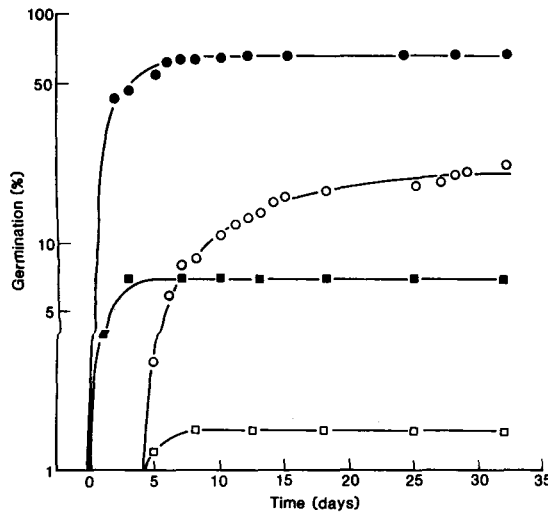
Fig. 11: The influence of distilled water (solid symbols) and fruit leachate (hollow symbols) on the germination of hand-picked (squares) and emu-ingested seed (circles) of nitre bush (*Nitraria billardieri*) (after Noble 1975b). Lines were only fitted for the distilled water treatments and are defined as follows:

emu-ingested (solid circles):

$$\log y = 73.0 \times \frac{10^{-0.4182}}{(x^{-1.2})} (r^2 = 0.96)$$

hand-picked (solid squares):

$$\log y = 21.7 \times \frac{10^{-2.14}}{(x^{-3})} (r^2 = 0.96)$$

La influencia del agua destilada (símbolos sólidos) y lixiviadores frutales (símbolos huecos) sobre la germinación de la semilla del arbusto nitre (*Nitraria billardieri*) recogida a mano (cuadrados) y la ingerida por los emus (círculos) (según Noble 1975b). Las líneas se ajustaron solamente para los tratamientos de agua destilada y se definen de la manera siguiente:

ingerida por emus (círculos sólidos):

$$\log y = 73.0 \times 10^{\frac{-0.4182}{(x^{-1.2})}} (r^2 = 0.96)$$

recogida a mano (cuadrados sólidos):

$$\log y = 21.7 \times 10^{\frac{-2.14}{(x^{-3})}} (r^2 = 0.96)$$

Germination of extremely large seeds has been observed in cassowary droppings (Majnep & Bulmer 1977, Stocker & Irvine 1983). Cassowaries are the only extant frugivores with sufficient capacity, and gape width, to effectively disperse many of the fruits of tropical rainforest species. One cassowary dropping contained 13 fruit of a *Beilschmiedia* species, each with a diameter of *c.* 5 cm and weighing 52 g (Stocker & Irvine 1983). Another enclosed several seeds of *Elaeocarpus bancroftii* whose fruit had a diameter of 4.5 cm.

A feature of the studies by both Crome (1976) and Stocker and Irvine (1983) was the preponderance of drupaceous fruit in the cassowary diet. Whilst the fruit of some species such as *Abrophyllum ornans* (Saxifragaceae) and *Apodytes brachystilis* (Icacinaceae) are technically not classified as drupes, they nonetheless have many of their characteristics (FHJ Crome, pers. comm.). One of these is the ability of the diaspore to pass through the digestive tract of the cassowary relatively undamaged. The large-fruited *Beilschmiedia* "berry" described by Stocker and Irvine (1983) passes through the cassowary more or less intact.

The fruit of two New Zealand species of *Beilschmiedia*, viz. tawa (*B. tawa*) and taraire (*B. tarairi*), are both classified as drupes (Allan 1961), those of taraire having mean dimensions of 31 x 16 mm. Seeds of both these lauraceous species require high humidity, moderate temperature and passage through the digestive system of the New Zealand pigeon (*Hemiphaga novaeseelandiae*) for maximal germination to occur (Myers 1984, West 1986). Myers (1984) found that seed ingested by captive pigeons gave significantly higher germination than intact seed collected from the forest floor (86% vs. 13% in 1982 and 95% vs. 58% in 1983). While rate of germination of pigeon-ingested seed was significantly higher than that of other seed, higher germination resulted when fruit was collected directly from the tree instead of from the ground.

In tropical ecosystems, dispersal of tree seeds by the terrestrial cassowaries occurs through a combination of gravichory when ripe fruit first falls to the ground, and endozoochory, when the fallen fruit is later ingested by the disperser. The reverse applies to smaller, non-ratite frugivores like the New Zealand pigeon which first ingest the fruit directly from the tree canopy before gravichory then occurs as seed is

voided directly on to the ground beneath favoured roosting trees.

