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Breeding biology of North Island robins (*Petroica australis longipes*) on Tiritiri Matangi Island, Hauraki Gulf, New Zealand

DOUG P. ARMSTRONG
Wildlife Ecology Group, Institute of Natural Resources, Massey University, Palmerston North, New Zealand

JOHN G. EWEN
Wildlife Ecology Group, Institute of Natural Resources, Massey University, Palmerston North, New Zealand
Current address: School of Zoology, Faculty of Science and Technology, La Trobe University, Melbourne, Australia

WENDY J. DIMOND
Wildlife Ecology Group, Institute of Natural Resources, Massey University, Palmerston North, New Zealand

TIM G. LOVEGROVE
Auckland Regional Council, Regional Parks Service, Private Bag 92012, Auckland, New Zealand

ANDERS BERGSTRÖM
Department of Zoology, University of Stockholm, Stockholm, Sweden,

BARBARA WALTER
Department of Conservation, Tiritiri Matangi Island, GPO Auckland, New Zealand

Abstract We studied North Island robins over 7 breeding seasons following their reintroduction to Tiritiri Matangi Island. All robins bred in their first year if a mate was available. They usually retained pair bonds for life but some females switched mates within or between breeding seasons. There were 2 instances of sequential polyandry, where a female laid a clutch with a new male while her previous mate was rearing her fledglings. The 1st clutches were usually laid in early September and the last clutches in late December or early January. Mean clutch size was 2.3 eggs, and clutches were largest in the middle of the breeding season. Females reared a maximum of 3 broods per year, and a maximum of six fledglings. Females that survived the breeding season fledged an average of 2.48 young, and 51% of clutches found before hatching fledged at least one young. Juveniles were fed for 4-7 weeks after fledging, and stayed in the natal territory for 7-10 weeks. Dispersing juveniles were often chased when entering other territories, but there were 4 instances of juveniles being fed by unrelated lone males. The juvenile survival rate declined as the population grew. Permanent territories were restricted to patches with a canopy of at least 6 m, totalling about 13.4 ha, and the breeding population levelled off at 65 in the 5th year. The decline in juvenile survival was similar for males and females, suggesting that both sexes needed to compete for territories even though there were always males without mates because of an initial bias in sex ratio. Males had delayed plumage maturation whereby they appeared similar to females or juveniles until after their first breeding season. We suggest this could be advantageous for territory acquisition because male territory holders cannot be preferentially aggressive toward juvenile males.

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INTRODUCTION

As Powlesland *et al.* (2000) note, North Island robins *(Petroica australis longipes)* are easy to study, but until now there has been no detailed account of their breeding biology. Powlesland *et al.* (2000) provide data on several aspects of robin breeding biology collected over 2 breeding seasons at Pureora Forest Park. This paper provides similar data collected over 7 years on the robin population on Tiritiri Matangi Island, and adds additional information permitted by having a longer time frame, a fully-banded population, and an island situation with no mammalian predators.

The Tiritiri Matangi population was established by translocation of 44 birds from the Mamaku Plateau, near Rotorua, in April 1992 (Armstrong 1995). A further 14 birds were translocated in June 1993. As with the Pureora robins, robins in the Mamaku Plateau have co-existed with a range of mammalian predators over the past century and may have become adapted to this, behaviourally (Maloney & McLean 1995), or genetically, or both. However, robins on Tiritiri Matangi exist in an environment free of mammalian predators. Kiore *(Rattus exulans)* were on the island during the first robin breeding season, but were eradicated in September 1993. The habitat is also quite different from the study sites at Pureora, which were relatively large (> 100 ha) continuous blocks of unlogged forest (Powlesland *et al.* 2000; Knegtmans & Powlesland 1999). In contrast, Tiritiri Matangi is a highly modified island, that currently has several small (< 5 ha) patches of closed canopy forest in a matrix of recently-planted regenerating forest (see below).

The aims of this paper are: (1) to reinforce and extend the observations of Powlesland *et al.* (2000), and (2) to compare the breeding biology of the Tiritiri Matangi and Pureora populations, given their contrasting habitats and management regimes, and possible genetic differences.

