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# Morphology and evolution of two takahe: flightless rails of New Zealand

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(With 7 figures in the text)

Two forms of a large and flightless rail (takahe) belonging to the genus *Porphyrio* and endemic to New Zealand have been described, although their taxonomy has been repeatedly questioned. Analyses of osteometric data from modern and Quaternary fossil material show such a degree of allometric distinctiveness that it is considered that the two forms are, indeed, different species as originally described, *Porphyrio mantelli* (Owen), *Porphyrio hochstetteri* (Meyer). It is suggested that this degree and type of difference could have resulted from the two species arising independently from similar volant ancestors.

## Contents

## Introduction

A large, flightless and presumed extinct rail (Aves: Rallidae) was described in 1848 from Quaternary fossil bones collected at Waingongoro in the North Island of New Zealand (Owen, 1848*a*). Owen (1848*a*) erected the genus *Notornis* on the basis of a small number of elements including a number of head elements and a single leg bone and named and described the species *N. mantelli* (Owen, 1848*b*).

A second species was later proposed from the remains of a recently killed bird found in the Fiordland area of the South Island. Meyer (1883) named this *N. hochstetteri*, proposing a new species on the basis of size differences of certain bone elements as compared to those of *N. mantelli.* Parker (1882) had previously described in detail the trunk of the specimen which later became the holotype of the species, and at that time two oil paintings were made from the skin. Additional material ascribed to *N. mantelli* by Owen included a number of leg bones (Owen, 1851), one of which (a tibia) was later re-identified as that of a swan (Forbes, 1892; Greenway, 1967). Meyer (1883) made use of these for comparison, and would have been struck by the considerable difference in tibial lengths between the two small samples. Forbes (1892) proposed the name *N. parkeri* for a specimen from the South Island held in Otago Museum, on the basis of differences between dimensions of this skeleton and those of the types of the other species. The taxonomy of these birds continued for some time to be confused and sometimes arbitrary in nature, but was always concerned with differences in size of northern and southern forms (Parker, 1886). A series of rationalizations (Mayr, 1949; Fleming, 1953; Greenway, 1967; Kinsky, 1970) has left us now with two subspecies of takahe included in the genus *Porphyrio* which otherwise includes volant forms. These are, *Porphyrio mantelli mantelli* for the North Island form and *Porphyrio mantelli hochstetteri* for the South (Ripley, 1977).

For this study, the most significant of these classifications was the merging of the two kinds as a single species. Although originally separated on account of differences in the length of some bones, the two were later said not to differ significantly (Forbes, 1923). Some confusion was added by Greenway (1967) stating that Peters (1934) had synonymized the two when, in fact, he had not. Ripley (1977) accepts this ad hoc synonymization, indicating that the differences recorded at that time were not sufficient to separate the two birds as species. However, Ripley (1977) goes on to offer a key to the two forms based on the presumably discriminatory differences in leg bone lengths.

The manner by which the systematic significance of observed differences in morphology are judged is not apparent in any of the literature relating to these (and other) flightless birds. It must be assumed, therefore, that the current taxonomy reflects the passive adoption of the vernacular and not a formal evaluation. Although in many cases increasing knowledge about polytypic 'species' allows their merging by virtue of the discovery of intermediates (Mayr, 1977), unbridled clumping can obscure actual species boundaries.

The bird now known as *P. m. hochstetteri* or more commonly by its Maori appellation 'takahe' is extant in Fiordland, south-west New Zealand (Ripley, 1977) and some individuals have been translocated to island reserves, but the species remains on the verge of extinction. The larger *P. m. mantelli* is known only from Quaternary fossil bones, although a single tantalizing observation of a living individual in the North Island in 1894 is recorded by Phillipps (1959) who noted also that the name used by local Maoris was 'moho'. Many well-preserved bones apparently representing both morphs have now been collected in swamps and caves. These provide the opportunity for an intensive comparison of the distribution and morphology of the two forms, and a more rigorous assessment of their origins.

The two islands on which material has been collected are today separated by a fast flowing channel known as the Cook Strait which is less than 30 km wide at its narrowest point. Geophysical evidence suggests that the two islands were connected most recently during the last (Otiran) glaciation (Stevens & Suggate, 1978) and breached about 16,000 years ago (Lewis, Carter & Davey, 1994). However, discrete island land masses were probably present in the vicinity prior to the formation of the two principal islands of contemporary New Zealand (Stevens & Suggate, 1978). The proximity and recent association of the two islands has encouraged the view that the two forms of takahe must be very closely related, and thus may represent only the extremes of a continuum of phenotypes spanning both islands.

In order to emphasize the nature of the morphological relationships of the two forms of takahe, data from an equivalent pair of birds have been incorporated in the analysis. Although not closely related to the takahe, these birds and the circumstance in which they were described possess many characteristics similar to the takahe. Two species of kagu (*Rhynochetus orarius*

Balouet and Olson, and *Rhynochetus jubatus* Verreaux and des Murs) are known from New Caledonia (Balouet & Olson, 1989). The rhynochetids are considered to be allied to the rails and are flightless running birds restricted to a single island. *R. orarius* was described from Quaternary fossil bones collected in lowland caves and found by comparison of dimensions to be larger than the extant upland *R. jubatus* (Balouet & Olson, 1989).

