

SOME FEATURES OF RECENT RESEARCH ON THE TAKAHE (*NOTORNIS MANTELLI*)

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Takahe were once widely distributed — the type specimen being sub-fossil and from Taranaki in the North Island. During recent centuries the size and range of the population has shrunk and only four living specimens, all from Fiordland, were recorded between 1849 and 1898 (Williams, 1960). There followed a gap of 50 years and the species was considered extinct. Then, in November 1948, takahe were rediscovered in the neighbouring Point Burn and Tunnel Burn* Valleys of the Murchison Mountains, Fiordland (Orbell, 1949).

Field studies started the same summer and during the next four years ten trips involving a total of 345 man days were made. Considerable information (Falla, 1951; Fleming, 1951; Gurr, 1951; Turbott, 1951; Williams, 1950, 1952) resulted but the returns did not compensate for the time involved, as there was no way of identifying individual birds. This precluded reliable work on many aspects of social behaviour and population ecology.

Studies have posed problems. Coupled with the need to learn as much as possible about the species has been the desire to keep interference to a minimum. However, in December 1952 it was accepted that banding was not only justifiable but essential, as it could provide the only method for checking vital population parameters in a near-extinct species. Nine birds were banded that summer (Riney and Miers, 1956). This initial banding heralded a more systematic approach and during the next six summers (to March 1959) trips were so timed that the capture-recapture programme not only gave information on adult population dynamics but also provided maximum data on breeding biology and recruitment (Kean, 1956; Williams, 1957, 1960; Williams and Miers, 1958).

When, in 1960, it was considered that adequate data had been collected on nesting and breeding behaviour, visits early in the breeding season were discontinued so that the disturbance could be kept to a minimum. Nevertheless, there was no evidence to suggest that breeding success had in any way been adversely affected by the presence of parties in October–December.

The general programme of banding and recapturing as many adults and chicks as possible continued until the 1960–61 season; then, in accordance with the policy of “minimum interference”, banding of adults ceased because the degree of disturbance was considered to be greater than with chicks. During both the 1961–62 and 1962–63 seasons only chicks were banded and a few records obtained of banded adults.

Band recoveries to February 1963 indicated that takahe had an apparent annual mortality rate of 26%–29% and nest records showed a mean productivity of 0.24 chicks (surviving to the age of about six weeks) per adult per year. As only six of eighteen chicks banded at six weeks were known to have reached the age of one year, data then available suggested adults were dying at three times their replacement rate. Furthermore, during the following summer (1963–64) only one chick was reared in the study area.

It became imperative to check the stability of the population and during the 1963–64, 1964–65 and 1966–67 summers a full banding/recapture programme was resumed.

TABLE 1. *Number of takahe banded and recovered*

Season	Banded		Recovered	
	A	C	R	S
19				
52–53	7	2	0	0
53–54	4	2	3	5
54–55	16	3	6	0
55–56	0	0	2	8
56–57	1	0	5	1
57–58	3	0	8	2
58–59	6	3	4	1
59–60	0	0	2	0
60–61	9	3	8	2
61–62	0	6	3	0
62–63	0	6	4	0
63–64	6	0	15	0
64–65	15	5	21	0
66–67	4	3	17	0

A = Adult, C = Chick, R = Recapture, S = Sight record.

* The upper reaches of the Tunnel Burn have been re-named Takahe Valley. This and the Point Burn comprise the study area where all banding has been done.

