The Takahe (*Notornis mantelli* Owen, 1848): A General Survey

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Abstract

AN account is given of the history, classification and description of *Notornis mantelli* Owen (Aves: Rallidae). As it is monomorphic, sexes are determined in the living bird by using a combination of weight and culmen measurements. Plumage sequences are outlined. After describing the present habitat there is a discussion of changes in distribution and their possible causes. Long-term climatic changes are considered the most important of these. Following sections deal with food and feeding habits, calls, display, pair bonds and territorial behaviour. Banding studies show that pair bonds probably last for life and that territory is held throughout the year and usually for a number of years—if not for life also.

Aspects of breeding biology dealt with are: breeding age (known to be at one year for at least one bird), length of breeding season, nesting behaviour, clutch size (1 or 2 eggs), re-nesting, incubation (shared by both sexes, period approximately 28 days) and egg fertility (at least 75%). Aspects of population ecology discussed are: embryo survival and hatching success (57% for the latter), chick production (0.25 to 0.45 per adult to the stage of leaving the nest), juvenile and adult mortality (provisional estimates are given) and population size and its regulation. Territorial behaviour limits population density but not, apparently, through the food value of the territory. The size of the territory seems to be governed mainly by what is here called "acquisitiveness" rather than being closely correlated with any obvious requisite in the environment. This view of territorial behaviour is briefly discussed.

GENERAL

HISTORY. The rediscovery of a colony of this large, flightless rail in 1948, on the western side of Lake Te Anau, in the South Island, caused interest throughout the world; and the flavour of the excitement of that time appears strongly in the discoverer's account (Orbell, 1949). The find was a most unexpected one for, in the century before, only five recent specimens had come to light and, as 50 years had passed since the last, the species was regarded as extinct. Brief histories of these specimens and of the subfossil type of the extinct North Island race are given in the table:

TABLE NO. I.

Discovery Date	Place	Described by	Comments
1847	Waingongoro R., Taranaki, N.I.	Owen, 1848a and b	In British Museum (Nat. Hist.). Type *N.m. mantelli*
1849	Dusky Sound, S.I.	Mantell, 1850	In British Museum (Nat. Hist.)
1851	Deas Cove, Thompson Sound, S.I.	Buller, 1873 (mention only)	In Dominion Museum, Wellington. Formerly in B.M. (N.H.)
1879	Nine miles S.E. of Lake Te Anau, S.I.	Meyer, 1883	Dresden Museum (now destroyed—Steinbacher, 1949). Type *N.m. hochstetteri.*
1884	Patience Bay, Lake Te Anau, S.I.	Parker, 1886	Skeleton only, in Otago Museum, Dunedin.
1898	Middle Fiord of L. Te Anau, S.I.	Benham, 1899a, b and c	In Otago Museum, Dunedin.

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* Since this paper was written, Mr. Williams has transferred to the staff of Lincoln College, Christchurch.—Editor.

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The 1849 and 1851 specimens are usually said to have come from Resolution Island and Secretary Island respectively (e.g., Buller, 1888 and Oliver, 1955). As the species is flightless and the distance to be covered by swimming considerable, this seems most unlikely, and Mantell says the first specimen was "caught in the gully of a sound *behind* Resolution Island" (my italics). Hector (1863: 460) says he was told by one of the captors of the second specimen that it came from Deas Cove, on the mainland, and R. Henry (in Dollimore *unpubl.*, p. 81–2) gives a verbatim account of its taking as well as that of two others (one from near Resolution Island) whose remains have apparently not been preserved. Only one complete adult specimen has been found since 1898. It was found dead in Takahe Valley in 1958.

Though the takahe first came to European attention through Mantell's discovery, it had been known to the Maori well before this in the southern part of the South Island for according to tradition, it was long hunted in parts of Fiordland (Beattie, 1949). In 1949 tradition was confirmed when a midden was found in Takahe Valley which contained takahe bones as well as those of other birds, including a species of bush moa (Duff, 1956). Radiocarbon dating of some of the associated material sets it in a period the middle of which is 1720 A.D. ± 60 years (Fergusson & Rafter, 1957). There seems to be no Maori legend explicitly referring to takahe in other parts of New Zealand, though subfossil and midden remains have been recorded from places mainly in the southern part of the North Island (Owen, 1872; Oliver, 1955; Greenway, 1958; Yaldwin, 1956; Falla, *pers. comm.*), and the eastern part of the South Island (Gurr, 1952). Reliable records for both islands are shown in Fig. 1.* As some of the coastal sites are middens they are only approximate guides to true distribution, for food was often carried for long distances.

CLASSIFICATION. On the North Island bones Owen founded *Notornis mantelli.* Meyer (1883) considered the skeleton from the 1879 specimen sufficiently different from the North Island bones to merit the founding of a new species, *N. hochstetteri.* But Forbes (1923) made public Parker's suggestion that the differences did not justify so great a separation. This opinion is in accord with modern ideas on taxonomy and has been endorsed by Peters (1934) and the New Zealand Checklist Committee (Fleming, *et al.* 1953), though Oliver remains staunch to the older view. Mayr (in Fleming, 1950) has suggested that *Notornis* and *Porphyrio* are congeneric, and Greenway accepts this opinion. In describing a new species of ectoparasite from the takahe, *Rallicola takahe,* Holloway (1955) remarks upon its close resemblance to the feather louse *R. lugens,* from pukeko, and suggests that this resemblance indicates that "*N. mantelli* and *P. porphyrio melanotus* are more closely related than at present indicated in the literature." Although this view has much to commend it, the genus has been retained in the present paper. *Notornis,* then, is a genus endemic to New Zealand comprising two subspecies: *N.m. mantelli,* in the North Island, now extinct, and *N.m. hochstetteri,* in the South.

GENERAL DESCRIPTION, WEIGHTS, SEX DIFFERENCES, MOULTS, ETC. Oliver (1955) and Buller give a detailed description of the adult *N.m. hochstetteri.* The following general account will thus suffice: The plumage has a loose and silky texture, that of the head, neck, breast, abdomen and thighs being indigo where exposed, but charcoal brown otherwise. Scapulars are peacock blue, changing to a metallic sage-green on the mantle. Back, rump and upper tail coverts are olive-green and the under tail coverts white. The primaries are indigo on the distal vanes but charcoal brown proximally. A striking contrast to the plumage is provided by the beak and legs—the former scarlet at the base and on the large frontal shield

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* Several of the South Island records are based upon unpublished identifications of material in Canterbury Museum (R. J. Scarlett, *pers. comm.*).

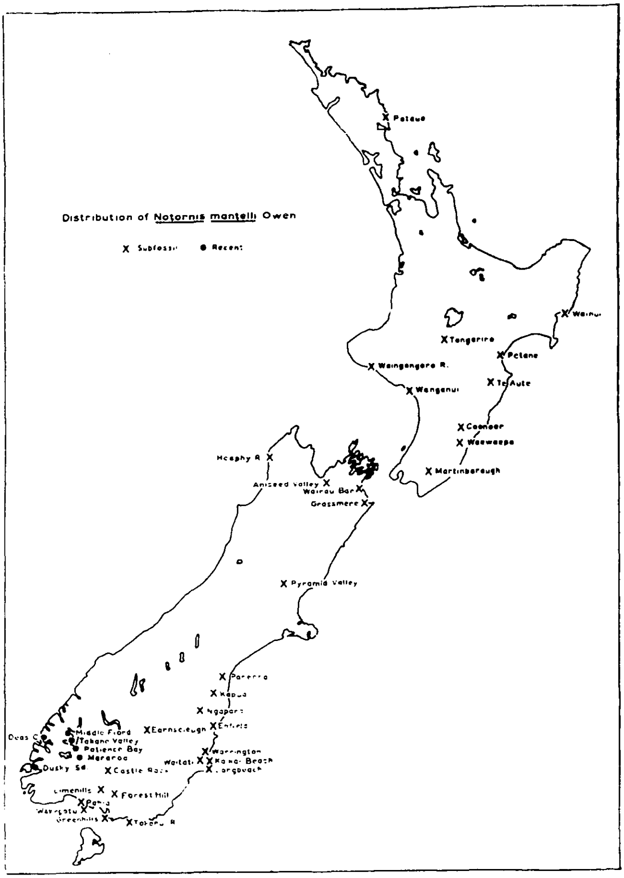

FIG. No. 1

but becoming wax-pink distally; the legs and feet bright red. Eyes are reddish-brown. Though the species is flightless the wings are of a moderate size (length 243 mm, range 221–260 mm), and there is a spur at the carpal flexure. Colour plates appear in Buller—of these that in the earlier edition is the better—and in Rothschild (1907) and Oliver (1955). The last is a photograph of a living bird, but the reproduction of colour is poor. Rothschild's plate is the best in this respect.