## Methods

### *Material*

A large number of Quaternary fossil bones of takahe has been collected from swamp and cave sites across New Zealand (Yaldwyn, 1956; Millener, 1981; Worthy, 1984; Beauchamp & Worthy, 1988) (Fig. 1). Bones of various species from such deposits have been dated to between 25,000 and 1000 years bp (Yaldwyn, 1958;

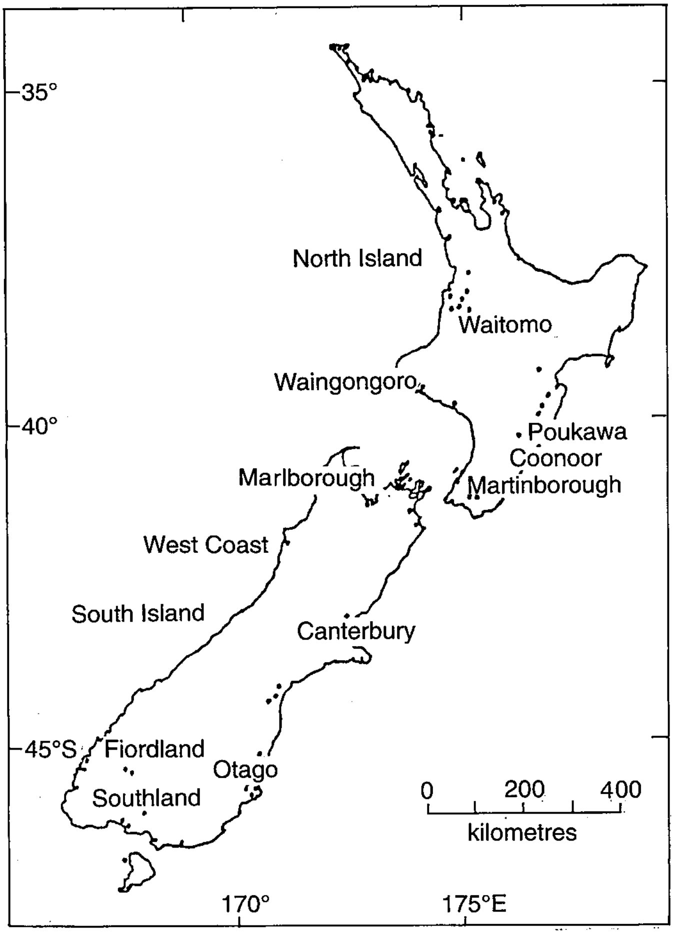

FIG. 1. Map of New Zealand with names of principal takahe Quaternary fossil locations, and (●) sites where material has been found.

Horn, 1980, 1983; Millener & Templer, 1981; Worthy, 1984; Worthy & Holdaway, 1993). These collections provided most of the material used in the present study (details in **Appendix 1**), although modern material from recently skeletonized corpses (Museum of New Zealand and Trewick) collected from the extant population in Fiordland was also included. These modern specimens were the only complete skeletons from the South Island.

### *Bone measurement*

Undamaged adult bone material verified by comparison as originating from takahe (more than 700 elements), held in the following collections, was examined and measured using Mitutoyo dial callipers graduated to 0·05 mm: Auckland Institute and Museum, Canterbury Museum, Museum of New Zealand Te Papa Tongarewa, Waitomo Caves Museum. Linear measurements were taken from all major elements, excluding vertebrae and toe bones. Four standard measurements (length L, proximal breadth PB, minimum latero-medial breadth MB, distal breadth DB) of long bones were made (Millener, 1988; Millener & Worthy, 1991), and lengths and breadths were taken from sterna, crania, premaxilla, and pelvi as follows. Sterna: median longitudinal dimension (Sternum L.), crania: median length from the supraoccipital process above the foramen magnum to the point of fusion of the crania and the premaxillary (Cranium L.), and breadth between the temporal fossa (Cranium B.), premaxillary: median length from fusion with crania to tip (Premax. L.), pelvis: median length between terminal synacral thoracic and synacral caudal vertebrae (Pelvis L.), breadth between widest processes of antitrochanter (Pelvis antitroch. B.), minimum horizontal width across anterior portion of ilium (Pelvis ant. iliac B.), and maximum breadth between processes of the posterior iliac crests (Pelvis post. iliac B.). Terminology follows Howard (1931).

Data from associated elements (i.e. individuals) were recorded together, though this circumstance was rare with fossil material. Only 5 partially complete skeletons of the North Island takahe were available, all collected from caves in the Waitomo area. These associated elements allowed more powerful comparisons to be made.

### *Data analyses*

Data were organized by collection site, but initial analysis used 2 groups composed of material found in each of the 2 islands, North Island (NI) and South Island (SI), as this reflected the traditional classification of the takahe. Independent *t*-tests with separate variances were undertaken to compare mean linear measurements of elements from these 2 groups. A graphical summary of relative mean values for all data was produced and univariate, bivariate, and trivariate plots of certain elements were generated. Prior to further analysis to examine the allometric nature of the 2 forms, a test of homogeneity of variances (Bartlett's test) was first applied to subsets of the length data for tarsometatarsi (Fig. 5a) and tibiotarsi (Fig. 5b) such that the data set was categorized according to the principal collection sites. These were: (in the SI) 1—Modern Fiordland, 2—Southland, 3—compilation of West Coast, Otago, Canterbury and Marlborough (and NI) 4—Martinborough, 5—Coonoor and Poukawa, and 6—Waitomo (Fig. 1). It should be noted that the sample size in group 3, small as it is, was composed, by necessity, of material from several sites around the South Island. The 2 major groups (SI and NI) and a comparative data set from 21 pukeko (*Porphyrio porphyrio melanotus*) collected from throughout New Zealand were subsequently compared using ANCOVA. Allometric relations were fitted by producing linear regressions of log values.

Data from kagu were used for allometric comparison. Proportionated dimensions and length/breadth ratios of leg elements were calculated for the 2 described forms (*Rhynochetus orarius, Rhynochetus jubatus*) and compared with equivalent data from the takahe.

## Results

Mean values of all 25 parameters measured on bones of North and South Island takahe were significantly different (Table I), apart from: humerus distal breadth, carpometacarpus length, and sternum median length, all of which are associated with the wing structure and presumably reflect the redundancy of this organ. The posterior iliac breadth of the pelvis was significant only at $P<0{\cdot}05$, despite seemingly distinct mean values, because only three bones were measured from the North Island (NI). Differences between the two island morphs for other elements are significant at $P<0{\cdot}001$ or $P<0{\cdot}01$ for the premaxilla length and cranium breadth.

All elements that differed significantly were larger in the NI group with the exception of the premaxilla, which was smaller in the NI group relative to the South Island (SI) (Table I). Coefficient of variation (CV) values of data produced by pooling across a broad spectrum of temporal and geographic samples did not differ greatly from the values derived from the modern Fiordland population. When data from the two groups (NI and SI) are pooled, CV values are higher (as expected), for example tarsometatarsus length CV = 11·3% (data not shown).