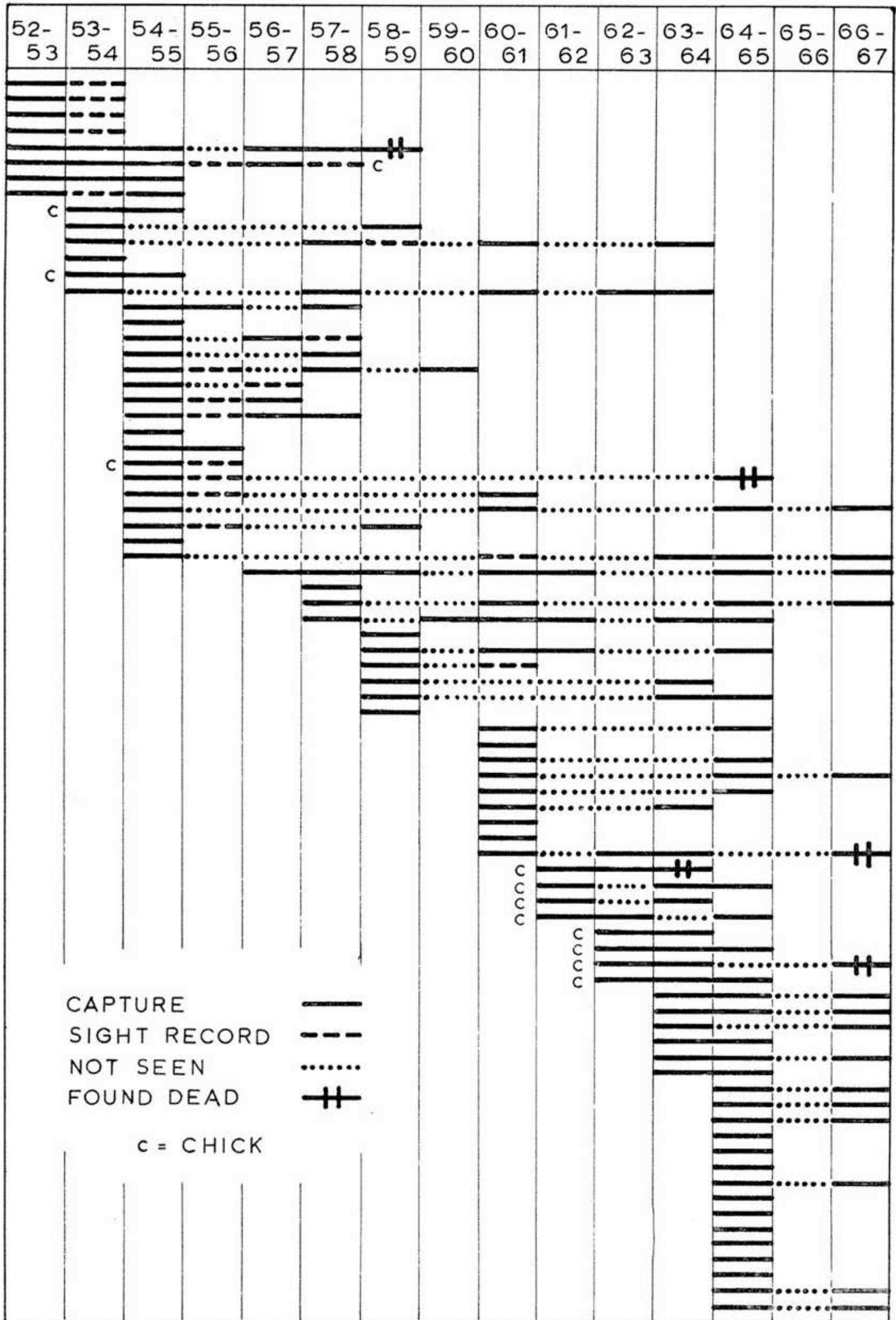


FIGURE 1. Minimum survival times for all takahē banded as adults. Only those chicks recovered in subsequent years are plotted.

BAND RECOVERIES

By the end of the 1966-67 season 104 birds (71 adults, 33 chicks) had been banded and 60 (48 adults, 12 chicks) of the 97 birds caught prior to 1966-67 were subsequently recorded in a total of 117 (112 living, 5 dead) recoveries (Table 1, Fig. 1).

There were no expeditions in 1959-60 and 1965-66 although during the former season an inspection party did identify two banded birds. In the summers of 1961-62 and 1962-63 no serious effort was made to recapture birds but a few adults accompanied by chicks were checked. In other seasons the effort and success have varied; consequently the percentage of birds recovered in any age class does not necessarily reflect the strength of that class in the population.

