

THE TAKAHE - A RELICT OF THE PLEISTOCENE GRASSLAND AVIFAUNA OF NEW ZEALAND

Of all the suggested causes of extinction or near extinction of certain species of avifauna only that invoking alteration of habitat following upon climatic change is satisfactory to explain the shrinkage of takahe range (G. R. Williams, 1960).

Summary: The takahe (*Notornis mantelli*), an endangered rail once widely distributed through New Zealand, had become restricted to Fiordland, and possibly Nelson and the Ruahine Ranges, by European times. Two contentious viewpoints have been advanced to explain the decline: climate and vegetational changes in the late Pleistocene and Holocene; and ecological changes induced by early Polynesians. These theories are examined in relation to the habitat requirements of takahe in its present restricted range, the historical and sub-fossil record, and the possible age of the sub-fossils. We conclude that the takahe is a specialised tussock grassland feeder adapted to the alpine region and that it is unlikely to have changed these feeding adaptations since the last glacial period of the Pleistocene; that the widespread sub-fossil distribution occurred in the glacial periods of the Pleistocene when alpine and sub-alpine grassland covered most of New Zealand; and that replacement of grassland and scrubland by forest when the climate ameliorated in the late Pleistocene-Holocene would have reduced takahe habitat restricting the bird to certain localities where it was vulnerable to hunting by Polynesians when they colonised New Zealand.

Keywords: Takahe; *Notornis mantelli*; Rallidae; Pleistocene; sub-fossil; distribution; habitat; grassland; *Chionochloa*; extinction; avifauna; Murchison Mountains; New Zealand.

Introduction

The sub-fossil record of takahe (*Notornis mantelli*) indicates that this endemic rail was, at one time or another, widely distributed through New Zealand (Williams, 1960; Reid, 1978). In European times taka he have been restricted to Fiordland but may have existed in Nelson and the Ruahine Ranges (Reid, 1978). The underlying causes of the decline of takahe and other near extinct or extinct species such as kakapo (*Strigops habroptilus*), the giant rail (*Aptornis otidiformis*) the eagle (*Harpagornis moorei*) and the moa species (*Dinornithidae*), have been the subject of speculation but they are still not well understood.

On the mainland of New Zealand 27 species of terrestrial and freshwater birds (based on a classification of 12 moa species (Millener, 1982)) with Quarternary fossil records are known to have become extinct prior to European settlement (Millener, 1981). Remains of all but two of the 27 species have been reported in association with Maori occupation sites (Millener, 1981) raising the question as to whether the early Polynesians were a factor in the demise of these birds, through hunting, habitat modification (e.g. forest fires) or the liberation of the Polynesian rat (*Rattus exulans*) and dog. Whether these birds were declining prior to the arrival of the Maori and had already become limited to small areas of preferred habitat, or whether they were more vulnerable than other species for some other reason, is unknown. There are, therefore, two

main viewpoints on the causes of the decline and extinction of these avifauna - one suggesting that factors associated with climatic and vegetational changes were responsible (Archev, 1941; Oliver, 1949; Williams, 1960), and the other implicating Polynesian man (Fleming, 1962; Millener, 1981; Diamond, 1982; Anderson, 1983).

Whether climate or man was the primary cause of the demise of the moa species and the giant rail as well as the decline of takahe, depends, to a large extent on whether these species inhabited forest or grassland - scrubland habitats. If they were inhabitants of the forest then an increase in forest cover in the late Pleistocene should have benefited them and the only satisfactory explanation for their decline would be the impact of the arrival of the Polynesians, approximately 1000 years ago. Conversely, if these species were grassland or scrubland herbivores, then the reduction of this habitat through climatic change in the late Pleistocene would have caused a concomitant shrinkage of their ranges.

The idea that the takahe was primarily a forest bird (Fleming, 1979a; Millener, 1981) has developed because sub-fossil bones have been found in areas that were forested in pre-European times and because some takahe sub-fossil material occurs in association with forest species from the extant fauna (see Millener, 1981).

Pleistocene glacial landscapes both in northern hemisphere continents (Hestor, 1967; Guthrie,

1966, 1968; Kurten, 1968) and on southern islands such as New Zealand (Fleming, 1962, 1979b) were dominated by grass and scrubland on outwash plains. Large mammalian herbivores flourished on the extensive grasslands in North America (Guthrie, 1966, 1968; Klein, in press), while in New Zealand a vigorous avifauna developed (Falla, 1953; Stevens, 1980) in the absence of terrestrial grazing mammals.

Large-scale climatic changes associated with glacial and interglacial phases occurred world-wide during the Pleistocene (Coe, 1980; Stevens, 1980). During these climatic fluctuations extinctions of many species occurred, with disproportionately more large mammals and island bird species disappearing in the late Pleistocene - Holocene (c 25,000 - 1,000 years BP) than before (Coe, 1980; Diamond, 1982). It has been argued that the large grazing herbivores of North America disappeared when the late Pleistocene grassland habitat shrank (Klein, in press). This spate of extinctions, however, coincided with the expansion of early hunting man into the New World and the Pacific region and has led many to conclude that man was responsible for the majority of the extinctions, particularly the megafaunal elements (e.g. Martin, 1958, 1967, 1973; Fleming, 1962; Mosimann and Martin, 1975; Coe, 1980; Diamond, 1982; Olson and James, 1982). Nevertheless, as Diamond (1982) points out, the question of whether the North American extinctions were due primarily to man or climatic changes of the late Pleistocene remains unanswered.