The relative amounts by which the mean size of the NI and SI groups differed was not the same for all variables (Fig. 2). For each variable the mean for the NI group was divided by that for the SI and the result presented as a percentage. A horizontal line at 100% therefore indicates parity between the two groups. The NI form would clearly have been taller than that found in the SI with leg elements between 106–124% longer. But not all parts of the body show the same amount

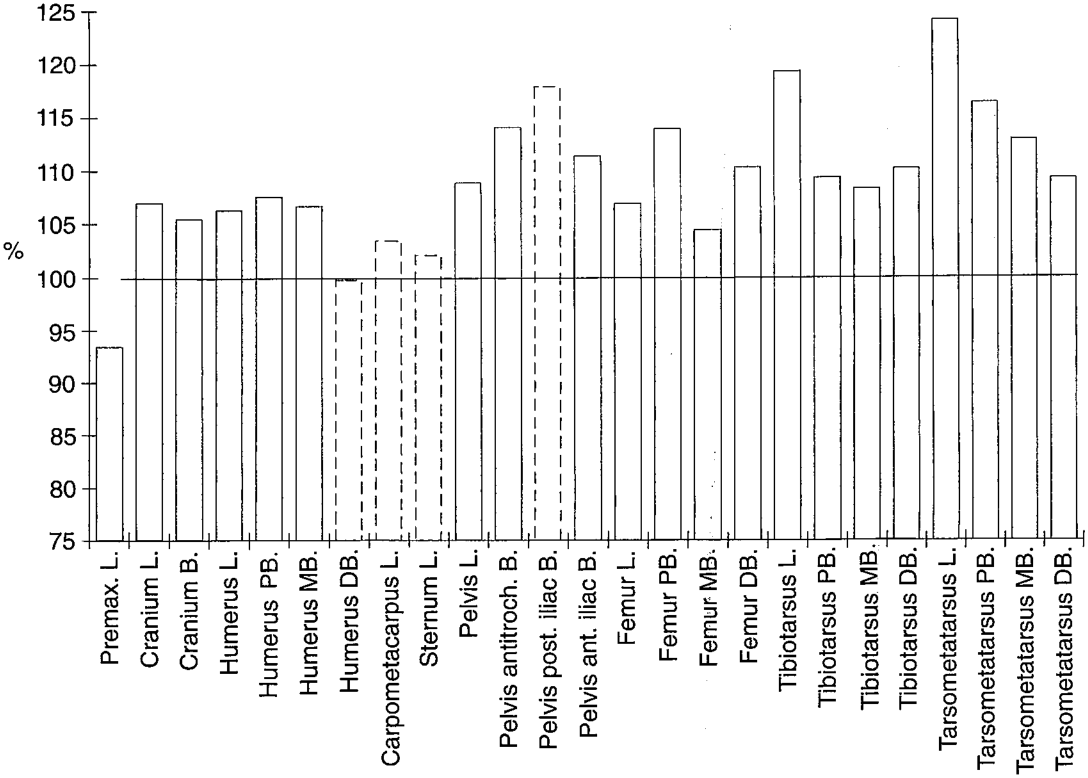

FIG. 2. Comparison of bone dimensions of takahe from North (NI) and South (SI) Islands of New Zealand. Mean values of NI dimensions given as % of SI values. 100% line represents parity of the two forms. Labels are as given in the text. Fully bordered bars show significantly different means ($P<0{\cdot}01$).

TABLE I

Summary statistics for all takahe material measured, presented in two groups and means compared (*, $P<0{\cdot}05$; **, $P<0{\cdot}01$; ***, $P<0{\cdot}001$). Labels as in text

| Bone variable measured | Group | N | RANGE | MEAN | *P* | S.D. | CV | CV mod. 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 |

TABLE I (*cont.*)

| Bone variable measured | Group | N | RANGE | MEAN | *P* | S.D. | CV | CV mod. SI |
|---|---|---|---|---|---|---|---|---|
| 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 |

of difference, i.e. the two forms are not the same shape, and it would not therefore be correct to describe one simply as being bigger than the other. Most noticeable is the fact that the NI form possessed a smaller premaxilla (and presumably smaller beak) than its SI counterpart. This difference is emphasized by the reverse trend in the length of the crania such that the premaxilla would appear not only absolutely smaller in the NI but relatively smaller as compared to the head and the rest of the body (Fig. 3).

