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POPULATION DYNAMICS OF THE NEW ZEALAND WHITEHEAD (PACHYCEPHALIDAE)—A COMMUNAL BREEDER[1]

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Abstract. On Little Barrier Island, New Zealand, Whiteheads (*Mohoua albicilla*) reach high densities—a crude estimate of maximum density was 87 birds/ha. Males and females appeared to occupy home ranges of the same size. The sex ratio of mist-netted birds did not differ significantly from 1:1, but most helpers at the nest were males. The annual survival rate of independent mist-netted Whiteheads of unknown age was at least 0.82, yielding an estimated life expectancy of 5.1 years. Using Fry's method (1980) of generating survival curves we obtained an s_{10} value (mean age reached by 10% of birds initially at risk) of about five. The longest-lived birds in the study reached at least six years and seven months. At least 65% of fledglings survived their first year. Some dispersed from their natal area in their second or third years but others did not. In the best-studied case, a pair of Whiteheads bred communally by associating with their surviving young. These young helped raise later progeny. Young Whiteheads were seen associating with a parent for up to two years and seven months. We think that communal breeding in Whiteheads is a mechanism that allows young adults to mark time until an opportunity for breeding arises.

Key words: Population dynamics; survival; longevity; communal breeding; Mohoua; *New Zealand.*

INTRODUCTION

The Whitehead (*Mohoua albicilla*) is a small, sociable, insectivorous forest bird. Females weigh 12–16 g; males weigh 16–21 g (Gill and McLean 1986, Gill and Veitch 1990). Whiteheads are endemic to the North Island of New Zealand where they persist in native and exotic forests in central and southern parts of the island (Bull et al. 1985), and on Little Barrier and Kapiti Islands where densities are particularly high. With its South Island congeners, the Yellowhead (*M. ochrocephala*) and Brown Creeper (*M. novaeseelandiae*), the Whitehead forms the subfamily Mohouinae endemic to New Zealand (Keast 1976).

Guthrie-Smith (1925) discovered that at most Whitehead nests on Little Barrier Island a "quartette" of mature birds fed the nestlings. He was uncertain whether quartets comprised two pairs or a male and three females, while at a few nests only a pair of adults seemed to be involved. Blanshard (1966) recorded three adults associated with a nest that he monitored closely, again on Little Barrier. Oliver (1930) favored the suggestion that two pairs used the same nest for breeding, whereas Falla et al. (1966) thought polygamy the most likely explanation. Our observations of color-banded birds (McLean and Gill 1988, this study) showed that Whiteheads on Little Barrier Island often bred communally in groups of up to eight (including the primary pair), and this is the modern interpretation of Guthrie-Smith's observations. A quartet was seen at Puketitiri in Hawke's Bay on the mainland (Guthrie-Smith 1925) so the phenomenon is not restricted to Little Barrier Island.

In this study we color-banded Whiteheads on Little Barrier Island to attempt to elucidate aspects of their population dynamics, especially social relationships, density, dispersion, dispersal, sex ratio, survival and longevity.

STUDY AREA AND METHODS

Whiteheads were banded and resighted in an area of about 60 ha within roughly 1 km of the bunkhouse at the southwest corner of Little Barrier Island (36°13′S, 175°3′E) which lies on the northern fringe of the Hauraki Gulf, northern New Zealand. The study area comprised flat land and low hills, most of it forested but including some open farmland on flats near the shore. The forest is mainly seral, dominated by *Kunzea* and *Lep-*

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TABLE 1. Summary of banding effort and resightings of banded birds during the five years of study.

Year	Banding (birds in squares)	Resightings (birds in squares)	Max. no. sqs/bird	Max. no. birds/sq
1 June 1984–March 1985	159 in 22	64 in 23	3	15
2 April 1985–March 1986	16 in 7	105 in 52	11	23
3 April 1986–March 1987	12 in 6	92 in 67	16	30
4 April 1987–March 1988	8 in 5	80 in 61	13	33
5 April 1988–March 1989	none	57 in 35	6	20
Total	195 in 25	158 in 92	16	33

tospermum with a dense broad-leaved understory.