In New Zealand evidence of the diminution of grassland and the extension of the forest cover in the late Pleistocene (since about 14,000 years BP) is well preserved in pollen records (Moar, 1971, 1982; McGlone and Moar, 1977; McGlone and Topping, 1977; McGlone, Nelson and Hume, 1978). The decline of grassland or scrubland avifauna would be expected to follow such a shift in vegetation patterns. By the time the Maori arrived approximately 75% of New Zealand was forested (Nicholls, 1980) and it is reasonable to suppose that the grassland avifauna of earlier times was already much reduced.

The problem of extinctions is complex and is unlikely to be solved using only archaeological or sub-fossil information. It needs to be demonstrated that extinctions of different species were contemporaneous to justify a monocausal explanation. For a proper evaluation of the causes of extinction we need to know the timing of the

declines and whether species became extinct simultaneously or at separate times. We also need to know the types of species vulnerable to extinction, their food habits, their habitat requirements and whether the habitat they occupied changed over time because of climatic changes.

Assemblages of sub-fossils in caves, dunes, and swamps provide important information on the paleoecology of extinct or near-extinct species. However, caution needs to be exercised when interpreting assemblages from such sites because they can reflect the nature and locations of trapping and preservation site rather than the habitat or distribution of the animals. Trapping sites may not exist in the preferred habitat of a species. For example, acid swamps are unsuitable for long-term preservation of bones, and consequently the distribution of non-acid swamps will determine the distribution of swamp-borne sub-fossils. The shape and size of caves have a pronounced effect on the fauna collected - for example, flightless species predominate in vertical shafts, the victims of pit-fall entrapment (Millener, 1981). Material collected in swamps and caves may have been washed considerable distances. Furthermore, the present-day vegetation at the preservation site may differ from that existing when the animal died; a cave site which is now situated in dense forest could have been in grassland in the Otira Glaciation Period of the Pleistocene (20,000 years ago). Therefore, it is important that the age of the sub-fossil material is known so that the contemporaneous climate and habitat can be judged. Important considerations in interpreting the paleoecology are the habitat requirements and morphological adaptations of species that are still extant, because these provide a key to the past.

It is our view that the takahe is primarily adapted to alpine grasslands. We arrived at this view by examining information on the habitats of takahe in its present range in Fiordland, its demonstrated food preferences, and the distribution of takahe in historical times and of their sub-fossil remains. We have concluded that the present habitat occupied by takahe represents its preferred ecological conditions, conditions that existed over much of the country during the glacial periods of the Pleistocene. Herbivores such as takahe, the giant rail, and some of the moa species would have flourished when extensive grassland and scrubland communities were present. The replacement of the grasslands and

scrubland by forest over much of the country in the late Pleistocene would have reduced the habitat available to these birds. This, in turn, would have meant that these species would have been restricted and vulnerable to hunting by Maori when they colonised New Zealand. The takahe is the sole survivor of this group of herbivores, a relic of the Pleistocene grassland avifauna. The historical and sub-fossil records of the past distribution of takahe are examined in the light of this interpretation.

The views we put forward support the explanations advanced by Gordon Williams (1960, 1962, 1964, 1973) for the decline of takahe. We wish to dedicate this paper to him as a tribute to the pioneering work he carried out on takahe and, subsequently, his support of our takahe research programme.

Food Preferences and Habitat Requirements of T akahe in the Murchison Mountains

Because the taka he is monogastric and possesses a very small caecum, fibrous material cannot be digested. Plant food which passes through the bird is structurally unaltered, only the readily extractable juices being digested. As a consequence of this apparently inefficient digestive system the takahe has an extremely specialised diet.

During the snow-free period (usually from October to May) taka he inhabit the alpine tussock grasslands between 1110 and 1430m. The tussocks provide food, shelter and nesting sites. Although there are about 250 species of potential food plants present in the grassland and adjacent beech (*Nothofagus* spp.) forest, the diet of takahe is extremely restricted, consisting mainly of three tussocks (*Chionochloa pallens*, *C. flavescens** and *C. crassiuscula*) and a mountain daisy (*Celmisia petriei*). Takahe eat only the basal meristematic portions of the tussock tiller and *Celmisia* leaf. The bird pulls out the leaf or tiller with its beak and then nips off and eats 1-2cm of the white basal section. The remainder of the leaf sheath and blade is discarded. It is unusual for green leaf material of any plant to be eaten. From October to January the tussock tiller bases form the major part of the diet but, from mid January to March the seeds of small grasses (*Poa* spp. and

Festuca spp.) are also taken and, when available, the seeds of the snow tussocks (the latter constitute a very important food source about every three years when flowering occurs). Although berries of *Coprosma*, *Myrsine*, *Cyathodes* and *Gaultheria* are extremely abundant at times, taka he do not feed on them. Similarly, the herbs *Ranunculus lyallii*, *Senecio lyallii*, *S. scorzonerooides*, *Anisotome aromatica*, *Ourisia macrocarpa*, *Bulbinella gibbsii*, *Astelia nervosa*, *Oxalis lactea* and *Coriaria plumosa*, which are abundant (and palatable to deer (Lavers, 1978)), are not eaten. Others, for example *Aciphylla takahe* and *Anisotome haastii*, are occasionally eaten - the basal parts of the stem being grubbed up.

The nutritional quality of *C. pallens* and *C. flavescens* tussocks varies according to site. Plants growing on fans and flush zones have a higher nutrient content than those of the same species growing on more mature soils. Takahe feed consistently at certain sites and choose individual plants high in nitrogen and phosphorus (Mills and Mark, 1977; Mills, Lee and Mark, 1978). Less nutritious plants usually have only one or two tillers taken or are left untouched. Thus, although there may be extensive areas of *C. pallens* and *C. flavescens* available, the plants may not be of sufficiently high nutritional quality to support takahe. The distribution of takahe territories is dependent on the presence of *C. pallens* and *C. flavescens* growing on fertile, young, well-drained soils. The tussock species which grow on mature, poorly-drained soils, namely *C. teretifolia* and *C. acicularis* are seldom or never eaten. In wetter areas of Fiordland, particularly to the west of the main divide where few takahe occur, *C. acicularis* is the dominant tussock species (takahe have never been observed feeding on this species).