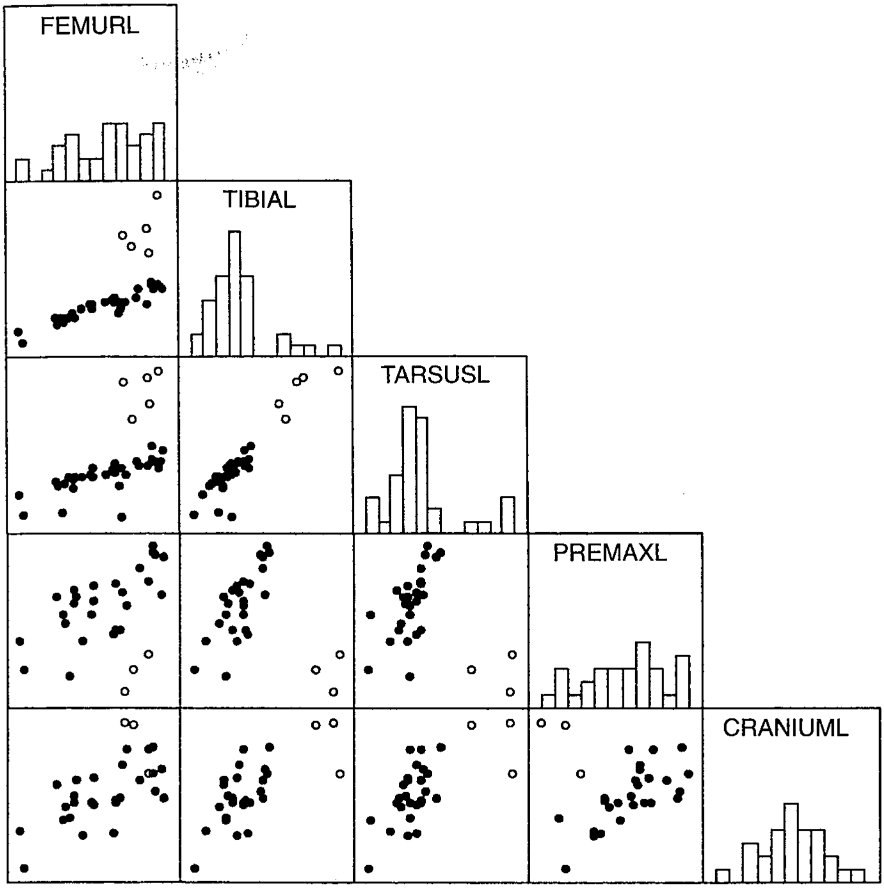

FIG. 3. Scatterplot matrix plots of lengths of leg elements, crania and premaxilla from NI and SI takahe individuals, with accompanying density bar graphs for each element.

The non-scalar relationship of body components is also exemplified by the relatively broader terminal (proximal and distal) breadths of leg bones (Fig. 2) and by the differences between the proportional lengths of these elements (i.e. femur, tibiotarsus, and tarsometatarsus). The tarsometatarsus for instance is relatively longer in the NI than the SI compared to the tibiotarsus despite this being, in absolute terms, the longest bone in the body. This latter relationship is emphasized by a trivariate plot of the lengths of the three leg elements from individuals (Fig. 4). The intercepts of the two distributions are evidently distinct despite the small sample size for NI takahe.

The absolute difference between the lengths of the tarsometatarsi and tibiotarsi of NI and SI birds is shown in Fig. 5. Despite the wide range of values encountered in both populations (Table I), the size frequency distributions are almost without overlap, and the means are significantly different (117·4 mm vs. 148 mm, $P<0{\cdot}001$ and 149 mm vs. 177·8 mm, $P<0{\cdot}001$, respectively).

Tarsometatarsus and tibiotarsus length data for collection site subgroups were subjected to Bartlett's test of homogeneity of variances. Low sample sizes did not prevent the overall ANOVA indicating significant differences between the groups ($P<0{\cdot}001$) with pairwise absolute mean differences and comparison probabilities being consistent with the NI, SI groupings (Table II). Within the NI subsets, site 5 (Poukawa and Coonoor) was the least similar, having relatively high scores in pairwise comparisons of absolute mean differences with the other NI subsets. This effect differed with the pairwise comparison being made, such that the overall separation of subsets into NI and SI groups was upheld. All SI subsets were relatively uniform, despite the high variance expected for group 3 which had been compiled from disparate geographic localities.

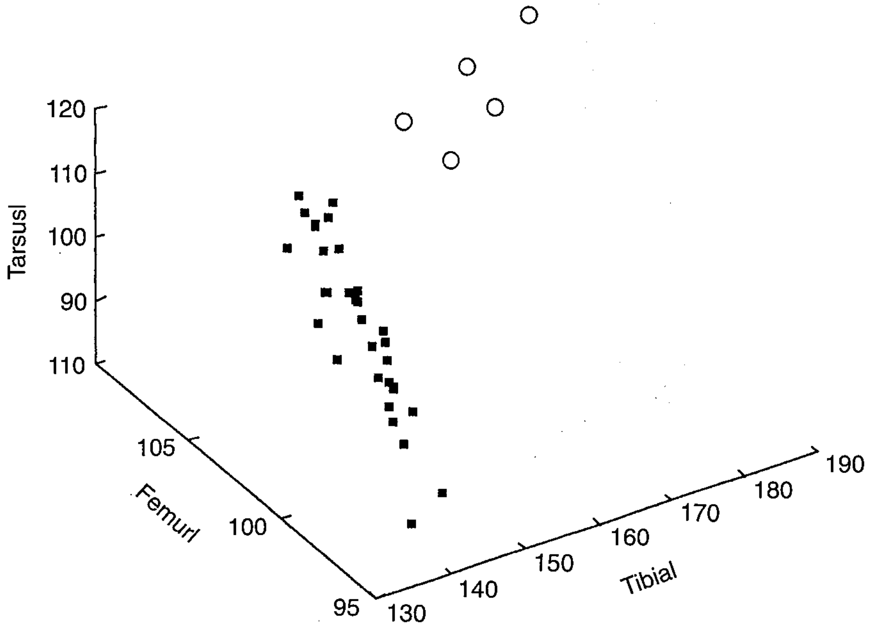

FIG. 4. Trivariate plot of lengths of all three leg bone elements from NI (○) and SI (■) individuals.