TABLE 2. *Adult recoveries, 1953-54 to 1966-67.*

	Years after banding											
	1	2	3	4	5	6	7	8	9	10	11	12
Cohort size	67	63	48	42	42	42	33	33	27	24	23	23
Raw recaptures	21	18	14	10	7	9	4	1	3	6	0	2
Minimum no. alive	48	41	30	21	17	14	8	7	7	6	2	2
Minimum % alive	72	65	62	50	40	33	24	21	26	25	9	9

Table 2 shows that only 21 of the 48 birds known to be alive one year after banding were recovered in that year, the other 27 being caught in subsequent years. This is a lower recovery rate than actually applies because it includes all banding seasons when, in fact, those birds banded in 1958-59, 1960-61, 1961-62 and 1964-65 were not subjected to a recapture programme during the following summer (Fig. 1).

Data show about 50% of banded birds known to be alive in any one year are recovered during that year. If a banding year is followed by consecutive annual recapture programmes there is a 0.5 probability of recapture of an adult the year following banding and this increases to a 0.7 probability of recapture from two consecutive follow up seasons.

PAIR BONDS

These persist throughout life. Never has a bird been found with a different mate while its partner of earlier seasons was known to be alive. An unconfirmed sighting suggests one pair may have been together for nine years. The longest known partnership has lasted seven years. Two pairs have been together for six years, two for five years, four for four years, four for three years and two pairs have been together for two years.

TERRITORY

The same territory is generally occupied throughout life. Only four (three females, one male) of 48 birds banded as adults and recaptured in subsequent seasons were observed in territories other than those in which they were banded. Three had moved after the death of their mates. A sight record suggests the fourth had moved with its five-year-old partner. In three other instances (all females) the birds retained their territories and new males moved in, so a change of territory does not necessarily follow a death. Williams (1960) gives details on territory size and use throughout the year. Although family groups tend to remain in the same areas, subsequent observations show that by March they may range across neighbouring territories without apparent friction. This suggests that once juveniles are self-sufficient territories are no longer defended. They enlarge, overlap and merge into a semi-communal "home range". During winter birds may move to lower altitudes. They have been seen by the shore of Lake Te Anau over 2,000 feet below Takahe Valley.

LONGEVITY

The maximum age takahe may reach is not known but two of a possible 19 adults banded at unknown ages were recaptured 12 years later (Fig. 1). They would be at least 14 years old. As there is only a 0.5 probability of recapture in any one year it is quite likely that three, or even four, of these birds were alive after 12 years.

The bands were in good condition on seven birds recovered nine or ten years after banding and there appears little likelihood of band loss during the first ten years. The two 12-year-old bands, on the other hand, had worn noticeably thinner and could come loose.

MOVEMENTS OF YOUNG BIRDS

Yearlings may remain with their parents. Seven of ten birds banded as chicks and recaptured when one year old were either with their parents or on the parents' territory. The eighth was on the margin of its home territory about 700 yards from where banded. The other two had moved during their first year. One was associated with a neighbouring family 1,000 yards from where banded and the other was keeping company with an adult 2,700 yards from the original territory.

Seven birds have been recovered when two years old. One was with its parents and another was a lone bird on the margin of its parents'

territory. The two birds that moved during their first year (i.e. 1,000 and 2,700 yards) were still in the same area. The fifth bird (like the preceding four) remained in Takahe Valley but had moved 1,800 yards from where banded as a chick. The remaining two (Fig. 2) had moved to the neighbouring Point Burn—distances of 2,200 and 2,900 yards respectively. To summarise: Of these seven, one was with its parents, three were keeping company (possibly paired) with other birds and one was found recently dead.

Four three-year-olds have been recovered. One, found dead, was 3,500 yards from where last located as a yearling. Another, not seen since it was a yearling, had moved to the Point Burn. The

other two had stayed in Takahe Valley — one still in the territory it occupied as a yearling; the other 1,500 yards from where it had hatched and remained during its first two years.

Altogether, 15 of 34 birds banded either as chicks or yearlings prior to 1966–67 have been recovered and five that were reared in Takahe Valley are now resident in the Point Burn (Fig. 2). The other 19 have never been seen again and some, at least, of these may well have moved to different valleys adjacent to the study area. Widespread movement of juvenile and sub-mature birds is to be expected considering both the long life and permanent territories of adults.



