NOTORNIS IN FEBRUARY, 1950.

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The chief objectives of a visit to Takahe Valley in February, 1950, were to learn the plumage of the immature bird after juvenile down is shed, and to study the behaviour of adults during the period of moult which most birds enter at the end of their breeding season. In addition, observations in February were expected to help fill one of the gaps in the annual cycle that previous visits (in November, January, August and December) had begun to outline, and would allow a final check on the success of the 1949-50 breeding season. As it turned out, some time was spent observing a pair with their well-grown downy chick which was the only young bird of the 1949-50 season located.

I am grateful to Mr. G. F. Yerex, Controller, Wildlife Branch, Department of Internal Affairs, for the invitation to join the February Party (No. 5 party), and to Messrs. H. J. Ollerenshaw and G. R. Williams, of the same department, who, armed with previous field experience, initiated me into the joys and responsibilities of observing Notornis. Their observations are credited by quotation of initials. Both in the field and in preparation of this article, I have had the benefit of reference to the reports of previous expeditions by Dr. R. A. Falla and Mr. E. G. Turbott, to whom thanks are recorded for this courtesy. I have tried to avoid repeating observations published elsewhere (Falla, 1949, and in this number; Turbott, in this number; and Williams, 1950).

GENERAL SURVEY IN FEBRUARY.

In another article in this number, Dr. R. A. Falla has outlined the status of the several Notornis pairs studied by the December expedition (No. 4 party) in the Upper Tunnel Burn and adjacent Point Burn valleys. Pair A were attending a single healthy chick on February 3, 1950. Pair B, recorded at a high altitude north of the Tunnel Burn in 1949, were not located in February, although fresh feeding-sign, droppings, and empty nests were evidence of their presence (H.J.O., G.R.W.). Pair C (status uncertain in December) still occupied their territory in February ruary; they appeared to be without young, but the decayed carcase of a fledgling was retrieved from their territory. Pair D, which had lost their chick in December, were still on territory near their nest but had apparently not laid again. Pair E, too, were located by H.J.O. three hundred yards up the valley beyond their nest. We found no evidence of other pairs in the Tunnel Burn area in February. In the Upper Point Burn, pair G were found, alone, on February 4, apparently without young; no chick droppings were seen. Neither birds nor fresh feedingsign were seen outside the known or inferred breeding territories of the pairs enumerated. Pair A fed with their chick over their extensive territory; other birds, apparently "idle" in respect to reproductive activities, still maintained their association in pairs and still occupied what had been breeding territories, where they were feeding quietly when encountered, and were in various stages of moult. They, at least, had not dispersed away from their nesting areas at this season.

BEHAVIOUR OF PAIR WITH CHICK.

From February 3 to 6, the chick of pair A, then about six weeks old, was active and elusive, not permitting photography, and in view of the decision not to handle birds, it was studied and sketched from a distance, with the help of binoculars. It was a vigorous rather gawky-looking youngster, standing about twelve inches high, with conspicuous muscular thighs out of all proportion to its body, giving a fanciful resemblance to a miniature moa. Compared with the chick photographed by J. H. Sorensen in January, 1949, the February bird was larger, head relatively smaller, down less intensely black, wing-spurs inconspicuous. The down, like that of other adolescent rails, had faded in the weeks of fledging to a rather patchy brownish black, and a distinct whitish patch had appeared at the vent, foreshadowing the white under tail coverts of the

adult. Possibly, at this stage, down was shedding from tips of growing contour feathers which might contribute to the colour, but bleaching of down near the vent is equally likely. The bill was blackish, with white tip; legs, viewed at a distance, a rather pale warm orange-cream in front, darker behind.

Throughout the four days of our stay, the family party wandered extensively over the snowgrass and scrub bordering the north, east and north-east shores of Kohaka-takahea Lake and margining the outlet stream to the lip of the glacial valley. This feeding territory was estimated to occupy more than 15 acres and to extend about 1000 yards. Occasionally the family entered the bush edge, feeding there on fine grasses in moist gullies beneath the open beech forest. The supposed female* and the chick fed together with the male generally 20 to 50 yards away, maintaining contact by sight and sound. The chick sometimes fed with some independence, one to ten yards from its parent, but she once followed it up when it remained out of sight behind shrubs for several minutes, and also made directly for the chick in spite of the presence of a human observer between. The adults grazed on snowgrass leafbases, and, particularly, on seed-heads (as described in January; Falla, 1949) or rooted among Poa and sometimes took gentian and other herbs. The chick sometimes shared leaf bases, grass tips, and leaves plucked by its parent, stretching up to pick them from her bill, but just as often bit off its own food; grass tips, Viola leaves and grass seeds. Once the adult was seen (by H.J.O.) vigorously rooting with her bill among fine green grasses at the bush edge, making excavations like a kiwi prod but shallower. At this stage there was no evidence that insect food was sought or taken, other than this behaviour reminiscent of December chick-feeding (see Falla, p. 98).