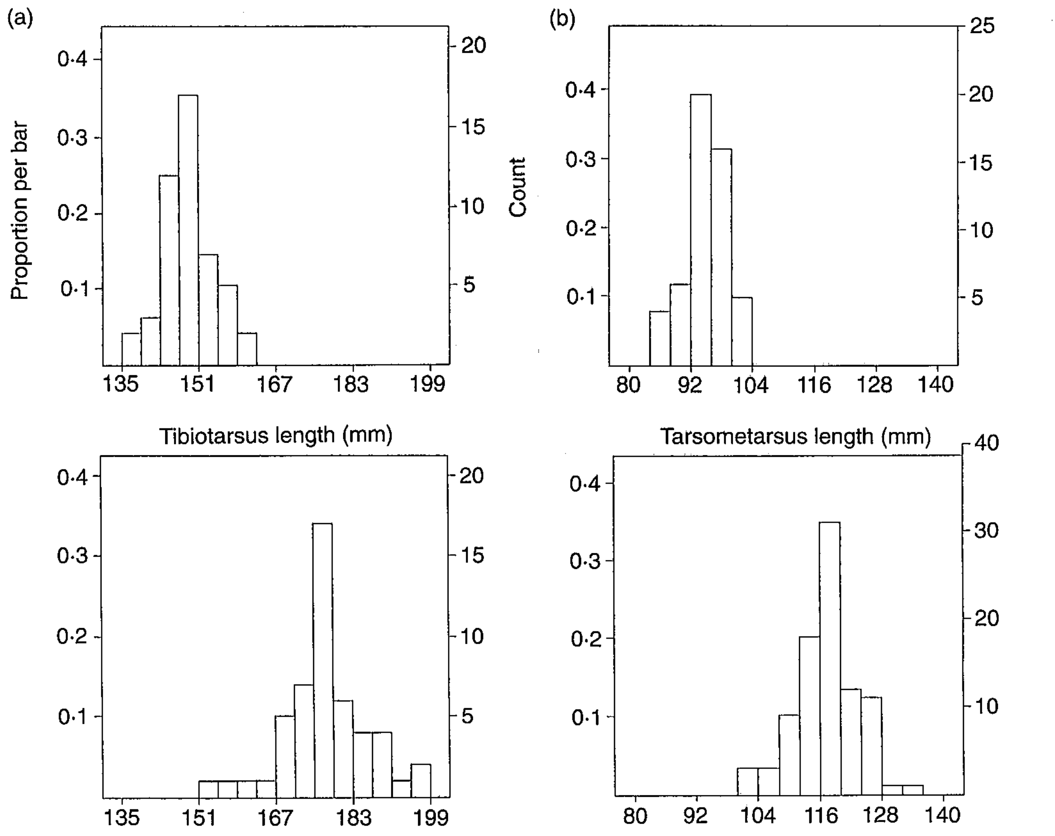

FIG. 5. Size frequency of lengths of all takahe (a) tibiotarsi and (b) tarsometatarsi measured, grouped according to origin in North Island (bottom) or South Island (top). Lengths in millimetres.

ANCOVA comparisons of log transformed data for the tarsometatarsi using the NI and SI groupings and a third data set from a sample of pukeko gave no significant difference between the gradients of all three in pairwise comparisons. However, although the intercepts of lines plotted for SI vs. NI, and SI vs. pukeko differed significantly ($F = 244{\cdot}18$, $P < 0{\cdot}001$ and $F = 22{\cdot}36$, $P < 0{\cdot}001$, respectively), those of NI and pukeko were not significantly different ($F = 2{\cdot}496$, $P > 0{\cdot}05$) (Fig. 6a). The same analysis for the tibiotarsus gave a slightly different picture. Although the plot of log length and breadth of the tibiotarsus looks even more convincing in its grouping of the NI takahe with the pukeko (Fig. 6b), the statistical analyses indicate a continuum of difference between all three groups. The gradients of NI and pukeko (with a very low F value of 0·1968), and NI and SI are not significantly different, yet the gradients of the pukeko and SI are just significant ($F = 4{\cdot}2611$, $P < 0{\cdot}05$) (Fig. 6). The intercepts of SI and pukeko, and NI and pukeko are not significantly different yet comparison of NI and SI strongly indicates difference ($F = 266{\cdot}775$, $P < 0{\cdot}0000$). Low sample size for the pukeko and high variance for all three groups has produced broad confidence bands around the intercepts such that pukeko, with a lower intercept of 4·0652, is not shown to be significantly different from SI

TABLE II

*Results of test of homogeneity of variances for lengths of takahe (a) tarsometatarsi and (b) tibiotarsi grouped according to collection site (1—Modern Fiordland, 2—Southland, 3—compilation of West Coast, Otago, Canterbury and Marlborough, 4—Martinborough, 5—Coonoor and Poukawa, and 6—Waitomo). Sites 1–3 are in the South Island and 4–6 in the North Island. Pairwise comparison probabilities (lower left) and absolute mean difference (top right) are given*

(a) *Tarsometatarsus length by site*

| | South Island | | | North Island | | |
|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 |
| 1 | | 0·43 | 0·87 | 22·44 | 25·82 | 21·34 |
| 2 | 1·0000 | | 0·43 | 22·00 | 25·38 | 20·91 |
| 3 | 0·9971 | 1·0000 | | 21·57 | 24·95 | 20·48 |
| 4 | 0·0000 | 0·0000 | 1·0000 | | 3·38 | 1·10 |
| 5 | 0·0000 | 0·0000 | 0·0000 | 0·3074 | | 4·48 |
| 6 | 0·0000 | 0·0000 | 0·0000 | 0·9805 | 0·0100 | |

(b) *Tibiotarsus length by site*

| | South Island | | | North Island | | |
|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 |
| 1 | | 1·58 | 2·56 | 24·13 | 32·67 | 26·03 |
| 2 | 0·9978 | | 4·14 | 22·54 | 31·08 | 24·45 |
| 3 | 0·9214 | 0·9052 | | 26·68 | 35·22 | 28·58 |
| 4 | 0·0001 | 0·0004 | 0·0001 | | 8·54 | 1·90 |
| 5 | 0·0001 | 0·0001 | 0·0001 | 0·3002 | | 6·64 |
| 6 | 0·0001 | 0·0001 | 0·0001 | 0·9969 | 0·0407 | |

(Intercept = 4·501), when NI with an intermediate intercept (4·2487) is significantly different. Overall, however, the implication is that the NI takahe differed more from SI takahe than it did from the flighted pukeko.

Examination of the mean bone dimensions from two morphs of kagu (Balouet & Olson, 1989) revealed a different relationship between lengths and breadths (minimum diameter) of elements than was found between NI and SI takahe. The degree and type of difference between dimensions of the leg bones of each pair of morphs was compared (Fig. 7). With all three leg bones (and others not shown) the relationship between the length and breadth of bones of the smaller and larger morphs is different. The 'larger' kagu (K1) has leg bones between 6–12% longer and 18–25% broader than those of K2. The opposite trend, as observed earlier, is found with the takahe such that, whilst longer, the leg bones of NI as compared to SI are relatively thinner.