Cassowaries probably play a similar role to the New Zealand pigeon in enhancing the germination of seed from large-fruited species of Australian rainforests. Such species are prominent in the Lauraceae, a family of particular importance in the cassowary diet. Crome (1976) found that fifteen species of this family accounted for 19% of all dietary items recorded. Cassowaries also facilitate short-distance dispersal of large diaspores such as those of *Beilschmiedia* spp. (Fig. 12), to either higher ground or ecotonal forest fringes. Longer distance dispersal is likely to be infrequent if, as with *Beilschmiedia* fruit eaten by the New Zealand pigeon, the time taken from ingestion to defaecation is only 2-3 hours, sufficient time nonetheless for the fleshy mesocarp to be stripped from the fruit.

Short passage times suggest that it is unlikely that enhanced germination can be attributed to increased permeability of the endocarp because little time would be available for grinding within the gizzard. Several factors, including the presence and absence of stones, may dictate the duration of the diaspore passage through the bird's gut. In their digestibility trials with captive emus fed diets differing in fibre content, Herd and Dawson (1984) found that mean retention time was 4.1 h for the liquid fraction and 5.5 h for the particulate fraction. Grain can also pass through the emu's gut in 3 hours although most food appears to take from 6-26 hours (Davies 1978). When surrogate stones in the form of glass marbles were fed to emus, 84-100 days elapsed before several were evacuated in a heavily abraded condition having lost up to 28% of their original weight.

This abrasion within the gizzard may be biologically significant for seeds ingested by emus during the summer when gizzard mineral content is high. Many of the seeds eaten by emus at this time are leguminous, such as *Acacia* species (Davies 1978), and may germinate more readily following abrasion and weakening of the strophiolar region of the seed's testa (Ballard & Grant Lipp 1965). The gizzard contents of one ostrich in South West Africa comprised a
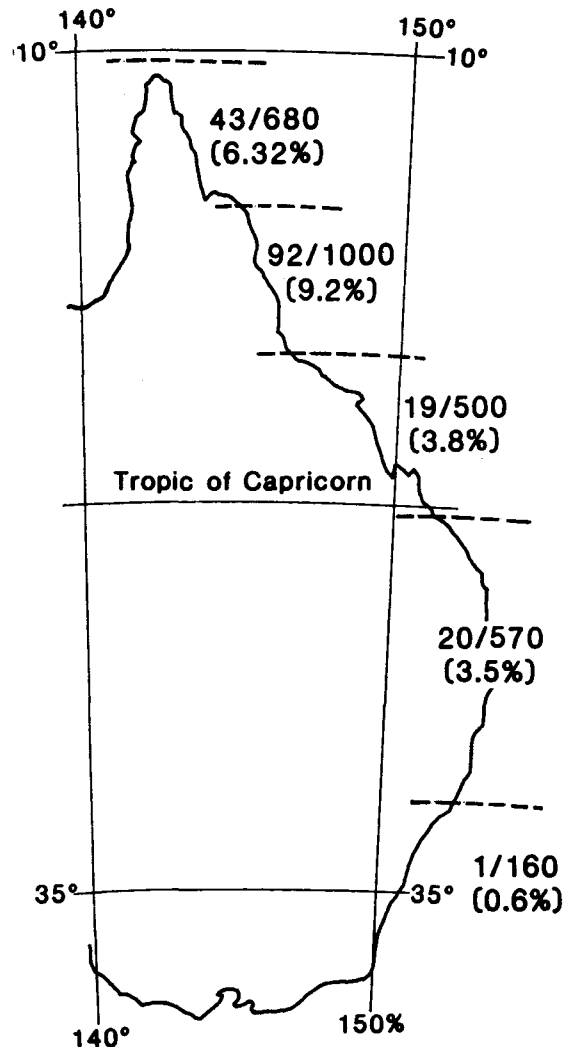

Fig. 12: Estimates of the number (and percentages) of large-fruited species in the woody rainforest flora of eastern Australia (after Stocker & Irvine 1983). Cassowaries (*Casuarius casuarius johnsonii*) are now only found in the two northernmost regions.

Cálculos estimativos del número (y porcentajes) de especies de frutos grandes en la flora maderera de la selva de Australia oriental (según Stocker e Irvine 1983). Los casuarios (*Casuarius casuarius johnsonii*) se encuentran ahora solamente en las dos regiones extremas del norte.

large quantity of seeds and pods of *Acacia albida* (17.4% by weight) and stones (31.2%) (Robinson & Seely 1975). The gizzard contents of another ostrich however contained no legume seeds despite a large quantity of stones being present. Seeds of hinau (*Elaeocarpus dentatus*) have been taken from kiwi gizzards where the nor-

mally rough endocarp has been worn smooth (Reid *et al.* 1982). These apparently had been retained as grinding aids for extensive periods and germination of viable seed may have been significantly improved following defaecation.