A map of the study area was traced from a 1:4,000 aerial photograph. This showed the flat open land (including shoreline, forest edge and various buildings and other landmarks) with great accuracy, but the position of the paths within the main block of forest on the hills could be determined only approximately. A grid system with 80 m × 80 m (0.64 ha) cells was superimposed on the map so that the positions of birds could be recorded. Birds were banded and resighted to an altitude of about 200 m, but the grid system had to ignore contours. Such inaccuracies meant that smaller grid-squares could not be justified.

From June 1984 to September 1987, but mainly in Year 1, 195 Whiteheads were color-banded in 25 squares (Table 1). Some 80% of these were mist-netted as independent birds (young-of-the year or older); the others were nestlings or fledglings caught by hand at or near the nest. Each bird was given a unique combination of a numbered metal band and three celluloid butt-ended color-bands. Unfortunately, the color-bands proved not to be light-stable and faded badly after about three years. Whiteheads were sexed from their mass and wing-length (Gill and McLean 1986, Gill and Veitch 1990) and behavior (McLean 1987).

For analysis the study was divided temporally into five years ending on 31 March (Table 1). This is an appropriate point to end the year because breeding and molting are largely over by then. After Year 5, mist-netting by other researchers continued to provide data on longevity of banded Whiteheads.

The density of Whiteheads in the study-area was so high, and observations of fast-moving sociable birds in the forest so difficult, that it was seldom possible to record the membership of entire groups. The observer encountering Whiteheads was usually reduced to concentrating on particular banded birds, checking and rechecking the band combinations, and recording these and the locality, before the birds moved away.

RESULTS

GENERAL

Of the 195 Whiteheads banded in 25 grid-squares, 158 were seen again dispersed over 92 squares (Table 1). Numerous unbanded birds were present in the study area. Observational difficulties meant that little chance existed to record interactions or develop an immediate feel for the social organization of Whiteheads in space or time. Instead we generally analyze the banding and grid-square data and present case-studies of the two best-known groups.

GROUP CASE-STUDIES

The "Bunkhouse" group. This group's home range included the isolated trees and open land around the bunkhouse where observations were relatively easy. Records during five breeding seasons give a picture of long-term group dynamics (Fig. 1). Where birds additional to those identified individually were noted with the group the number is given (Fig. 1). The group size was up to eight.

Male-267 and female-266 were a breeding pair when banded in November 1984. They had three nestlings at a nest that month but none survived. A later nest in January 1985 held another three nestlings one of which (male-196) fledged. In this season no visitors to the nest other than the primary pair were seen, though sometimes a third bird was in the close vicinity.

The same pair had a nest in November 1985 with two nestlings of which one (bird-311) survived. Male-196 fed the nestlings and fed bird-311 after it fledged. He was seen feeding female-

