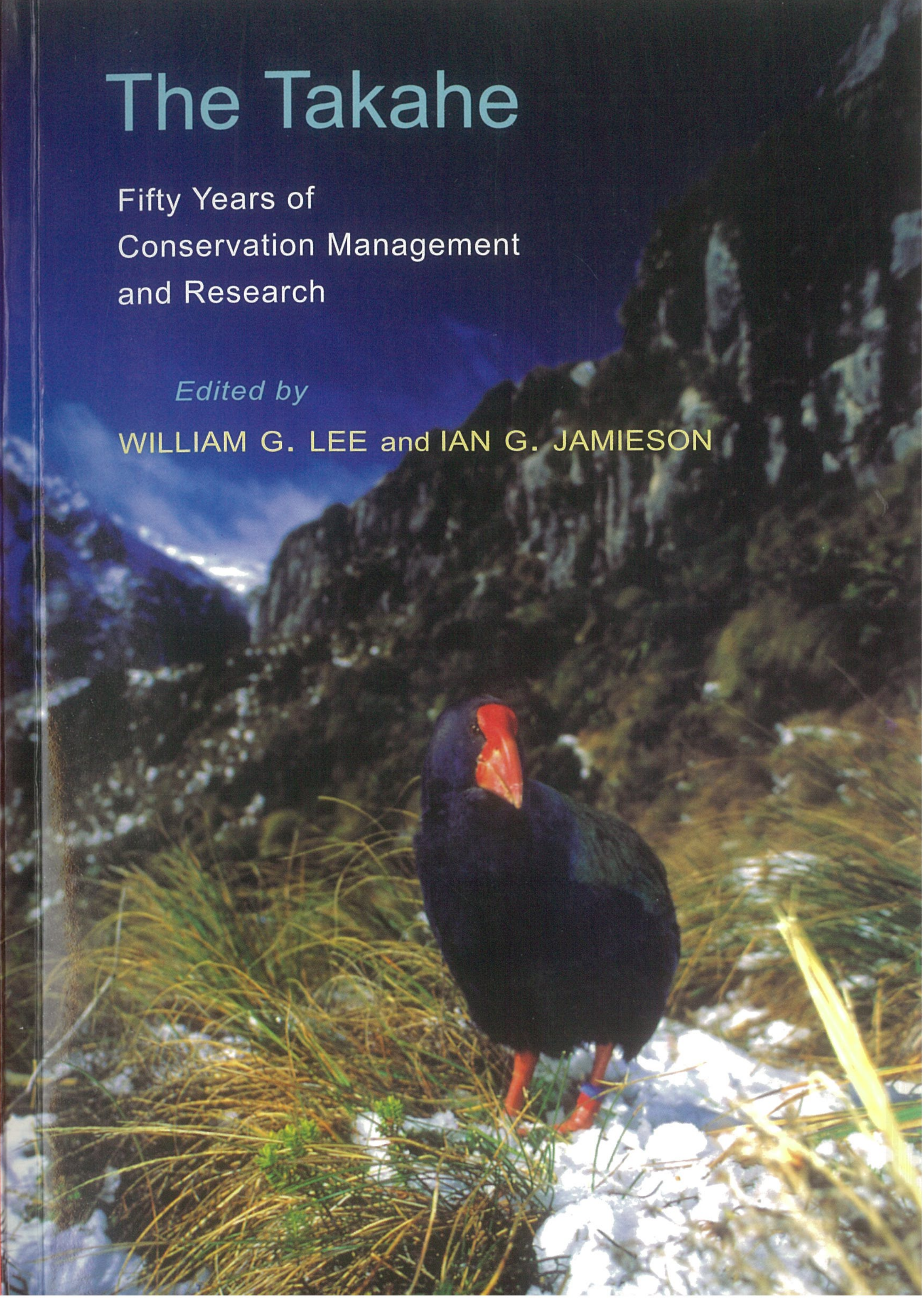
# The Takahe

## Fifty Years of Conservation Management and Research

Edited by

WILLIAM G. LEE and IAN G. JAMIESON



THE TAKAHE *Edited by* William G. Lee and Ian G. Jamieson four

# Origins and prehistoric ecology of takahe based on morphometric, molecular, and fossil data

STEVEN A. TREWICK AND TREVOR H. WORTHY

A large, flightless and presumed extinct rail (Aves: Rallidae) was described in 1848 from Quaternary fossil bones collected at Waingongoro (South Taranaki), North Island New Zealand (Owen 1848a). Owen, whilst recognising similarities with *Porphyrio,* erected the genus *Notornis* on the basis of a small number of head and leg bones. He named and described the species *N. mantelli* after the collector of the material, Walter Mantell (Owen 1848b).

A second species was proposed later that century from the remains of a recently killed bird found in the Fiordland area of the South Island. Meyer (1883) named it a new species, *N. hochstetteri*, based on size differences of certain skeletal elements compared with those of *N. mantelli.* Subsequently, however, a series of informal rationalisations (Mayr 1949; Fleming 1953; Greenway 1967; Kinskey 1970; del Hoyo *et al.* 1996) saw the relegation of these two species to subspecies status and their inclusion in the existing genus *Porphyrio* with the flying species *Porphyrio porphyrio*. The extinct North Island form was *Porphyrio mantelli mantelli* and the South Island form *Porphyrio mantelli hochstetteri* represented by a single extant population in the alpine grasslands of Fiordland (Ripley 1977). The volant species *Porphyrio porphyrio* (swamphen) currently consists of around 13 subspecies defined by plumage and size differences that are distributed predominantly in the Southern Hemisphere west from Africa to the western Pacific. *Porphyrio p. melanotus* (pukeko) occur in New Zealand, Australia and New Guinea.

Recent studies of morphological variation of takahe and genetic variation within *Porphyrio* indicate that North Island and South Island takahe are distinct species and that these most probably evolved independently from flying ancestors (Trewick 1996a, 1997). The original species names were therefore reinstated. Together with updated information on the distribution, age and palaeoecology of fossil takahe, this evidence raises interesting questions about the evolution and ecology of the two takahe species.

## ORIGINS OF TAKAHE

In addition to providing evidence of the relative abundance, habitat use and distribution of past takahe populations (see below), fossil bones have formed the basis for morphological (Trewick 1996a) and genetical (Trewick 1997) studies that have been instrumental in integrating historic and modern evidence.