IMPLICATIONS FOR SEEDLING ESTABLISHMENT

Dense seedling populations in a faecal dropping of an emu or cassowary rapidly induce self-thinning through intraspecific competition for "biological space" (Ross & Harper 1972). Because individual *Nitraria* hummocks may attain dimensions up to 3 x 13 m in horizontal plan (Noble & Whalley 1978a), substantial mortality must occur. Up to 1000 *Nitraria* seeds have been found in a single faecal deposit of *c.* 15 cm diameter (see Plate 1) so that even if only 50% of germinated, seedling density would be at least 15 cm^{-2} (Noble 1985). Only the earliest, and most vigorous, seedlings will ultimately assume dominance and develop into a mature, reproductive plant, providing it occupies a suitable "gap" amongst established plants.

Interspecific competition from cool-season annuals, especially annual medics (*Medicago* spp.) as shown in Plate 2, was also a major regulatory influence four to six months after the onset of germination (Noble & Whalley 1978b). Hand weeding of all annuals within individual plots resulted in 8% of the original seedling population of *Nitraria* surviving for eight years. After four years, even the weeded populations showed a marked decline in density as shown by the hazard functions calculated as $-\log_e (1 - p)$ in Fig. 13.

Hazard functions are derived by computing the probability of death of a seedling of *Nitraria billardieri* in either treatment in a given time interval. For each treatment, there is a pair (n, r) of recorded numbers: n being the number of shoots alive at the beginning of the time interval and r being the number of these shoots that die during that time interval. The probability p of death in that time interval is estimated by $p = r/n$ and the
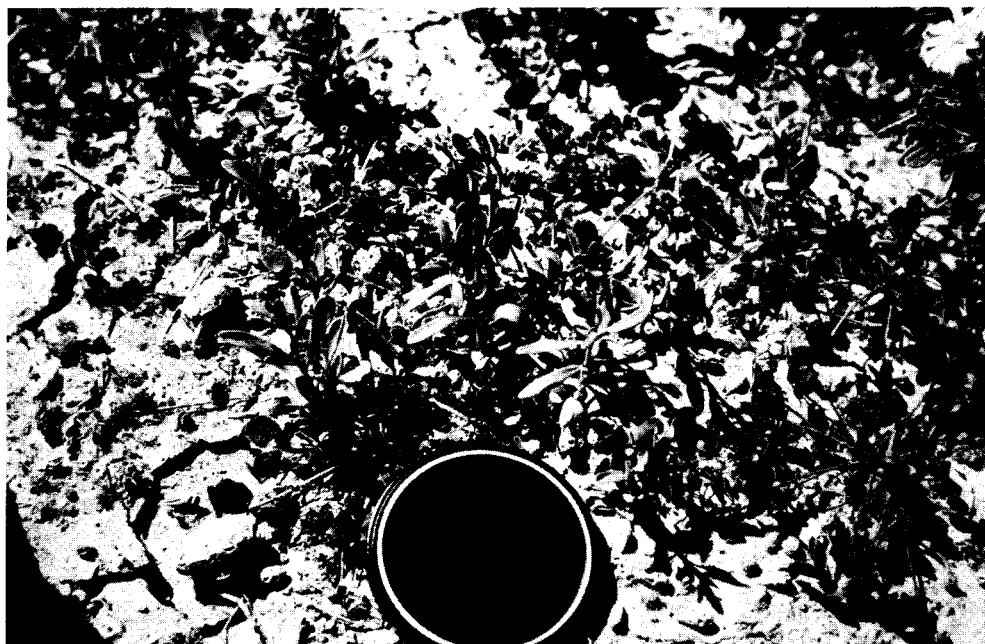

Plate 1. Seedlings of *Nitraria billardieri* emerging from an emu dropping on a clay soil in southwestern Australia. (Reference: approx. 5 cm wide).