In winter the alpine grasslands are usually covered with up to a metre of snow for at least two months of the year. It was believed for many years (Williams, 1960; Mills et al., 1980) that these conditions forced the takahe to descend to lower elevations and forage in the beech forest. Recent, as-yet-unpublished, radio-telemetry studies have shown that the preferred winter habitat is the scrub - grassland zone at or above tree-line. The soils of this zone are also young, being derived from alluvium, scree or talus. The winter diet of takahe in these areas is predominantly the rhizomes of the summer-green fern *Hypolepis millefolium* and the leaf bases of tussocks *C. flavescens*, *C. pallens*, *C. crassiuscula*

* *C. flavescens* in Fiordland possibly includes two taxa.

and *Celmisia petriei*, supplemented by the leaf bases of sedges and rushes (*Carex coriacea*, *Uncinia affinis*, *U. clavata* and *Schoenus pauciflorus*) and, if available, the forest tussock *C. conspicua*. The commencement of feeding on the rhizomes of *Hypolepis millefolium* coincides with the peak in the rhizomes' annual cycle of carbohydrates and nitrogen (Mills et al., 1980). The high carbohydrate concentrations in the rhizomes are required by takahe to meet the metabolic requirements of thermoregulation in the sub-zero temperatures of mid-winter. A high carbohydrate diet is not required at other times of the year, and as a result, *Hypolepis millefolium* is rarely eaten outside the period from April to September.

The radio-telemetry study has shown that the forest generally is not important to the bird in winter if there is adequate food available in the grassland-scrub zone.

Implications of present food preferences and feeding behaviour

The takahe, in its present range, has a very restricted diet despite the presence of a wide variety of potential food plants, and possesses specialised feeding adaptations suited to its relatively infertile alpine grassland environment. Most alpine and sub-alpine soils have low levels of phosphorus and nitrogen. Plants adapted to growing on these soils are correspondingly slow-growing and have low levels of these essential nutrients.

Takahe have specialised behavioural and morphological features that suit them to the alpine zone. The behavioural features include: eating the most nutritious part of the plant (the basal meristematic portion and the seeds); switching from species to species to take advantage of seasonal changes in plant chemistry of each species; and selecting the most nutritious individuals of a particular species. The morphological features are the large size of the bird and the possession of a powerful beak, which are necessary to pull out and cut the tussock tillers. For *C. flavescens*, an average force of 15.5 kg is required to break the tiller at the junction of the stem and the leaf sheath, and 13.0 kg is required for *C. pallens* (Table 1). A smaller bird could not break the tillers and hence would be unable to eat the most nutritious part of the plant. For this reason takahe chicks are dependent on their parents for the provision of food for three or four months after hatching.

Table 1: Force (kg) required to pull out *Chionochloa* tillers.

Species	Number			
	measured	Mean	S.D.	Range
<i>C. crassiuscula</i>	150	8.70	2.93	2.6 - 17.5
<i>C. pallens</i>	150	13.04	4.21	4.6 - 23.3
<i>C. flavescens</i>	150	15.48	4.82	2.4 - 25.1

Small birds would be able to exploit the meristem of tussocks only by digging up parts of the plant, which would destroy the slow-growing tussocks.

The mode of feeding by takahe does not endanger its main food species. *Celmisia petriei* and the preferred tussocks recover after the removal of moderate numbers of leaves and tillers. In fact, greater tillering is induced when up to a quarter of the tillers are removed from a tussock (unpubl. data). When the central leaves of *Celmisia petriei* are broken off near the base of the meristem the remaining stubs continue to grow. In contrast, sustained deer grazing on the green leaf material ultimately kills a tussock (Mark, 1969).

The evolution of large body size, as well as being mechanically advantageous, also confers thermoregulatory and energetic advantages which are essential to species on low nitrogen diets (Mattson, 1980) and living in a cold environment. These morphological and behavioural adaptations suggest that takahe have been predominantly tussock feeders for a very long time.

If the bird had occupied a variety of niches, e.g. forest, scrub, and tussock grasslands, one would expect this to be reflected in a wide diversity of foods eaten in its present range, but this is not so. Some birds do feed on the leaf bases of *Schoenus pauciflorus*, *Uncinia clavata* and the rhizomes of *Hypolepis millefolium* (Mills et al., 1980) in winter, but these foods are rarely eaten in other seasons. Furthermore, some information indicates that takahe would not have flourished on the types of tussock that presently exist in the lowland, sub-alpine or drier mountain areas. The principal tussocks of these regions are *C. rubra*, *C. macra* and *C. rigida*. Generally, these species have lower levels of nitrogen, phosphorus and soluble sugars than the alpine species *C. flavescens* and *C. pallens* (Fig. 1) (see Williams et al., 1977; Connor, Bailey and O'Connor, 1970; Mills and Mark, 1977). A study of a population of takahe feeding in the sub-alpine zone on *C. rubra* in Takahe Valley

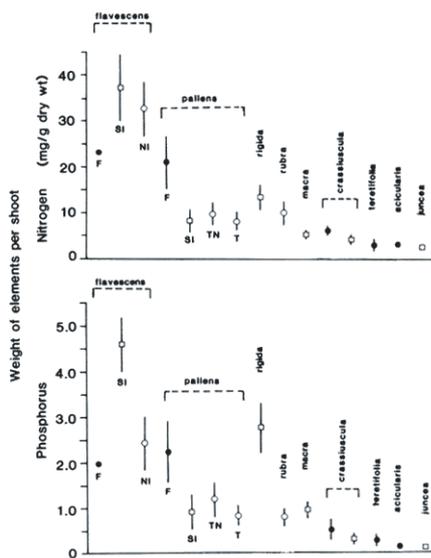


Figure 1: Weight of nitrogen and phosphorus per shoot (mg/g dry weight) for several taxa and regional groups of *Chionochloa*. Vertical bars denote 95% confidence intervals. • Fiordland; □ South Island excluding Fiordland; ○ North Island; T Tararua; TN North of Tararua (data from Williams et al., 1977).

revealed that these birds were significantly lighter in weight, and had a lower rate of chick and adult survival than those living in the alpine areas (Mills, 1975, 1978).