STUDY AREAS AND METHODS

Study area

We studied the Tiritiri Matangi robin population over its first seven years (1992/93 - 1998/99), and our research on this population is continuing. Tiritiri Matangi (36°36'S, 174°53'E) is a 220 ha island in the Hauraki Gulf, 3.5 km east of Whangaparaoa Peninsula and 28 km north of Auckland. The island has had a long history of human use and habitation, first by Maori (Kawerau and Ngati Paoa) then by European farmers from the mid 1850s to 1971. It was made a scientific reserve in 1980, and subsequent management included planting about 400,000 native seedlings of a wide range of species from 1983 to 1995 (Mitchell 1985; Cashmore 1995), eradicating kiore in 1993, reintroducing bird and plant species (Galbraith & Hayson 1994), and controlling weeds (for details, see http://www.massey.ac.nz/~ DArmstro/tiri.htm). When robins were reintroduced in 1992, the island had about 15 ha of forest in gullies and coastal areas, mainly surrounded by the early regenerating forest (Mitchell 1985; Armstrong 1995). One forest patch (Wattle Valley) is dominated by Australian crested wattle (*Albizia lophantha*) trees that spread from plantings in the mid 1900s, but the other patches consist of native coastal broadleaf forest fringed by manuka (*Leptospermum scoparium*) and kanuka (*Kunzea ericoides*).

Capture and banding

The original robins were caught in the Mamaku Plateau using electronically operated clap traps baited with mealworms (Armstrong 1995). Most robins produced on the island were banded on the nest, usually at 9-15 days of age, except in the 1997/98 breeding season when we did not monitor nesting. Almost all nests could be reached by climbing trees or by leaning an aluminium ladder on the nest tree or an adjacent tree. Nestlings were always taken away from the nest for banding, sometimes individually and sometimes all at once. No nests were deserted after banding. Birds that fledged without being banded were usually captured with a handnet 2-4 weeks after fledging, after they started to feed for themselves but before they left the natal territory. The handnet was made by threading plastic garden netting onto a loop (about 25 cm dia) of 8-gauge wire which was attached to a bamboo pole at a 135° angle. Fledglings were easy to catch with the handnet if they could be enticed to take mealworms in a relatively open area. Robins produced in 1997/98 were caught using a claptrap at the start of the 1998/99 breeding season. Maloney & McLean (1995) also used a handnet to catch adult South Island robins (*P. australis australis*) on Motuara Island. However, we found that adults were generally too wary to be caught with a handnet, and could be caught much more easily with a clap trap. All robins were given a unique band combination, with 2 colour bands (size B butt bands) on 1 leg, and 1 colour band over the metal band on the other leg.

Monitoring

In 6 of the 7 years, all forest patches were surveyed at the beginning (early-mid September) and near the end (early-mid January) of each breeding season, and usually at least once during the winter and several times over the course of the breeding season. Based on mark-recapture analysis (Armstrong & Ewen, unpubl. data), these surveys detected 96% (on average) of the robins alive at the time. The surveys at the beginning of the breeding season determined the pairs, and all pairs found were subsequently monitored until they finished nesting. This consisted of visiting pairs to determine if they were nesting, and then to band young and measure reproductive success. The frequency of visits varied, but was typically about once per week. In 1997/98, the research consisted of a single survey to determine pairs, hence we report pair bonding data for that year but no data on reproduction.

We usually found nests by feeding mealworms to the male, who would then call the female off the nest to feed her (males rarely fed females on the nest). Males normally called the female from any location in the territory, but sometimes ate all the mealworms if fed more than about 50 m from the nest. We then watched the female until we found the nest, repeating the procedure if necessary. The criterion for determining whether a female did not have a nest was observing her for 30 min continuously without her going to a nest. Nesting females normally returned to the nest within 7 min, and the maximum time a nesting female was observed off a nest was 17 min.

After young fledged, we determined whether or not they were alive by feeding mealworms to both parents and observing where they took them. While young were well concealed for the first few days, we could usually find young and determine their colour combinations at any time after fledging.

RESULTS

Habitat use

Robins held breeding territories only in forest patches with a canopy at least 6 m high. These included 13 different patches, ranging from about 0.15 ha to 3.8 ha. (11 of these are shown in fig. 2 of Armstrong (1995)). The breeding population, measured as the minimum number of birds known to be alive in mid-September, reached 65 in 1996/97, and stayed at exactly that level for the two subsequent years. This equates to an average of 4.9 birds ha^{-1} over an estimated 13.4 ha of robin habitat. The number of robins per patch was correlated closely with patch size (r^2=0.98, using mean values for numbers alive at the start of the breeding season over the last 3 years). The most preferred areas seemed to be in the middle of the larger patches, as these were always filled immediately after a bird died. These areas had canopies of 8-20 m, with open forest floor, damp gullies, and tree ferns (*Cyathea dealbata* and *C. medullaris*). All territories included a gully, except for a few territories on the upper fringes of the largest patch. Most territories did not include the recently-planted areas. One pair used one of the older planted areas from 1995/96 onwards, and built several nests there, but the territory also included one of the remnant patches.