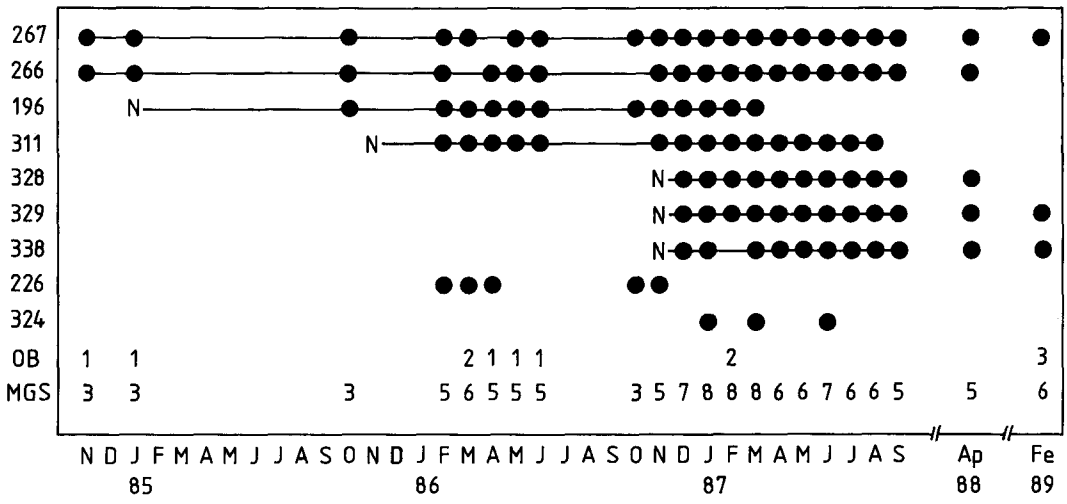

FIGURE 1. Composition of the "Bunkhouse" group between November 1984 and February 1989. Birds-267 and -266 were the primary pair (see text). Spots show when birds were seen in the group. OB indicates the number of other birds seen with those represented by the spots. MGS = minimum group size; further birds may have been present. N indicates the month when this bird was raised as a nestling by the group.

266 (his mother) in November 1986. A nest in November 1986 held three nestlings all of which survived (bird-328, male-329 and male-338). Male-196 was seen feeding nestlings; he, bird-311 and the primary pair were seen feeding the fledglings. The length of association of male-267 with his offspring is summarized in Table 2.

Male-226 was netted and banded in August 1984. During 1986 he occurred regularly with the "Bunkhouse" birds, but both before and after this period he was seen with other birds (in October 1985, for example, he fed a female not a part of the "Bunkhouse" group, and in December 1986 he fed fledglings in a neighboring group). Male-324 was banded as an adult in November 1986. He was seen occasionally with the "Bunkhouse" group and at other times with non-"Bunkhouse" birds. Male-267 chased him in April 1987. Males-226 and -324 seemed to be loosely associated with the "Bunkhouse" group and were never seen feeding nestlings or fledglings.

TABLE 2. Association of banded parents and offspring, showing how long they were seen together after fledging. In the first three cases only one parent was banded; the other cases are discussed in the text.

Offspring	Parent	Time together after fledging
bird-306	male-249	1 year 5 months
male-313	female-189	1 year 10 months
bird-194	male-258	2 years 7 months
bird-110*	female-191	2 years 7 months
bird-111*	female-191	1 year 6 months
bird-112*	female-191	1 year 11 months
male-196#	male-267	2 years 2 months
bird-311#	male-267	1 year 9 months
bird-328#	male-267	1 year 5 months
male-329#	male-267	2 years 3 months
male-338#	male-267	2 years 3 months

* "North-west Landing" group.
# "Bunkhouse" group.

Male-196 was not seen after March 1987. Bird-311 was last seen with the group in August 1987; in September 1987 and twice over the subsequent year it was seen at a distant location with other birds (see Dispersal of Juveniles).

The "North-west Landing" group. In December 1984 we caught and banded three adults (male-190, female-191 and male-192) near their nest. The nest contained three nestlings that we also banded (birds-110, -111 and -112). Male-190 was considered to be the primary male and father of the nestlings because he was larger and heavier than male-192 and had a bright white head (brownish in male-192). Male-190 was not seen again after this breeding season.

In July 1985, male-192 and the three juveniles were seen in the vicinity of the old nest. In the same area in winter 1986, male-192, female-191

and the three younger birds were several times seen together and with unbanded Whiteheads. Male-192 displaced bird-112 in an agonistic interaction.

In the 1986–1987 breeding season, female-191, male-192, bird-110, bird-112 and at least one unbanded adult were seen in their usual home range with several unbanded fledglings. Bird-112 was twice seen to feed female-191 (his mother). Male-192 fed fledglings.

These observations show a persistent association of Whiteheads with a parent. Male-192, apparently a helper when banded, may have been female-191's son from a previous season, and they were seen in the same home range for another two years. The association of the banded fledglings with female-191 is summarized in Table 2.

DENSITY

The difficulties of studying Whiteheads in the field have reduced us to consideration of maximum rather than average density. The greatest number of banded birds recorded in one grid square during one year was 33 in square L14 (near the bunkhouse) during Year 4 (Table 1). This equates to about 52 banded birds per ha. In April 1988 (start of Year 5), records of birds seen during seven consecutive days of intensive monitoring in nine forested or partly forested squares near the bunkhouse (including L14) showed that about 60% were banded (n = 111 sightings). Allowing for unbanded birds on this figure, the density of Whiteheads in forest near the bunkhouse was up to about *87* birds per ha. This crude figure is probably an over-estimate since it is based on sightings in one square for a whole year, and not all birds may have been present in the square at one time.