Apart from its brighter and more varied plumage, the takahe is similar in general appearance to the pukeko, though much heavier (2–3 times), more robustly built and with shorter legs. Fleming (1951, 1958) has compared the general body structure of the adults of the two species particularly in regard to the differences in physiology, structure and function that arise through that of weight. There is no obvious sexual difference in the plumage and the bird stands about 20 inches (50 cm) high.

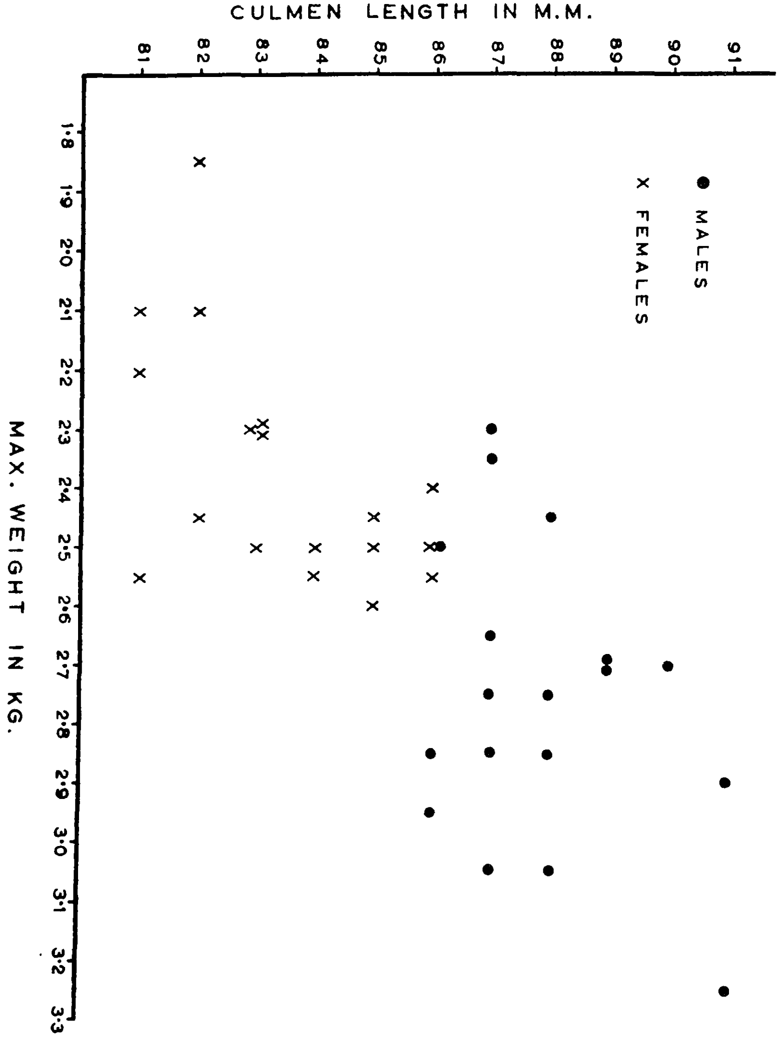

FIG. No. 3.—Scatter diagram showing sexual dimorphism of adults of *N. m. hochstetteri*.

Thirty-six living adults have been weighed and measured during the investigation and it has been assumed that—as in other of the *Rallidae*—the larger in a pair of birds is the male. By using either culmen measurements or weight the sexes apparently can be separated fairly accurately (Williams & Miers, 1958a): with but three exceptions, assumed males have culmen lengths greater than 87 mm and, with four exceptions, maximum weights greater than 2·60 kg. A scatter diagram of culmen lengths and maximum weights shows only one male falling entirely within the assumed-female range (see Fig. 3). However, as this bird was mated with an even smaller one of culmen length 82 mm and weight 2·10 kg the assumption that it is a male seems justified. (The 1898 specimen—a sexed female (Benham, 1899a)—has a culmen length of 82 mm, and recently the bird found dead in 1958 was sexed by dissection and found to be a female, as presumed). The not very numerous records available of seasonal weight variations indicate for both sexes, over the time for which there are records, that weight is at a minimum about December, when the birds are busiest with nests and young (see Table No. 2). As the four assumed males with weights less than 2·60 kg have been recorded only at this time, this may be the reason for their lightness. In the absence of any other simple method for sexing takahe in the field, the present one seems satisfactory—that is, any yearling or adult whose weight is not greater than 2·60 kg, and whose culmen length is not in excess of 86 mm is a female, all others are males. It has been tested by seeing if such changes of mate as are known to have occurred involve the right sexes. No contradictions have yet appeared. A method for sexing the pukeko also dependent on culmen and weight measurements was checked by dissection and found to be 93·7% reliable (Williams & Miers, 1958b).

TABLE NO. 2.

Weight (18 males)			2.65 kg.	Range	2.30–3.25 kg.	
(18 females)			2.30 kg.	Range	1.85–2.60 kg.	
Culmen (18 males)			88 mm.	Range	86–91 mm.	
+ Shield (18 females)			84 mm.	Range	81–86 mm.	
	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Mean male wt.	2.60	—	2.50	2.65	2.60	2.90
N	2	—	4	14	3	5
Mean female wt.	2.30	—	2.00	2.25	2.40	2.45
N	2	—	4	10	7	6

Weights taken to nearest 0.05 kg., lengths to nearest mm.

The plumage sequences, now being studied in captive birds (Williams & Welch *unpubl.*) may be summarized as follows: The *nestling* is closely covered in black fur-like down except in the position of the future frontal shield where it is sparse. The bill is white from the external nares to the tip but black elsewhere. Legs are dark horn with a purplish tinge. At about one month down begins to be replaced by juvenile feathers to the tips of which it clings, and at about three months this moult is complete giving the *juvenile* plumage. Though similar to the adult, it is duller on head, neck, breast, mantle and back. The bill and developing frontal shield are almost black except for a paler tip to the upper mandible and the legs and feet are horn-coloured. A partial moult into a *first winter plumage* soon follows, the new feathers being mainly confined to the back and mantle. Though brighter than the juvenile they still lack the richness of those of the adult. Legs and bill are now beginning to turn red, the former uniformly, the latter at the base and frontal shield only, elsewhere it is bluish-horn. The *first summer plumage* is still slightly browner on back and mantle than the adult, and the vanes of the distal primaries are greenish-indigo instead of the clear indigo of the adult, and although the rest of the bill has become pink there is still a bluish cast that is quite distinct. Yearlings and adults undergo a general post-nuptial moult which begins about mid-January and lasts throughout February and March. At this time takahe are quiet and secretive and large numbers of feathers are found under the shelter of tussocks, bushes or rocks where the birds have rested for long spells and aided the progress of the moult by plucking out feathers themselves.

Approximate weight at hatching is known from an embryo which died a few hours beforehand and was 61 grams. Twin chicks less than a week old weighed 96 grams and another set judged less than a fortnight old weighed 103 and 131 grams respectively. In captivity, three survivors of these four chicks reached the final stages of their body-weight growth curves at approximately seven months; wild young are in the adult weight range before they are twelve months old.

Internal anatomy has not recently been discussed. The skeleton of the nineteenth century specimens received considerable attention and detailed accounts with comparisons with related species may be found in Owen (1848b), Meyer (1883), and Parker (1882, 1886). Benham (1899b & c) studied the viscera—mainly the alimentary canal, larynx and syrinx. A recent observation of interest has been the great size and muscular development of the gizzard in both chick and adult. Benham, too, remarked on this in the adult he examined. He also published a paper (1899a) on the skin of the 1898 specimen. Recently Verheyen (1957) has given a general account of the characteristic morphology of the sub-family *Porphyriinae* to which *Notornis,* together with *Porphyrio* and *Porphyrula,* belongs.

N.m. mantelli is known only from bones. Those examined so far (Parker 1886, Yaldwin) suggest, surprisingly, that this race was larger than that from the colder South Island, but a more critical examination is necessary to take account of age and sex classes.