Research by Williams et al. (1978), and a review by O'Connor (1980), have emphasised that *C. flavescens* and *C. pallens* have an affinity for, and are adapted to, young soils that retain an appreciable proportion of total inorganic phosphorus in the primary apatite or calcium-bound form. Research by Archer (1973, 1976) has indicated that there is rapid ageing of alpine soils, with very little apatite present in the fine fraction of soils only 1000 years old. Thus these tussocks are dependent on unstable terrain for re-establishment. O'Connor (1980) has pointed out that the persistence of *C. flavescens* and *C. pallens* in an environment where stable soils age rapidly can be explained only by postulating conditions of persistent or recurrent land instability. He notes that the distribution of these two species is in general concurrence with the axial tectonic belt as defined by Walcott (1978). It should not pass without notice that the historical and recent distributions of taka he (Figs. 2 and 3), also generally correspond with the

position of the axial tectonic belt.

T all tussock grasslands that have persisted on the lowlands are generally on peaty, poorly-drained soils. Whilst these tussock grasslands may look like takahe habitat, in fact they are not because the nutrient levels are much lower than in the alpine tussocks (Fig. 1). In present-day conditions, tussock grasslands that develop on richer, younger soils are quickly replaced by scrub and forest. The only time in the past when it was possible for nutritious tussock species, such as *C. flavescens* and *C. pallens*, to have been abundant on the lowlands was during the cold periods of the Pleistocene, when extensive areas of young soil existed on the alluvial outwash plains. In the

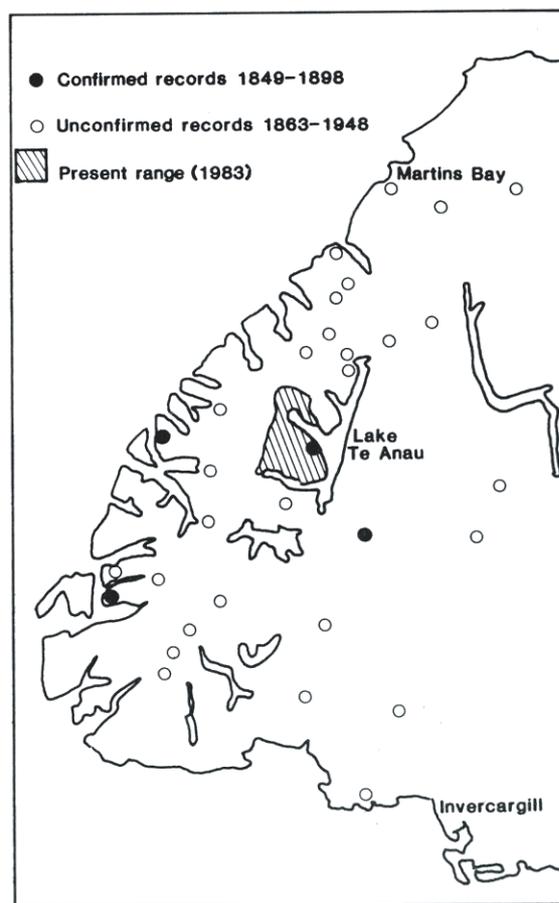


Figure 2: South-west area of South Island showing the locations of unconfirmed sightings and early captures of takahe. (from Reid, 1978).

Otira Glaciation period during the late Quaternary, sub-alpine grassland and scrub covered much of the area south of latitude 380 (Stevens and Suggate, 1978; Grant-Taylor, 1978) (Fig. 4b) and even north of this latitude extensive areas of grassland existed (M. S. McGlone, pers. comm.). The forests of the South Island remained as small refugia (Wardle, 1963). It is our conclusion that these conditions would have been particularly suitable for takahe and implies that the bird flourished over a wide area.

Historical Distribution of Takahe

Prior to the official re-discovery of takahe by Dr G. B. Orbell in 1948, only four confirmed sightings of takahe had been made in European times. These records, together with Maori traditions (Beattie, 1949) and numerous unconfirmed but likely reports in the latter half of the nineteenth century, led Reid (1978) to conclude that takahe were then "spread somewhat irregularly and discontinuously over about 15-16,000 km²: from Preservation Inlet in the south-east to north of Milford Sound; and to

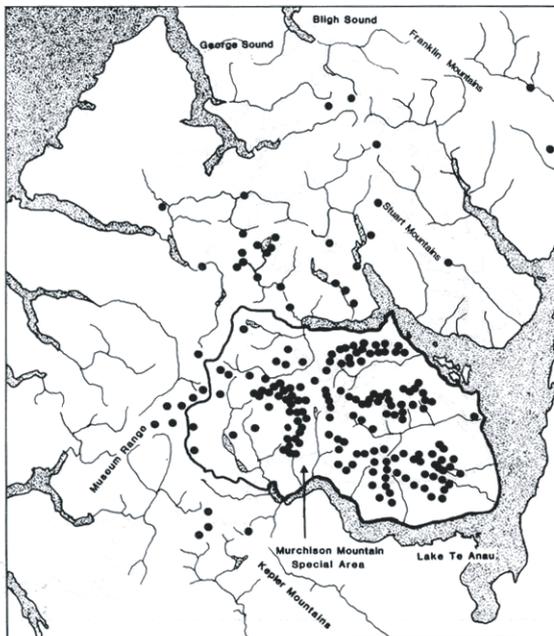


Figure 3: Sightings of takahe or their sign in Fiordland from 1948 to 1972. (from Reid, 1978).