DISPERSION

For each banded Whitehead we summed the number of grid squares in which it was seen (y) during Years 1–5 inclusive, including the banding square and a minimum of intervening squares between non-adjacent records. We plotted this as a function of the number of records for that bird (x) including initial banding as a record. Variable x was less than the total number of sightings and captures of a given bird. It was the sum over five years of the number of records of that bird in different squares in each year, discounting multiple records within a square within a year. When y was plotted as a function of x for 128 mist-netted birds (50 females, 78 males), y increased in direct proportion to x until about x = 10 where the curve began to level off. We therefore restricted the analysis to birds for which $x \geq 10$.

There was no significant difference in number of squares occupied between 28 mist-netted males and 15 females (t-test, $P = 0.4$), so we conclude that home ranges were the same size for both sexes. We combined the data for sexed and unsexed birds. On average, birds occupied 11.0 squares (range 6–22, n = 55, SD = 4.20). This translates to an average home range size of 7.0 ha (range 3.8–14.1 ha). However, these are crude estimates which are likely to over-estimate the true situation.

Considering the "Bunkhouse" group over the entire study, the primary pair and their progeny were seen mainly in 11 squares, an area of 7 ha. This excludes the post-dispersal sightings of bird-311 (see Dispersal of Juveniles), and a brief foray into eight additional squares made by male-267 and male-196 (along with non-"Bunkhouse" birds) in January 1987 (D. G. Allen, pers. comm.).

Intensive observations of the "Bunkhouse" group in 1987 using finer grid squares (Allen 1988) showed that their home range was up to 3.5 ha before breeding and as small as 1.3 ha during the breeding season, increasing again when fledglings were being fed. This suggests that estimating range size by tallying up the large grid squares overestimates by a factor of two.

The greatest number of grid squares in which one bird was seen in one year was 16 (Table 1), an area of about 10 ha. The bird in question (male-327) was banded as an adult in late November 1986, so the records refer to only four months and to the breeding season. His breeding and social status was unknown.

SEX RATIO

In a sample of 75 Whiteheads that were sexed from measurements and mist-netted outside the breeding season without lures and with no prior assumptions as to their sex, 43 were males, a ratio of males to females of 1.34:1. This ratio is not significantly different from 1:1 ($\chi^2 = 1.61$, $P = 0.204$).

SEX OF HELPERS

We identified 11 banded Whiteheads of known sex as helpers on the grounds that they fed nest-

TABLE 3. Annual survival rates of Whiteheads netted as independent birds (4 months or older). Data for 4 consecutive years; based on numbers alive between October and January of one year, and still alive during the same period next year.

Year (x)	No. alive Year x	No. still alive Year x + 1	Survival rate
1	92	75	0.82
2	103	84	0.82
3	92	54	0.59
4	61	37	0.61

lings or fledglings judged not to be their own progeny because other birds in the group were believed to be the primary male and female. Of these 11 birds, 9 were males and 2 were females. The skew differs significantly from an even sex ratio ($\chi^2 = 4.46$, $P = 0.035$). The sample is small, but provides a strong indication that Whitehead helpers were predominantly males.

SURVIVAL AND LONGEVITY

Adults. Table 3 shows the annual survival rates of Whiteheads caught in mist-nests. This includes birds of all ages not known to be recent fledglings, i.e., birds at least four months old. Survival rates appeared to be significantly lower in the last two years. This, however, is an artifact caused by (1) most banding being at the start of the study (Table 1) and subsequent resightings tracing an ageing cohort, and (2) the last years of the study lacking the benefit of sightings in following years. We believe that the data for the first two years are valid, and establish that at least 80% of Whiteheads in their first year or older survive from one year to the next. Of the 195 Whiteheads banded during the study, 81.0% were seen again (Table 1), echoing this high survival rate.

A survival rate of at least 0.82 (Table 3) indicates a mortality rate (m) of 0.18 at most. The average expectation of further life is 2-m/2m (Gibb 1961). The life expectancy of Whiteheads (young-of-the year or older) on Little Barrier Island is therefore at least 5.1 years. Table 4 gives a representation of the data using Fry's method (1980). The expression relating the log of n (%) to t yields an s_{10} value of about 5, i.e., the mean age reached by 10% of the Whiteheads initially at risk was five years.