Since the above was written I have been able to compare the bones of the recent South Island adult female referred to in this paper with the skeletal material of extant and extinct forms held in New Zealand museums and with the full-scale plates of the Waingongoro bones described in Owen's original papers. There can now be no doubt whatsoever that the North Island subspecies was considerably larger than that from the South Island (as seemed fairly likely in any case from Oliver, 1955, and Falla in Greenway). However, leg bones from what is possibly

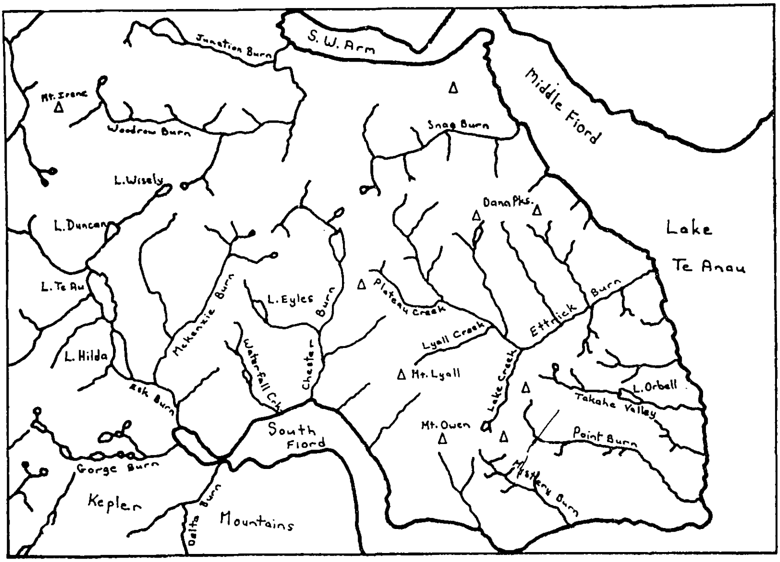

FIG. No. 4.—The Murchison Mountains area west of Lake Te Anau—the present range of *N. m. hochstetteri.*

a single mature bird from the Martinborough Cave, North Island, fall within the size range of the South Island race and are smaller than any other North Island material. (The bones are held jointly by the Canterbury Museum, Christchurch, and the Dominion Museum, Wellington.) The simplest explanation is that these belonged to an abnormally small adult *N. m. mantelli.*

PRESENT RANGE. This includes the Murchison Mountains which lie between the Middle and South Fiords of Lake Te Anau, and part of the Kepler Mountains situated between the South Fiord of Lake Te Anau and Lake Manapouri (see Fig. 4). Though there have been occasional reports of takahe being seen elsewhere none has yet been confirmed.

HABITAT. Most of the range is rough and mountainous. Peaks rise steeply to between five and six thousand feet and ridges and divides are kept narrow and jagged by the action of frost and snow. Streams are numerous and swift-flowing, there are many lakes and tarns and, in areas of poor drainage, bogs. Rainfall is probably at least 100 inches a year with a sharply-decreasing gradient of intensity eastward and there is a heavy winter snowfall (Turbott, 1951). Below the tree-line the dominant vegetation is evergreen beech forest, mainly *Nothofagus menziesii* (silver beech) and *N. cliffortioides* (mountain beech) with the degree of dominance of each varying from place to place. Above the forest is a band of subalpine scrub made up mainly of *Dracophyllum uniflorum, Hebe buxifolia,* and *Olearia moschata.* Above this again the tall tussocks are dominant—*Danthonia flavescens* and *D. teretifolia* on well-drained slopes and *D. crassiuscula* and *D. oreophila* elsewhere (Baylis, 1956, *unpubl.*). Rarely, but importantly as far as the takahe is concerned, tall tussocks are dominant well below the tree-line. When this is so the species most commonly occurring is *D. rigida.*

Takahe are generally to be found at about 3,300 to 3,800 feet where the forest has given way to scrub and snow tussocks—mainly *D. flavescens.* Occasionally tussock and scrub tongues run down through the forest to lower altitudes and takahe may then be found on these tongues. In winter and early spring, when snow lies thick on the tussock-covered mountain tops, the birds move into the forest until a thaw occurs.

Takahe Valley, where the species was rediscovered and where numbers are far more concentrated than elsewhere, is unusual in that the three-mile-long valley floor is fairly flat, wide and treeless (see Fig. 5); and although about five hundred feet below the tree-line (which here lies between 3,400 and 3,500 feet) it is, for the most part, covered in a luxuriant growth of red tussock, *Danthonia rigida,* with *Festuca novaezealandiae* and *Poa colensoi* prominent among the grasses. In boggy places sedges (especially *Carex* spp.) are common. On each side of the valley floor forest-covered slopes rise steeply to the subalpine scrub and the tall-tussock meadows above. A stream collects much of the drainage of the upper valley and of the cirque at the head and meanders through occasional patches of bog to empty into a lake about 1,200 yards long and 250 yards wide situated at the lower end of the valley. The lake is drained by a stream which discharges through a gap in some limestone bluffs beneath which the takahe often shelter in the winter, and after a series of water-falls and caverns it finally reaches Lake Te Anau nearly 2,500 feet below.

The Point Burn, the area of next highest takahe concentration, lies immediately to the south and is separated from Takahe Valley for the most part by a low forest-covered ridge that rises between 300 and 400 feet. The valley of the Point Burn is typical of those in the Murchison Mountains and the rest of Fiordland in that it is narrow with its floor covered in beech forest except for an occasional clearing where mainly red tussock occurs. The lowest clearing in which takahe nest in this valley is at an altitude of about 2,400 feet and this is the lowest altitude at which the birds are known to continuously live and breed.

There is little doubt that distribution is correlated with that of the two species of tall tussock, *D. rigida* and *D. flavescens,* upon which the birds mainly depend for food, cover and nesting sites, and that the relatively dense population in the Takahe Valley—Point Burn area exists there because of the unusually favourable habitat. Baylis has made the general comment that " the wet Fiordland mountains are botanically the *least* favourable part of the South Island for survival of the takahe since this is the region in which the large *Danthonias* are most extensively replaced at comparatively low altitudes by smaller species such as *D. crassiuscula* and *D. teretifolia.*" This then poses the problem of why takahe now exist only in this area and not also in apparently favourable ones elsewhere where the preferred species of *Danthonia* do occur.

CHANGES IN DISTRIBUTION AND POSSIBLE CAUSES. Notwithstanding a tentative identification (Phillipps, 1959) of the legendary North Island " moho " or " mohoau " with the takahe, there is no clear reference to the species in Maori legends of the North Island and in those of the northern part of the South Island. This implies that it has long been rare or extinct there, and the fact that only subfossil or very old midden remains have been found supports this view. None of these have been accurately dated, but the midden material at Wairau Bar and Lake Grassmere has been assigned by Duff to the Moa-hunter culture of 950-1550 A.D. and the rest is unlikely to be any more recent. Bones found at Pyramid Valley are associated with those of the large moas which became extinct before 1450 A.D., according to Duff. Inland deposits further south, for example, those at Earnscleugh and Castle Rock, show a similar association. Some, at least, of the Otago and Southland records are from middens—the one in Takahe Valley being dated, as we have seen, at approximately 1720 A.D. In none of the deposits so far critically examined have *Notornis* remains been abundant which implies that the species has not been common during the thousand or so years man has been in New Zealand. Only in western Otago are there reliable records of sightings in European and pre-European times, though Gurr (1952) accepts records given by Park (1888) implying a notable further shrinkage in range in this area within the last century. It is clear from present knowledge that Park's claims to have heard takahe are wrong. The acceptable records are Maori traditions which tell of hunting the birds in the mountains between Lakes Monowai and Te Anau, the evidence, gathered over the last eleven years, of the species' distribution in the Murchison and Kepler Ranges and the five specimens found before 1900. A rough parallelogram including Dusky Sound, Doubtful Sound, the Middle Fiord of Lake Te Anau and the junction of the Whitestone and Mararoa Rivers delimits this recent range.

So early a scarcity of remains coupled with a major shrinkage in distribution exonerates all those suggested causes resulting from European settlement, such as habitat destruction, predation by—or competition with—introduced animals or epidemics from newly-introduced diseases. Any part played by the early Polynesians in hunting the birds or unfavourably altering their habitat has probably only accelerated a natural trend towards extinction. In this regard it should be remembered that the present population has survived in spite of being hunted until at least the beginning of the European era; and that even the presence during the last half century or so of possibly inimical exotic mammals such as stoats, red deer and Australian opossums does not seem to have had a detrimental effect. This may not be so in the future if the numbers of any of these mammals should greatly increase. Competition for food with any surviving native species is highly improbable because of the takahe's very specialized feeding habits. Whether any competi-

FIG. No. 2.—Head and neck of *Notornis* (right) compared with that of *Porphyrio*.

FIG. No. 5.—Takahe Valley and Lake Orbell, Murchison Mountains. Note the wide valley floor, untypical of this part of New Zealand, and the extensive alluvial flats covered with *Danthonia rigida*—about 500ft below the tree-line.