The chick uttered a fairly constant cry: either a slow "wee-a" or a continuous repeated "weedle, weedle, weedle." Both parents, but generally the supposed female, used the "cowp, cowp" call (Falla, 1949) to keep contact with the chick. The weka-like call was heard perhaps on an average three times a day, usually when the pair was well separated, once at night (suggesting nocturnal activity), and once when the adults were on opposite sides of the stream. One bird begins a loud repeated "coo-eet," and the second joins in generally "out of phase" so that the call is continued as a two-part canon:

The weka has a similar duet call.

The amount of country covered by the family party during four days of feeding was striking; in a few hours, quite spontaneously, they would move several hundred yards. They twice voluntarily crossed the stream. We shared the experience of the January (1949) party in finding a large number of fresh-looking empty nests. One such nest, east of the lake and south of the stream, contained a shred of faded brownish nestling down and had recently been occupied; it was some hundred yards from the nest in which the chick had hatched and was apparently a brooding nest functioning for temporary shelter.

IMMATURE PLUMAGE.

The dead fledgling found in pair C's territory on February 3rd, is possibly the bird observed as a well-grown downy by Mr. K. H. Miers on December 6th some distance away, across the Upper Tunnel Burn. Its remains, consisting of feathers, bill sheaths, crop and skeleton, will be described by Dr. R. A. Falla elsewhere. When it died, the bird was, like

^{*} Identification of sexes was based on slightly more robust characters of the supposed male, and on the consistent association between the chick and the supposed female, but the inference lacks more definite confirmation.

all fledgling rails, considerably smaller than an adult and was in almost complete first plumage, with a little down still attached to the tips of the pin feathers still largely in sheath. The bill had not acquired adult characters: it retained the dark colour of the downy chick's, and the frontal shield had not attained adult proportions. Body plumage resembled that of the adult in essential characters but the colours perhaps lacked the brilliance of an adult in full plumage. Thus the first teleoptyle plumage of Notornis, like that of Porphyrio, seems to be rather similar to the adult plumage.

MOULT.

Most adults were in less-brilliant plumage than in December (H.J.O.). Odd dropped feathers were found scattered through the feeding area and others concentrated at definite "moulting places." In the Point Burn, the pair identified with G were in rather brighter feather, and moulted feathers perhaps more abundant than elsewhere. The moulting places were almost invariably beneath the overhanging crown of a twiggy shrub of Coprosma rigida and were generally on a lush carpet of fine-leaved bright geen Poa growing round its trunk. Beneath the shelter of the shrub, groups of feathers and accumulations of droppings showed that a bird stood on the sunny northern side, facing the sun, and probably preened there, returning to the same spot several or many times to tramp into the grass on later visits the feathers dropped on earlier occasions. About 30 feathers and about 40 droppings were counted in a typical moulting place. The feathers came from practically every part of the body and included primaries as well as contour feathers. Such moulting places were found in the Point Burn and in several of the Tunnel Burn territories, including that of pair A (with chick). No birds were seen in occupation of moulting places, but on the morning of February 5th the inferred male of pair A was found sunning himself and preening below a rock face half a chain away from his feeding mate and chick. Cast feathers were also found in a brooding neet.

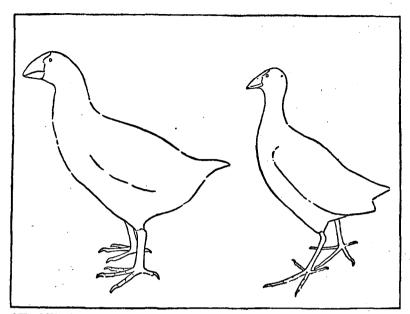
As reported in the press ("Evening Post," Feb. 14, 1950) there is evidence that Notorm's and other birds have at some time used the dry powdery floors of nearby limestone shelters for dusting during the moult. There was no sign of this habit in February, 1950, and Miers (1950) suggests that the feathers were plucked by Maori hunters.

SOME GENERAL REFLECTIONS ON NOTORNIS.

The stimulating experience of studying Notornis in the field has prompted the following observations on the bird's functional morphology, some of which, although trite in their general application to animals, have not previously been made, so far as I know, in respect to Notornis.