The mean values of 25 parameters measured on leg, wing, head and pelvic bones of North Island (NI) and South Island (SI) takahe differed significantly except for humerus distal breadth, carpometacarpus length, and sternum median length (Table 4.1). These latter elements are all associated with the wing structure and their lack of variation presumably reflects its redundancy in these birds. All elements that differed significantly between islands were larger in NI takahe with the exception of the premaxilla, which was larger in SI takahe. Statistics of modern specimens from the extant population in Fiordland did not differ significantly from those of other (fossil) SI individuals (Trewick 1996a).

Homogeneity tests of the variances of leg bone lengths indicated that regardless of age, type and location of populations/deposits takahe populations were similar within islands. The measurements of leg bones of NI specimens differed significantly from SI ones. The degree to which dimensions of particular bone elements differed between NI and SI takahe varied (Figure 4.1). NI takahe were evidently taller than SI takahe, with leg bones between 6% and 24% longer. However, other dimensions showed disproportionate size differences indicating that NI takahe and SI takahe differed in shape as well as in overall size. Most obvious is the fact that NI takahe possessed a smaller premaxilla (and presumably beak) than SI takahe, both in absolute terms and in proportion to the body and head (see Figure 4.2).

The relative proportions of the length and breadth of the major leg bones indicate that while NI takahe were taller, they were also relatively lighter in weight, having comparatively slight legs. An analysis of covariance (ANCOVA) carried out on NI takahe, SI takahe and pukeko leg bones indicates that NI takahe were, despite considerable difference in height, more similar in shape to Pukeko than to SI takahe (Figure 4.3). This indicates separate evolution of two takahe species and suggests more recent divergence from respective flying ancestors of the NI than SI takahe.

A fragment of the small ribosomal subunit (12S) of the mitochondrial DNA genome consisting of 388 homologous sites was aligned for eight *Porphyrio* taxa. For each taxon at least two independent sequences were obtained from one to four individuals. DNA sequences from *Porphyrio p. melanotus* individuals from New Zealand, Chatham Island and eastern Australia were identical to one another. Two distinct haplotypes were encountered in the two *P. p. pulverulentus* (Philippines) individual samples. Three modern *P. hochstetteri* had identical haplotypes. The sequence from *P. mantelli* was achieved by the alignment of several short sequences obtained using a number of different PCR primer pairs. This indicates that, despite the relatively good quality of the bones used for extraction, the DNA was extensively fragmented, which is typical of so-called 'ancient' sources.

TABLE 4.1: Comparison of means and their associated statistics of various bone measurements between North Island (NI) and South Island (SI) takahe (*= P<0.05; ** = P<0.01; *** = P<0.001).

| Bone variable measured | Group | N | Range | Mean | P | SDev | %CV | %CV modern SI |
|---|---|---|---|---|---|---|---|---|
| Premax. L. | NI | 21 | 47.2-67.8 | 58.6 | | 5.02 | 8.57 | |
| | SI | 30 | 56.6-67.4 | 62.7** | | 2.69 | 4.29 | 4.40 |
| Cranium L. | NI | 20 | 48.4-60.1 | 54.1 | | 2.51 | 4.64 | |
| | SI | 31 | 45.8-53.6 | 50.6*** | | 1.88 | 3.73 | 3.60 |
| Cranium B. | NI | 18 | 40.1-51 | 42.4 | | 2.50 | 5.90 | |
| | SI | 31 | 37.8-42.9 | 40.2** | | 1.26 | 3.13 | 3.10 |
| Humerus L. | NI | 71 | 77.7-99.3 | 88.0 | | 4.53 | 5.15 | |
| | SI | 44 | 74.1-90.2 | 82.8*** | | 3.57 | 4.31 | 3.10 |
| Humerus PB. | NI | 68 | 16.6-22.9 | 19.7 | | 1.20 | 6.08 | |
| | SI | 45 | 16.5-20.8 | 18.3*** | | 1.00 | 5.43 | 4.90 |
| Humerus MB. | NI | 74 | 4.7-6.9 | 5.9 | | 0.40 | 6.76 | |
| | SI | 45 | 4.4-6.3 | 5.6*** | | 0.42 | 7.60 | 5.70 |
| Humerus DB. | NI | 66 | 10.8-14.9 | 13.4 | | 0.87 | 6.48 | |
| | SI | 44 | 11.8-14.7 | 13.4 | NS | 0.72 | 5.41 | 5.00 |
| Carpometacarpus L. | NI | 16 | 41.1-51.3 | 46.1 | | 2.74 | 5.94 | |
| | SI | 23 | 41.2-47.7 | 44.6 | NS | 1.55 | 3.48 | 3.50 |
| Sternum L. | NI | 10 | 57.5-73.8 | 64.9 | | 5.22 | 8.04 | |
| | SI | 28 | 15.5-20 | 63.6 | NS | 2.62 | 4.12 | 4.30 |
| Pelvis L. | NI | 9 | 83.6-93.5 | 89.4 | | 3.78 | 4.23 | |
| | SI | 35 | 70.7-89.6 | 82.2*** | | 4.50 | 5.48 | 5.00 |
| Pelvis antitroch. B. | NI | 6 | 54.2-60.7 | 58.2 | | 2.33 | 4.00 | |
| | SI | 36 | 47.4-55.7 | 51.0*** | | 1.83 | 3.58 | 3.30 |
| Pelvis post. iliac B. | NI | 3 | 58.45-65.8 | 61.2 | | 3.97 | 6.48 | |
| | SI | 30 | 47.2-59.6 | 51.9* | | 3.12 | 6.01 | 5.50 |
| Pelvis ant. iliac B. | NI | 6 | 26.1-29.1 | 27.5 | | 1.10 | 3.99 | |
| | SI | 37 | 20.5-27.1 | 24.7*** | | 1.40 | 5.67 | 5.50 |
| Femur L. | NI | 69 | 96.5-120.6 | 110.4 | | 5.00 | 4.52 | |
| | SI | 43 | 94.1-111.5 | 103.3*** | | 4.23 | 4.10 | 3.50 |
| Femur PB. | NI | 74 | 20.2-29 | 24.6 | | 1.47 | 5.98 | |
| | SI | 44 | 19.22-23.5 | 21.6*** | | 0.96 | 4.45 | 4.10 |
| Femur MB. | NI | 96 | 8.8-11.5 | 10.1 | | 0.57 | 5.59 | |
| | SI | 44 | 8.41-10.7 | 9.7*** | | 0.57 | 5.83 | 4.80 |
| Femur DB. | NI | 72 | 21.4-28.2 | 24.9 | | 1.40 | 5.60 | |
| | SI | 42 | 20.2-25 | 22.6*** | | 1.04 | 4.58 | 4.30 |
| Tibiotarsus L. | NI | 51 | 153.4-199.9 | 177.8 | | 9.38 | 5.28 | |
| | SI | 48 | 137.7-160.4 | 149.0*** | | 5.27 | 3.54 | 3.10 |
| Tibiotarsus PB. | NI | 47 | 16.3-22.2 | 19.9 | | 1.37 | 6.92 | |
| | SI | 47 | 15.7-20.1 | 18.2*** | | 0.89 | 4.91 | 4.20 |
| Tibiotarsus MB. | NI | 66 | 7.1-10.7 | 9.3 | | 0.76 | 8.12 | |
| | SI | 52 | 7.4-10 | 8.6*** | | 0.69 | 8.05 | 6.20 |
| Tibiotarsus DB. | NI | 54 | 17.4-21.6 | 19.3 | | 0.95 | 4.93 | |
| | SI | 49 | 15.2-19.7 | 17.5*** | | 0.94 | 5.40 | 4.00 |
| Tarsometatarsus L. | NI | 89 | 101-132 | 117.4 | | 6.28 | 5.35 | |
| | SI | 51 | 84.8-102.3 | 94.6*** | | 3.95 | 4.18 | 4.00 |
| Tarsometatarsus PB. | NI | 74 | 19-24.5 | 21.2 | | 1.07 | 5.06 | |
| | SI | 52 | 15.5-20 | 18.2*** | | 0.92 | 5.04 | 4.10 |
| Tarsometatarsus MB. | NI | 101 | 7.6-12 | 9.7 | | 0.65 | 6.62 | |
| | SI | 54 | 7-9.8 | 8.6*** | | 0.53 | 6.12 | 5.90 |
| Tarsometatarsus DB. | NI | 79 | 19.3-25.1 | 22.4 | | 1.21 | 5.39 | |
| | SI | 50 | 18.3-22.6 | 20.5*** | | 1.04 | 5.06 | 4.30 |

