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BIOGEOGRAPHIC THEORY AND THE NUMBER AND HABITAT OF MOAS

Summary: From the relationship of the number of bird species to land area in New Zealand, the expected number of moa species is about 8 to 12. Of these, half should have lived in forest and half in open habitats. This may help to explain the uneasiness biogeographers have felt with 28 described species of moas, and the question of whether they were forest birds or not.

Keywords: Moas, biogeography.

Introduction

Ten years ago I graphed the relationship between the number of forest bird species in New Zealand and the area of available forest (Flux, 1977; Fig. 1). This was to illustrate the application of island biogeographic theory (Preston, 1962; MacArthur and Wilson, 1967) for a group of National Park rangers, and to emphasise the importance of conserving the remaining native forest. At question-time someone asked how the 28 species of moas fitted into this theory. This embarrassingly large group of birds deserves further consideration in view of the current debate on whether moas were forest or open-country species, and what effect they were likely to have had on vegetation.

Material and Methods

Using the checklist of New Zealand birds (Kinsky 1970) and information from other members of Ecology Division, I listed 27 native forest birds for the South Island, 26 for the North Island, 22 for Stewart Island, and 13 for the Chatham Islands, which rely on that habitat and were present in 1840 when Europeans settled. Estimates of the areas of forest in various tenures were taken from the New Zealand Yearbook (1976) to emphasise the relative importance of National Parks and State Forest Land. The dashed lines in Figure I are the curves tracking the decline in number of bird species, as the forest cover declined to zero from an assumed 66% in each island. The curve is calculated from Darlington's "rule of thumb" (MacArthur and Wilson 1967) that "division of area by ten divides the fauna by two", based on Arrhenius' power function (Connor and McCoy 1979).

Results and Discussion

The number of forest bird species when Europeans colonised is well documented and forms a relatively firm baseline. Some subjectivity, of course, is involved in deciding which species are restricted to forest. The area of forest in 1840 is far less certain, but the curves at 66% are so flat that an error of ± 20% (i.e. 46%-86 % forest cover) changes the expected number of species by only ± 2 for the two main islands, and less for the others.

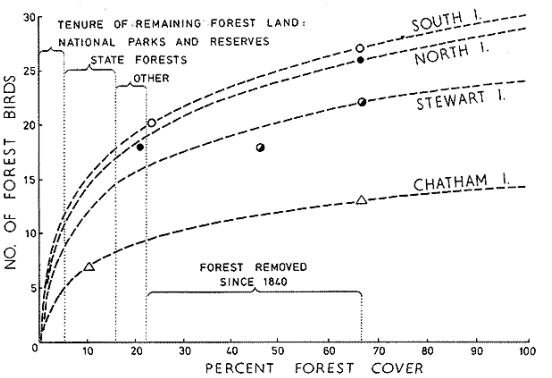

Figure l: *Relationship of number of forest bird species to forest area in the four main islands of New Zealand. The right-hand points are the number of species present in 1840, with dashed curves fitted to indicate the expected number at other percentages of forest. The left-hand points are the present totals of forest birds, entered above the present forest cover. [Figure copied from Flux (1977). Since then kakapo, and possibly kokako, have been discovered in Stewart Island, making the fit of observed to expected totals even closer.]*

The left hand points in Figure 1 are the present totals of forest bird species for each island entered above the present forest cover. For example, when the Chatham Islands were 66% forested there were 13 native species; now, with 10% forest there are seven. The fit against the number of species expected (dashed lines) is remarkably good. Stewart Island shows the greatest discrepancy with two species too few, but the

kakapo *(Strigops habroptilus)* has been rediscovered there since the original figure was drawn, and kokako *(Callaeas cinerea)* may still exist - the graph offers hope.

How many moas does Figure 1 indicate should have been present when the Maori arrived? Forest probably covered 95% of the North Island, 90% of the South Island and 100% of both Stewart and Chatham Islands. At these percentages (which are not critical) we could expect only three moas in each of the main islands, say a total of 4-6 species allowing for overlap, not the 28 of Oliver (1955). Fortunately, recent taxonomic revisions reduced the number of species to 13 (Cracraft 1976), then 12 (Millener 1982); and Caughley (this volume) suggests that eight species lived in the South Island and six in the North Island.

Unless the number of moa species can be even more drastically reduced by taxonomic lumping, which is unlikely, it seems that several species of moa did not live in forest but in more open habitats - swamps, coastal or riverine areas, and alpine grassland. For a group that evolved in isolation for 85 million years, with frequent climatic and volcanic disruption to forest, this seems highly probable. The relatively uniform forest structure would allow three widespread species, feeding on the surface, shrubs, and low trees respectively, in each island. The rest would have been part of the open country avifauna so dominant in the sub-fossil record - pelican, swan, geese, ducks, harrier, eagle, rails, owlet-night jar, and crow. These species would have been in decline as forests spread after the ice ages.

The natural increase of the open country avifauna following Maori and European forest clearing is already evident (e.g. plovers, heron, swallow, etc.) and the ready acclimatisation of introduced birds is another indicator of the ecological "vacuum". The rules of biography apparently allow South Pacific islands of the size and remoteness of the North or South Island to support about 50 resident land birds species (my estimate from Figure 9 of Slud 1976): their expected mix, from the ratio of forest to open land, is illustrated in Figure 2. Even if moas were really "mammals", they should obey the rules. "Their evolution in a land lacking mammals is comparable with the adaptive radiation of the deer and antelopes of northern continents. . ." (Fleming, 1974), but the area and latitude of New Zealand would support only two or three ungulates (my calculation, based on East 1981 for area, and Slud 1976 for latitude; and of the dozen species introduced, only the red deer group and goats have become widespread in forest).

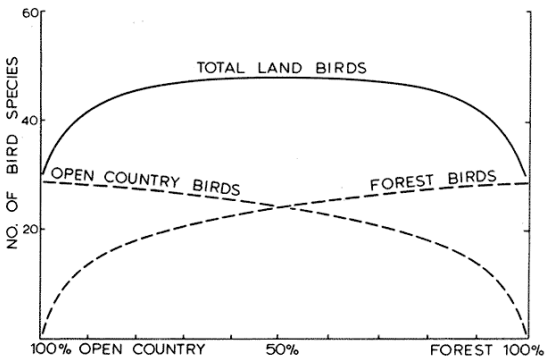

Figure 2: *Ratios of forest bird species to open country species expected at different percentages of forest cover for one of the main New Zealand islands. Note that the total number of species is relatively constant over most of this range, an indication of the relative unimportance of habitat compared with land area and latitude.*

Several zoogeographers have been concerned at the excessive number of moas. Thus McDowall (1973) wrote, "It seems most unsatisfying that New Zealand has 28 moa species but less than 100 other land birds of diverse character and habits, and that New Zealand has more than threequarters of the entire ratite bird group." He suggested several supposed species might be growth, sexual or geographic forms. Caughley (1977) agreed: "The hallmark of a useful zoogeographic model is its generality, the extent to which it accounts for the distributions of many species, not just one or two. But any attempt to produce such a model runs headlong into 25 species of moas doing something else". To my knowledge, however, no one has applied biogeographic theory to estimate just how many moas there should have been, or what their habitats were. I would suggest a total of 8-12 species, evenly distributed between forest and open country.

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