Brotes de *Nitraria billardieri* emergiendo de una defecación de emu sobre suelo de arcilla en Australia suroccidental. (Referencia: aprox. 5 cm de ancho).
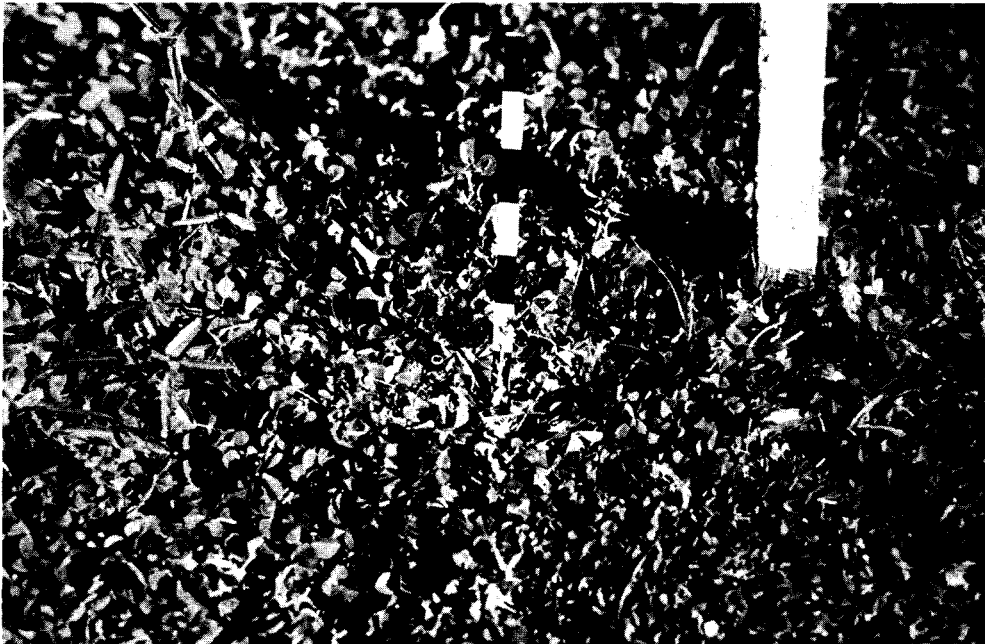
Plate 2: Seedlings of *Nitraria billardieri* struggling to survive strong competition from annual herbage composed mainly of annual medics (*Medicago polymorpha* and *M. truncatula*). The scale is shown in 2.5 cm intervals.

Brotes de *Nitraria billardieri* luchando por sobrevivir la fuerte competencia del herbaje anual compuesto principalmente de medicagos anuales (*Medicago polymorpha* y *M. truncatula*). La escala se muestra en intervalos de 2.5 cm.
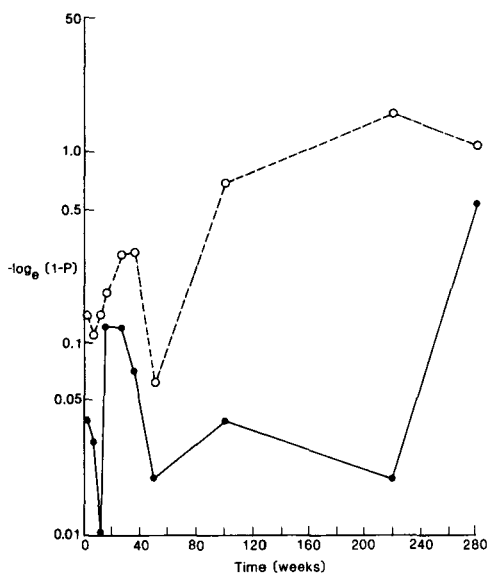

Fig. 13: Hazard functions or age specific failure rates for weeded (hollow circles) and non-weeded (solid circles) seedlings (1973 cohorts) of nitre bush (*Nitraria billardieri*) in southeastern Australia.

Tasas de funciones por azar o falla específica debida a la edad para brotes desmalezados (círculos huecos) y nodesmalezados (círculos sólidos), (1973 conjuntos) de arbustos nitre (*Nitraria billardieri*) en Australia suroriental.

model used (Bartlett & Noble 1985) has the form:

$\log_e [-\log_e (1 - p)]$ = time component + treatment component. These functions, together with seedling survivorship data (Noble 1985), illustrate that established plants of *Nitraria billardieri* are close to maximum carrying capacity (K). Successful recruitment of seedlings can therefore only occur on a one-for-one basis following the death of an established individual (Harper 1977).

Gut retention times obviously have a significant influence on the post-dispersal seed shadow generated by dispersal agents on the simple prediction that the longer the seed is retained in the gut, the higher the probability that long-distance dispersal will prevail. However, once frugivores have stripped seed of their nutritious pericarp, there is no further advantage in carrying "ballast" which is heavy and space consuming (Snow 1971). Emus feeding on fruit of *Nitraria billardieri* concentrate faecal deposits around female fruit-bearing plants with minimal dispersal of seed. The fluid nature of the faeces suggests low gut reten-

tion times probably induced by the high water content of the fruit (see Plate 3). Undoubtedly some seeds are periodically deposited in favourable sites some distance away from mature plants but seed dispersal curves would be highly skewed.