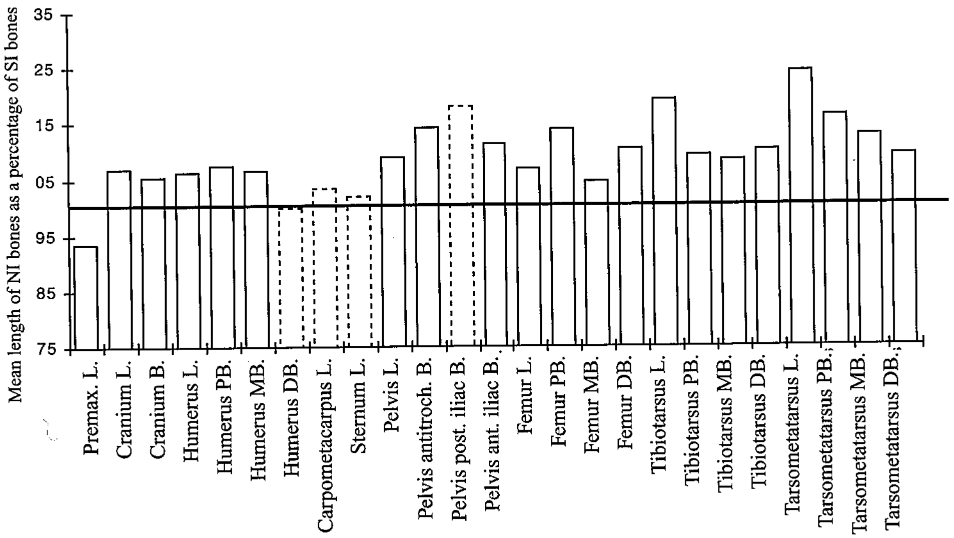


**FIGURE 4.1**: Comparison of bone dimensions between North Island (NI) and South Island (SI) takahe. Mean dimensions of NI takahe are given as the % length of values for SI takahe, with the 100% line representing parity of the two species. Dashed borders indicate means of NI takahe and SI takahe that were significantly different at $P<0.01$. Labels are from Trewick (1996a).

**FIGURE 4.2**: The skulls of North Island takahe *P. mantelli* (left) and South Island takahe *P. hochstetteri* (right). (Photo by Rod Morris)

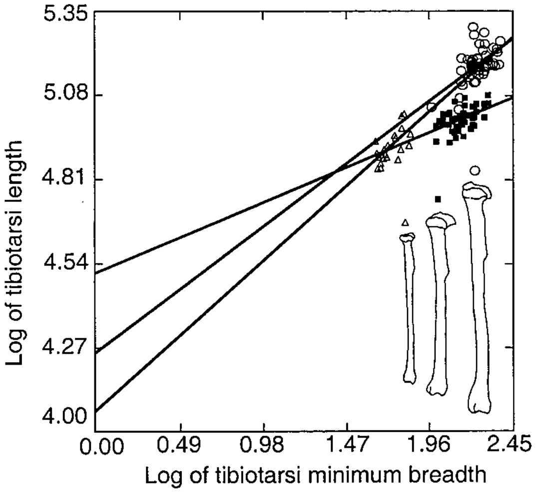


**FIGURE 4.3**: Log-transformed lengths and minimum shaft breadths of tibia of North Island takahe (open circles) and South Island takahe (filled squares), and pukeko (open triangles). Details of regression equations are given in Trewick (1996a).

