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SOME PRELIMINARY DATA ON THE POPULATION DYNAMICS OF THE TAKAHE (*Notornis mantelli*, Owen)

By *G. R. WILLIAMS*
Wildlife Branch, Department of Internal Affairs

As far as information at present available permits, this paper deals with breeding season data, and particular emphasis is given to clutch size, egg fertility, egg production and chick survival.

Discussion of population size, display, pair formation and various aspects of behaviour will appear elsewhere. I have used the papers of Falla (1949, 1951), Kennedy (1955), Williams (1952, 1955) and Williams and Miers (1957), together with unpublished field notes in preparing the table.

DURATION OF THE BREEDING SEASON

Eggs may be laid as early as the beginning of October and an approximately week-old chick (resulting perhaps from renesting or double brooding) has been seen as late as 31 March. Most of the nest records are for November and December, but this may be a reflexion as much of the peak period of investigation as of the true period of maximum nesting effort. Though a five to six-month breeding season may seem rather long it is matched by that found by Gullion (1954) for the American coot (*Fulica americana*) in California.

BREEDING AGE

We know from two birds banded as chicks that successful breeding may occur in the first season after hatching, but it is not yet known whether this may be taken as the general rule. Banding has also shown (as might in any case have been expected from the previous fact) that at least some birds breed annually. At present there is no reason to doubt that all mature birds will *pair* annually if not already paired, though, as will be seen later, this may not always result in the laying of eggs.

CLUTCH SIZE

This may be either one or two: eggs have been found in 36 nests and there are 20 records of one-egg clutches, but of these (to go to an extreme) we can be quite sure of only seven, for only in these seven instances were observations such that the presence of a second egg at any time can be utterly discounted. Although there are only 16 records of two-egg clutches, what is known of the behaviour of adults when hatching occurs makes it fairly certain that the larger clutch is nevertheless at least as common as the smaller. For example, three instances are known of the second egg of a clutch being deserted after the first had hatched; had these nests been found only *after* desertion a reasonable conclusion might have been reached that they were deserted one-egg clutches — and especially would this have been more likely to have been the opinion when, during the earlier years of the investigation, it was not generally known that the finely broken-up pieces of the hatched egg are usually to be found out of sight beneath the large nest bowl. (Kozicky and Schmidt, 1949, report that the same state of affairs may also occur in nests of the clapper rail, *Rallus obsoletus*, and desertion of part of the clutch has been reported in other rails — for example, by Gullion in the American coot and by Alley and Boyd, 1947, in the European coot, *Fulica atra*.) Furthermore, until late 1952 when opinion became favourable for the beginning of a banding campaign recommended as early as 1949, particular birds with nests or chicks could not be positively identified — hence some other originally two-egg clutches could have been missed since birds that had hatched one of two eggs could not always be associated with the remaining egg and nest. No three-egg clutches are known — the careful examination of one deserted nest associated with three eggs indicates that two eggs had been laid, incubated and deserted and then one egg laid in the deserted nest bowl (see photograph). Four instances are known of takahe incubating empty nests which seem never to have contained eggs, and in at least one of these instances incubation, which must have lasted between seven and eight weeks (Miers, *pers. comm.*), was being shared, as is usual in this species, by both birds. (It will be shown elsewhere that the incubation time for takahe eggs is approximately four weeks.)

The average clutch size for takahe — lying between one and two — is certainly one of the lowest of any of the *Rallidae*; in fact, a wide but not exhaustive search through the literature readily available (Bent 1926, Cayley 1933, Whistler 1935, Roberts 1940, Witherby *et al.* 1941, Serventy and Whittell 1948, Austin and Kuroda 1953, Oliver 1955) has not disclosed any as low. In itself, of course, this fact is not necessarily significant as far as survival is concerned; however, it is interesting because of the commonly accepted opinion that clutch size in many birds is adapted to the food requirements of the young (Lack, 1954).