1966-67 BREEDING SEASON

- PAIRS THAT BRED
- ⊖ PAIRS NOT KNOWN TO BREED
- SINGLE BIRD HOLDING TERRITORY
- ⊗ PAIRS REMOVED
- △ "PERMANENT" TERRITORIES NOT USED

Chains 20 0 120

← MOVEMENTS OF BIRDS
BANDIED AS CHICKS(c) OR YEARLINGS(y) TO
THE POINT BURN

FIGURE 2. Takahe Valley (upper) and Point Burn study area enclosed by black line. "Permanent territories not used" refers to two territories that have been continuously occupied since they were first recorded, with the exception of 1966–67. "Movements of young birds" includes all records of transfer to the Point Burn.

PHOTO BY COURTESY DEPT. LANDS AND SURVEY

BREEDING AGE

Williams (1957) recorded two birds as breeding in their first year—a female recovered with its male parent on a nest containing one egg and a male incubating a nest 2,700 yards from where it was banded. However, it is now known that yearlings are not evicted from their parents' territory and this suggests they are not of breeding age. The first of the above records is probably an example of the family sharing incubation—an extension of the fact that with some rails the chicks are often cared for by the young of a previous brood (Van Tyne and Berger, 1959). In the second record there is no evidence that the eggs were fertile. Studies of captive birds have shown that eggs may be laid in the absence of copulation and yet still be incubated by both birds of a pair.

Although the six two-year-olds recaptured in the wild were not known to be breeding, a female of the same age has laid one egg in captivity. As birds tend to leave the parents' territory during their second year it may be assumed that by the age of 24 months takahe are physiologically capable of reproducing but, because of environmental limitations, lack of opportunity or behavioural and social inexperience most two-year-olds probably fail to breed.

Evidence indicates that the three three-year-olds recaptured were breeding and that at least two had hatched chicks but whether these fledged is not known.

MORTALITY AND SURVIVAL

First year mortality (from banding to about 12 months of age).

Of 30 chicks banded prior to the 1966–67 season only 12 have been recaptured. Two of these were later found dead; one died in its second year, the other in its fourth year (Fig. 1). This low recapture rate does not entirely reflect mortality but arises, at least in part, from chicks moving to other areas on reaching maturity. The 12 live recoveries came from 18 chicks banded in seasons that were followed by two or three consecutive seasons of "high search effort" and this recovery of 67% is considered a truer figure for juvenile survival.

Adult mortality

Three adults have been recovered dead; two died in the sixth year, the third in the tenth year after banding (average = 7 years).

Recoveries (Fig. 1) have been used to calculate mortality rates in several ways. Three composite dynamic life tables gave similar values. The first, based on the total number known to be alive in each age class, gave a mortality rate of 17.1%; the second (based on raw recapture for all years) gave a rate of 15.3% and the third (raw recapture for "equal" search years) gave a mortality of 16.5%.

Total recoveries, when treated as "time specific" data, gave a mortality rate of 13.3%.

The use of Jolly's stochastic model (Williams, 1965) gave, in some years, a probability of survival greater than unity. In determining the mean probability of survival these years have not been deleted but each value has been accepted as unity because all adults banded in at least two of eight seasons survived the first 12 months. This treatment may overestimate survival because of the acceptance of a value for it of unity in some years; nonetheless, it gives a mean probability of survival of 0.87 which is in agreement with both the mortality rate obtained from treating recoveries as "time specific" data, and with the known survival of birds recovered in consecutive "high search effort" seasons.

Thirty-four of 67 adults have been subjected to several intensive recapture programmes starting in the year following banding and 30 (88%) at least survived the first year. Nineteen of a possible 24 birds subjected to intensive recapture programmes during their second, third and fourth seasons after banding were known to have survived for 24 months and a minimum of five from twenty birds subjected to the same attention in the tenth and eleventh years after banding were alive after 10 years. These recoveries suggest the adult mortality rate is 12%–13%.

All calculations place the mortality rate between 12%–17%. It is not possible to say which value is more correct. With the environmental extremes encountered in the Murchison Mountains it is unlikely that the same proportion of a small population would die each year. The annual mortality probably fluctuates appreciably, from less than 12 to more than 17 per cent, but the results of all methods of calculation suggest a mean mortality rate of 15 per cent.