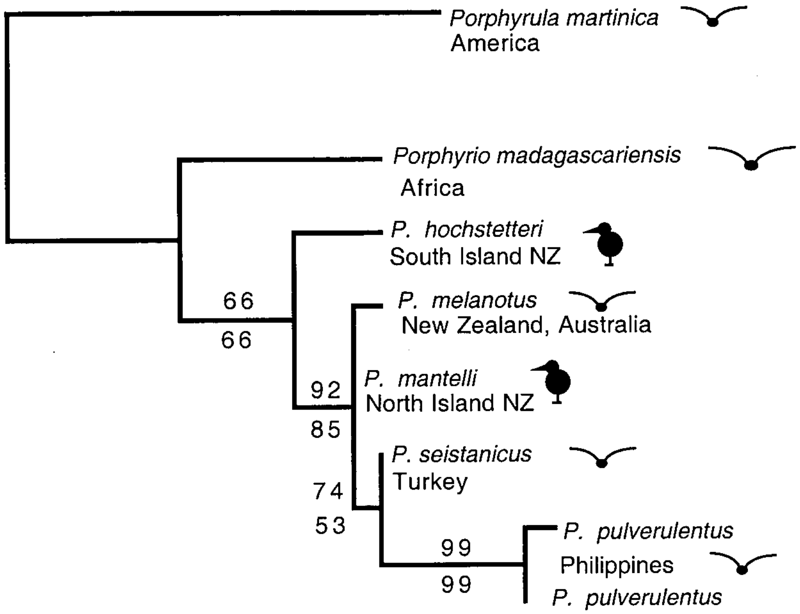


**FIGURE 4.4**: The single shortest unweighted parsimony tree constructed from 12S sequences of Porphyrio. Support for nodes is indicated by % bootstrap values derived from 1000 replicates. Fat and flying bird icons indicate volancy of respective species.

Phylogenetic analysis with maximum likelihood, parsimony and distance methods all produced trees with similar topology. Bootstrap resampling indicate good support for the nodes of particular interest to this study (Figure 4.4). The purple gallinule *Porphyrula martinica* (America) was used as the outgroup as it is morphologically and behaviourally the most similar rail to *Porphyrio*. In all trees, *Porphyrio* was monophyletic, and the most basal taxon in the present analysis was the African swamphen *P. p. madagascariensis*. There was, however, little apparent geographic pattern in the genetic relationships of the group. Sequences from the two takahe (*P. mantelli* and *P. hochstetteri*) indicate that they have distinct evolutionary histories and are paraphyletic with respect to *P. porphyrio*.

Morphological and molecular data indicate that the SI takahe was probably derived prior to the NI takahe, and from a different lineage (subspecies in the current taxonomy) of flying *Porphyrio*. The genetic difference between pukeko and NI takahe, and identity within New Zealand and between Australian pukeko indicate that the current pukeko population in New Zealand is not the one that founded NI takahe. Thus, it is apparent that there have been at least three separate invasions of New Zealand by flying *Porphyrio* and this is consistent with the existence of many distinct *Porphyrio* populations on islands throughout the Indian and western Pacific Oceans (Mayr 1949; Ripley 1977).

Independently derived takahe-like birds are known to have evolved on other islands (Olson 1977; Steadman 1988; White 1962), most notably New Caledonia (Balouet & Olson 1989; Balouet 1991; Trewick 1995). Conditions there were unlikely to be the same as New Zealand and yet very similar species evolved. Two species of takahe in New Zealand is therefore evidence for the evolutionary benefits of increased size with the concomitant loss of flight. Morphometric differences suggest a more recent origin of NI takahe than SI takahe, as the first phase in the evolution of flightlessness (or conversely its cause) is size increase. This is probably achieved by simple scaling up from the founding species (pukeko in this case). Fine-tuning selection would be expected to operate subsequently to alter the body form in more subtle ways. This is what we see in the NI and SI takahe and is supported by the genetic evidence.

## FOSSIL RECORD

It is 10 years since Beauchamp & Worthy (1988) reviewed the fossil distribution of takahe and documented 74 sites on the North Island and 37 on the South Island. Since then, most of the museum collections have been checked by T.H. Worthy resulting in the discovery of unpublished records and some wrongly identified bones, e.g. the 'Lake Ngaroto' and 'cave at Punakaiki' records, which were pukeko and New Zealand coot, respectively. In addition, continued collecting has resulted in a significant number of new sites. All of the known fossil sites and records of NI and SI takahe and the pukeko are presented in Figure 4.5 and Appendix 4.1. (see page 43). These records are summarised below.

**FIGURE 4.5**: Location of takahe fossil bones found in North Island and South Island of New Zealand.

### NORTH ISLAND TAKAHE PORPHYRIO MANTELLI

NI takahe are recorded from 83 discrete fossil deposits, distributed throughout the North Island, from near sea level to about 1000 m a.s.l. Eighteen were from dunes, 53 from caves (42 from the South Auckland – King Country karst area), seven from middens, three from swamps and two from loess sites. The dune sites indicate a coastal distribution in the Late Holocene (<5000 yrs before present 'BP') from the Far North (North Cape, Cape Maria van Diemen) to Coromandel and the Wairarapa. NI takahe were abundant in the Late Holocene deposits of Poukawa swamp of Hawke's Bay (Horn 1983), and midden deposits in the coastal Taranaki – Manawatu region indicate it was present throughout these areas as well. Of the 42 cave deposits in the South Auckland – King Country region, few have been dated. Some are definitely of Pleistocene age, e.g. the Gardners Gut sites, but in F1c site, which is the richest site in the region with at least 22 individuals represented, the deposit was 1000–2000 years old (Worthy 1984).

### SOUTH ISLAND TAKAHE PORPHYRIO HOCHSTETTERI

SI takahe are reported from 54 discrete sites scattered throughout the South Island. No takahe bones have been found on Stewart Island or any other offshore island. Five sites were dunes, although a further five were surface finds in dunes associated with middens. Twenty-eight were in caves, six were swamps, one was in loess, and nine were middens. SI takahe bones have been found in Pleistocene and Holocene sites. Most dated sites are Holocene, often of Late Holocene age, and most are below 300 m a.s.l. Only one site bearing takahe bones has been found above the tree line in the subalpine zone, wherein the last naturally occurring population lives. This is despite the existance of several hundreds of potential sites that contain the bones of other bird species in limestone-karst areas of Northwest Nelson and in Fiordland. In contrast, despite the few caves available in lowland sites in Canterbury and Otago, takahe bones have been found in several of them. Similarly, takahe has been found in two of the four fossil-bearing swamps in each of North and South Canterbury, and in two of the seven such swamps in North Otago. The Tuarangi Cave fauna is more than 38 000 years old yet the takahe bones found there are indistinguishable from modern takahe and distinct from fossils collected in the North Island, demonstrating that the form of the extant SI takahe is not a recent phenomenon.

