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BIRDS OF A FEATHER

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THE BREEDING ECOLOGY OF MOAS

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From their skeletal anatomy it is apparent that moas occupied in New Zealand the ecological niches of large herbivores and of the larger cursorial birds, i.e. birds whose locomotion is mostly or wholly by walking. The concept of niche is useful because within it an organism's morphology, physiology and behaviour are seen as an intergrated system directed towards enabling the animal to make a living in nature in the face of competition from other species. Niche should be distinguished from habitat which is the place where an organism lives, whereas its niche is its occupation or way of life (Odum 1959).

According to niche theory a particular morphology such as that of a cursorial bird will tend to be linked to particular breeding adaptations such as the type of nesting dispersion and clutch size. For the prehistorian, breeding ecology is of interest not only because of its relationship to population dynamics, but also for the reason that the animals taken by hunters and gatherers are more vulnerable during the breeding season than at other times. Hence any deductions about moa breeding ecology from what we know of their bones, set within the context of niche theory, may be a profitable exercise for New Zealand prehistorians.

Lack (1968) has documented the ways in which breeding adaptations in birds are integrated in the major ecological groupings of littoral, marine, freshwater, wading and cursorial birds. He compiled data for most of the bird families of the world, looking for regularities between feeding habits and breeding patterns, as well as seeking functional explanations of these regularities. In this paper I shall bring together the available empirical data on moa nesting and, using these within the framework of Lack's deductions, suggest relationships between moa breeding patterns and Polynesian hunting techniques.

Breeding dispersion in cursorial birds

Among the cursorial birds, Lack includes 430 species belonging to 25 families. Two of the most important orders of cursorial birds are the Galliformes, which includes pheasants, turkeys and hens, and the Charadriiformes, which includes the plovers. The seven families of ratites (Table 4.1) which are now considered to constitute a monophyletic group (Lack 1968:99), are all cursorial birds. Six of these families still have living representatives but the family to which the moas belonged is wholly extinct. Other New Zealand cursorial birds are the kiwi, weka, takahe, New Zealand dotterel, banded dotterel, wrybill, shore plover, the extinct New Zealand quail and several

Table 4.1 The genera of ratites

Cassowary	Casuarius
Emu	Dromiceius
Kiwi	Apteryx
Moas	Dinornis Pachyornis Euryapteryx Emeus Anomalopteryx Megalaapteryx
Ostrich	Struthio
Rhea	Rhea
Tinamous	Crypturellus Nothoprocta Nothocercus Rhynchotus

Table 4.2 Scientific names of New Zealand birds mentioned in the text

Banded dotterel	Charadrius bicinctus
Bellbird	Anthornis melanura
Black-backed gull	Larus dominicanus
Extinct eagle	Harpagornis moorei
New Zealand dotterel	Charadrius obscurus
New Zealand falcon	Falco novaeseelandiae
New Zealand quail	Coturnix novaezealandiae
Shore plover	Thinornis novaeseelandiae
Takahe	Notornis mantelli
Tui	Prothemadera novaeseelandiae
Weka	Gallirallus australis
Wrybill	Anarhynchus frontalis

non-breeding migrant dotterels (see Table 4.2).

Most cursorial species are solitary nesters, the main function of this dispersion being concealment of the nest and the sitting bird from predators. The few cursorial birds which are colonial (pratincoles, sand grouse and a seed-snipe) breed in loose colonies in which the nests are dispersed and the cryptic eggs hard to find (Lack 1968:100). The chicks are nidifugous, i.e. leaving the nest soon after hatching and often picking up food for themselves from their first day. Lack argues that these adaptations are the best strategy for raising the maximum number of young given a cursorial habit, ground nesting, a plant diet and the presence of egg and chick predators. Lack cites plant diet as a factor because herbivorous birds generally require larger volumes of food than insect eaters and so have a logistical problem in feeding their chicks. They solve this either by a change of diet (tuis and bellbirds feed insects to their nestlings), or by the nidifugous adaptation in which the newly hatched chick is able to move itself to the food supply instead of having the food brought to it. All the living ratites are solitary nesters and nidifugous, even the kiwi, which is not primarily a herbivore.

Moas as herbivores

Morphologically moas were well adapted to living on the ground. Besides being flightless and heavy boned, they had the metatarsi shortened and strengthened almost to the proportions typical of the Galliformes (Owen 1879:107), presumably for effectively scratching in the soil for food, rather than just for weight bearing. The herbivorous habit is evident in the heavy crushing bill, the long neck and legs to aid browsing, the overall pachydermal proportions and from the few gizzard contents competently analyzed. Identifiable gizzard contents have been found in only a few swamp deposits and most have contained fruits of forest and shrubland species (Oliver 1949, Falla 1941, Gregg 1972). Four of the gizzards from Pyramid Valley contained seeds of matai (Podocarpus spicatus), a tree which rarely fruits within five metres of the ground, but which does drop fruiting twigs very readily. After strong winds in summer and autumn, the ground under a matai tree is littered with twigs, and a moa scratching there would find a layer of half-rotting leaves and seeds, equivalent to a poor quality silage, as well as a dense mat of noduliferous roots of the matai and of any other nearby podocarps. Such an area represents a relatively high-calorie focus for a herbivore. It has also been plausibly argued that the unusually high proportion of divaricating shrubs in New Zealand is an evolutionary response to browsing by moas who are thought to have fed in a different way from mammals, probably pulling and breaking more than nipping and chewing (Greenwood and Atkinson 1977). As herbivores then, moas could have effectively browsed shrubs and the lower branches of trees, the taller species reaching up to four or five metres above the ground. They could also have been efficient scratchers of the litter layer on the forest floor.