FERTILITY

In the past, fears have been expressed about the apparent very low fertility of takahe eggs without it being made very clear which is supposed to have come first — the low fertility or the small population. Knowing more, as we now do, about the fate of eggs and about nesting behaviour the situation no longer seems quite so unfavourable though their fertility may yet prove to be lower than the average of those of other rails. Of the 52 eggs recorded the status or ultimate fate of 40 is known* Of these, infertile eggs or those in which development had ended at an early stage amounted to 12 (or 30%); those of known fate — destroyed — but unknown fertility made up 5 (or 13%). The remaining 23 (57%) were regarded as actively developing and all but three of these seem to have given rise to *advanced* embryos or chicks. (This figure has been arrived at by adding together live or dead embryos found *in ovo*, live chicks actually seen in the nest or its immediate precincts and, with less justification, chicks reported in the feeding territory surrounding the the nest from which hatching is suspected.) So, of the 35 eggs (12 + 23) whose fertility was ascertained — though discrimination between truly infertile eggs and those in which only early development occurred has usually not been made — *at least* 66% may be regarded as having been fertile, and from these, in turn, 15 birds hatched to leave the nest. How do these figures compare with those given in the literature for some other rails?

In his study of the American coot Gullion found that 24% of 119 eggs laid were 'addled' (by which he apparently means infertile as well as dying early in development). However, there was no information on fertility for 31 of the total number of eggs. Disregarding these, then, the proportion 'addled' when calculated on the remainder (88) is found to be 31%, which means that almost the same percentage (69%) of eggs hatched or gave rise to advanced embryos as has been found for the takahe. That the two calculations agree so well is no doubt fortuitous, but the comparison at least shows that the degree of *apparent* infertility among takahe eggs may not be so very different from that found in one instance for a thriving species. However, Gullion's figures may not be representative. In fact he quotes other workers who found a much higher fertility (at least 90%) for this and other species of rail; and Alley and Boyd, in their study of the European coot, found that 91% of all eggs laid hatched.

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*Most, if not all, of the 12 eggs whose individual fates are unknown disappeared without any definite trace or issue between the brief expeditions that were characteristic of the earlier years of the takahe investigation.

A comparison of the degree of fledgling success in the three species would have been of considerable interest. Unfortunately, this will be information exceedingly hard to get for the takahe because of the difficulty of re-locating chicks a short time after they have left the nest and are able to take refuge in the thick cover. We do know from the records of those nests for which there is clutch size data that, calculated from the total number of eggs laid, 29% gave rise to chicks that left the nest, but we have no useful data on subsequent mortality throughout the first year of life. On the basis of assumptions of the extent of this mortality, comparisons with the European and American coots could then be made, but in my opinion, under such conditions, the comparisons would be of little value.

RE-NESTING

Four instances of re-nesting have been recorded. Two of these rely to some extent on circumstantial evidence — an occupied nest in a territory has later been found to be deserted with a new and occupied nest situated very close nearby. In one of these instances egg measurements from the two nests were in excellent agreement (Bell *unpubl.*). On the third occasion a positively identified banded adult was seen with a chick a few days old about ten weeks after having been seen in almost precisely the same place with another chick. Though this earlier chick could not be traced we cannot assume that it was certainly dead for chicks of approximately three months of age are particularly difficult to catch sight of in the tall tussock and low scrub — more so than very much younger chicks which cannot move so easily through the thick cover. (Incidentally, if the incubation time for takahe eggs is about four weeks and the second chick was approximately one week old when first seen, then the second clutch with this particular adult concerned must have been laid at least four weeks after the first had hatched.)

The fourth instance of re-nesting concerns the nest already referred to associated with three eggs. The freshest of these, containing a dead embryo slightly decomposed, lay in the nest bowl; a foot away outside the bowl lay another, slightly cracked but not pipped, which also contained an advanced embryo but noticeably more decomposed than the other; a foot way again in a direct line was the third egg, broken open and empty, and, from the appearance of the shell, about the same age as the second. It did not have the appearance of one from which a chick had hatched. The most satisfactory reconstruction of the history of this nest is that a double desertion from unknown causes had occurred — the first following a two-egg clutch and the second a one-egg clutch. No egg fragments were found in or about the nest bowl which might suggest a second *two*-egg clutch from which one chick had successfully hatched.