### PUKEKO PORPHYRIO PORPHYRIO MELANOTUS

Fossil bones of the pukeko *Porphyrio p. melanotus* are rare in New Zealand. Only Poukawa Swamp in Hawke's Bay has significant numbers of bones (Horn 1983). There, 410 bones are recorded from Layer 1, and two bones from Layer 2, but as Layer 2 was defined as 'below 7 cm above the Taupo Ash', it is probable that all of these bones are from above the ash. Fossil pukeko bones have been found at only one site in a cave (Maniapoto's Cave, Te Kuiti), although they regularly fall in them now in the Waitomo district and their fresh bones are found (T.H. Worthy, pers. obs.). Sparse finds of their bones have been made in dunes but all of the specimens in collections from dunes appear to be of recent age. Pukeko bones have been found in 11 archaeological sites, but apart from Ototara and Marfells Beach, these are not 'archaic' sites in the sense that moa-hunting was not significant during their deposition.

There is no fossil evidence that pukeko was present in New Zealand until after 1000 years ago. The spectacular assemblage from Poukawa (Horn 1983) is ample demonstration of that, but older fossils are unknown from elsewhere in New Zealand, despite many dated sites and large available faunas. Pukeko are also absent from the large faunas from the earliest archaeological sites (Wairau Bar, Paremata, Shag Mouth, Pounawea, Papatowai), which date from about 500–700 yrs BP (Anderson 1989). Dates for the oldest sites with pukeko bones are Ototara 475 ± 70 yrs BP; Timpendean 436 ± 50 yrs BP; Cannibal Bay 390 ± 39 yrs BP; and Long Beach, 400-800 yrs BP (Anderson 1989). These dates, and the absence from older sites, indicate that pukeko established in New Zealand between 600 and 400 years ago. Genetic evidence supports the suggestion that pukeko are a recent arrival in New Zealand as individuals here are closely related to those in Australia. This evidence plus plumage characteristics (colour similarity of New Zealand to Australian birds versus dissimilarity to middle Pacific pukeko) shows that, despite traditions of pukeko introduction during Polynesian colonisation of New Zealand, modern pukeko came from Australia.

## PALAEOECOLOGY

Fossil bones of takahe are common in caves, dunes, swamps, and middens throughout New Zealand. They derive from both Pleistocene and Holocene time periods, but are more abundant from the latter. We restrict the discussion to Holocene records because deposition in such sites was under climatic conditions and vegetation essentially similar to the immediate pre-human situation (McGlone 1988).

NI takahe were distributed in the Holocene throughout the North Island, from North Cape to the Wairarapa. They have been found in most available fossiliferous dunes indicating a near sea level distribution in only the last 1000–5000 years. It has been commonly found in the Waitomo karst, which was primarily vegetated with podocarp-hardwood forest throughout the Holocene. While many of the sites are undated, those in which takahe were most abundant were only 1000–2000 years old and were interpreted as being near tarns (Worthy 1984). Many other sites are surface finds whose age can be predicted by the associated moas. The habitat preference of the most abundant moa in surface deposits (*Anomalopteryx didiformis*) was closed canopy forest (Worthy & Holdaway 1993, 1994), which became the main vegetation in the region in the last 10 000 years. Prior to this the vegetation consisted of grassland-shrubland in which *Euryapteryx curtus* was the commonest moa (T.H. Worthy, unpubl. data). These data support the suggestion that many of the undated takahe fossils from surface deposits in Waitomo are likely to be of Holocene age.

SI takahe have a similar widespread distribution, predominantly at low elevations. However, they were rare or absent from the high rainfall areas of the West Coast and Northwest Nelson during the Holocene. They were present at coastal localities near Nelson, in Marlborough and all eastern districts through Canterbury, Otago and into Southland. These areas were characterised by a mosaic of forest, shrublands and grasslands during the Holocene (Gurr 1952; McGlone 1988; Worthy & Holdaway 1996; Worthy 1997), and such a vegetation physiognomy presents an abundance of forest or tall scrub margins. A former subalpine distribution is indicated by only one fossil site on Mount Arthur (Nelson area). This distribution suggests that SI takahe preferred to live in regions where edge habitat was available, where monocotyledons, which are now among their preferred food, can grow in the high light conditions, yet which offer the shelter of adjacent scrub and forest in which to retreat. The distribution of NI takahe, despite being a distinct species, indicates a similar preference, especially when relative abundance is considered. This explains their abundance around the lake margin at Poukawa, or the tarn at the F1c site, and widespread occurrences in dunes.

Mills *et al.* (1984) proposed that takahe were grassland-feeding specialists adapted to the alpine region. Beauchamp and Worthy (1988) found agreement with Fleming (1979) and Millener (1981) contending that takahe once occupied many lowland and forested sites. Beauchamp and Worthy (1988:105) said that the distribution of fossils in cave sites suggested 'that takahe lived in forest', but they went on to conclude 'takahe ... were in a variety of habitat dominated by forest' (Beauchamp & Worthy 1988:107). It was not said that takahe fed on plants characteristic of lowland forest, and the distribution within such was explained by saying 'takahe may have lived in areas ... with sufficient other monocotyledons ... which are well dispersed over all altitudes ...' (Beauchamp & Worthy 1988:108). This latter statement was overlooked by Mills *et al.* (1988) who focussed on the statement that takahe lived in forests. They provided a list of several tussock species that were potential food plants at low altitudes in edge habitats near or within forests, thus supporting Beauchamp and Worthy (1988). Our essential point now (as then) is that both takahe were distributed at all altitudes. We are in agreement with Mills *et al.* (1988) that takahe preferred edge habitats. But we disagree with the suggestion that takahe existed only in a few remnant populations through the Holocene. Forest edge and other grassland habitats were widespread and existed around all forest clearings, along river banks, around lakes, in the subalpine zone, and in coastal dune vegetation mosaics. Such habitats were especially plentiful in the low rainfall (<1200 mm) zones of the eastern regions in both islands, and in other areas such as the Waitomo karst in the form of forest with frost hollows (in dolines) supporting tussock. Most such sites do not offer conditions conducive to fossil preservation: few available dunes and only two lake sites are fossiliferous, and karst containing pitfall traps is very patchily distributed. Despite the limitations on the fossil record, takahe fossils have been found throughout the country, indicating a widespread distribution.

In general, takahe bones were most abundant in areas where significant edge habitat was available, as around lakes, or dunes. The sparse distribution through most of the Waitomo karst, yet abundance in a site near an inferred tarn, supports this apparent attraction to edge habitats. Similarly, the abundance of takahe in the caves of the Puketoi Range and Coonoor probably reflects the presence of grassland or shrubland areas at the higher altitudes of this region. The abundance of takahe in the South Taranaki – Manawatu archaic archaeological sites supports these observations as this was one of the largest areas of mosaics of forest-shrubland-grassland on dune systems available in the North Island. The widespread lowland distribution in Holocene sites of Canterbury, Otago and Southland, but absence from Westland and Northwest Nelson is further evidence of this, because only in the east would have significant areas of open habitats been present.