Breeding dispersion in moas

The empirical evidence that moas were solitary nesters is slim. Ambrose (1970) described natural deposits of moa bone (mostly Megalapteryx),

egg shell, droppings and nesting material in small rock shelters at Benmore, Waitaki Valley. Each rock shelter could have held at the most only a few nesting birds at one time. Hartree (in Falla 1962) was able to recognize the remains of solitary nests of Anomalopteryx on ledges and in sheltered cavities in limestone country that once carried fairly heavy forest in Hawkes Bay.

As herbivorous cursorial birds it is likely that the moa chicks left the nest soon after hatching. In a country lacking small mammals it does not seem likely that birds as large as moas would have solved the logistics of feeding chicks by supplying them with animal protein. In the emu, the chicks are led about by the male who establishes a small territory with plenty of open ground as dense undergrowth is difficult for the young emu chicks to scramble through (Eastman 1969). The bones of emu chicks are well ossified when they hatch and the chicks leave the nest as soon as the last of the clutch has hatched. Hector (1871) was able to compare the dried embryo of a moa chick in a whole egg found at Cromwell with an emu chick at the same stage of development and found that the patterns of ossification of the bones were very similar. If, as this suggests, the moa chick was nidifugous, moa adults may also have had to establish small chick feeding territories in a recognizable type of open forest, a behaviour pattern which could have been learnt and utilized by the human hunter.

Though mammalian predators were absent from New Zealand before man arrived, we cannot assume that there was no predation pressure on nesting moas. The extinct eagle, the New Zealand falcon, the black-backed gull and the weka (Table 4.2) were all possible chick predators, the last two being capable egg predators also. Only the eagle was large enough to have attacked the sitting adult. In the evolution of nest and chick dispersion then, it seems likely that moas were subjected to similar pressures and evolved similar adaptations to cope with those pressures as other cursorial birds.

Clutch size in cursorial birds

Lack has developed the argument that in nidicolous birds, where the young are fed in the nest, clutch size has evolved through natural selection to correspond with that brood-size from which on an average most surviving young are produced, the limit normally being set by the amount of food that the parents can collect for their nestlings (Lack 1968:165). Nidifugous birds are released in part from this limitation and raise some of the largest clutches known. A male rhea has been known to incubate 60 eggs, laid in his nest by several females, and hens of various species of the Phasianidae (pheasants and partridges) lay up to 17 eggs in a clutch. At the other extreme, there are several cursorial species which lay only one egg, the kiwi being a well-known example. Since fledging success is not affected by the food which the parents can bring to the brood, Lack suggests that the critical factor may be the food available to the laying bird, which she may use to produce either one large or several smaller eggs. In general, eggs of nidifugous birds are larger than those of nidicolous species, since the young must be larger at hatching so that they can fend for themselves (Lack 1968:199).

Ostriches, emus and rheas which live on the open plains lay average

clutches of 8 to 30 eggs and tend to be polygamous, with several hens laying in an nest guarded and incubated by one male. The forest ratites, however, (the cassowaries, kiwis and some tinamous) lay small clutches of one to eight eggs and tend to be monogamous. The functional value of this correlation between clutch size and habitat presumably has to do with the hunting techniques of chick predators.

The little empirical evidence available on clutch size in moas suggests that they follow the forest ratite pattern. In the nests of Anomalopteryx found by Hartree in Hawkes Bay, there tended to be the remains of only one egg or one chick (in Falla 1962). An entire skeleton of Dinornis robustus found in a cave near Tiger Hill, Alexandra was in a crouching position over the bones of four chicks (Ewen 1895). Also the eggs of moas seem to have been larger relative to body size than those of ostriches, suggesting that the moa female may have put the available energy into laying fewer, larger eggs than do ostriches. Lack estimated that large moa eggs would have weighed about 7.0 kg whereas ostrich eggs weigh only about 1.6 kg (Lack 1968:208). Certainly one would expect predation pressure in the New Zealand forests to be less than on the African savannah, and hence it would be better strategy for a moa to use the available energy in hatching fewer and larger chicks who would have a better chance of survival.

Discussion

Though the factors of solitary nesting, small clutches and nidifugous chicks suggest that moa adults, chicks and eggs would not be an easy or predictable harvest for Polynesian man to gather during the breeding season, there must have been sufficient regularities in moa breeding behaviour to enable man to gather their eggs. Moa egg shell is relatively common in moa hunter sites. The evidence from Hawkes Bay and Benmore shows that at least some moas favoured sheltered crevices and rock shelters as nesting sites. Such locations tend to be limited in number in most New Zealand lowlands where moa populations were largest, and those accessible to moas would also have been accessible to man. Knowing the favoured sites and the timing of nesting, it may have been a relatively successful hunting technique to visit cliffed and rocky areas at the right season. Faithfulness to nesting sites and to particular types of terrain as chick rearing territories could have made moas relatively vulnerable to human predation and could have been part of the pattern of events leading to their extinction.

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