Mossburn and the Irthing River in the east" (Fig. 2). Takahe are presently confined to the Murchison and Stuart Mountains of Fiordland National Park. In the 1950s, however, the bird had a much wider distribution that included part of the Kepler Mountains and a larger area of the Stuart Mountains (Fig. 3).

Takahe would never have been very numerous over much of Fiordland. For instance, Reischek (1888) unsuccessfully searched 50 km² of Dusky Sound in "good grass country" near where the first living specimen was captured 38 years previously. Other explorers, such as Hector, Park, Hay, Henry and Wilmot, undertook extensive surveys in Fiordland and, amongst other things, were on the look-out for takahe; none were seen, whereas kakapo and kiwi were frequently encountered. An old Maori informed Bathgate (1899) that he had been told by the Aparima Maoris some 50 years previously that takahe were plentiful, but "went in patches" between Preservation Inlet and Lake Hauroko.

Similarly, if the bird was abundant on the red tussock (*C. rubra*) lowlands of eastern Fiordland or Southland it should have been seen more frequently in the 1870's, when areas were under pastoral development.

Areas where takahe were likely to be concentrated in Fiordland during Maori times would have been the Murchison Mountains, Stuart Mountains, parts of the Kepler Mountains, and the Hauroko-Poteriteri area - all areas of extensive alpine grassland. Elsewhere the steep topography and the presence of unpalatable tussock species (such as *C. acicularis*), particularly in the wetter areas west of the main divide, would have precluded the presence of other than small numbers of takahe.

During European times takahe may have also survived in the Nelson and the Ruahine Ranges. Reid (1978) documents four unconfirmed sightings in the Nelson district between 1866 and 1935 and Phillipps (1959) presents convincing evidence of their existence in the Ruahine Ranges of the North Island late last century.

Recent takahe decline

The main cause of the decline of takahe in Fiordland over the past 50 years has been competition for food from introduced red deer (*Cervus elaphus*) (Mills and Mark, 1977; Mills, 1977; Mills, Lavers and Crawley, 1982). Browsing and grazing by deer have adversely affected the grassland, scrub and forest habitats

of takahe. The diet of deer in the tussock grasslands is varied but they have distinct preferences, which coincide, to a considerable degree, with those of takahe. Grasses and herbs make up the bulk of the diet of red deer (Lavers, 1978, unpubl. data). When deer colonise an area the palatable herbs form an important component of the diet. As deer numbers increase and the palatable herbs are eliminated, deer concentrate more of their feeding on tussocks, intensifying competition with takahe. Takahe and deer feeding on tussocks show distinct preferences for certain species, the most preferred containing the highest nutrients (Mills and Mark, 1977). Repeated grazing on the green leaves of the same tussock plants by deer, severely weakens and can kill the tussocks (Mark, 1969, Mills, Lavers and Lee, unpubl. data). The weakening, by lowering the nutrient content or elimination of the most nutritious plants, must have had a detrimental effect on the breeding success and survival of takahe, a species which depends on a rapid throughput of high quality food.

Takahe have persisted in the Murchison Mountains because of the extensive tussock grasslands and the high grassland: forest ratio. Because of the extent of the grasslands the impact of grazing by deer has not been as great as elsewhere in Fiordland and competition with takahe for food has been less intense. Another major factor in the persistence of takahe has been that the Murchison Mountains was one of the last areas in Fiordland to be invaded by deer. From early liberations between 1901 and 1910 near Manapouri (Logan and Harris, 1967), red deer moved 30 km northwards into the Murchison Mountains, via the Kepler Mountains, arriving in some western catchments in about 1930 (Parkes et al., 1978). It was not until the late 1950s that deer had begun to invade and build up numbers in the eastern sector of the Murchison Mountains (Parkes, Tustin and Stanley, 1978; K. Miers, pers. comm.). In contrast, in the southern part of the takahe range at Hauroko there was a liberation of deer in 1901, and peak deer densities would have occurred around 1920-1930 (see Riney, 1964). The Hauroko area was heavily infested with red deer by 1947 (Wodzicki, 1950). A similar pattern of increase occurred in the northern part of the takahe range in Fiordland after the release of wapiti (*Cervus elaphus nelsoni*) in 1905 (Donne, 1924) and following the spread of red deer into the area by 1940 (Tustin, 1970; Batcheler and McLennan, 1977).

Sub-fossil Records

Distribution

The distribution of sub-fossil remains (Fig. 4a) indicates that takahe once occurred over a wide area of New Zealand. Recent excavations (R. J. Scarlett, pers. comm.; Millener, 1981; Horn, 1983) have extended the sub-fossil distribution reported by Williams (1960) and Reid (1978). Most North Island remains are from caves (31 of 58 sites) or dunes (23, including possible middens), three are from swamps and two are early Pleistocene fossils (Millener, 1981). Usually only a single bird was present in each find but at the Poukawa Swamp site remains of at least 72 takahe were found; in a Martinborough cave 18 were present; and in a midden at Kaupokonui, Taranaki, 16 were found (Millener, 1981).

In the South Island the sub-fossil distribution is mainly confined to the eastern regions. Again most remains are from caves (13 of 27 sites) and only three from swamps. At 11 sites bones were found in or near to middens.