A Takahe emerging from its nest. The vegetation in the foreground has been clipped off by the bird and used in making the nest bowl.

Colour Photo: P. Morrison, Wildlife Branch.

tion existed in the past with the gramnivorous moas is a question to which there can now be no answer.

Of all the suggested causes of extinction or near-extinction of certain species of the native avifauna (discussed at length in relation to the kakapo, *Strigops habroptilus*, in Williams, 1956) only that invoking alteration of habitat following upon climatic change is satisfactory to explain the shrinkage of takahe range that seems to have occurred before traditional and historic times. A similar view in regard to the various genera of moas has been advanced by Archey (1941), Oliver (1949) and Duff. It is significant that the pattern of retreat has been similar with moas and takahe: disappearance in the North Island followed by diminution in the South with final stands being made in the south-west. There are even other species which have a rather similar pattern of a retreat towards the south, for example, the kakapo (Williams, 1956), kea, *Nestor notabilis* (Oliver, 1955, if his North Island records are accepted in spite of Fleming's (1956) doubts) and laughing owl, *Sceloglaux albifacies* (Williams *unpubl.*). A history of long-term climatic changes in New Zealand with their associated changes in vegetation is given by Raeside (1948), Holloway (1954) and Deevey (1955). There is general agreement in setting a date about 1300 A.D. before which a climate existed favourable for maintaining forest on the eastern side of the South Island and, no doubt, over most of the North Island. After this a change occurred which encouraged the spread of tussock grasslands. At a very much earlier but less certain time a severe post-glacial climate existed which was unsuitable for forest. We would therefore expect the numbers and habitat of grass-eating birds to diminish up to about 1300 A.D. but perhaps to increase thereafter. Though hunting by the early Polynesians has sometimes been put forward (cf. Deevey) as at least the proximate cause of extinction of most of the genera of moas, there are objections to this view—as Duff has pointed out. And whether hunting has been the cause of the restriction of the takahe and some other birds to their present ranges is even less certain. Even when the Polynesian population of New Zealand was greatest it is hard to believe that hunting was so efficient in the great expanses of remote, difficult and sparsely-populated country that extinction of this and other species could be brought about by this means alone. After all, extinction is the fate of more than 99% of all species that have ever existed (Andrewartha & Birch, 1954) and with most of these man can have had little to do. Human interference by hunting, habitat destruction or introduction of predators has doubtless hastened some recent extinctions and has been the proximate cause of others, but in our concern with these, little attention has so far been given to the possible effects within historic times of climatic changes upon populations of specialized and isolated species. Such species are always more sensitive than others to minor changes in the environment. Birch (1957) has recently discussed the role of weather in determining the distribution and abundance of animals, and has reviewed Kalela's studies of the changes in the northern limits of birds and mammals in Finland and Germany. These changes are essentially similar to those I have outlined for takahe and kakapo.

Why the present range of the takahe should be so restricted when apparently wholly suitable habitat occurs close by (as well as further afield in the South Island) in localities much less accessible to both man and introduced mammals, is a question to which there seems no satisfactory answer. Greenway's discussions of extinct and vanishing birds of the world emphasises, at a century's distance, the continued relevance of a statement made by Darwin (1859) in *The Origin of Species:* "Rarity is the attribute of a vast number of species of all classes in all countries. If we ask ourselves why this or that species is rare, we can answer that something is unfavourable in its conditions of life; but what that something is we can hardly ever tell."

BEHAVIOUR

FOOD AND FEEDING HABITS. For a species living in what seems to be an inhospitable environment the diet of the adult takahe is remarkably simple. Whenever available the succulent bases of *D. rigida* and *D. flavescens* are the main items throughout the year. Leaves or leaf bases of other grasses are eaten, notably those of *Poa colensoi, Festuca novae-zealandiae, F. mathewsii* and *Hierochloe alpina,* and in season the seeds and flowers of all species so far mentioned are readily consumed too. The birds seem to relish the succculent bases of *Carex sinclairii* for they wander along the banks of streams or along the margins of pools where it grows most abundantly and lay it waste. Another item is the leaf base of the mountain daisies, *Celmisia* spp., but this is not popular as it does not occur frequently in droppings in spite of the species' widespread distribution. Insect remains appear only rarely in adult droppings, so the fully-grown birds are almost solely grazing animals. In captivity, however, they have readily killed and eaten young chicks, guinea pigs and white rats that have strayed into their pen. This is surprising, as meat had not until then been included in their artificial diet.

When snow lies thick and frozen on the tussock grasses takahe are forced to feed in the forest. The droppings, now almost black instead of bright green or amber are composed almost entirely of stalks of the fern *Hypolepis* sp. (Mason, *pers. comm.*). The only species of this fern recorded from the main colony area is *H. millefolium.* I have seen a takahe readily eating the seed-heads of sweet vernal *Anthoxanthum odoratum,* and Miers (*pers. comm.*) has seen another eating the seed-heads of cocksfoot, *Dactylis glomerata.* Both of these introduced grasses now grow about the hut in Takahe Valley, having presumably been brought in as seeds attached to bags containing stores. Another introduction, timothy, *Phleum pratense,* may be eaten occasionally, too.

D. rigida and *D. flavescens* are readily taken by the red deer occupying the same range as the takahe. However it is incorrect, at present, to refer to competition existing between the two species as there is an abundance of both tussock grasses. Continued grazing by undiminished herds of deer could eventually alter this state of affairs.

Takahe feed by holding down the shoots with a claw, as does a parrot, and then nipping through low down with the powerful beak. Sometimes a bird may even grub below the ground or pull shoots up bodily if the clump is not too big. Then, still grasping the shoots parrot-fashion, the dead material is stripped off before the chosen portion is eaten and the rest discarded. The foot is not used for picking up material directly—this is done by the bill and the material then transferred. (Pukeko often feed in a similar way on pond vegetation.) In a place where birds have been feeding actively the rejected tussock shoots lie in swathes almost as though they had been scythed. When feeding on the seed-heads of the *Danthonias* takahe sweep the partly-open bill smoothly along the stalks and strip the seeds from them. As the bird moves its head from stalk to stalk and runs its bill upwards turning its head at the same time, the observer obtains the impression of graceful weaving action. Elliott (1957) describes a similar method of feeding used by the Gough Island moorhen, *Porphyriornis nesiotus comeri.*

Chicks, like young birds generally, are mainly insectivorous for their first few weeks, and Gurr (1951) has given a list of some of the species eaten: the larvae and pupae of flies and butterflies and parts, at least, of worms and other non-insect matter such as spiders and harvest-men. From late December to mid-February the shores of Lake Orbell, in particular, support great swarms of flying insects—blowflies (*Calliphora quadrimaculata*), of which the chicks are particularly fond, dragonflies and damsel flies, and, among the tussocks, pyralid moths, especially *Crambus* sp.

When the chicks are perhaps rather less than two months of age they appear to have already changed over to a predominantly vegetarian diet, and even at a much earlier age I have seen a chick taking *Viola filicaulis* from a parent's bill. When the chick is being fed, one parent picks up the food and passes it on to the chick or accepts that collected by the other parent and then passes it on. Pukekos and wekas, *Gallirallus australis,* behave similarly. Chicks ingest grit at an early age—I have found quartz grains in the droppings of a bird less than a fortnight old.

Kean (1956) has compared the availability of foods in two Takahe Valley territories, using results from an analysis of droppings to support a contention that food resources of a territory are reflected in the degree of success attained in raising chicks. However, his analysis is only of plant foods and covers only one season.

Droppings are a sure sign of active occupation of an area. When fresh they are most commonly bright green (the colour of the vegetation itself), cylindrical and about as long as the little finger. If not soon destroyed by heavy rain, they dry and bleach and finally become almost white and hay-like. In sheltered places they may lie for years. Kean has described the changes in appearance that occur in the open with time and these are often useful for roughly dating events and for tracing birds. Because chick droppings are of a different size they may be used for establishing one's presence when no other evidence is available.

In captivity, takahe have been found to be very dependent on water, even in cold weather. Not only do they drink and bathe very frequently, but artificial foods such as lettuce and fruits are carried to water and immersed before eating. This degree of dependence—hitherto unsuspected of being so great—perhaps explains why takahe do not occupy some parts of their main range previously thought to be suitable, for in a dry spell these places become temporarily devoid of water.