FIG. 6. Log transformed lengths and minimum shaft breadths of (a) tarsometatarsi and (b) tibiotarsi of NI (○) and SI (■) takahe, and pukeko (△). Tarsometatarsi: NI, Lntars = 4·2583 + 0·222*Lntarsmb, $F_{1,87} = 5·7012$, $P < 0·05$, $r^2 = 0·062$; SI, Lntars = 3·8603 + 0·3192*Lntibmb, $F_{1,49} = 10·217$, $P < 0·01$, $r^2 = 0·173$; pukeko, Lntars = 3·997 + 0·3256* Lntarsmb, $F_{1,15} = 6·6663$, $P < 0·05$, $r^2 = 0·308$. Tibiotarsi: NI, Lntib = 4·2487 + 0·4150*Lntibmb, $F_{1,47} = 22·7846$, $P < 0·0000$, $r^2 = 0·326$; SI, Lntib = 4·507 + 0·2302*Lntibmb, $F_{1,46} = 16·5019$, $P < 0·0001$, $r^2 = 0·264$; pukeko, Lntib = 4·0652 + 0·4882*Lntibmb, $F_{1,19} = 15·3188$, $P < 0·0001$, $r^2 = 0·44$.

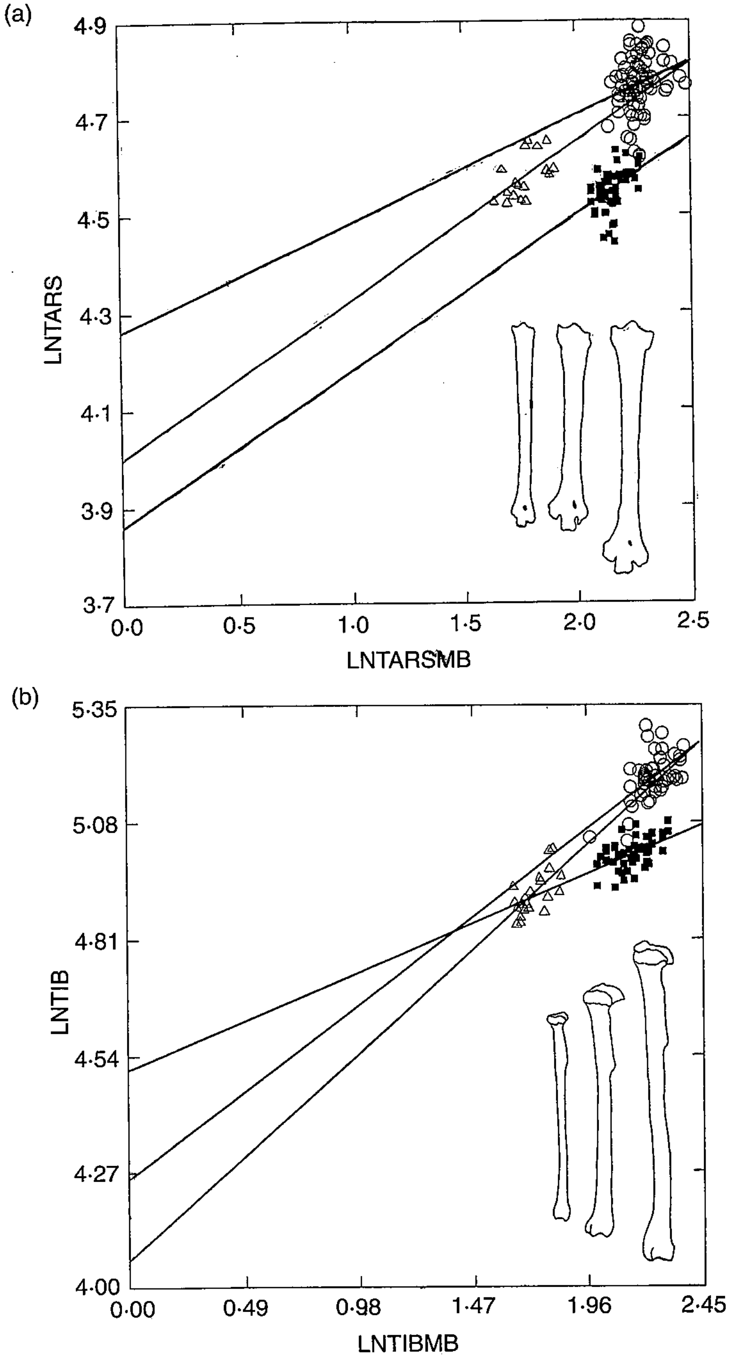
(a)
LNTARS
4·9
4·7
4·5
4·3
4·1
3·9
3·7
0·0
0·5
1·0
1·5
2·0
2·5
LNTARSMB
(b)
LNTIB
5·35
5·08
4·81
4·54
4·27
4·00
0·00
0·49
0·98
1·47
1·96
2·45
LNTIBMB

FIG. 6

TABLE III

*Length/minimum shaft breadth ratios for leg bones of takahe and kagu. KI = 'larger' and K2 = 'smaller' kagu, T NI = 'larger' and T SI = 'smaller' takahe. Index of difference was generated by subtracted ratio of smaller animal from larger, the sign indicating the direction of ratio shift*

| Bone | K1 | K2 | Difference | *T* NI | *T* SI | Difference |
|---|---|---|---|---|---|---|
| Femur | 11·9 | 12·8 | −0·90 | 10·9 | 10·6 | +0·30 |
| Tibiotarsus | 24·8 | 25·9 | −1·10 | 19·1 | 17·3 | +1·80 |
| Tarsometatarsus | 19·3 | 22·6 | −3·30 | 12·1 | 11·1 | +1·00 |

Calculated from data in Balouet & Olson, 1989

Calculation of length to breadth ratios and comparison of these between the two morphs of both kagu and takahe (Table III) emphasized the different relationship of the length and breadth of the leg bones. The 'larger' (K1) form of kagu has, for all three leg bones, smaller length/breadth ratios than the 'smaller' form. The reverse is true for the takahe where the 'larger' (NI) morph has larger length/breadth ratios for all three elements. T-tests cannot be applied to these data as variances were not available for the kagu, however, the consistency of the sign of difference values seems conclusive. It is evident that the two kagu were allometrically scaled versions of one another whilst the two takahe certainly were not.