The Pleistocene was characterised by a widespread reduction in forest cover in most present land areas south of latitude 38°S. Habitats were probably grasslands and shrublands with more of the latter in the west (McGlone 1988) because of higher rainfall there. The presence of these shrubland-grassland mosaics in western regions would have presented the edge habitats takahe favour, and allowed them to live there. Thus we would predict that takahe would be a component of most Pleistocene faunas, but that in the Holocene they became restricted to areas where edge habitats survived – the forest-shrubland-grassland mosaics of dry eastern regions, dune field, or subalpine zones, and lacustrine or riparian environments. This is not the same as being a specialist subalpine inhabitant – preadapted is not the same as adapted to. Their grazing habits, willingness to utilise grasslands and some forest plants as evinced by the use of fern rhizomes in Fiordland (Mills *et al.* 1980), ability to move through forests and locate feeding areas (S.A. Trewick pers. obs.), large size and relatively low metabolic rate (McNab 1994), are all features that render takahe capable of survival in a temporally and spatially heterogenous environment. Conversely, there is little to indicate any specialisation to and thereby constraint to subalpine conditions (but see chapters 5 and 8).

## IMPACT OF HUMAN SETTLEMENT

Why takahe declined so rapidly in recent times can be simply and logically attributed to predation. As with so much of New Zealand's fauna, takahe are neither behaviourally nor physically adapted to avoid terrestrial predation (see also Bunin & Jamieson 1995, 1996a). In evolving flightlessness, takahe gave up the very features that enable their relatives to escape many attackers. Takahe are large birds and were undoubtedly easy and attractive prey for Polynesian hunters and their dogs and as such would have been among the first casualties of over-hunting. Given the fact that evidence of Maori hunting (for most birds) is neither widespread nor evenly distributed, and that many of the investigated archaeological sites were not deposited during the early period of Polynesian–

fauna interaction, and that for most sites faunas are small, takahe remains are present in surprisingly many sites (Worthy 1999).

Several forest birds were hunted to extinction including *Anomalopteryx didiformis, Dinornis novaezealandiae, D. struthoides*, but it was the species that preferred to live in the more open habitats (forest-shrubland-grassland mosaics) of drier eastern regions that suffered most. An entire suite of large species including several of the moas, a coot *Fulica prisca*, geese *Cnemiornis* spp., a duck *Euryanas finschi*, a rail *Gallinula hodgenorum* and *Aptornis* spp. was extinguished in pre-European times. That these drier eastern mosaic habitats were the ones almost totally destroyed by Polynesian burning (McGlone 1988, 1989) and that their inhabitants were probably easier to hunt in the last remnants of available habitat, made them more susceptible to extinction. Takahe, with their preference for edge habitats, would have been easy to find, and having a low fecundity would have had little capacity to survive human/mammalian predation, habitat loss aside. The NI takahe may have survived until European times (Phillipps 1959), and it is probably only by virtue of their ability to persist in a wide range of conditions including those of subalpine Fiordland that SI takahe (like kakapo) survived to European times. Even after the arrival of humans in New Zealand, the Fiordland area remained isolated from the impacts of hunting and burning and predator introduction. It is more than likely that with the added impact of deer and stoats, which arrived in the area following European colonisation, that SI takahe would have succumbed without the captive-rearing and population replenishment programme that has dominated conservation efforts in the last 15 years (see chapters 6 and 7).

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## APPENDIX 4.1

List of sites in which fossil bones of takahe and pukeko have been found. (Midden sites have their archaeological site number in brackets after their name.) Under the column heading Region: KC-S. Auck. = King Country–South Auckland. Under Site type: C = cave, D = dune, S = swamp, M = midden. Age: H = Holocene, P = Pleistocene. For Ref. see list at end of appendix.

North Island Takahe

| Site | Region | Site type | Age | Ref. | Catalogue |
|---|---|---|---|---|---|
| Cape Maria Van Diemen | Northland | D | H | THW | CM Av30291 |
| Cape Maria Van Diemen | Northland | D | H | 1 | |
| Mt Herangi West | Northland | D | H | THW | MNZ S25837 |
| Spirits Bay | Northland | D | H | 1 | |
| Tom Bowling Bay, #1 | Northland | D | H | 1 | CM Av21919 |
| Tom Bowling Bay, #2 | Northland | D | H | 1 | |
| Tom Bowling Bay, #3 | Northland | D | H | 1 | |
| Waikuku Bch #1 | Northland | D | H | 1 | |
| Waikuku Bch #2 | Northland | D | H | 1 | |
| Waikuku Bch #3 | Northland | D | H | 1 | |
| Henderson Bay South | Northland | D | H | 1 | |
| Tokerau Bch main | Northland | D | H | 1 | |
| Tokerau Bch south | Northland | D | H | 1 | |
| Pataua | Northland | D | H | 1 | MNZ S23252 |
| Ocean Beach | Northland | D | H | 1 | MNZ S23371 |
| Opito Bay | Coromandel | D | H | THW | CM Av16658 |
| Port Jackson (N35-36/88) | Coromandel | M | H | 2 | |
| Helictite Hole | KC-S. Auck. | C | | 1 | |
| MacDonalds Mud Cave | KC-S. Auck. | C | | 1 | WO169 |
| Black Sands Cave | KC-S. Auck. | C | | 1 | WO183 |
| Goddards Cave | KC-S. Auck. | C | | 1 | |
| Maze Cave | KC-S. Auck. | C | | 1 | |
| St Benedicts Caverns | KC-S. Auck. | C | | 1 | |
| Gardners Gut, Bone Pssage | KC-S. Auck. | C | P | THW | WO18 |
| Gardners Gut, Zweiholen | KC-S. Auck. | C | P | THW | WO |
| Maniapoto's Cave | KC-S. Auck. | C | | | WO80 |
| F1b | KC-S. Auck. | C | | 3 | WO3 |
| F1c, layers 2&4 | KC-S. Auck. | C | H | 3 | WO63 |
| F1c, layer 8 | KC-S. Auck. | C | | 3 | WO63 |
| Dawson Moa Bone Cave | KC-S. Auck. | C | | 1 | WO15 |
| Luckie Strike Cave | KC-S. Auck. | C | | 1 | WO5 |
| Opening Day Cave | KC-S. Auck. | C | H | 4 | WO2 |
| Haggas Hole | KC-S. Auck. | C | P | 1 | WO230, 383; CM Av18826-831, 19143,19230, 28205 |
| Fred Cave | KC-S. Auck. | C | | 1 | WO220 |
| Waipuna Cave | KC-S. Auck. | C | | 1 | |
| Little Theatre Cave | KC-S. Auck. | C | | 1 | WO391 |
| Bens Hole, Twin Tomo | KC-S. Auck. | C | | 1 | WO85 |
| Anns Cavern | KC-S. Auck. | C | | 1 | |
| Paryphanta Cave | KC-S. Auck. | C | | 1 | WO429 |