CHICK AND ADULT MORTALITY

Nothing definite is known about either of these two population parameters — the chance of finding dead fledglings in the thick cover is remote (only one — unbanded —has been found so far and this was in 1950) and we are not justified in assuming the death of a chick if we are later unable to trace it in an area where it had previously been seen. It is rather more significant that all the expeditions into the main colony over the past eight years have found only two recently-dead adults (unbanded birds in 1949 and 1951), for the birds are large and their remains would be conspicuous except in the thickest cover: and the methods of observations are such as to ensure a fairly full coverage of most of the snow-tussock areas, especially those of the two valley floors which are the dwelling places of most of the population of the main colony. The implication is that the species (once past the fledgling stage, at least) is a relatively long-lived one. In all, 35 takahe have been banded up to January 1957 (though some or all of the five marked in the initial banding of December 1952 with plastic colour bands *only* — Riney and Miers 1956 — and so far untraced, may have since lost these and been unknowingly rebanded with aluminium *and* cemented plastic bands). Of these 35, 16 have been positively identified between one and four years after their first capture (four years being the theoretical maximum time so far for the earliest-banded birds). Since some of the earlier-banded birds through loss of their colour bands (apart from the five already mentioned) can no longer be identified except by capture and reading of the numbered aluminium band, the number surviving one or more years after banding must be higher than the known total of sixteen. At present, of course, there is insufficient data for the preparation of a reliable life table.

REPLACEMENT RATE

At the present state of knowledge it is impossible to make any estimate of replacement rate that will satisfy all critics, and by 'replacement rate' is meant the rate at which new adults of breeding age are produced; in fact, Lack (1954) has drawn attention to the many difficulties that stand in the way of any accurate calculation of this property, and he lists the criteria needed to make such a calculation. For example, we should need to know at least: (i) the breeding age, (ii) the proportion of non-breeding to breeding adults, (iii) the mean number of broods per breeding female and (iv) fledging success and first year mortality. Now, in the case of the takahe, for example, any estimation of the *proportion* of mated pairs which breed each season must be tentative; this is just another result of the difficulty of observation and of the proper interpretation of behaviour. Thus, we do not know whether birds incubating empty nests ever lay in the same season, but judging from the time some are prepared to sit to no purpose (54 days in one case) it seems unlikely that they will. From the nest records it appears that about 11% of pairs may not breed annually for this reason.) Then again, though we can be reasonably sure from behaviour whether a pair whose nest has not been found is caring for a chick that may be up to a month old, after this age – when it is able to move about more freely – the chick's presence is difficult to establish short of an actual sight record which is not easily obtained.* But the complication arises that this family group may now wander occasionally from what we recognise as its territory and so be counted, if it has not been definitely identified beforehand, as another breeding pair elsewhere; though it must be stated that the species is generally remarkably territorial throughout the year. Furthermore, we cannot estimate (outside of our nest record data) the number of unproductive pairs, for we have no way of being sure whether mated pairs for which no chicks have been found are *really* without chicks or have never laid; nor can any estimate be made at present of the proportion of unmated birds in the population. If we added to the data from our nest record cards, information on pairs with a chick – information not so far included because of the absence of data on the size of the clutch from which the chick must *have hatched,§ this would cause a bias suggesting a higher replacement rate* than actually exists; for it would be equivalent to assuming that all attempts at raising young outside those included on the nest record cards had been successful, which is absurd; therefore the most satisfactory course of all seems to be to calculate replacement rate from nest records *only* rather than from the number of young produced by all the adults in the main study area (which, incidentally, over all years gives a figure of between 0.5 and 0.7 per pair). From the table we see that there are records of 36 nesting efforts about which we have clutch size data and four of these were the result of re-nesting. Therefore we have a total over all years of 32 effective nesting pairs. To this must be added the four pairs that incubated empty nests. This then raises the total to 36 effective nesting pairs:

36 pairs produced 15 chicks which left the nest.

1 pair, then, produces 0.42 chick per year or, in round figures:

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*The *seldom-heard call of the partly-grown bird is characteristic, however,* and the finding of small fresh droppings (or of tracks accompanying adults) may be taken as fair evidence of its existence.

§One such addition would be the third instance of re-nesting referred to earlier, there are no clutch records of the two nests that must have existed.

1 bird, then, produces 0.20 chick per year to the stage of leaving the nest. With the help of some assumptions and/or approximations we may make a rough preliminary estimate of the life equation for the takahe. The first two of these are (i) that over the last eight years there has been a mean stable population (though the extreme long-term trend may well be towards extinction); and (ii) that the breeding age is one year. Now, working from the quantitative material at our disposal we may say that the maximum replacement rate must be 20% – that is, that *all* chicks leaving the nest survive to breed; and this, of course, means in turn – following upon the assumptions we have made – that the annual adult mortality of birds of one year of age or more must also be 20%. Though there is no useful information of first year mortality we can at least be sure that there is some and that it may be considerable. If only 50% of young birds leaving the nest survive to breed then the replacement rate would be, of course, 10%, as would then be the annual adult mortality. Whatever provisional estimates we may make of first year mortality (and because of the smallness of the population and the difficulty of observation estimates may have to be provisional for a long time yet) it appears that the species must be a long-lived one. For example, an annual adult mortality of 10% implies an average expectation of further life (ex) of between 9 and 10 years if, as in most birds, adult mortality is taken as being independent of age.* Other evidence supports this view: Thus only two adult birds have so far been found dead in the main colony areas and survival among banded birds has been high so far.