## Discussion

The rails as a group are generally accepted to be poor fliers (Ripley, 1977). Certainly, many, if not all, might be termed behaviourally flightless as this means of locomotion is not common in

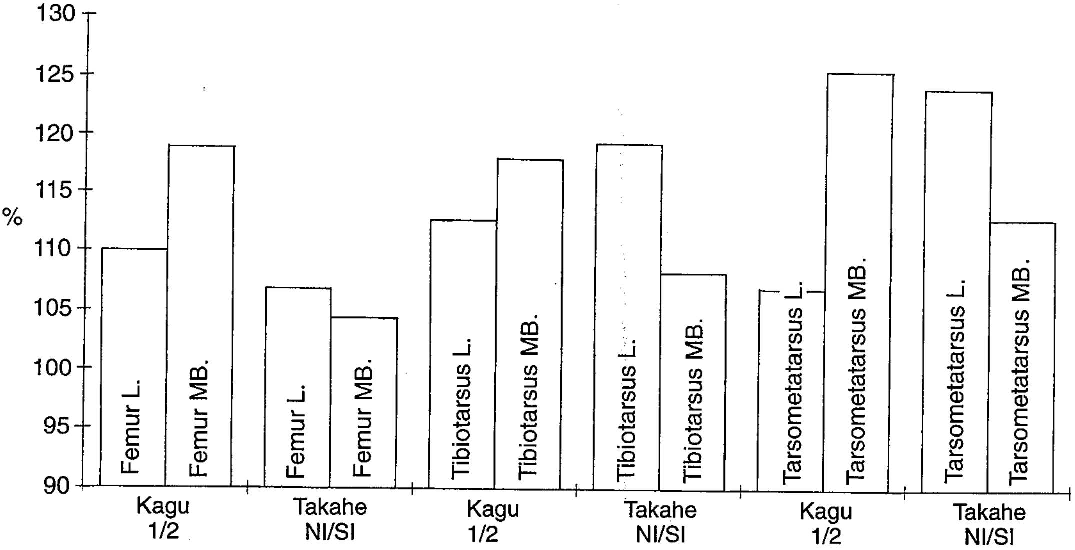

FIG. 7. Comparison of leg bone dimensions (length and minimum shaft breadth) of takahe and kagu. In each case, values are proportionated such that the mean for the 'larger' form (takahe = NI, kagu = K1) are divided by those of the 'smaller' (takahe = SI, kagu = K2) and expressed as a percentage.

the day to day lives of most rails. This is not to say, however, that they cannot fly under certain circumstances and, judging by the number of oceanic islands populated with rail species, they can clearly fly for considerable distances. The presence of subspecies of the volant purple swamphen (*Porphyrio porphyrio*) on numerous land masses from north Africa to the southern Pacific (Ripley, 1977) presumably demonstrates that such birds are capable of transoceanic colonization. Dispersal by flight seems to be the only appropriate explanation for their presence given the wide geographic range of the species. Furthermore, examination of fossil material in New Zealand (Millener, 1981) and New Caledonia (Balouet & Olson, 1989) indicates that, in both cases, modern populations of *P. porphyrio* are the product of recent colonization that postdates extinction or near extinction of the endemic flightless species.

If the takahe evolved *in situ* from a volant ancestor such as *P. porphyrio* (Fleming, 1951, 1979; Olson, 1973*a*; Sibley & Ahlquist, 1990; Baker, 1991), then it must have done so as a result of an earlier colonization event than that which brought the modern pukeko. This suggests, therefore, that at least two (and possibly more) episodes of dispersal have brought *P. porphyrio* or an ancestor of that species to New Zealand and other islands. The question arises as to whether different colonizations by a volant ancestor could give rise through parallel evolution to flightless forms so similar as to be considered the same species, i.e. takahe.

The data show that morphologically the two forms of takahe are sufficiently distinct to warrant specific status, what remains unresolved is how they arose. In the absence of predators, it has been suggested that evolution of large size, and consequently flightlessness, offers energetic advantages to the product of such a genesis (Darwin, 1859; Fleming, 1958). Metabolic data for *Porphyrio* have been analysed and found to support this conclusion (McNab, 1994). A flightless form might therefore evolve from a volant ancestor and subsequently diverge to give rise to two forms parapatrically, or more unlikely, sympatrically. In the latter case, it would be difficult to argue that these were not different species. For two forms to arise parapatrically, significant and consistent differences in the environment would be required to allow natural selection to fix morphological differences in the genotype. The distribution of late Quaternary and Holocene aged bones show (Fig. 1) that takahe were distributed across New Zealand in recent geological history (Beauchamp & Worthy, 1988), a time when substantial changes in climate were taking place. This implies that both forms of takahe were tolerant of a range of conditions and environments, and that the different forms were not specifically honed for a particular habitat. Furthermore, the apparent frequency with which flightlessness evolves amongst rails in particular, implies that there are consistent advantages to be gained from this 'adaptation' in a wide range of environments. In most cases, freedom from mammalian predators seems to be the common factor. Predation might be seen as the principal constraint on ancestral volant forms in their natural habitat to such an extent that they are prevented from following a more economical lifestyle, and are therefore 'pre-adapted' to a flightless lifestyle. Rapid change to this state is therefore to be expected given the opportunity (Olson, 1973*b*). Once flightlessness has been achieved and fixed, the assumption that further significant change will take place as easily might be presumptive.

An alternative to the single colonization followed by allopatric speciation model presented above is that two forms of takahe in New Zealand each evolved from a similar colonizing ancestor on separate occasions. This scenario is suggested because of the high incidence of flightlessness in rails generally (and the implied advantages of this) and supported by the observed allometric and not simply isometric (Gould, 1966) differences in morphology of the two takahe.

McMahon (1973) has shown that the dimensions of terrestrial biological forms abide closely with the principles of elastic similarity, so that the length of a structure changes at a rate which is the 0·666 power of diameter. Relationships of other parameters such as mass follow similar power functions. Exactly what exponent describes the relative length and breadth of components (legs for instance) of an organism, and thus the relationship of the values of these parameters between phylogenetically related organisms, will depend on the composition of structural components and the lifestyle of the organisms (McMahon, 1975; Alexander, 1977). The effect of this relationship was noted, with regard to takahe by Fleming (1958).