Where ratites are selectively eating flowers, browsing may influence fruit production. Robinson and Seely (1975) reported large quantities of *Acacia giraffae* flowers in ostrich gizzards. Greenwood and Atkinson (1977) claimed that browsing of shrubs by moas in New Zealand had a strong selective influence on their morphology with divaricate shrubs (Tomlinson 1978) now comprising nearly 10% of that country's woody flora. The relative evolutionary significances of moa browsing and climate in this respect are open though to speculation (McGlone & Webb 1981, Wardle 1985). Compared with other ratites, the moas were unique in having the capacity to browse twigs and leaves of such shrubs, presumably selecting buds and young leaves because they were both more digestible and more nutritious than those on older twigs (Lowry 1980, Atkinson & Greenwood 1980).

Examination of preserved moa gizzards has revealed that seeds from a wide range of plant species were also an important component of the moa's diet including those from drupes of *Elaeocarpus hookerianus* (Burrows 1980). Moas, particularly *Dinornis* spp., specialized by feeding on twigs of shrubs, vines and trees to a much greater degree than extant ratites (Burrows *et al.* 1981, Atkinson & Greenwood 1989), grouse (*Lagopus* and *Tetrao* spp.) being the only other birds habitually feeding on twigs. Different species of moa may have utilised distinct niches distinguished by differences in feeding height, bill shape and gizzard development. Moas could digest this woody material because of the strong musculature of the massive gizzard and enclosed gastroliths (Atkinson & Greenwood 1989). In this context, the large gizzard stones associated with mihirungs suggests that these birds may have also browsed woody plants.

Atkinson and Greenwood (1989) have recently completed a comprehensive analysis of the evidence for the co-evolution of certain moa traits such as increased cutting power of the bill, increased gizzard

Plate 3: Emu faeces composed almost entirely of seeds of *Nitraria billardieri.* The purgative action of the fruit is clearly evident.

Heces de emu compuestas casi totalmente de semillas de *Nitraria billardieri.* La acción purgante de la fruta es claramente evidente.

development, and increased height *inter ilia*, and the evolution of at least 11 different growth habits in native plants. The main benefit possibly to be derived by tree seedlings from ratite browsing is the suppression of rapidly growing understorey species which would otherwise interfere with their regeneration. Wardle (1985) has discussed the possible role of moa-browsing in promoting the regeneration of podocarp-dominant forests. Any evidence for co-evolution between fruit ingestion by moas and subsequent seed dispersal and seedling development traits is, however, likely to be less compelling.

The fruit of one podocarp species, *Podocarpus spicatus*, was found to occur frequently in the gizzard contents examined by Burrows *et al.* (1981) indicating that they may also have acted as dispersal agents for these conifers. The mihirungs may have had a similar dispersal role within the Tertiary rainforests which covered most of what is now arid Australia (Martin 1982). The pollen record includes such conifers as *Podocarpus, Dacrydium* and *Phyllocladus* (Truswell & Harris 1982). It appears unlikely that contemporary forest ratites have a critical role in the establishment of coniferous seedlings, only a single seed of *Podocarpus dispermus* being found in Australian cassowary dung (Stocker & Irvine 1983).

EVIDENCE FOR MUTUALISM

Putative relationships between plants and ratites are portrayed in Fig. 14. Whilst simplistic, this model highlights the ecological significance of the ratite faecal microsite in promoting rapid germination and seedling establishment of woody plants in habitats ranging from xeric shrublands and grasslands to humid rainforests.

Indirect influences such as the predation of insects and trampling are relatively unimportant in terms of seedling establishment. Whilst all extant ratites are omnivorous, there is no reliable evidence indicating that predation of insects has any significant bearing on the establishment of seedlings, either within or without faecal
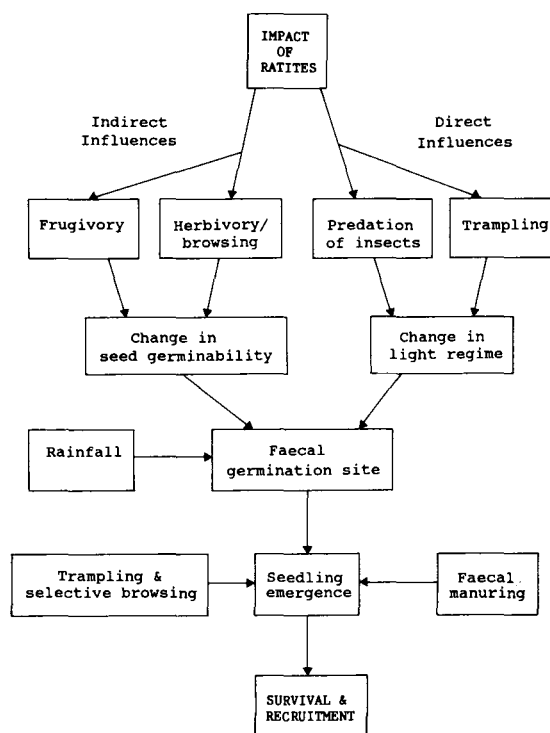