CALLS. The "contact" call, used by birds of a pair that have become separated or in territorial dispute at a distance, is an almost monosyllabic "klowp" uttered on a rising inflection. It resembles the disyllabic but rather more flute-like call of the weka, common in the same range. The two have been confused in the past because takahe will frequently answer wekas against whom they are very aggressive during the breeding season. Fleming's (1951) description of a pair of takahe calling in a "two-part canon" is an example of this confusion, for though this kind of stimulus and response occurs with takahe, the transliteration of the call as "coo-eet" is more accurately descriptive of that of the weka. Occasionally the contact call is heard late at night which implies some nocturnal activity.

The alarm note is percussive, described in Maori tradition as sounding like the knocking together of pieces of greenstone underwater, but nowadays less picturesquely transliterated as "oomp". It is heard when takahe are aware of the presence of an observer, and also serves as a warning to chicks to remain under cover. Again, the weka has a similar call but more staccato and continuous and given with a greater frequency. A quieter version of the alarm note is used between birds of a pair when close together and undisturbed, and this, with a soft rhythmical "kau" superimposed, serves as a recall note for chicks.

A variety of clucking sounds, rather like those of the common fowl, are made by undisturbed adults when feeding; and, rarely, if suddenly alarmed at close quarters, takahe utter a loud screech.

Chicks' pipings have little that is characteristic about them, but immatures or yearlings readily call, when alarmed, in a distinctive way—rather like the distress call of the pukeko. Even in the absence of any other evidence, this call may be taken as proof that a young bird is present. Three chicks taken from Takahe Valley when only a few days old developed the "contact" call at about 4½ months, and the alarm note at about 7 months of age.

DISPLAY. Thick cover makes observation difficult in the wild, and little has been recorded. The following brief notes are in part based upon observations of captive birds:

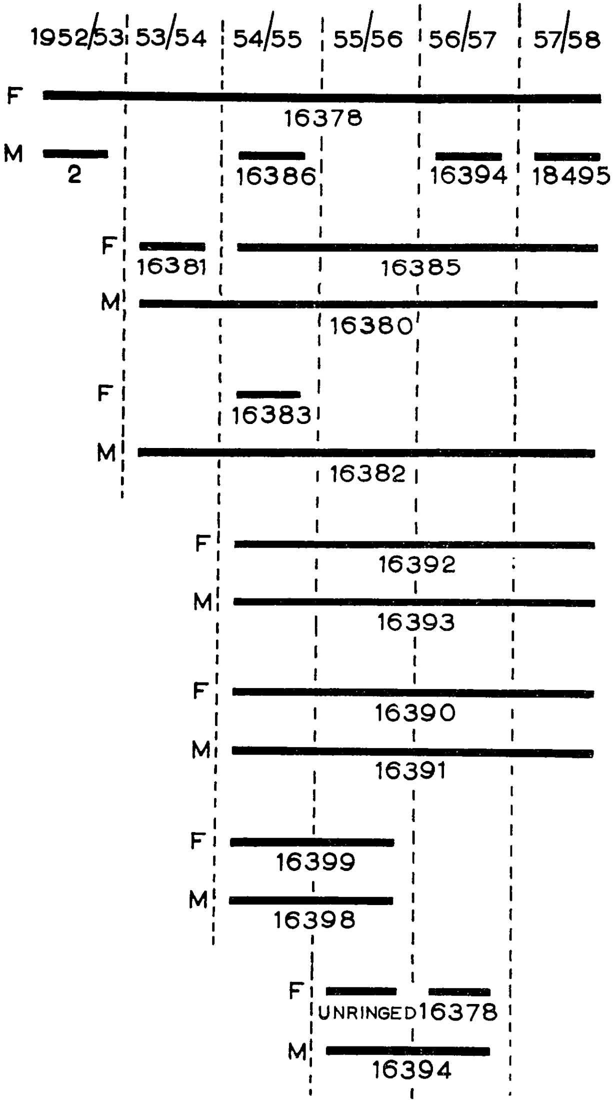

Fig. No. 6.—The persistence of pair bonds in the takahe. Only No. 16378 is known to be dead; the bars show the breeding season in which particular birds have been recorded. With the exception of No. 16391 the territories occupied by unbroken pairs or the "senior" bird are the same throughout.

(i) ALARM. When a bird is uneasy the tail is continuously and rhythmically flicked upwards to expose the white under-tail coverts. In the presence of other takahe this no doubt acts as a warning signal. This display, characteristic of the *Rallidae,* is recorded for almost all species. Once, an alarmed adult, being stalked, took to the water, dived, and kept itself totally submerged by grasping underwater vegetation with its feet. It remained thus for five to ten seconds until it was picked up and placed on dry land. (See Witherby *et al.,* 1941, for similar behaviour of the moorhen, *Gallinula chloropus.*)

(ii) EXTREME THREAT. In territorial dispute, either just before attack or interspersed with fighting, the wings are held high and arched, the neck feathers ruffed out and the wing coverts made prominent. If attack ensues blows are struck with beak and neck. An account by Moon (1957) of an intimidatory display by an incubating pukeko resembles this closely. Gullion (1952), under the name " paired display ", describes similar behaviour in the American coot, *Fulica americana.*

(iii) MUTUAL DISPLAY. Falla (1951) describes such between birds of an incubating pair thus: " The sitting bird was called off by its mate. The bird responding darted with a crouching run to the caller and straightened up facing it with the two bill tips almost touching and both necks upstretched. After some seconds one bird, I think the original caller, crouched and moved round the other with a gyratory movement which presented the spread white under-tail coverts to the other's view. Drooped wings and fluffed-out flank feathers gave the general impression of a round white target ringed with blue." A very similar display, with mutual neck-nibbling, occurs in mated birds that have not yet bred and is probably a preliminary to coitus. Gullion's " arching " display seems to be an equivalent in the American coot.

(iv) " GAPING ". Occasionally birds will continually raise their heads and open their bills wide as if calling, but no sound emerges, nor does it appear that nearby birds are responding. This behaviour may go on for some time. It may be elicited after disturbance from sleep, which suggests it is a form of threat; on the other hand, it is quite commonly seen when the birds are bathing. I have not seen this behaviour described for other rails.

PAIR BONDS. Pairs once formed probably last until the death of one of the partners. Fig. 6 gives details of the duration of pair bonds and of changes that have occurred. In four of the five changes there has been no subsequent record of the superseded bird, though it could have escaped observation or, even less likely (as will be seen presently) have moved out of the study area altogether. In the fifth change the first mate was unbanded and so could not be identified later.

TERRITORIAL BEHAVIOUR. The obvious year-round occupation by a pair of a fairly well-defined home range or territory* is an aspect of behaviour that has often been commented on (Falla, Williams, 1952; Williams and Miers, 1958a). Even in the depth of winter when snow lies deep on the valley floor, most of the birds are still in at least part of their summer range though, as they keep mainly to the shelter of the forest at this season, they are not easily seen. However, whenever an extensive thaw occurs they immediately move out into the exposed tussocks. Other rails are known to hold territories throughout the year, for Cramp (1947) has described such behaviour for the European coot, *Fulica atra* and Gullion (1953) for the American coot.

Various evidence shows that mated pairs or family groups of takahe are attached at least semi-permanently to an area: The characteristic droppings do not occur randomly distributed over the whole of the country occupied by the species in the main colonies, but are concentrated (fresh and old alike) in well-marked localities

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* The area occupied is certainly a territory during the breeding season. Whether it is defended at other times is not certain—if not, it would then be a home-range. In the meantime, for simplicity's sake, I will refer to the occupied area as " territory ".