Pair bonding

Females always paired before their first breeding season after fledging, and all females had mates in each of the 7 years. There were always more males than females in the population: 79% in 1992/93, 70% in 1993/94, 61% in 1994/95, 60% in 1995/96, 62% in 1996/97 and 55% in 1998/99. This was entirely the result of a biased sex ratio in the original translocation (Armstrong 1995), as the sex ratio of recruits has been close to 50:50 and survival rates have been very similar for males and females (Armstrong & Ewen, unpubl. data). Females were clearly paired to one male at any time, hence there were always unpaired males. Each pair or lone male had a distinct territory, with adjacent territories usually having clear boundaries. Lone males occasionally displayed to females at the territory boundary (wings spread, frontal patch displayed, attempting to get behind female), presumably to solicit copulation, and were always chased by her mate when they did so.

Pair bonds were usually retained throughout the breeding season, and in subsequent seasons until one of the pair died (Tables 1, 2). The longest pair bond lasted 6 breeding seasons before the female died. The male and the female remained in the territory for the whole year, but outside the breeding season they often had little interaction and seemed to subdivide the territory. A few females switched mates during the breeding season (Table 1) or between breeding seasons (Table 2), even though the original male was still alive. Of the 6 females switching mates during the breeding season, one moved to a new bush patch after two unsuccessful nests, and paired with another male, then returned to the original male the next year. Two switched between adjacent territory holders for

Table 1 Pair bond retention within breeding seasons by North Island robins (*Petroica australis longipes*) on Tiritiri Matangi Island, Hauraki Gulf, New Zealand.

	Pairs at start[1]	Together at end[2]	Male dead	Female dead	Female with new male	Female alone
1992	7	7				
1993	11	9		1		1
1994	14	13			1	
1995	21	19	1		1	
1996	23	21		1	1	
1998	27	17	2	4	3	
Total	103	86	3	6	6	1

[1] Number of pairs found in September, when breeding usually started (in 1993, this excludes pairs involving birds probably killed by the Brodifacoum poison drop in late September)
[2] Number of those pairs still together in December, by which time most clutches had been initiated

Table 2 Pair bond retention between breeding seasons by North Island robins (*Petroica australis longipes*) on Tiritiri Matangi Island, Hauraki Gulf, New Zealand

	Pairs at end of year[1]	Together next year[2]	Male dead	Female dead	Both dead	Female with new male
1992-93	7	3	1	1		2
1993-94	9	6	1			2
1994-95	14	8	1	2	2	1
1995-96	20	13		5	1	1
1996-97	22	12	3	5	2	
Total	98	57	13	16	6	6

[1] Number of pairs found in December of previous year
[2] Number of those pairs still together in September the following year

successive clutches, and were fed on the nest by 1 male while the other male fed her previous fledglings. One of these switched back to the original male for subsequent seasons, whereas the other remained with the new male. In 2 instances, a female switched to an adjacent older male when his mate died. Another female subsequently switched to one of these abandoned males, who was also older than her previous partner. Of the 6 instance of a female switching mates between breeding seasons, 2 involved the females that switched back to their previous mates (see above). The other 4 all involved switches to adjacent territory holders, 3 of the 4 original pairs having failed to fledge any young.

While there were a few instances of females switching to older males when the males became available, there was no overall tendency for females to pair with older males. For each year, we counted the number of new pairs involving 1st-year versus older males, and related this to the pool of available males in both categories (this pool excluded males remaining in the same pair as the previous season, and excluded males that died before September). On average, 49% (26/53) of the available 1st-year males and 54% (50/92) of the available older males obtained mates (Table 3). These proportions are similar to those expected if females were choosing at random from the available pool (Table 3). It is probably unrealistic, however, to expect females to choose from all males on the island (see discussion). We therefore considered an alternative model in which a female first settles in a patch, then chooses at random from the available males in her patch. The number of 1st-year males that paired is slightly less than that expected based on this model (Table 3), but not significantly (goodness-of-fit test based on total paired versus expected for 1st-year and older males; $\chi^2 = 2.09$; df = 1; $P = 0.148$).