The longest-lived birds in the study were males-238 and -246, both of which were netted and

TABLE 4. Survival of 153 Whiteheads netted as independent birds (4 months or older), expressed according to Fry's method (1980); t = years since birds were banded, n = cumulative number of birds known to have survived at least t years.

t	0	1	2	3	4	5
n	153	104	83	46	27	16
n (%)	100	68.0	54.3	30.1	17.7	10.5

banded at unknown age in August 1984 and last seen in August 1990. These had minimum life-spans of six years and seven months, as they could not have hatched after January 1984. Male-214 and female-224, also banded in August 1984, were last seen in May 1990, giving minimum life-spans of six years and four months.

Fledglings. Considered here is the survival in their first year of Whitehead fledglings, of which 20 were banded in Year 1, six in Year 2 and five in Year 3. Of these 31 birds, 20 were known to be alive a year later, a survival rate in their first year of at least 65%. This is a minimum because some of those not resighted after a year may have dispersed rather than died. Any birds leaving the main study area were unlikely to be recorded in their new location.

DISPERSAL OF JUVENILES

After fledging, bird-311 spent its first 21 months with its natal group (see The "Bunkhouse" group and Table 2), and was last seen with them in August 1987. In September 1987, April 1988 and February 1989 it was seen with other birds about 0.5 km from its natal home range. This bird had a protracted association with its parents and siblings including the opportunity to feed fledglings, and we speculate that only after this experience did it disperse in search of breeding prospects of its own. Numerous other juveniles were long associated with their parents (Table 2). However, several other banded offspring of known parents were resighted 6–10 times, but never with their parents.

Bird-284 fledged in November 1984 and was seen next month 0.12 km from the nest in which it was raised. However, in January 1985 it was seen with a large flock of Whiteheads 0.28 km from its natal site, and not seen again. This could be a simple case of a juvenile dispersing from its natal area within six weeks of fledging. However, at last sighting bird-284 may have been with its natal group within the larger flock. Bird-285

fledged in November 1984 and was seen again only once—0.45 km away in February 1986. In the time between, bird-285 may have had a long association with its natal group.

Figure 2 shows the distance of dispersal of 26 young Whiteheads. For each bird, the maximum distance it was seen from the grid-square in which it fledged is recorded as a function of time elapsed since fledging. During their first year juveniles dispersed no more than 350 m, but some moved up to 650 m from their natal area in their second and third years. Any greater dispersal, beyond the study area, was unlikely to have been detected. For birds recorded more than 200 m from the nesting square, distance dispersed seemed to be positively correlated with time. A second group of birds were still within 200 m of the natal area 10–40 months after fledging. This suggests that juveniles were either dispersers or non-dispersers. No correlation with sex was apparent for the few juveniles of known sex.

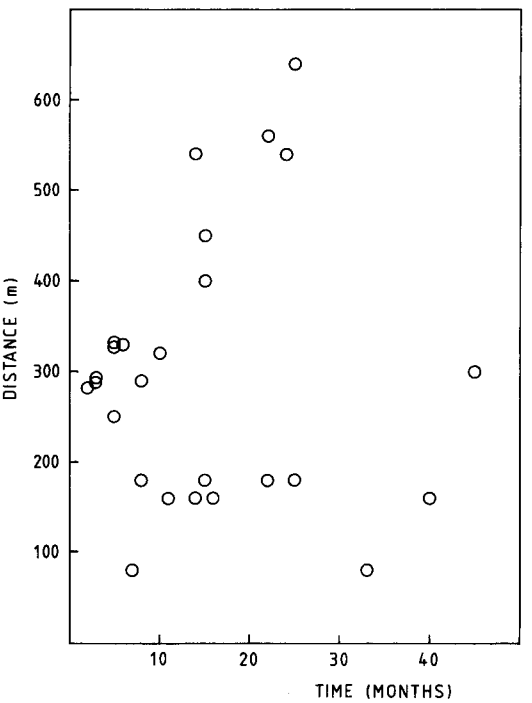

FIGURE 2. Dispersal of juveniles. Maximum distance from their natal square recorded for 26 fledglings as a function of time elapsed since fledging.