Fig. 14: A simple model illustrating the various influences of ratite activities on seed germination and seedling establishment.

Un modelo simple que ilustra las diversas influencias de las actividades de las rátidas en la germinación de las semillas y establecimiento de los brotes.

germination sites. Similarly, trampling by ratites appears to be of little significance in determining the fate of seedlings although the larger extinct ratites such as the moas, elephant birds and mihirungs, may have created "light gaps" in forests because of their sheer size, but only if they fed in flocks which is uncertain. Moas were more likely to forage singly or in small groups (Atkinson & Greenwood 1989), possibly to avoid predation by the enormous forest eagle *Harpagornis moorei* (Braithwaite & Holdaway 1987).

Despite the limitations imposed by a worldwide paucity of contemporary plant and ratite data, ecological studies of the two Australian ratites, the emu and the cassowary, suggest that both birds have had a significant influence on vegetation history in certain habitats. Wheter or not they have had an even longer influence over geological time is uncertain but Truswell and Harris (1982) refer to fruits

of *Santalum* spp. being found in Miocene deposits in arid South Australia. They suggested that the genus *Santalum* was therefore a late migrant into arid regions originating from stocks in coastal rainforests. Whether this migration was facilitated by emu or other ratite dispersal is unknown although there is no doubt about the modern emu's predilection for ripe fruit of *Santalum* species.

Many of the fruits eaten by ratites have evolved traits characteristic of ornithochory (van der Pijl 1972). Such features as an attractive edible part, signalling colours when mature, and inner protection of seed against digestion, can be applied to most of the fruit consumed by Australian cassowaries (Stocker & Irvine 1983) and emus (Noble & Whalley 1978a). Here dispersal is endozoochorous when whole fruits are ingested by the disperser and the seed eventually regurgitated or defaecated undamaged (van der Pijl 1972). Whilst the dispersal "syndrome" of bird-dispersed propagules includes several attributes, Herrera (1981) has also pointed to the importance of matching external fruit size, particularly of tropical species, to the gape widths of avian dispersal agents. Snow (1973) has described the disproportionately wide gape of some tropical frugivores such as some Cotingidae, a family of small South American passerines, as constituting an adaptation to feeding on large-seeded fruits.

Whether there has been coevolution by emus and *Nitraria* with both acting as selective forces on each other, is uncertain. In his study of coevolution between plants and avian dispersers in Mediterranean Spain, Herrera (1982) found definite support for the hypothesis that fruit quality traits evolved to meet disperser demands. He found that fruit that ripen during the dry Mediterranean summer, like *Nitraria billardieri*, when water demands of dispersers were highest, also had the highest water content.

Selective forces are distinguished according to whether they act either as dependent or independent variables. The physical environment generally acts as an independent variable by selecting for optimum energy

content of endosperm and embryo tu support subsequent seedling growth. Seed predators act as a dependent variable by selecting instead for increased thickness of endocarp (Smith 1975). If this is so for ratite predators, gut retention time may need to increase to compensate if gizzard scarification of the endocarp is important for promoting postdispersal germination. As mentioned earlier, experimental evidence tends to refute this hypothesis.

Extensive recruitment of seedlings of *Nitraria billardieri* cannot occur on heavy soils such as those found on the Riverine Plain of south-eastern Australia in the absence of emus. Prior avian ingestion of fruit is however not obligatory for successful germination to occur in sandy substrates. It has also been alleged (Sargent 1928) that seeds of the zamia palm (*Macrozamia fraseri*) in Western Australia, often larger in size than a walnut, will only germinate after they had been eaten by the emu however this has since been found not to be obligatory.