POPULATION REGULATION

As far as we can tell the number of takahe in the main colony is notably stable from year to year and pairs can usually be found, no matter what the season, in fairly well defined areas. Because the adults are long-lived and mate perhaps for life, the implication is that chicks unable to find an unoccupied territory or an unmated bird in occupation of one must generally leave the vicinity of the colony. Rather rarely from present evidence they may succeed in establishing a territory in already occupied ground. Thus population regulation seems dependent – in the main colony at least – upon the species' territorial behaviour. However, from observations made in the main colony over a number of years I am convinced that this territorial behaviour does not limit population density through regulation of food supply or cover. Whether or not the takahe *prefer* the shoots or seeds of the snow tussocks on which they feed, these do supply the great bulk of their food and always appear to be growing in superabundance for both food and cover needs in all territories every year. In other words, the size of the territories appears to bear no close relation to the food and cover requirements of the pairs and young inhabiting them. Thus I am in general agreement with Lack (1954) and Hinde (1956) on the particular point that the food value of the territory is not significant in this regard. Regulation comes about merely because year-round occupation of territories by long-lived birds that may mate for life forces the young to move elsewhere. Though a few chicks have been banded there is little chance of recovering them outside the main colony because the nature of the terrain is such that it is seldom visited. The movement of greatest amplitude at present known is however that of a chick which travelled some 2000 yards from the territory in which it was hatched and banded to that in which it bred twelve months later. Other aspects of territorial behaviour are to be dealt with, more properly, in forthcoming publications.

At this point we must stop until the rather slow accretion of information

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*Ex (adult) can be readily found from the equation:

$$Ex = \frac{2 - m}{2m} \text{ years}$$

where m = average annual mortality rate independent of age in a population of stable and appropriate age distribution.

makes a re-examination of the whole subject possible. Though it may rightly be maintained that some of what has been said depends upon assumptions and for that reason the paper may be somewhat premature, it has been offered, nevertheless, because really reliable information will take a very long time to obtain, and a statement of some kind is surely due after nearly nine years of even intermittent work on a species of such general interest.

THANKS

In the course of preparing this paper I have had, in addition to my own unpublished field notes, access to unpublished reports furnished the Wildlife Branch by a number of visitors to Takahe Valley. I have tried to acknowledge particular sources of information in the text, but in addition would like to thank the following for making their reports available for consultation: Mr L. C. Bell, Dr D. S. Farner, Mr H. L. Secker, Mr E. G. Turbott, Mr J. S. Watson, Dr K. E. Westerskov and Mr K. H. Miers. I should also like to thank Mr Miers for critically reading the manuscript.

Breeding season	One-egg clutches	Two-egg clutches	Total eggs	Fertile	Infertile or early develop. only	Destroyed & fertility unknown	No details	Re-nesting	Incubated empty nests	Known chicks leaving nests	Chicks surviving elsewhere	Mating pairs elsewhere	
1948-49	2	–	2	1	–	–	1	–	–	–	1	1	
1949-50	2	3	8	3	3	–	2	–	–	2	–	1	
1950-51	1	–	1	–	1	–	–	–	1	–	5	6	
1951-52	3	2	7	3	2	–	2	–	1	3	7	9	
1952-53	4	3	10	3	2	–	5	1	1	2	5	5	
1953-54	2	2	6	2	1	1	2	2	–	1	4	2	(3?)
1954-55	3	3	9	5	1	3	–	–	1	4	3	5	
1955-56	3	3	9	6	2	1	–	1	–	3	–	1	
Totals	20	16	52	23	12	5	12	4	4	15	25	30	(31?)

REFERENCES

Alley, R., & H. Boyd, 1947. The hatching and fledging success of some Coot. Brit. Birds 40: 199-203.

Austin, O. D., & N. Kuroda, 1953. The birds of Japan, their status and distribution. Bull. Mus. Comp. Zool. Harvard 109: 279-637.

Bent, A. C., 1926. Life histories of North American marsh birds. U.S. Natl. Mus. Bull. No. 135.