| Site | Region | Site type | Age | Ref. | Catalogue |
|---|---|---|---|---|---|
| Footwhistle Cave | KC-S. Auck. | C |  | 1 |  |
| Masons Dry Cave | KC-S. Auck. | C |  | 1 | WO390; CM Av28206 |
| Cutthroat Cave | KC-S. Auck. | C |  | 5 | WO1 |
| Hilltop Cave | KC-S. Auck. | C |  | 1 | WO384 |
| Dinornis Cave | KC-S. Auck. | C |  | 1 |  |
| Swiss Cheese Cave | KC-S. Auck. | C |  | 1 | MNZ S1066;CM Av28253 |
| Porthole Cave | KC-S. Auck. | C |  | 1 | CM Av20620,23638, 24629, 27175, 27178, 27187-8, 27190, 27192, 27195, 28789 |
| Spotlight Cave | KC-S. Auck. | C |  | 1 | CM Av25004, 25044 |
| Tomo A, near Spotlight | KC-S. Auck. | C |  | 1 | CM Av26406 |
| Rorisons Quarry | KC-S. Auck. | C | H | 1 |  |
| Pukeroa Cave | KC-S. Auck. | C |  |  | WO53, MNZ S23861 |
| Roses House Cave | KC-S. Auck. | C |  |  | WO235 |
| Briars Cave | KC-S. Auck. | C |  |  | WO30 |
| Cave on Mahoe Rd | KC-S. Auck. | C |  |  | WO73 |
| Ecch Cave | KC-S. Auck. | C |  |  | WO75 |
| Cave on Kape Te Kanawa's | KC-S. Auck. | C |  |  | WO192 |
| Osbournes Caves | KC-S. Auck. | C |  |  | WO257 |
| Mudball Cave | KC-S. Auck. | C |  |  | WO284 |
| Waipapa Cave | KC-S. Auck. | C |  |  | WO401 |
| Togyp Cave | KC-S. Auck. | C |  |  | WO218 |
| Waikawau Bay | KC-S. Auck. | D | H | 1 |  |
| Quarantine Island | Napier | L | P | 1 |  |
| Scinde Island | Napier | L | P | 1 |  |
| Bushface #1 | Hawke's Bay | C | H | THW | CM Av25131 |
| Poukawa B | Hawke's Bay | S | H | 6 | MNZ |
| Poukawa D | Hawke's Bay | S | H | 6 | MNZ |
| Te Aute | Hawke's Bay | S | P(?) | 1 | MNZ S23323 |
| Waewaepa #2 | Puketoi Rnge | C |  | 1 | MNZ |
| Waewaepa #6 | Puketoi Rnge | C |  | 1 | MNZ |
| Waewaepa #9 | Puketoi Rnge | C |  | 1 | MNZ |
| Coonoor | Puketoi Rnge | C |  | 1 | MNZ S28440; CM Av11385, 11387-390 |
| Puketoi Site 25 | Puketoi Rnge | C | H | THW | Manawatu Mus |
| Ramsay's neck | Puketoi Rnge | C |  | THW | Manawatu Mus |
| Opua Moa Hunter site (P20/105) | Taranaki | M | H | 7 |  |
| Ohawe (N129/77) | Taranaki | M | H | 8 |  |
| Kaupokonui (N128/3) | Taranaki | M | H | 9 | CM Av26846, + |
| Te Rangatapu/Waingongoro (N129/33) | Taranaki | M | H | 1 , 10 | CM, BMNH |
| Foxton (N148/1) | Manawatu | M | H | 1 |  |
| Harrisons Hole = Martinborough #1 | Wairarapa | C | H | 1 | MNZ S28441, 24736;CM Av11381-4, 11386, 21765, 22241, 22859,22946, 24736, 30256, 36385, 36390-1 |

| Site | Region | Site type | Age | Ref. | Catalogue |
|---|---|---|---|---|---|
| Haurangi 12 | Wairarapa | C | H | 1 | MNZ S24590 |
| Fissure 2 | Wairarapa | C | H | 1 | MNZ S24591 |
| Fissure 1A | Wairarapa | C | H | 1 | MNZ S24592 |
| Mataikona | Wairarapa | D | H | 1 | MNZ S22455-6 |
| Paremata (N160/50) | Wellington | M | H | 11 | MNZ S24593 |