Millener (1981) has warned that mistakes can be made in ascribing sub-fossil remains in dunes to midden material. Many reports of moas and other birds reputed to come from middens are more likely to be of bones eroded from underlying dune sands and subsequently mixed with midden waste by downslope gravity movement before collection (Millener, 1981; Millener, pers. comm.; Millener quoted by Fordyce, 1982). There is doubt as to whether material from Ocean Beach, Port Jackson and some of the takahe material at Kaupokonui sites in the North Island and the Grassmere site in the South Island, are of midden origin (Millener, pers. comm.). The Kaupokonui site has been examined by Millener (pers. comm.). He found an intact takahe skeleton below a midden site, but considers it unlikely that it was associated with the midden. The problems of assessing primary and secondary association in these sites are such that in most cases a solution will be reached only by direct dating of the small bird bones (Millener, 1981).

Age of sub-fossil bones

The age of most of the sub-fossil material is not known with any precision, and there are problems with the different dating techniques. Many sub-fossil deposits have no clear stratigraphy and the conventional carbon - 14

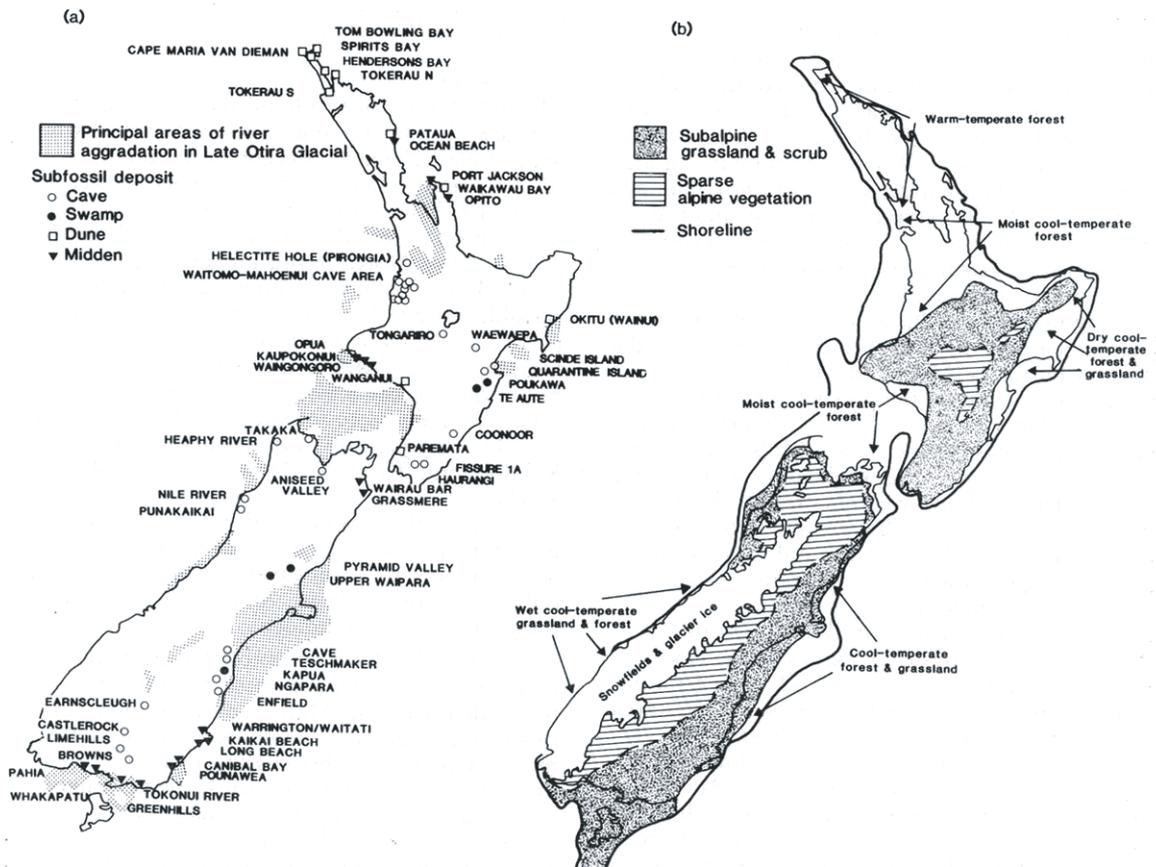


Figure 4: (a) Distribution of takahe sub-fossil remains; (b) Late Quarternary (late Otira Glacial Period) paleogeography (from Stevens and Suggate, 1978).

dating technique can not be used on takahe bones because they do not provide sufficient material for analysis (approximately 5 kg is required).

Excavations of Poukawa Swamp near Hastings (Horn, 1983) have provided the best-dated sequence of avian sub-fossils in New Zealand, as well as an indication of their abundance. Three layers of the swamp can be aged because of the presence of known-age ash showers from volcanic eruptions. In the two lowest layers, 7000-4000 years BP and 4000-1000 years BP, takahe represented approximately 16% of the ground bird community and 4% of all individuals of the different species present. In the top layer (less than 1000 years old) there was a marked reduction in the proportion of takahe; only two

takahe were found. It is possible that some or all of the five bones present in this layer could have come from a lower layer through mixing by recent agricultural cultivation (P. Horn, pers. comm.). Even if the two takahe in the top layer are genuinely associated with it, they represent only 3% of the ground-bird community, a decrease of 13% from previous layers. Horn (1983) believes that takahe began to decline before the arrival of the Maori and so "while fires and hunting activity in the last 1,000 years may have completed their local extinction, factors operating prior to this era initiated their decline". No takahe bones have been found in Maori middens in the vicinity of Poukawa or elsewhere in Hawkes Bay.