The two forms of takahe have neither the same size or shape, by comparison the two species of kagu are very similar in shape but differ in size. The two kagu are biologically (or mechanically) scaled versions of one another. A simple explanation for this could be that the two forms of kagu diverged from an ancestor of the same shape in response to environments favouring smaller and larger size. In contrast, if the two takahe diverged from an already large and flightless ancestor, it must have been in response to different specific selection pressures. The wide distribution of both forms across the respective islands, and that both forms were parapatric when a landbridge crossed the Cook Strait (Lewis *et al.*, 1994), would seem to preclude the existence of such specializing selection.

ANCOVA analysis indicates that the pukeko and NI takahe are more similar to one another in form than either is to the SI takahe. The length/breadth data show that, although taller than the SI takahe, the NI takahe would not have been substantially heavier (and may have been lighter), and generally would have looked more like a tall *P. porphyrio* than a tall SI takahe. Therefore, I suggest that the two forms diverged from a similar volant ancestor on different islands. The SI takahe may represent the product of an older colonization, seeing as it seems to have diverged most from the pukeko, the postulated ancestral form. The first of these possibilities would therefore imply that the NI version is a more recent product, having gained the advantages of large size and a flightless lifestyle but not all the subtleties of plumper form.

Examination of the literature reveals that the independent evolution of two forms of takahe in New Zealand may not be unique. Balouet & Olson (1989) described a new species, *P. kukiwedei*, from fossil bones on New Caledonia and this species is similar in shape (although possibly slighter) but not quite as tall as the NI takahe of New Zealand. Rothschild (1907) gives details of another large blue rail, *Apterornis coerulescens*, supposedly recorded on Reunion Island but leaving no physical evidence. This bird has also been ascribed to *Porphyrio* (Olson, 1977). White (1962) observed a white form (*Porphyrio albus*) on Lord Howe Island of which two specimens remain. This 'White Rail' suffered as so many species of flightless birds, at the hands of humans being "easily struck . . . down with sticks" (White, 1962). This observation at least confirmed the inability of the species to fly. It appears, therefore, that on several occasions, similar volant ancestors have given rise, as a result of similar circumstances, to flightless forms. Paradoxically, what may transpire to be most intriguing about this is not how different these birds were, but how similar.

The application of genetic techniques will help to elucidate the actual relationship of these rails. In the meantime, the morphological differences vindicate the original taxonomy of takahe, and the original names should be readopted by virtue of priority. Thus the North Island takahe is *Porphyrio mantelli* (Owen) and the South Island takahe is *Porphyrio hochstetteri* (Meyer).

## Conclusion

The evolution of flightlessness in birds is relatively common in certain conditions, most often associated with the environment of oceanic islands. In such cases, the lack of constraints such as mammalian predators 'releases' an organism from the apparently costly requirements of maintaining flying ability. This may happen several times from the same volant ancestor in different locations. The presence of allometric differences between certain flightless species would seem to indicate that parallel evolution can give rise to species phylogenetically more closely related to their ancestors than to species that are in gross terms morphologically similar.

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## Appendix 1

*The osteological material used in this study included, to the best of my knowledge, all that registered up to September 1992 in collections at Waitomo Caves Museum (WO), Canterbury Museum (AV) and the Museum of New Zealand (NM, DM or prefix S for subfossils) and is covered by the registration numbers listed below. In the case of modern material and a small number of fossils, registration numbers refer to associated elements, otherwise a single number may cover a range of elements collected at the same site at the same time, or it may refer simply to a collection site as not all such material has been individually registered*

*Porphyrio hochstetteri*: AV5,424; AV11,678; AV13,720; AV15,039; AV16/404; AV17822; AV20,467; AV22,890; AV25217; AV31,332; AV32,389; AV32,535; AV36,139; AV5789; DM146; DM488; DM489; NM11949–51; NM12032; NM13564; NM14966–68; NM17177; NM17611; NM19302; NM19304; NM19313–14; NM19350; NM19810; NM20829; NM21467; NM21557; NM22076; NM23590; NM2372; NM24057; NM24709; NM24710; NM24712; NM24713; NM24715; S22069; S22669; S22719; S22723; S23253; S23255; S23322–4; S23407; S23490; S23517; S23707; S23827.

*Porphyrio mantelli*: Unreg. specimen at Kauri Lodge Waitomo (NM)c/138cave; (NM)M1/136; AV11,381–390; AV12521; AV16,658; AV18,826–30; AV20,620; AV21,765; AV22,241; AV24,926; AV26,406; AV27,461; AV28,205; AV19,143; AV21,170; AV25,004; AV25,044; AV27,175; AV27,461; S10075; S10139–10142; S10211; S10363; S10460; S11063; S11090; S11103; S12224–6; S12400; S12519; S13109; S13114; S13590; S13593; S13778; S13817; S16848; S17294; S17315; S17577; S18024; S18090; S18372; S18627; S18721; S18723; S18798; S18833–4; S18834; S192229; S19688; S20205; S20431; S20556; S20609; S20671; S20898; S21129; S21386; S21508; S21600; S21603; S21648; S22137; S22138–43; S23521; S24593; S24736; S3190; S3929; S3989; S4074–6; S4082; S5519; S5521; S5657; S5703; S6038–6044; S6128–6131; S6324; S6817; S6926; S7542–3; S8071–8090; S8101; S8203; S8227; S9708; S9987; WO169; WO18.4; WO192; WO2.4; WO218.1; WO220.1; WO23.5; WO230; WO235.2; WO257; WO284; WO3.4; WO53.4; WO63; WO63.4; WO80; WO85.1.

*Porphyrio p. melanotus*: AV10185; AV12634; AV12636; AV13735; AV14536; AV17139; AV17140; AV17752; AV22392; AV25202; AV27922; AV30907; AV34900; AV5225; AV6425; AV7709; S11246; S11408; S15029; S16694; S16695; S23522; S23533; S23535; S23537; S23979; S24223; S24252; S617, plus other material discarded after use.