TABLE 3. *Takahe survival calculated from stochastic model.*

Left-hand figures in each pair of columns — all birds, right-hand figures — adults only.																
l	m_l		n_l		s_l		Z_l		R_l		M_l		$M_l - m_l + s_l$		P.s	
52-53	0	0	9	7	9	7	0	0	8	7	0	0	9.00	7.00	0.90	1.03
53-54	7	6	13	10	9	6	1	1	8	5	8.12	7.20	10.12	7.20	1.05	0.98
54-55	6	3	25	19	25	19	3	3	16	14	10.69	7.07	29.69	23.07	0.72	0.79
55-56	10	8	10	8	10	8	9	9	8	7	21.25	18.29	21.25	18.29	1.00	1.18
56-57	6	5	7	6	7	6	11	11	5	4	21.40	21.50	22.40	22.50	0.94	0.86
57-58	10	9	13	12	13	12	6	6	7	7	21.14	19.29	24.14	22.29	1.13	0.99
58-59	4	4	13	10	13	10	9	9	5	5	27.40	22.00	36.40	28.00	0.54	0.70
59-60	3	3	3	3	3	3	11	11	2	2	19.50	19.50	19.50	19.50	0.75	0.72
60-61	10	10	22	19	22	19	3	3	14	14	14.71	14.08	26.71	23.08	0.78	0.74
61-62	3	3	9	3	9	3	14	14	7	3	21.00	17.00	27.00	17.00	0.92	1.00
62-63	4	2	11	3	11	3	17	15	9	3	24.78	17.00	31.78	18.00	1.10	1.37
63-64	16	9	21	14	21	14	10	9	11	8	35.09	24.75	40.09	29.75	0.69	0.67
64-65	20	16	40	31	40	31	3	2	16	16	27.50	19.87	47.50	34.87		
66-67	16	16	25	20	17	16										

Mean probability of survival	all birds	adults
Based only on those years where P. survival less than 1	0.78	0.81
Based on all years, but where P. survival greater than 1 taken to = 1	0.85	0.87

Notes:

l = the banding season.

 n_l = total number of birds caught. Z_l = number previously banded, not caught in season l but in a later season. R_l = number released in season l and caught later. M_l = number of banded birds in the population, $(s_l Z_l / R_l) + m_l$.P.s = probability of survival from l to $l+1$. $(M_{l+1}) / (M_l - m_l + s_l)$. m_l = number of banded birds caught. s_l = number of birds released.

POPULATION DATA

The figures given are the cumulative total of reliable observations made since the study began. The sample sizes differ because it has not always been possible to duplicate the same records each year. For example, the data on chick production are based on two sets of observations:—

- the proportion of breeding pairs that hatched chicks (43 of 61 pairs); and
- the proportion of these that hatched two chicks (20 of 53 pairs).

The latter contains 10 more pairs because during two seasons, although records for pairs that successfully hatched chicks are known, neither the history nor proportion of breeding pairs that failed to produce young is available.

Proportion of paired to unpaired adults

This varies and the number of unpaired birds in any season probably largely reflects the breeding success of the preceding one or even two seasons. In 1963-64 only 72% of the birds recorded were paired whereas in both the 1961-62 and 1966-67 summers 87% were paired. All observations indicate a 0.82 probability that an adult will either be mated, or keeping company, with another bird.

Proportion of breeding to non-breeding pairs

A pair may breed in one year but not in another: For example, conditions preceding and during the 1963-64 season were extremely severe with very few examples of flowering among any of the five species of snow tussock and only three pairs of birds were known to have bred (one successfully). The following summer at least 12 pairs, and in 1966-67 a minimum of 13 pairs bred. Both were good seed years for all tussock species. In many instances the breeding record is not known but 88 (70.4%) of 125 pairs are known to have bred.

Clutch size

This is known with certainty for only 32 of the 88 occasions in which breeding is known to have occurred. Twenty-five pairs (78%) laid two eggs and seven laid one egg — an average clutch size of 1.78. Williams (1960) mentions a nest with three eggs and in 1965 a nest with four eggs was found. Both are probably examples of re-nesting which both circumstantial and unequivocal evidence indicate may be fairly common.