The systematic affinities of Notornis (recently emphasised by Mayr, 1949) are with gallinules of the genera Porphyrula and Porphyrio. The pukeko is the New Zealand representative of this group, which comprises moderate-sized waterfowl of swamp and lake-shore with adequate powers of flight, occupying relatively large distribution areas, chiefly in the Southern Hemisphere. We may infer that Notornis sprang from similar stock and developed its peculiar characters in New Zealand. The pattern of differentiation from the supposed ancestral form is one that is shared by other island birds, and it may help us to appreciate the distinctive characters of Notornis if we try to assess their functional significance in relation to the bird's environment.

The outstanding characters of Notornis, compared with its nearest relatives, are its large size, stout legs and neck, short toes and tarsus, flightlessness and oversized beak. All who have studied the bird since its re-discovery have been impressed with its herbivorous habits, which suggests that it once had the role of a grazing animal in the extensive tussock-grasslands of New Zealand (Duff, 1949).



SKETCHES OF NOTORNIS (left) and PORPHYRIO (right), based on photographs, to show differences in size and proportions.

Increase in size has been a common tendency among vertebrate animals, particularly among vegetarians, and has a simple physiological basis, recently emphasised by Watson (1949). The food requirements of an animal consist of a maintenance ration, the amount required to maintain life, and a production ration, which provides the energy for all activity, locomotion, reproduction, growth, etc. The maintenance ration is related to the weight of an animal, but is not proportionate to it, increasing roughly as the animal's surface area, i.e., as the two-thirds power of the weight, but the production ration is directly proportional to the energy used, and thus to the weight of the animal. "Thus the total food consumption of an animal is built up by a maintenance ration varying as the square of a linear dimension, plus a production ration varying with its cube'' (Watson, 1949, pp. 50-51). This means that, for the same amount of activity, a larger animal has greater thermodynamic efficiency than a small one, and to this advantage is attributed the increase in size that characterised evolution of the horses, the elephants and other groups. Clearly, a gallinule weighing 6 pounds (Williams, 1950, p. 218) has a similar physiological advantage over one half that weight* provided that other factors allow the survival of a bird of that size.

There are simple aerodynamic reasons why flight is more difficult in large birds than in small ones. "The bigger a heavier-than-air machine, whether living or not, the faster it must fly to keep itself from crashing?" (Wells, 1938), and to develop this speed more power and relatively larger wing muscles are needed. Other things being equal, the efficiency of a wing is a function of its surface area, which is proportional to the square of a linear dimension. The load to be carried, however, is proportional to the cube of a linear dimension so that a bird exactly twice the linear size of another would have to support eight times the weight of its smaller fellow with only four times the area of

^{*} Two male pukeko weighed 1 lb. 142 oz. and 2 lb. 7oz.

wing. A gallinule about twice the weight of a pukeko would have much less efficient wings unless the proportions of the wing and its muscles changed in compensation. But the energy used in flight is a debit against the production ration of a bird, and is a more expensive item in a large bird than in a small bird.

Feather weight, in birds of different sizes, is known to be almost directly proportional to their body weight, but the number of feathers increases at a lower rate, even lower than does the surface area (Brody, 1945, p. 639). Thus larger birds have relatively fewer feathers of relatively greater weight per unit area of skin, than smaller birds. For mechanical reasons, however, the weight of the supporting quill of a feather is relatively greater and that of the vanes relatively less in large birds than in small birds (Brody, p. 640). These are additional reasons why large birds have become flightless when flight was no longer necessary for survival. In most birds, needless to say, flight is so important that its maintenance is essential for survival. This has kept their average size low.

Difference in size also accounts for the robust legs and neck of Notornis in comparison with those of a pukeko, for the strength of a supporting column is related to its cross-section (i.e., to the square of a linear dimension). To keep pace with a cubic increase in weight, the cross-section of limb bones must increase disproportionately. Allee and others (1949, p. 132) note that the capacity of a column to support weight varies inversely as the square of its length (Euler's principle) so that "the leg bones of a heavy vertebrate tend to be shorter than those of a related lighter species." The tarsus of Notornis (82-90 mm. according to Buller and Oliver) is, in fact, a little shorter than that of the slender-legged lighter pukeko (99-100mm., 3 measurements). The long toes which support the pukeko on the boggy ground of its swamp habitat are unnecessary and indeed undesirable in a terrestrial feeder which tends to shun swampy ground (Miers, 1950).