### South Island Takahe

| | | | | | |
|---|---|---|---|---|---|
| Paturau, Twin Forks Cave | NW Nelson | C |  | 12 | MNZ unreg |
| Heaphy River Mouth | NW Nelson | C |  | 12 | CM Av16404 |
| Honeycomb Hill | NW Nelson | C | P | 13 | MNZ S22669, 22719, 22723,23704, 23827 |
| Honeycomb Hill, Graveyard | NW Nelson | C | P | 13 | MNZ |
| Honeycomb Hill, His & Hers | NW Nelson | C |  | 13 | MNZ S23517 |
| Honeycomb Hill, Aven 12 | NW Nelson | C |  |  | MNZ S23490 |
| Honeycomb Hill, T Entrance | NW Nelson | C |  |  | MNZ S23516 |
| Honeycomb Hill, Hives Passage extn. | NW Nelson | C |  |  | CM Av36400 |
| Sims Cave | NW Nelson | C |  | 14 | MNZ S32734 |
| Mansons Cave | NW Nelson | C |  | 14 | CM Av17822 |
| Bone Cave | NW Nelson | C |  | 14 | CM Av21332 |
| Takahe Tomo, Hodge Ck Cv | NW Nelson | C | P | 15 | MNZ S34495 |
| Hodge Ck Cave | NW Nelson | C | P | 15 | MNZ S34460 |
| Farriers Cave, Mt. Arthur | NW Nelson | C | H | THW | MNZ S35514 |
| Aniseed Valley | Nelson | C |  | 12 | MNZ S146 |
| Rotokura (O27/1) | Nelson | M | H | 16 |  |
| Anapai (N25/59) | Nelson | M | H | 16 |  |
| Metro Cave, Triclops Entr. | West Coast | C | P | 17 | CM Av20467 |
| Wairau Bar | Marlborough | M |  | 12 |  |
| Marfells Beach | Marlborough | D/M | H | 18 | CM Av11678, 13675, 17497 |
| Cave near Waiau | N. Canterbury | C |  |  | CM Av12530 |
| Ledge, Weka Pass | N. Canterbury | C |  | 19 | MNZ S33613 |
| The Deans, Waipara | N. Canterbury | S | H | 19 | CM Av33240 |
| Pyramid Valley | N. Canterbury | S | H | 19 | CM Av5789, 5842, 5921, 5922, 6041, 7453, 15039, 18930, 33833 |
| Waikari Cave | N. Canterbury | C | H | 19 | MNZ S33717, CM unreg |
| Tuarangi Stn, Tomo 2 | S. Canterbury | C | P | 20 | MNZ S33848 |
| Tuarangi Cave | S. Canterbury | C | P | 20 | MNZ S33866 |
| Kings Cave | S. Canterbury | C | H | 20 | MNZ S33792, CM Av22890, 23056, 23810, 24771, 24795, 25294 |
| Opihi River | S. Canterbury | L | P | 20 | MNZ unreg |
| Pothole, Totara Valley | S. Canterbury | C |  | 20 | S. Cant Mus NHO23 |
| Mt Harris swamp | S. Canterbury | S | H | THW | MNZ S36260 Kapua |
| Swamp | S. Canterbury | S | H | 12 | CM Av5425 |
| Earnscleugh Cave | Otago | C | H | 21 | CM Av5424, OM Av |
| Ngapara | Otago | C | H | 21 | MNZ S23255, OM Av1500, 1502 |

| Site | Region | Site type | Age | Ref. | Catalogue |
|---|---|---|---|---|---|
| Totara Swamp, Enfield | Otago | S | H | 21 | NOM unreg |
| Macraes | Otago | S |  | 21 | MNZ S23407 |
| Ototara (=Teschemakers) | Otago | M | H | 21 | Otago Uni. Anthro colln |
| Waitati | Otago | D | H | 22 | OM Av |
| Pounawea (H47/1) | Otago | M | H | 23 | CM Av34083 |
| Awamoa (J41/3) | Otago | M | H | 24 |  |
| Ross's Rocks (I43/22) | Otago | M | H | 23 |  |
| Warrington (I44/177) | Otago | M | H | 23 | MNZ S23254 |
| Long Beach (I44/23) | Otago | M | H | 25 | MNZ S23253, CM Av13720, 13742 |
| False Island (H47/6) | Otago | D | H |  | CM Av36080 |
| Cannibal Bay (H46/28) | Otago | D/M | H |  | CM Av34426 |
| Kaikais Beach (I44/127) | Otago | D/M | H |  | CM Av11476 |
| Pahia | Southland | ?M | H | 26 | SM A.40.39 |
| Wakapatu | Southland | D | H | 26 | SM A.46.10, A39.7 |
| Greenhills Back Beach | Southland | D | H | 26 | SM unreg |
| Tokanui Mouth | Southland | D/M | H | 26 | SM unreg |
| Colac Bay | Southland | D | H | 26 | SM unreg |
| Forest Hill Tomos | Southland | C |  | 26 | OMAv6858-6865 |
| McKerchars Cave | Southland | C |  | 26 | SM unreg, CM Av32389, 32535, 36139 |
| Castle Rocks | Southland | C | H | 26 | MNZ S23322-4 |

Pukeko (only the latest most relevant literature is cited)

| Site | Region | Reference |
|---|---|---|
| Ototara S136/2 | Otago | 21 |
| Whalers Bay Cave | Kaikoura | 27 |
| Timpendean | Canterbury | 19 |
| Te Awamate Pa | Manawatu | 28 |
| Long Beach | Otago | THW |
| Cannibal Bay | S. Otago | 23 |
| Port Jackson | Coromandel | 1 |
| Lake Ngaroto | Waikato | 1 |
| Delaware Bay | Nelson | 16 |
| Kohika | Bay of Plenty | 29 |
| Marfells Beach | Marlborough | 18 |

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### five

# Fifty years of takahe conservation, research and management:
## What have we learnt?

### WILLIAM G. LEE

The unexpected discovery of a population of takahe (*Porphyrio hochstetteri*), an endemic, flightless rail, on 20 November 1948 in the Tunnel Burn (subsequently renamed Takahe Valley), on the western shores of Lake Te Anau, Southland, New Zealand, created international interest and was widely reported (Orbell 1949). Known only from a few early European sightings, the takahe had not been seen in the 20th century and was generally considered to be extinct (Henry 1900). The finding of a population of takahe initiated a major effort by government agencies to conserve the species, which has continued uninterrupted for 50 years. Research and management work on takahe has been unprecedented in the history of threatened species conservation in New Zealand. Initially these involved establishing a 650 km$^2$ special area for the protection of takahe centred on the Murchison Mountains within Fiordland National Park, but efforts have been greatly extended subsequently to include a range of techniques and approaches.

In this chapter, I want to provide an overview of the history of research and management of the takahe. An historical approach enables us to see the development of different management options and research emphases, while also providing a context for understanding the origin of some of the contentious issues associated with takahe conservation. Obviously as a participant in some of these debates I am not a neutral observer, but I hope that I am able to adequately describe the background to these decisions and the evolutionary process that resulted in the current integrated recovery plan for the species (Crouchley 1994). Biological conservation inevitably occurs within the context of scientific research, government policy, and community aspirations, and all have been influential in the efforts to sustain the takahe.

The takahe holds a special place in avian conservation in New Zealand. One of the distinctive elements of the pre-human indigenous biota was the dominance of flightless bird species in terrestrial ecosystems, a diversity perhaps facilitated by the paucity of mammalian herbivores and predators. Of the flightless ground-herbivore guild present during the Holocene, which included moa and several rails, only the takahe has survived human settlement to the present day (Atkinson & Millener 1991). The takahe is a precious remnant of this guild.