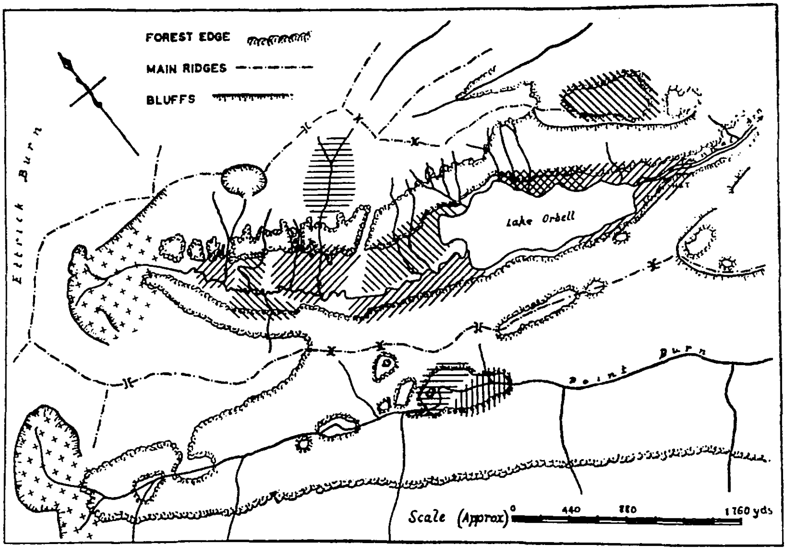

Fig. No. 7.—Line hatching shows approximate extent and boundaries of the "permanent" takahe territories in Takahe Valley. The cross-hatching on the N.E. shore of L. Orbell indicates an occasional extension of the territory of the pair on the northern bluffs. Stippled areas show the other occupied parts of the main colony which are not well known because of the difficult terrain.

that are usually separated by expanses where fresh droppings are scarce. Feeding signs, equally characteristic, show the same distribution. This is not just a reflexion of the distribution of preferred food plants and water, for these are usually widely and abundantly spread and often occur in places where there is little occupation. Furthermore, calling and sight records are most frequent in the vicinity of those places where they have been reported in other seasons and years. Nests, too, are made in well-used localities season after season, even though sites similar in every way are widespread. All these criteria for establishing territorial behaviour show excellent agreement; but it is the sighting or recapture of banded birds that supplies the most reliable data for fixing the approximate boundaries and period of occupation. Williams and Miers (1958a) have discussed the subject in detail and have included a map, reproduced in Fig. 7, which shows the location and approximate boundaries of a number of permanently-occupied areas. The size of each remains fairly constant—the smallest being about 5 acres, the largest about 20; though these are only provisional estimates.

If it is assumed that a bird has been in continuous occupation provided that it has never been seen settled elsewhere and no alien birds have been seen living in its territory, then we have the following occupation records up to the end of the 1958–59 breeding season (see Fig. 8): Seven seasons in a territory—1 bird (No. 16378), six seasons—1 (No. 16377), five seasons—3 (Nos. 16380, 16384, 18488), four seasons—4 (Nos. 16385, 16389, 16390, 16391), three seasons—6 (Nos. 16382, 16386, 16392, 16393, 16394, 18492), and two seasons—10 (Nos. 2, 3, 8, 9, 16376, 16379, 16383, 16396, 16397, 16398, 16399).

If pair bonds and territories are semi-permanent young birds, unless they oust one of their parents, must generally move over considerable distances in search of a

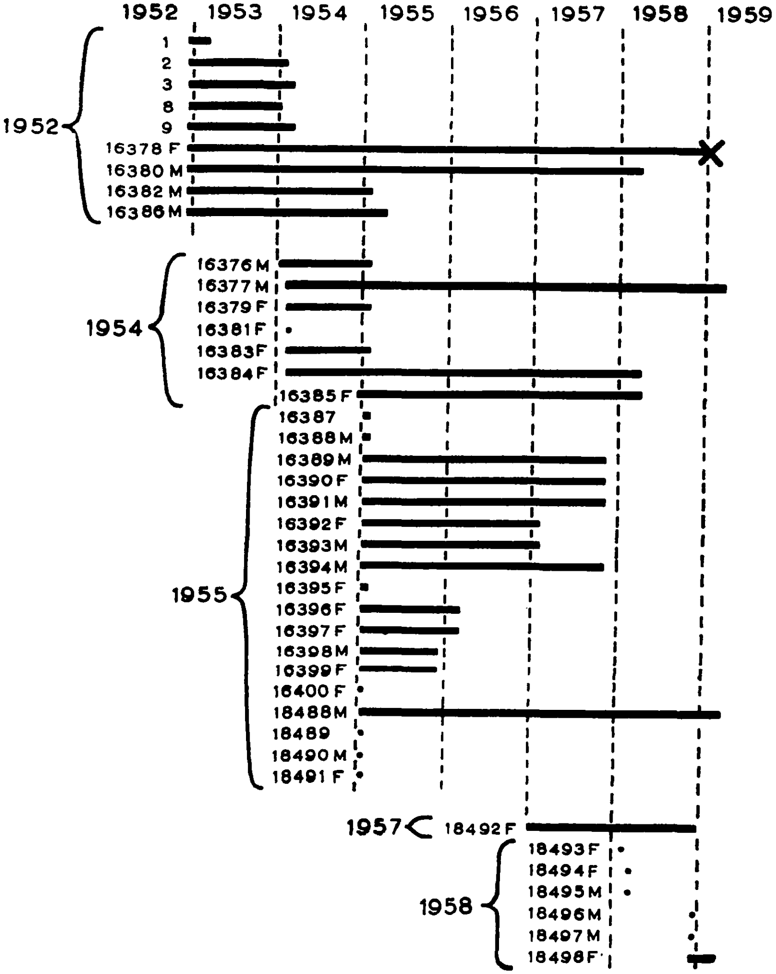

FIG. No. 8.—Minimum survival times of all takahe banded up to the end of 1958. No. 16378 was found dead in November, 1958. All were banded as adults or yearlings except the following, which were banded as chicks: Nos. 16376, 16380, 16383, 16387, 16397 and 18489.

place to establish themselves, and there is evidence from banding records that this is so. For example, No. 16380, banded as a chick, was found a year later established in a territory about 2,000 yards away. This is the greatest distance a takahe is known to have moved over. Occasionally there are movements well beyond territorial boundaries that do not seem to be connected with wandering of young or displaced birds but rather to have arisen from disputes, the temporary straying of a chick or from disturbance through capture. Two temporary shifts of over 1,000 yards are known to have been made by adults shortly after being banded, and these involved the crossing of adjoining occupied areas. The movements of one of these birds, No. 16388, is shown in Fig. 9. An undisturbed pair not seen beyond its territory in five years was found to have left it unoccupied, while others in the main colony were still in theirs and to have moved fully three-quarters of a mile away from the main colony altogether. One of the birds of this pair is No. 16380 in Fig. 9. Movements of two other birds in Takahe Valley are also shown in Fig. 9. They are typical of the wanderings that are the general rule in that they extend little, if at all, beyond recognizable territorial boundaries.

METHOD OF OBTAINING DATA. As a means of studying behaviour in this species banding has not been entirely satisfactory. The birds spend most of their life in thick cover much taller than themselves and are wary and difficult to shepherd into open ground where the colour combinations may be seen. Loss and fading of the plastic colour bands must also be contended with, though both of these difficulties have been largely overcome since nitrocellulose lacquer has been used to seal the bands and colours subject to fading have been withdrawn from use. All the 20 uncemented bands put on between late 1952 and early 1954 appear to have now been lost, but only six of the 27 cemented bands are known to have suffered the same fate since. There is no evidence that any numbered aluminium bands have been lost.

The nature of the cover and terrain in which the birds live and their behaviour make the use of any sort of trap for their capture impracticable. If capture is necessary it must be done by hand. This is difficult, for the birds can run fast and have the advantage of concealment. Three men are needed for efficiency and a minimum of disturbance.

Field work consists of a daily traverse on foot of five to ten miles of forest, bog and mountain meadow, with frequent climbs and descents of 1,000 feet or more. Heavy rain or snowfall limit the amount of observation that can be made on any

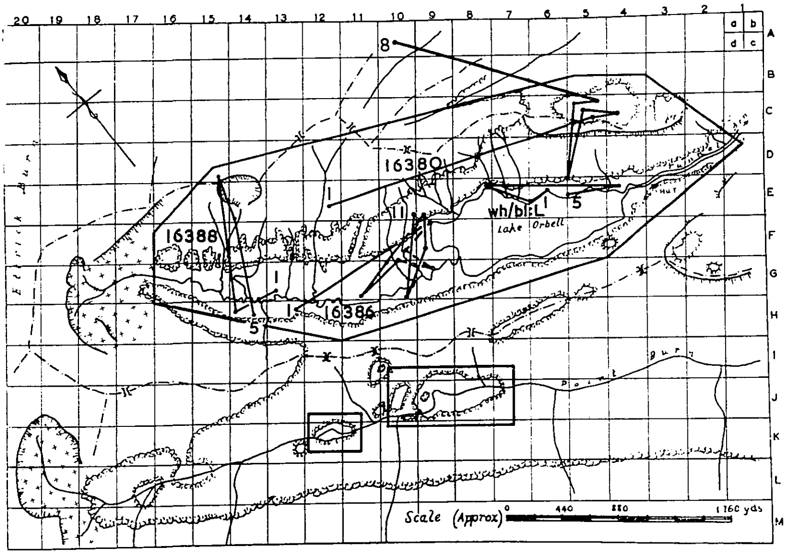

FIG. No. 9.—Movements of four selected takahe. Digits indicate first and last observed positions and therefore the total number of observations. Further details in text. The three areas enclosed by heavy lines are those that have been censused.

one visit, and the distance of the Murchison Mountains from major settlement limits the frequency of expeditions.