What is critical in the case of Riverine Plain *Nitraria billardieri* is that speed of germination is significantly increased enabling seedlings to rapidly establish themselves while moisture conditions remain favourable within the faecal microsite and surface soil. Similar constraints must also apply to cassowary-dispersed seeds which require quite specific moisture, and probably light, conditions for successful seedling recruitment. Some *Beilschmiedia* species for example, not only require the removal of the fruit's mesocarp by appropriate dispersal agents but also the maintenance of high moisture, either within a large faecal dropping of a cassowary, or alternatively, burial beneath forest leaf litter (Knowles & Beveridge 1982, Wright 1984). Such seedlings are unable to tolerate the effects of direct sunlight unless very high moisture conditions are maintained.

There is no evidence available suggesting that any plant-ratite mutualism exists similar to that proposed by Temple (1977) for the near-extinct tree *Calvaria major* of Mauritius and the extinct dodo (*Raphus cucullatus*) although recent observations suggest that these seeds can germinate

without ingestion (I. Atkinson, pers. comm.). Nonetheless, the semantics of mutualism are complex. The term itself is often applied to obligatory associations while protocooperative associations are facultative (Hallam 1980). Although there may be exceptions, symbiotic mutualisms tend to be coevolved and obligate whereas facultative mutualisms are frequently non-symbiotic and not coevolved (Bourcher et al. 1982). In his scheme for classifying biological associations, Starr (1975) defined mutualism as a "mutually beneficial symbiosis", a definition which would apply to those ratite and plant relationships where there was a positive gain at both trophic levels.

Absolute dependence in mutualistic associations of temperate zone systems can be often too costly, due to prolonged winter breaks. Bristow in May (1982) claimed that "...temperate zone mutualisms are rarely obligate, but rather than by relying on simple environmental cues and behavioural mechanisms a high degree of fine tuning may be achieved with almost no loss of flexibility". The ratio of energetic reward of the fruit pulp, or mesocarp in the case of drupes, to the indigestible seed is equivalent in temperate and tropical fruit (Herrera 1981). The real difference is that many tropical fruits have large seeds and correspondingly rich pulp while most temperate fruits have small seeds and smaller nutritional rewards (Howe & Smallwood 1982).

It is the quality, as well as the quantity, of the fruit as a food source which determines the demographic significance of any frugivore —or omnivore— plant association. Nevertheless, studies indicate that the rich mesocarp pulps commonly found in tropical fruits are not necessarily related to close coevolution between large-seeded plants and their "specialised" dispersers (Snow 1971, McKey 1975, Howe & Estabrook 1977). Data on the composition of Elaeocarpus dentatus drupes in New Zealand are shown in Table 8a. This tree produces heavy fruit crops which may last for several months through the autumn and winter (Fitzgerald 1976). Because of its high nutrient status, and especially as a source of available energy, it has been

shown to enhance winter reproduction of the introduced Australian possum (Trichosurus vulpecula) in broadleaf-podocarp forests in New Zealand (Bell 1981). Whether the fruit has similar demographic significance for kiwi populations is unknown although the preponderance of hinau fruit in some kiwi gizzards suggests that there could be considerable nutritional benefit for these birds when fruit is abundant (Reid et al. 1982).

Observations of large emu flocks (up to 80 birds) feeding on fruit of Nitraria billardieri (Noble 1975a) demonstrated that the emu is an apostatic generalist feeder or feeder that concentrates on the source of food in greatest supply at any point in time, leaving this when the supply becomes limiting (Harper 1969). Data on the food quality of native drupes is limited but the nutritional value of both N. billardieri and Elaeocarpus dentatus fruit is not insignificant (Table 8). N. billardieri fruit particularly, in terms of both its nutrient and water contents, provides a valuable source of fresh food during summer (December-February). When fruit production of N. billardieri has been reduced following poor insect pollination in wet springs (Noble 1985), the catholic tastes of emus (Davies 1978) enable them to find alternative summer food sources.

In the tropical rainforests of northern Australia, the cassowary breeding season coincides with the period of maximum fruit production from July through to October (Crome 1976) (Fig. 15). Fruits produced by species from the Lauraceae are particularly important in this respect, not only because they produce most of their fruit during this period but also because the fruit itself is highly nutritious (Crome 1976, Stocker & Irvine 1983). The mesocarps of some lauraceous species contain 8-14% protein and 19-44% fat, with water contents ranging from 54-75% (Snow 1962). Crome (1976) found protein contents (% fresh mesocarp) of two lauraceous species, Endiandra montana and E. muelleri, to be 0.77 and 2.89% respectively. Elaeocarpaceae is another important family in the cassowary diet and the protein content of the mesocarp of Elaeo-

TABLE 8 (a)

Composition (dry weight basis) of the mesocarp of hinau (*Elaeocarpus dentatus*)
fruit in New Zealand (after Williams 1982)

Composición (en base al peso seco) del mesocarpio del fruto del hinau (*Elaeocarpus dentatus*)
en Nueva Zelanda (según Williams 1982).