Chick production

Infertility and embryo survival were discussed by Williams (1960). There are no further data on

these aspects as all subsequent visits have been made between January and March. To date, records of 61 nests obtained in seasons when all nests were checked show 43 (70.5%) hatched chicks. In some seasons only nests with chicks were visited; of these 20 out of 53 (38%) hatched two chicks and 33 hatched one—an average of 1.38 chicks per successful breeding pair.

Chick survival to the age of six weeks

Subsequent checks show that 47 of 50 pairs that hatched chicks had living young of about six weeks of age, see Table 4.

TABLE 4. *Chick production and survival (based on total sample of 50 successful pairs).*

With chicks at 6 weeks	Brood sizes at 6 weeks			No. of chicks at 6 weeks
	2	1	0	
47 (94%)	15 (30%)	32 (64%)	3 (6%)	62 (1.24 chicks/pr)

Productivity

Fusion of all data gives the following average picture of a breeding season. Yearlings are included with adults because (unless caught) it is difficult, due to the species' wary behaviour, to identify birds in the field. The number of birds present on a territory may be determined but not always their status:—

1. 82% of adults (1 year and older) are paired.
2. 70% of pairs (57–58% of all birds excluding chicks) breed or, more correctly, there is a 0.7 probability that any pair will breed, but not necessarily the same pair(s), each year.
3. 78% of breeding females lay 2 eggs, 22% lay one egg.
4. 71% of breeding pairs hatch chicks; 27% hatch two and 44% hatch one chick.
5. 66% of breeding pairs (49% of all pairs) have chicks surviving to the age of about six weeks; 21% have two chicks and 45% have one chick.

TABLE 5. *Average productivity (all years).*

Per	Eggs laid	Chicks hatched	Chicks alive*
Breeding pair	1.78	0.97	0.88
Pair	1.25	0.68	0.62
Adult	0.51	0.28	0.25

* Surviving to the age of about 6 weeks.

Recruitment and mortality

Nest records give an average clutch of 1.78 eggs and a survival to six weeks of 0.88 chicks per breeding pair. Therefore between egg laying and the banding age of chicks there is a 50–51% combined loss of eggs and chicks. As recoveries of banded chicks suggest one third die during their first year this means only 32–33% of eggs laid survive to become yearlings.

Field counts show that 57.5% of takahe breed and the adult mortality rate is calculated to be 15%. As there are no recoveries known to have occurred beyond 14 years all birds are assumed dead by the end of their fifteenth year.

Birds may be capable of breeding at two years but it is not known what proportion of these, or of three-year, or even of four-year-old birds secure mates and territories. Also, as the proportion of established breeders that breed each year varies, knowledge of breeding age is of little value in determining the productivity required to maintain the population. However, available data permit the productivity (or number of eggs per breeding pair to ensure equilibrium) to be obtained from the following expression —

$$X = \frac{2}{A(R + S_2 + S_3 \dots S_n)}$$

where X = Number of eggs required per breeding pair.

A = Percentage of adults (1 year and older) that breed.

R = Recruitment or first year survival (on basis of eggs laid).

S = adult survival series (from composite dynamic life-tables).

This method gives a requirement of 1.76 eggs per breeding pair which is very close to that obtained (1.78) in nest counts and implies a stable population.

Mortality calculations of 67% in the first year and 15% thereafter imply the population will be maintained if no yearlings or two-year-olds breed so long as 80–85% of birds aged three or more years lay (=56–59% of all adults).

Population size

The populations in the great cirques at the head of Takahe Valley and the Point Burn have not previously been determined. Annual counts made between 1950 and 1959 in the rest of the study area gave a fairly consistent number of birds. Field parties recognised a total of 12 different territories. Ten were occupied off and on during most years and regarded as "permanent" — the other two were used occasionally. The number of pairs identified varied but never exceeded ten (i.e. 1951–52, 1952–53, 1955–56 — 8 pairs; 1950–51, 1953–54, 1956–57, 1957–58 — 9 pairs; 1954–55, 1958–59 — 10 pairs). Sign indicated other pairs, though not located, might have been present, and the population (Williams and Miers, 1958) was placed at 10–12 pairs. As 20% of birds are not paired the total population would be in the order of 25–30 adults. A Lincoln Index technique agrees closely with field observations and estimates. It gave an adult population of 26 birds in 1954–55 and 28 birds in 1955–56.