Cayley, N. W., 1933. What bird is that? A guide to the birds of Australia. Angus & Robertson, Sydney.

Falla, R. A., 1949. Notornis rediscovered. Emu 48: 316-322.

Falla, R. A., 1951. The nesting season of Notornis. Notornis 4: 97-100.

Gullion, G. W., 1954. The reproductive cycle of American Coots in California. Auk 71: 366-412.

Hinde, R. A., 1956. The biological significance of the territories of birds. Ibis 98: 340-369.

Kennedy, J. G., 1955. Takahe research 1954-1955 season: A summary. Notornis 6: 164-166.

Kozicky, E. L., & F. V. Schmidt, 1949. Nesting habits of the clapper rail in New Jersey. Auk 66: 355-364.

Lack, D., 1954. The natural regulation of animal numbers. Oxford Univ. Press.

Oliver, W. R. B., 1955. New Zealand Birds (2nd edition). A. H. & A. W. Reed, Wellington.

Riney, T., & K. H. Miers, 1956. Initial banding of **Notornis mantelli, 1952.** Notornis 6: 181-184.
Roberts, A., 1940. The birds of South Africa.
Serventy, D. L., & H. M. Whittell, 1948. A handbook of the birds of Western Australia. Patersons Press, Perth.
Whistler, H., 1935. Popular handbook of Indian Birds. Gurney & Jackson, London.
Williams, G. R., 1952. **Notornis** in March 1951. Notornis 4: 202-208.
Williams, G. R., 1955. Summary of takahe investigations for 1953-54 study season. Notornis 6: 112-114.
Williams, G. R., & K. H. Miers, 1957. A brief summary of takahe research for the 1955-56 season. Notornis 7: 69-71.
Witherby, H. F., et al., 1941. The handbook of British birds Vol. V. H. F. & G. Witherby, London.

HEN ISLAND IN WINTER

By B. D. HEATHER

In mid-August 1953, fourteen members of the Auckland University College Field Club visited Taranga (Hen I.). Four O.S.N.Z. members, I. A. Atkinson, B. D. Heather, R. R. Moynihan and C. B. Trevarthen, were present, but, because of other scientific work and two nights and a day of continuous rain, the success, ornithologically, of the five days' visit was small.

The usual boisterous crossings to and from Leigh were made with Mr Norman Warren in the *Gunner,* and we landed in Old Woman Cove on the South Coast. Camp was sited a chain into the bush immediately east of the main stream of the Cove. This afforded a chance of comparing the merits of this and the traditional western site as I experienced it in December 1948. (Sibson, *Notornis* 3: 183-8.)

In summer, the south site should offer a more reliable landing, a central position with quick access to the main ridge once the best route is known, an abundance of water, a minimum of the enervating summer sun, and a good area for all birds.

In winter, however, this site is damp, sunless and chilly. When rain falls, the gullies quickly become raging torrents and water flows, unceasing and unchecked, down the steep, thin-soiled slopes. In fine weather the winter sun scarcely touches these south slopes and birds seem to favour the more equable conditions of the north and west sides.

We would therefore suggest that the south site be used for summer visits and the west site for winter visits.

For accounts of various scientific aspects of Taranga, see *Tane*, journal of the A.U.C.F.C., Vol. 6, 1953-54, an issue of note for students of Northland and Bay of Plenty offshore islands. This includes (pp. 20-25) a full geographical account, with map, of Taranga by G. A. Cochrane.

In the following list, the outward voyage on 17/8/53 is designated 'outward', and the return to Leigh on 23/8/53 as 'inward'.

BLUE PENGUIN
Numerous and vociferous ashore at night. Fresh dropping trails frequent on the coast, but the few holes investigated by day were empty. Outward: 5.

MOLLYMAWK (Sp ?)
Outward: 2 adults.

GIANT PETREL
Outward: 8. Inward: 3.

CAPE PIGEON
Outward: 1.

FLESH-FOOTED SHEARWATER
Outward: 1, possibly 2. Inward: 1 near Taranga.

BULLER'S SHEARWATER
None was seen, despite as careful a watch as sea conditions allowed.

J. PRICKETT, PHOTO

G. R. WILLIAMS, PHOTO

PLATE IX. Top – White Ibis: Kawhia, June 1957.
Bottom – 'Three-egg' nest of Takahe at head of Point Burn Valley, Murchison Range, January 1956.