There is evidence that a similar decline occurred at other localities. In Northland, takahe bones have been found in dune deposits which have had associated moa bones and landsnail shells, radio-carbon dated at 4980 to 1130 years BP (mean 2543 ± 214 years) (data analysed from Millener, 1981). These dune sites were formed after the sea level reached its post-glacial peak about 6500-5000 years ago (Millener, 1981). Apart from a doubtful midden record at Ocean Beach (Millener, pers. comm.) no takahe bones have been found in Maori occupation sites in Northland.

Elsewhere in New Zealand takahe appear to have been rare during Maori times. Only a few takahe bones have been found in middens and it is uncertain whether all of these can be ascribed to human occupation. Those that are in middens are probably very old. The midden sites at Wairau Bar and Grassmere are from the moa-hunter period (950-1150AD) (Duff, quoted by Williams, 1960).

Another point which supports the view that takahe have been rare in the last 1000 years is that there is no clear reference to takahe in Maori legends of North Island or in those of the northern part of South Island (Williams, 1960). In contrast, in Southland and Fiordland where takahe have persisted, the species was known to the Maori (Beattie, 1949; Bathgate, 1899; Turbott, 1967; Reid, 1974, 1978) and referred to as the "pass bird found high up in the mountains" (Douglas, in Pascoe, 1957).

The apparent absence of takahe bones in swamps is another reason to believe that takahe had a reduced range over the past 6,000 years. Many of the existing swamps developed only after the sea level stabilised at its post-glacial maximum (Millener 1981). None of the limited number of moa bones that have been carbon-dated from swamps are older than 9500 years BP (Millener, 1981; McCulloch and Trotter, 1979; Gregg, 1972). Only six locality records for takahe come from swamps. This contrasts with moa which have 20% of the locality records in the North Island from swamps (data from Millener, 1981). To some extent a larger number of moa bones would be expected to be reported from swamp sites because of their size and conspicuousness and further excavations would be required to locate takahe bones. Nevertheless, with the exception of the Poukawa site, where at least 72 takahe were found, the number of takahe found at specific swamp sites is small. Extensive

diggings have been carried out at Pyramid Valley in North Canterbury but only seven takahe bones have been found (Scarlett, 1955). Associated moa bones at Pyramid Valley have been dated at 3450-3740 years BP (Gregg, 1972; McCulloch and Trotter, 1979).

The point we are making is that if takahe were widespread throughout New Zealand at about 6000 years ago it would be expected that taka he bones should be represented in swamp sites even although the bird is not an inhabitant of swamps. Bones can be washed in from some distance away or the bird could have become trapped. If the apparent lack of takahe bones in swamps is real then this information indicates either that the decline of takahe started prior to that of the moa species or the rate of decline was much faster.

The limited evidence available in the form of dated bones from caves indicates that the bones are old. There are five sites where takahe bones are present where dates for associated moa bones are available. The dates of these sites range from 15,300 years to 3500 years BP (see Millener, 1981).

Precise dating of takahe bones is needed, especially of those attributed to midden sites, to clarify the situation.

Sub-fossil evidence of takahe habitat preferences

There is an apparent anomaly in that takahe were absent from a large number of swamp sites where other avian sub-fossils (particularly the moa species) have been found and yet were plentiful at the Poukawa site. This could mean that the Poukawa Swamp had characteristics that made it suitable for takahe or that favourable habitat existed in the hinterland. Dr M. S. McGlone (pers. comm.) suggests that the absence of takahe from many New Zealand swamps may be due to low nutrient status of the swamps. He has examined the pollen records of many New Zealand swamps and believes that prior to the arrival of the Polynesians there were few swamps of high nutrient status. It was only the destruction of the forest in surrounding catchments and the swamp forest on the sites which permitted the tall swamp herbs, rushes reeds etc., characteristic of high fertility swamps, to thrive. In McGlone's experience Poukawa Swamp is one of the exceptions, having a raupo (*Typha*) dominant band of vegetation around the edge from its inception. This, he believes, is due to the nutrient-rich limestone soils on the surrounding hills.

We disagree with McGlone's explanation. Firstly there are other swamps (e.g. Glenmark, Hamilton, Enfield, Ngapara, Kapua, Te Aute, and Pyramid Valley) which lie within limestone basins (Millener, 1981), but only the last three have had takahe amongst the recovered avian remains. In the case of Pyramid Valley, raupo has been identified on one layer of the swamp (Harris, 1955) but takahe could not have been very abundant there because only seven bones, representing at the most only 3 or 4 individuals (Scarlett, 1955), have been found. Secondly, whilst raupo rhizomes can be expected to contain high levels of carbohydrates and certain nutrients the food would not be readily available because the morphology of takahe (short legs, heavy build) indicates that it is not adapted to feed in a swamp (Fig. 5). Furthermore, in its present range in the Murchison Mountains takahe do not favour swampy sites. *Carex coriacea*, *funGus gregiflorus* and *Schoenus pauciflorus*, which grow in damp situations, are eaten in late autumn and winter but form only a small component of the diet. It is likely that takahe could subsist on a diet of some swamp plants, but if they were a preferred food in the past then why not now? If fertile swampy sites were not widespread in the past then it is hardly likely that a preference for these habitats would account for a once widespread distribution of the bird.

In this regard comparisons are often made between takahe and its close relative the pukeko (*Porphyrio porphyrio*). Bull and Whitaker (1975) suggested that the takahe may have occupied the

same niche presently occupied by the pukeko. They argued that when pukeko became established the resultant competition reduced the range of takahe. This is highly unlikely because the available evidence from sub-fossil and midden remains indicates that the pukeko is a recent immigrant from Australia, having become established in sufficient numbers to maintain a viable population only in the last few hundred years, well after the decline of takahe began (Millener, 1981). This interpretation is supported by the excavation at Poukawa (Horn, 1983).