Subsequent checks of the same areas in 1963–64, 1964–65 and 1966–67 are in agreement (Table 6) and indicate no apparent imbalance in the rates of recruitment and mortality throughout 17 years. The population has compensated for four eggs, four chicks and three adults taken into captivity between November 1957 and September 1963.

TABLE 6. *Number of birds and territories. Takahe Valley and Point Burn, excluding head basins.*

Season	Total adults	Pairs breeding	Single* birds	Total	
	Number of territories occupied				
1963–64	28	2	9	1	12
1964–65	27	7	4	1	12
1966–67	29	8	4	1	13

* Very few unpaired birds are solitary; they are mainly members of family groups which suggests that although classed as adults during field censuses many are not of breeding age.

As there are now known to be three pairs in the Takahe Valley head basin and five or six pairs in the upper reaches and head basin of the Point Burn (Fig. 2) the population of the entire study area includes 19–21 pairs in a total of 47–50 adults.

PROSPECTS OF SURVIVAL

Takahe are restricted to an area of some 200–230 square miles of mountainous country bordering the western shores of Lake Te Anau. The maximum number living at any time during this century (or even earlier) probably has never been much above the estimated 370–420 birds surviving today. Results of several exploration parties show there are fewer takahe at the western end of their range where some watersheds contain as few as two or three pairs. An evaluation of old sign, and of numbers present in relation to habitat available in this climatically less favourable part of their habitat indicates a continuing population shrinkage from the west where birds have disappeared from at least two peripheral valleys during the last decade. Birds in the eastern valleys appear to be maintaining their numbers. Counts and calculations based on band recoveries in two of these (Takahe Valley, Point Burn) show the population to be stable but the limitations of field methods and demographic techniques in detecting a long term trend are obvious when the duration of the study, population size and terrain are considered.

It is rather remarkable that this remnant species has not only persisted but also (apparently) managed to maintain numbers for so long. The "retreat" by takahe into an inaccessible habitat has undoubtedly contributed to their survival. However, a more important factor is that the small colonies (from two or twelve pairs) in the numerous cirques and watersheds are not isolated. There are routes, negotiable to and used by takahe, linking them.

The population has been very small and geographically confined for many decades and limited back breeding (and possibly inbreeding) may have occurred throughout the generations. Isolated populations are relatively poor in genetic variability — "and appear to become vulnerable to extinction, particularly if they live for long periods in a very uniform environment" (Mayr, 1954).

Although there is a tendency for juveniles to move from their home valley many will probably settle within a rather limited radius of their place of birth. Therefore the value of these movements by young birds depends largely on the colony sizes and spacings in the various watersheds. The probability of young birds either not finding mates or forming successive non-viable

intra-family unions may have contributed to the disappearance of takahe from two of the sparsely populated western watersheds.

There is no basis for expecting a declining and small population to stabilise at its present level particularly as this flightless vegetarian's "natural habitat" is now shared with browsing ruminants and predatory stoats. (During the 1966-67 season one chick and one adult were killed by stoats, one nest was predated and another adult was probably killed by a stoat in Takahe Valley alone.) Earlier records of stoat predation have been mentioned in a discussion on environmental hazards (Reid, 1966). "Populations with depleted genetic variability . . . are not very plastic. . . . such populations rarely have the capacity to adapt themselves to severe environmental shocks. The arrival of a new competitor or of a new enemy or a drastic change of vegetation or of the physical environment is apt to lead to extinction." (Mayr, 1954).

As the birds inhabiting the eastern part of the range still possess the reproductive capacity to maintain numbers and even replace members so far taken into captivity, it is essential that this procedure be followed now while the population is numerically strong enough to withstand the necessary losses. In future years, fewer should survive and a less variable gene pool result, and the self regulating mechanism operating now may not be able to compensate for the removal of breeding stock.

ACKNOWLEDGEMENTS

Throughout this study many officers of the Wildlife Service have participated in field trips. The unsurpassed performance by field parties during the last four years is attributable mainly to Messrs. C. D. Roderick and D. J. Stack of the Wildlife Service and M. Evans of the Forest Service. Unpublished field notes and reports by G. R. Williams and K. H. Miers provided much of the data, and the assistance of my colleague, M. Imber, is also recorded with thanks.

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