AGE AT FIRST BREEDING

Male-196 in the "Bunkhouse" group clearly did not breed during its first two years. Bird-311 and probably all the other young in Table 2 did not breed as yearlings. In 1989 and 1990, 80 Whiteheads were transferred from Little Barrier Island to Tiritiri Matangi Island (220 ha) which previously lacked Whiteheads. Yearlings then showed evidence of breeding (Anonymous 1990) which suggests that some factor present on Little Barrier, such as high density, causes delayed reproduction among the Whiteheads there.

DISCUSSION

Evidence from the "Bunkhouse" birds suggests that a breeding pair and their progeny form the core of Whitehead groups. The primary pair had no helpers at first and bred poorly. They later raised three fledglings with the assistance of two earlier progeny. Birds of unknown genetic relatedness associated with the group, but the primary pair were joined in feeding nestlings and fledglings only by their own progeny from previous broods. In 1985 and 1986 both surviving progeny joined the group as helpers. During the 21 months in its natal group before bird-311 dispersed to join unrelated birds, it gained experience at raising young.

In terms of the classification of breeding systems proposed in Table 2.1 of Brown (1987), Whiteheads have all-purpose territories, but more work is needed on defense of the territory and the extent to which helpers assist with this. Whiteheads appear to be singular-breeding. We presume that only one female in the unit breeds because the clutch-size is small (mode = 3) and the color of eggs varies less within clutches than between (McLean and Gill 1988). The helpers are mainly males. Whiteheads seem to be monogamous.

Little Barrier Island lacks all mammalian predators except *Rattus exulans,* and Whiteheads are the most abundant land bird on the island (Turbott 1961, Kikkawa 1964). Kikkawa (1964) and Gravatt (1970) gave figures for the density of breeding Whiteheads (pairs and singing males) that translate to only 1.0–5.4 birds/ha. It is now clear that census figures based on an assumption of simple pair-formation without helpers are rather meaningless for Whiteheads. Our crude estimate of maximum abundance is perhaps the opposite extreme, and further work is needed on average density.

The high survival and life expectancy of independent (mainly adult) Whiteheads may be

typical of small New Zealand forest birds. Grey Warblers (*Gerygone igata,* mean weight only 6.4 g) had an annual adult survival rate of at least 80% at Kaikoura (Gill 1982). However, the high survival of fledgling Whiteheads in their first year is remarkable. At Kaikoura only 23% of successfully fledged Grey Warblers were seen again (Gill 1982). Both at Kaikoura and on Cuvier Island almost no fledgling Fantails (*Rhipidura fuliginosa*) were recorded after one year (Powlesland 1982, McLean and Jenkins 1980). These figures could merely reflect the non-dispersal of communally breeding Whiteheads as against dispersal in the other species, which do not breed communally. However, dispersal of Fantails from Cuvier Island was unlikely since it is 15 km from the nearest land.

This study has shown that the communal breeding of Whiteheads on Little Barrier Island is associated with the following attributes of the population: high survival of fledglings and adults, the non-dispersal of many juveniles and their long association with a parent, and high density. McLean and Gill (1988) showed that productivity is low—the modal clutch-size was three and groups raised less than 1.5 fledglings per season.

The high survival presumably occurs because the climate is mild all year with no great shortage of food in winter, and because Little Barrier Island has few predators. The only likely predators of Whiteheads are a relatively inoffensive rat, an owl (*Ninox novaeseelandiae*), a forest kingfisher (*Halcyon sancta*) and a large cuckoo (*Eudynamys taitensis*). High longevity is balanced by low productivity. We think it unlikely that communal breeding in Whiteheads is an adaptation to increase productivity. The high density and longevity of Whiteheads may prevent yearlings from breeding by denying them access to space. In these circumstances, the occurrence of helpers may be a mechanism that allows young adults to mark time safely within a familiar territory until an opportunity for breeding arises, as has been suggested in other bird species (e.g., Brown 1969). This needs to be tested by further studies that seek to separate cause and effect among the factors attending communal breeding in Whiteheads.

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