BREEDING BIOLOGY

BREEDING AGE. Williams (1957) described two birds as breeding in their first year. One was found incubating on a nest 2,000 yards from where it was banded as a chick in another territory, the other was associated with one of its parents and a nest containing one egg. There can be no doubt that the first bird was breeding in its first year; but as it is now known from a number of observations that family groups may remain together until at least the start of the next breeding season, sharing of incubation duties could be the explanation of the behaviour of the second bird. The extent to which breeding occurs in yearlings is unknown, but three yearlings in captivity (2 ♂, 1 ♀ and 1 adult ♀) failed to breed. In the wild, birds may pair but not lay in the same season, and this is known to have happened with four different pairs.

BREEDING SEASON. Most laying occurs from late October to late November, though eggs have been found in early October and an approximately week-old chick, perhaps resulting from re-nesting, has been seen at the end of March. These may be extreme or untypical phenomena, but a five to six-month breeding season has been reported by Gullion (1954) for the American coot and by Moon for the pukeko in New Zealand.

NESTING BEHAVIOUR. Neither nest building nor egg laying has been observed in the wild, though a bird has been seen scraping dry grass together in a place where a nest was later found. Most commonly the nests are placed under or between large tussocks of *D. rigida* or *D. flavescens,* and they consist of grass bowls about 12 to 15 inches in diameter and at least 3 inches thick in the centre. From the appearance of the ground beneath, it seems that a saucer-like scrape in the earth is made first and the vegetation trimmed accordingly before the bowl is fashioned. The thick bower of living tussock above keeps it dry in wet weather and the thickness of the bowl keeps the nest cavity above ground water. Usually there are two entrances which connect with runways. A " latrine " within about two yards, with its pile of droppings, gives the location of the otherwise well-concealed nest away. Where snow tussocks grow intermingled with subalpine scrub the nest may be under the imbricating foliage of *Dracophyllum uniflorum,* but even so the bowl is still made of the shoots of the tall tussocks. In captivity, both birds of a pair have taken part in building a fairly typical nest. Both brought nest material but the female was mainly responsible for making the bowl.

A feature of any nesting area is a number of " trial " nests. Some of these have probably served a purpose in that their building has helped to synchronize the sexual cycles of each of the pair, though we do not at present know whether both sexes take part. Others are almost certainly true nests that have been begun but abandoned when soaked by heavy rain or snow. After a chick has hatched and is able to leave the nest proper, " brood " nests, very similar to the real ones, may be built to shelter the wandering young; and Witherby *et al.* describe behaviour of this kind in the moorhen.

CLUTCH SIZE. One or two eggs are laid. A nest with three eggs was most likely one in which one egg and then, at a later date, two eggs were laid. Of 44 clutches recorded (see Table No. 3) 23 are of two eggs. Though the remaining 21 nests contained one egg when found, some certainly held two eggs originally, as will be seen later. There are only eight nests in which positively only one egg was laid. Whether there is variation in the mean clutch size or of hatching success with the season or with the age of the female are points about which there is no information. Takahe probably have the lowest mean clutch size of all rails.

Twenty-four eggs have been measured: Length, 68–78 mm, mean, 73·5 mm.; breadth, 47·5–52·5 mm, mean, 49·0 mm. They are pale buff and marked irregularly with blotches of brown and mauve.

Takahe occasionally re-nest: apart from the three-egg nest described above, three other re-nestings have been recorded; two rely on circumstantial evidence—an occupied nest has later been found deserted with a new and occupied one nearby in the same territory. In one of these egg measurements from the two nests were in excellent agreement. For the third record there is unequivocal evidence: an identified banded adult was seen with a newly-hatched chick some ten weeks after having been seen in almost precisely the same place with another. Though the first was not found again its death cannot be assumed, for birds of about three months of age are particularly difficult to see in the tall tussock and low scrub.

INCUBATION. Though the incubation period is not known exactly, two independent estimates agree in fixing it at close to four weeks: (1) A nest was found in which incubation had been going on for about 10 days, judging from the size of the latrine, which is a reasonable guide. Eighteen days later one of the two eggs was very close to pipping, for the chick was moving about vigorously inside and could be heard "peeping" from a yard off; the other chick was alive but silent and not so far advanced. Unfortunately, this was the last visit that could be made.

(2) In 1957 four eggs were taken (two 2-egg clutches) in the first attempt to raise the species in captivity. These eggs were very fresh and, judging from candling and from the size of the nest latrines, could have been incubated for only about two days before they were removed. Under a bantam one reached a stage of development so advanced that the chick could be heard calling from within. This took 26 more days. The chick failed to pip the shell and died, but was found to have been within a few hours of hatching.

As is usual among the *Rallidae,* incubation is shared by the sexes. Eggs are not covered when the nest is left, and this, too, is usual ralline behaviour. Secker (1952, *unpubl.*) on one occasion heard what he believed to be egg-turning to continue for 10 minutes after one bird had been relieved by another. On taking its place on the nest a bird will sometimes rearrange the cover within reach to improve concealment, and will often gradually turn its red bill from sight when approached by an observer. Both sexes sometimes sit on empty nests as if incubating eggs; one pair for as long as seven to eight weeks, another for at least a month judging from the size of the latrine and the state of the droppings. Two more pairs have "incubated" on nests that have never held eggs. Observations of two captive pairs suggest that at least one of the birds in each of these four wild pairs may have been a yearling (see above, under "Breeding Age").

EGG FERTILITY. Of the 67 eggs recorded, the status or ultimate fate of 48 is known and the data available are summarised in Table 3.

TABLE NO. 3.

Breeding season	Two-egg clutches	Apparent one-egg clutches	Total eggs	Examined for fertility	Judged fertile	Judged "infertile"	No data
1948–49	—	2	2	1	1	—	1
1949–50	3	2	8	6	3	3	2
1950–51	—	1	1	1	—	1	—
1951–52	2	3	7	5	3	2	2
1952–53	3	4	10	5	3	2	5
1953–54	2	2	6	3	2	1	3
1954–55	3	3	9	6	5	1	3
1955–56	**3**	3	**9**	8	6	2	1
1956–57			No expedition this season.				
1957–53	3	—	6	4	4	—	2
1958–59	4	1	9	9	9	—	—
Totals	23	21	67	48	36	12	19

Though the overall estimate of fertility of the 48 eggs examined is only 75%, the true figure will be higher, for the table shows a clear tendency for the estimate to increase with time as the technique for making it has been improved. In fact, during the last two seasons, when a candler has been used all eggs examined have been found fertile. Included among the "infertile" eggs of earlier observations must have been some in which the embryo had died early in development. Whatever the true percentage of fertility it will certainly be less important as a factor affecting survival of the species than viability of the embryos and survival of the hatched young. Indeed, "fertility" is often used as a synonym for embryo viability or hatching success, which is incorrect though the difference may be small in many species. Of the 17 eggs, for which there are no data on fertility, five are known to have been destroyed, the other 12 disappeared without any trace or issue between the brief expeditions characteristic of the earlier years of the investigation.

POPULATION DATA

EMBRYO SURVIVAL AND CHICK PRODUCTION. Three late embryos have been found dead in deserted eggs, and some of the twelve "infertile" eggs of earlier observers undoubtedly contained decomposed early embryos. Survival is probably most directly affected by three factors—the operation of lethal genes, deficiency disease, or parental neglect. Occasionally malposition of an otherwise healthy embryo could make hatching impossible too, and this is known to have occurred once. Nothing is known of lethal genes in takahe or of deficiency diseases either, but deficiency of trace elements may cause death of common fowl embryos, and Dr. Muriel Bell (*pers. comm.*) has informed me that with cobalt deficiency this occurs at about the eighteenth day of development. South Island soils derived from granite are severely deficient in cobalt (Andrews, 1956); those in the Takahe Valley area, though not yet examined for cobalt content, are derived from granites and are heavily leached as well (Cutler, 1954 *unpubl.*, McKellar, 1956).