Crude protein %	Lipid %	Ash %	Crude fibre (acid detergent) %	Available carbohydrate (N.F.E.*) %	Water soluble sugars %	Methanol -soluble sugars %	Gross energy kJg-1
3.4	1.7	3.2	21.8	69.9	10.0	2.9	18.0

* Nitrogen-free extract

TABLE 8 (b)

Comparative composition of entire nitre bush (*Nitraria billardieri*) fruit at different stages of
maturity in southeastern Australia (after Noble & Whalley 1978a).

Composición comparada del fruto entero del arbusto nitre (*Nitraria billardieri*), en diferentes
etapas de maduración en Australia suroriental (según Noble y Whalley 1978a).

Maturity	Soluble solids % sucrose	Titratable acid (% w/v as citric)	pH	Vitamin C (mg/100 ml)
Immature (green-yellow)	15.5	1.73	3.9	
Near-ripe (bright red)	16.7	0.96	4.3	8
Fully ripe (red-purple)	18.5	0.78	4.6	

KEY WORDS:

Ratites = rátidas.
size = tamaño
distribution = distribución
habitat = hábitat. Exactly the same as in English but it is not a widely known word. For this reason I put "medio
ambiente natural" (natural environment) - habitat" the first time the word appears in the abstract.
seed dispersal = dispersión de las semillas.
seedling establishment = establecimiento del brote (1 seedling), establecimiento de los brotes (more than 1 seedling).
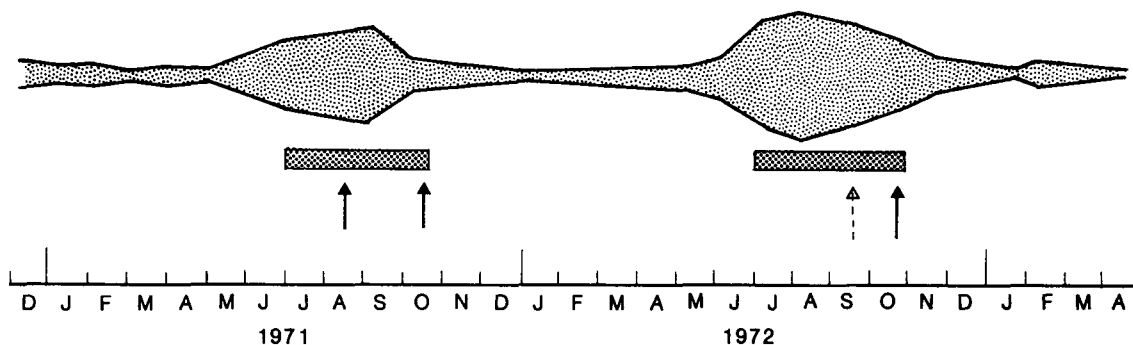

D J F M A M J J A S O N D J F M A M J J A S O N D J F M A
1971   1972

Fig. 15: The relationship between breeding seasons of the Australian cassowary (*Casuarius casuarius
johnsonii*) and fruit production in tropical rainforest (after Crome 1976). The stippled area represents
the amount of fruit available and bars represent breeding season. Arrows represent known hatching
dates while the broken arrow indicates the suspected hatching date of one chick.

La relación entre las estaciones de reproducción de los casuarios (*Casuarius casuarius johnsonii*) y la producción frutal
en la selva tropical lluviosa (según las barras representan la estación de reproducción). Las flechas representan las fechas
conocidas de incubación, mientras que la flecha quebrada indica la fecha sospechada de incubación de un polluelo.

:arpus grandis (1.64%) recorded by Crome
1976) is not dissimilar to that recorded for
:. dentatus (Table 6a) given differences in
moisture content.

Because all the extant ratites are essential-
ly omnivorous, it is unlikely that their
associations with plants, particularly those
producing drupaceous fruit, are obligatory
symbioses. They do nonetheless, have the
capability to exploit periodic abundances
of such food sources, either for reproductive
or simply maintenance purposes.

Few studies of plant dispersal systems
have actually demonstrated increases in
either fitness or population growth rate
by organisms at either trophic level (Boucher
et al. 1982, Wheelwright & Orians 1982).
This general lack of specificity in seed
dispersal conforms to the hypothesis
(Howe & Smallwood 1982) that coevolu-
tion reflects adaptation to arrays of similar
organisms rather than to particular species.

ACKNOWLEDGMENTS

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