In grass-eating mammals, there is a direct relationship between size and the relative area of the teeth that triturate, bruise and disrupt the grass to allow digestion of its cell contents. The consequent effects on the shape of the face in horses have been discussed by Watson (1949). In grass-eating birds some of the functions of teeth are served by the sharp shear-like edges of the horny beak-sheaths and by the hard spiny armature of the palate and tongue: still more trituration goes on in the gizzard. Now, to maintain their triturating functions in a larger bird, the relevant parts of the palate must increase in proportion to increasing food and body weight, that is, in proportion to the cube of a linear dimension. Brain size does not increase proportionately with increased weight, but varies more nearly as its two-thirds power, and this accounts for many differences in the shape of the face in vertebrates. "The value of the exponent for birds is considerably less than for mammals, meaning that, in comparison to small birds, large birds have relatively smaller brains than mammals" (Brody, 1945, p. 626). The differences between Notornis and Porphyrio in the proportions of the head and beak may be due in large part to inevitable functional consequences of the differences in their body weight. Comparison of the oblique frontal view of the head of Notornis published by Buller with a similar view of Porphyrio suggests that the former has a smaller brain than the latter, relative to its large beak, jaws and cheek muscles.

Most of the characters of Notornis discussed above would follow naturally as a result of an increase in size which leads to greater metabolic efficiency. In most birds, flight is too valuable an attribute to jeopardise by gain in weight, but, as Romer (1945) points out, "for many birds which seek their food on the ground, flight is necessary mainly as a protection from enemies. With freedom from carnivores, there is no reason why flight should be maintained." Rails spend much of their time skulking through the undergrowth, and by avoiding flight a bird "can escape from the mechanical limitations which flight

imposes" (Wells, 1938). New Zealand has long been quoted as an area where many flightless birds developed in the virtual absence of predators.

The fate of many animals adapted to a special set of conditions has been extinction, which, in general, can be attributed to a change in the environment; for specialised animals lose the power to adapt themselves to changed conditions. "Forms on the verge of extinction" according to Romer (1949) "are frequently found to be individually large; abundant in numbers; and . . . herbivorous rather than carnivorous."

Notornis, certainly large and herbivorous, was probably abundant when it ranged the tussock grasslands of both islands of New Zealand before the onset of conditions which led to its restriction. Like the moa, Notornis had survived the vast climatic changes of the Ice Age, but it had apparently become restricted to Western Southland by the time European settlement began a century ago. Despite much discussion, no one has satisfactorily accounted for the extinction of the moas and their contemporaries, which coincided in time with the restriction of the range of Notornis. What has seldom been emphasised is that the extinction (or near-extinction) of large herbivorous animals in New Zealand is not an isolated phenomenon but is paralleled in many parts of the world in post-glacial times. Romer (1945) concludes that the only widespread change of conditions to which such extinction can be attributed is that due to the development and spread of man. The arrival of Polynesian man with his domestic animals (dog and rat) seems to be the chief ecologic change in New Zealand during the few thousand years prior to 1774 and is the basis of perhaps the most popular (and in the writer's opinion, the best) hypothesis for the extinction of moas. If dogs came with the first Polynesian settlers, and if, contrary to tradition, they tended to become wild and hunt in packs, they would have been important factors in the extermination of flightless birds. Certainly, changes in climate and vegetation during post-glacial times may have reduced their range, but such changes as are known, in New Zealand and elsewhere, were small compared with the large scale fluctuations of the glacial and inter-glacial periods which New Zealand flightless birds survived.

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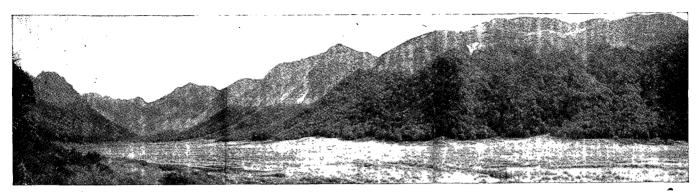
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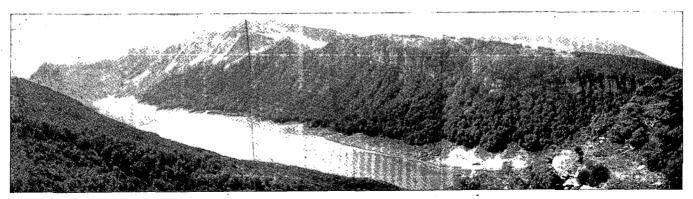
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UPPER TUNNEL BURN VALLEY.—In the 1949-50 season, the broad valley-floor, clothed in snowgrass and bog vegetation, supported three or four breeding pairs of **Notornis**. The view shows the area occupied by pairs C (right), D (left of centre) and E (head of valley, left).

Photo: C. A. Fleming.



GENERAL VIEW, LOOKING NORTH ACROSS KOHAKA-TAKAHEA LAKE, towards limestone bluffs forming the north side of Tunnel Burn Valley. Notornis pair A ranged the strip of snowgrass margining the lake (centre and right); traces of pair B were found on the ridge above, and other pairs occupied the valley-head (left). Photo: C. A. Fleming.