As for parental neglect, some of the "deserted one-egg clutches" of the past have really been deserted clutches from which one chick has hatched, the second egg then being left (or even destroyed). That this is the correct interpretation is strongly indicated by the data given in Table No. 3. Observations over the last five breeding seasons have been more thorough and continuous than during the first five, and the proportion of two-egg clutches found has shown a corresponding increase from 40% to 62·5%. Two well-developed embryos are known to have been deserted and there could well have been more. The reason for this seems to be as follows: the laying interval between eggs in a two-egg clutch is about 48 hours, and incubation begins with the laying of the first egg. This is not known from direct observation but is inferred from knowledge of the differing degree of development of embryos from seven clutches. An interval is known to occur at hatching, and this will also be about 48 hours. With such an interval brooding and parental behaviour towards the hatched chick apparently sometimes overcomes the drive to complete incubation of the remaining egg, and the nest is deserted when the chick leaves it. Other rails are known to sometimes desert part of the clutch (Gullion, 1954; Alley and Boyd, 1947). Such behaviour in the takahe is one reason why only three sets of hatched twins have been observed out of the 23 theoretically possible. (Other reasons are failure to find, or even look for, a second chick or the death of one soon after hatching).

Of the 48 nests recorded, full details of clutch size and fate of eggs are known for only 12 (or 16, if the four that never contained eggs are included). Nine of these twelve nests contained clutches of two, the others clutches of one; and from these 21 eggs 12 chicks hatched. The remaining nine eggs either contained dead late embryos, were addled (i.e., more likely deserted fertile eggs rather than infertile ones), or were destroyed by the takahe themselves before fertility could be investigated. This gives a likelihood of hatching of 57% and a mean productivity of 1·0 chick per laying pair. Three clutches were totally unsuccessful. A truer estimate will take into account those pairs known not to have laid. However, to include all four would give undue weight to the frequency with which non-laying occurs in the nest records as a whole, which is once in every twelve. By including one of these non-laying pairs in the calculation proportionate representation is restored. Thus, 13 pairs hatch 12 chicks, or 0·9 chick per pair. This should be a maximum estimate of chick production, for a higher proportion (75%) of two-egg clutches is included in the sample than occurs in the nest records as a whole (52%), and all three known sets of hatched twins are included also.

A minimum estimate of chick production may be obtained, and one calculation of this has been given in an earlier publication (Williams, 1957). A new estimate may now be made: from all 48 nests 21 recently-hatched chicks have been observed. Forty-two pairs produced these (48, less four known to have re-nested, less another two whose eggs were taken in the 1957–58 season for the first attempt to raise the species in captivity). One pair, then, produces 0·5 chick surviving to leave the nest. This is a minimum figure because, as already pointed out, some chicks have certainly not been accounted for—either because they have not been seen or because of their death soon after hatching.

Chick productivity in this species therefore lies between the limits of 0·5 and 0·9 per pair, or 0·25 and 0·45 per adult.

An approximate check on this estimate may be made by using the provisional figure for hatching success of 57%. Forty-two pairs have laid a minimum of 67 eggs. If 57% of these hatched, 38 chicks would result—a productivity of 0·9 chick per pair. At present it is not possible to decide whether 57% is likely to be above or below the true figure, but the agreement of this estimate of productivity with the upper of the two limits found by other means suggests that the true chick productivity is likely to lie closer to 0·9 than 0·5.

JUVENILE AND ADULT SURVIVAL. Little is known of chick survival for few have been banded. Of the seven that have (the last in 1955), survival times for each up to the last sighting have been as follows: 1 week, 2 months, 11 months, 12 months, 13 months, 5 years and 3 months, and one not seen again. The banding and recapture programme begun late in 1952 (Riney and Miers, 1956) has furnished some preliminary data on adult survival. Fig. 8 summarises all returns and recoveries up to early 1959. Only one banded bird has been found dead and, as it was at least one year old when banded, it was at least seven years old at death. Only two other adults have been found dead in the main colony area over the last eleven years, both before banding was begun. The implication from this and the data in Fig. 8 is that takahe, having reached the yearling stage, have a good expectation of further life.

By assuming (i) that over the last 11 years there has been a stable population in the main colony (annual estimates of numbers support this), (ii) that the breeding age is one year (there is some evidence for this), and (iii) that adult mortality is independent of age (an assumption generally accepted as being true for birds), it is possible to make provisional calculations of expectation of further life for adults.

If all chicks leaving the nest survive to breed the replacement rate or annual adult mortality would lie between the limits of 25% and 45%. But there is sure to be considerable first-year mortality. If this were only 50% replacement rate would lie between 12·5% and 22·5%, which implies an average expectation of further life for adults of between 4 and 7·5 years If 67%, then annual adult mortality would lie between the limits of 8·3% and 15% with an average expectation of further life of between six and 10 years.

With 50% first-year mortality 2·2 to 4 pairs would be needed to produce a chick surviving to breeding age; with 67% mortality the necessary number would lie between 3·3 and 6.

A first-year mortality of 67% is by no means high for birds (Lack, 1954). Alley and Boyd found it to be that for the coot, and Gullion (1954) found mortality to be already 46% for the American coot even at fledging.

If takahe are as long-lived as these preliminary calculations indicate, it will be some years before a satisfactory life table can be constructed.

POPULATION SIZE AND ITS REGULATION. Various expeditions to the north, west and south of the Takahe Valley-Point Burn area have shown that beyond these two valleys the population density is much less—perhaps one or two birds to the square mile, though this is only an estimate. With a density of this order occurring over the known range the total population of the species can be only a few hundred.

Counting of the pairs in the main areas of the Takahe Valley-Point Burn colonies (shown enclosed by heavy lines in Fig. 9) has indicated that there is little annual variation, the number always lying between ten and twelve (Williams and Miers, 1958a). As territories are held throughout the year and often for a number of years, the observer's familiarity with them makes a direct census more trustworthy than it would be otherwise. However, unmated wandering adults are not satistorily accounted for, though long observation makes it certain that they are not numerous. The total adult population, then, in the main areas probably lies between 25 and 35. Another estimation that should take account of unmated adults may be made by using a Lincoln Index technique: The main areas were repeatedly and thoroughly traversed in the 1954–55 and 1955–56 breeding seasons and, from the ratio between birds seen with aluminium bands and those without, estimations made of the adult populations for each of these seasons gave figures of 29 and 33 respectively. The provisos attendant upon the use of a Lincoln Index to calculate population size are well-known, but, as with the direct census of mated pairs, familiarity with the terrain and the birds' habits removes a number of objections and makes the results of the calculations rather more trustworthy than they would otherwise be. For example, it is unlikely that any birds were counted twice or that banded ones were unavailable for census through being outside the census areas. Conversely, immigration of unmarked birds was unlikely also. As the species is known to be fairly long-lived once about a year old and as marking with metal bands was begun only in early 1954, loss of bands through mortality is likely to have been very small. Therefore, the agreement between the two population estimates is probably not fortuitous.

Two parts of the Takahe Valley-Point Burn area—the great cirques at the head of each valley—are difficult country and not so well known as the rest. However, the number of adults living here (the stippled areas in Fig. 9) is less than the combined total of those in the other parts of the main colonies. To sum up: observations over the last seven years clearly show that there has been little variation in the adult population and estimates would fix it as very close to 50 birds.

Territories or home ranges in the main colonies are almost constant in number and position from year to year and it is only very rarely that takahe succeed in establishing themselves on ground already occupied. Nor do new pairs appear in unoccupied ground and this compels one to believe that where such ground is not obviously unsuitable it is part of a defended area even though behaviour in defence of it has not been seen. Territorial behaviour is, therefore, regulating population density and, through it, population size in these colonies. What, then, determines the extent of the territories? Long familiarity with them and with the takahe's food habits and cover needs convince me that the area each pair occupies is far in excess of what is needed to supply adequate food and shelter throughout the year, though all the evidence for this is at present qualitative rather than quantitative. Thus, insofar as food is concerned, I agree with Hinde (1956), who states, in discussing the possible functions of territory in birds: " In a few species territory is primarily concerned with food, but in most the food value of the territory is not significant ". Consideration of territorial behaviour in takahe has led me to wonder whether it is not, in this species at least, essentially an attempt to indulge in " acquisitiveness " for space to the fullest extent physically possible. Obviously there must be a close connexion between the " acquisitiveness " of an individual and its chances of survival. If it does not hold enough of its environment to assure a sufficient supply of essential commodities it, and its offspring, will perish; on the other hand, there is no disadvantage in staking out a claim to more than needed so long as the organism does not exhaust itself by trying to hold too much. (Natural selection could be expected to act in the obvious way here.) If this concept of territorial behaviour is correct we would expect it to have a value for survival but not expect a very frequent close correlation between population density and the supply of a limited essential commodity. It may well be significant that attempts to find such close correlations in nature are generally not very successful, for it is hard to believe that natural selection could work so exactly as to closely fit the complexities of behaviour and the needs of the organism to the almost infinite variability of the environment.

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