Millener (1981) expressed the view that because takahe remains are often found in association with sub-fossil remains of extant forest species, takahe was primarily a forest inhabitant. This is not necessarily true. Takahe territories in the present range are close to beech (*Nothofagus* spp.) forest, but the forest habitat is only utilized when heavy snow prevents feeding in the tussock grasslands or sub-alpine scrub zone. The same situation could have existed during the glacial periods of the Pleistocene, with the bird taking refuge in pockets of forest during winter but preferring the grassland habitat for most of the year. This would not preclude the possibility of takahe dying in forests.

If takahe was a forest inhabitant it would have been rare in the glacial periods of the Pleistocene, when forest existed only as small isolated remnants in two-thirds of New Zealand (see Wardle, 1963; Stevens and Suggate, 1978; Grant-Taylor, 1978), and have become more abundant when the forest expanded to cover most of North Island between 14,000 and 12,000 years ago and over most of South Island between 12,000 and 10,000 years ago (M. S. McGlone pers. comm.). If the habitat was favourable, why, then, did the species decline? The answer that is frequently advanced involves the ecological changes induced by the Maori through hunting, burning of extensive areas of forest and the introduction of the Polynesian dog and rat (Fleming, 1962; Millener, 1981). The two views that takahe was a forest species and that the Maori caused its decline and near extinction, are not compatible. By the time Europeans arrived approximately 53% (14 million hectares) of New Zealand was still covered in forest (Nicholls, 1980). It would have been physically impossible for the Maori to have penetrated all of this forest and removed the takahe if takahe were as widespread as the sub-fossil record indicates. The same applies to the giant rail, kakapo (in North Island) and the moa



Figure 5: The takahe a large stout bird with short legs, certainly not adapted for wading around in swamps.

species. Species which were or are definitely forest species, e.g. New Zealand pigeon (*Hemiphaga novaeseelandiae*), huia (*Heteralocha acutirostris*), kiwi (*Apteryx* spp.), kakapo (*Strigops habroptilus*) and weka (*Gallirallus australis*, which is partially a forest bird), were extensively hunted for food and feathers by the Maori, but were still abundant when Europeans arrived. For example, in 1874 a single expedition collected over 600 huia skins from forested areas of the Tararua Ranges (Enys, 1875). The New Zealand pigeon which lays only one egg and has one clutch per year would be vulnerable to hunting, especially in view of the fact that it was readily attracted to trapping sites - yet it remained common. The species which supposedly suffered the most at the hands of the Maori (takahe, giant rail, the moa species, flightless goose (*Cnemiornis*), extinct crow (*Palaeocorax*), giant eagle) all have the same characteristics in that they all could be birds of the open country or the forest margins.

The amount of grassland or scrub present in New Zealand when the Maori arrived is considered to have been small as approximately 75% of the country was thought to have been covered in forest (Nicholls, 1980). Birds existing in small pockets of habitat would have been extremely vulnerable to being hunted to extinction.

Conclusions

Our research has shown that the takahe is primarily an obligate, specialist tussock-feeder dependent on highly nutritious tussocks which grow only on young soils. It is our belief that takahe are behaviourally and morphologically adapted to live in the alpine grasslands, and it is unlikely that the species has drastically changed its diet and method of feeding since Pleistocene times. The evolution of large body size has enabled the bird to exploit the most nutritious part of the tussock plant by wrenching tillers with its powerful bill. Large size also confers energetic and nutritional benefits on a species living in a cold climate. The extensive alluvial outwash plains which existed in the Pleistocene would have been extremely favourable for the spread of *C. pallens*, *C. flavescens*, or other nutritious tussocks and takahe would have flourished in that environment. In the post-glacial Holocene, the spread of forest would have reduced the habitat

available to takahe thereby causing a major reduction in range.

The sub-fossil record shows that takahe have, at one time or another, occurred over a wide area of New Zealand. However, because the ages of the bones are not known with any degree of precision, the relative abundance of takahe at any given period and the timing of the decline are not accurately known. The only information available which gives some clue to the timing of the decline is the comparative absence of takahe bones from swamp sites. Many of the swamps that have avian bones present developed in the period when the sea level stabilised at the postglacial maximum, 5000-6500 years ago. The lack of takahe bones in many of these swamps indicates that the bird was not abundant in or near swamps at this time, and had declined.

It is known that the bird survived in Northland and Hawkes Bay in the early Holocene and in the Ruahine Range, Taranaki, Nelson, Otago and Southland in early Maori times. The climatic and vegetational conditions during these times would have been markedly different from those experienced during the glacial periods of the Pleistocene, and presently in Fiordland. Undoubtedly the bird survived on a diet which was different in plant species composition from that presently preferred in the Murchison Mountains, but takahe could still have been predominantly a grassland feeder existing in grassland pockets in forest clearings and grassland areas on alluvial soils. Our argument is that in such circumstances the population would have been low, with an isolated distribution. With such a restricted distribution the bird would have been vulnerable to hunting by the Maori. The Maori may well have eliminated the bird from some regions but the ultimate cause was the reduction in suitable habitat. The same pattern of decline could have occurred with the moa species, the giant rail, and the extinct eagle. The Maori merely dealt the *coup de grace* when these species were concentrated in a restricted habitat.

The survival of takahe in Fiordland to the present day is remarkable, especially considering the effects of introduced mammals, which, in recent times, have severely reduced the population size and distribution. Nevertheless, the fact that the bird continues to live and breed in the Fiordland mountains augers well for its future. However an active management policy will be needed to increase the population and to restore the bird to parts of its former range. Our research

shows that the species is adapted to life in the alpine zone and so the major thrust of future management of takahe must be aimed at preserving them in that environment.

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