Breeding season

Combining all years, the mean date that females laid their first recorded clutches of the year was 26 September (Table 4), and the mean date that they laid their last recorded

Table 3 Pairing of available male North Island robins (*Petroica australis longipes*) on Tiritiri Matangi Island, in relation to age.

	1st-year males[1]			Older males		
	Paired/ available[2]	Expected at random[3]	Expected constrained[4]	Paired/ available	Expected at random	Expected constrained
1992	3/10	2.69	2.89	4/16	4.31	4.11
1993	2/5	2.73	4.00	10/17	9.27	8.00
1994	1/3	1.50	1.67	7/13	6.50	6.33
1995	8/16	8.73	9.00	4/6	3.27	3.00
1996	3/7	3.04	3.67	7/16	6.96	6.33
1997	0/2	1.40	0.67	14/18	12.60	13.33
1998	9/10	8.13	9.00	4/6	4.88	4.00
Total	26/53	28.22	30.90	50/92	47.79	45.10

[1] All birds produced on Tiritiri Matangi were of known age, and translocated males were divided into 1st-year versus older birds based on plumage

[2] "Paired males" includes those paired at the start of each breeding season, and "available males" includes all males that were not still in pairs formed the previous year

[3] "Expected at random" is number of males in each category expected to be paired if females chose at random from all available males on the island

[4] "Expected constrained" is the number of males in each category expected to be paired if females settled in a forest fragment, then chose among the available males in that fragment

[5] We assumed that the translocated males were in their second year if they had adult plumage, hence these values will slightly underestimate the true mean ages

clutches of the year was 13 November (Table 5). Nesting started latest in the first 2 years, when most of the females involved had been recently translocated (7/7 in 1992/93 and 6/10 in 1993/94). Nesting also finished earliest in these 2 years. The earliest clutches were laid in mid to late August, in 1994/95, and were at the beginning of September in subsequent years. Other than the first 2 years, the latest clutches were laid in late December or early January. The dates for last clutches were extremely variable among birds, with some females having only a single recorded clutch in September. This partially reflects low reproductive effort by these birds, but these data also include females that died during the breeding season (Table 1). In addition, some clutches may have failed before they were found.

The latest time that a fledgling was still being fed by its parents was mid-March, in 1994/95. The earliest that the last fledglings became independent was late January, in 1992/93, and usually all fledglings were independent by late February. The breeding season therefore typically lasted about 6 months, from early September until late February.

There were 4 instances in which a monitored female had no clutches recorded in a year (1 in 1992/93, 1 in 1993/94, 1 in 1996/97, 1 in 1998/99), and these are excluded from the above statistics. The 1st and 3rd involved an unusual pair that was also the longest-lasting pair. The male fed the female and repeatedly tried to copulate with her throughout most of each breeding season. They produced at least 6 clutches during their other years together but none of the eggs ever hatched. The other two involved a female that disappeared midway through the breeding season, and a female that moved to a new bush patch midway through the breeding season and remained unpaired until the next year.

Nest building and site selection

Only females built nests, and nests were constructed of materials similar to those reported by Powlesland *et al.* (2000).

Of 131 nest sites recorded, 41 (31%) were in crowns of tree ferns. In addition, 7 nests were attached to the sides of tree fern trunks (protected by old fronds), 1 was in the fork of a branching tree fern, 1 was wedged between

Table 4 Egg-laying dates[1] for first clutches of North Island robins (*Petroica australis longipes*) on Tiritiri Matangi Island.

	Mean[2]	Earliest	Latest	SD[2]	*n*
1992/93	15 Oct	29 Sep	10 Dec	27.9	6
1993/94	11 Oct	11 Sep	6 Nov	16.3	9
1994/95	2 Sep	15 Aug	5 Oct	13.8	14
1995/96	25 Sep	1 Sep	6 Nov	17.9	21
1996/97	27 Sep	3 Sep	2 Nov	19.7	22
1998/99	2 Oct	1 Sep	6 Dec	23.7	25
Overall	26 Sep	15 Aug	10 Dec	19.7	97

[1] When a laying date was unknown it was estimated from the date of hatching or chick age, allowing 19 days for incubation. If the eggs did not hatch, the midpoint between the earliest and latest possible laying date is used

[2] Means and standard deviations were calculated by converting each date into the number of days after 1 January

Table 5 Egg laying dates[1] for last clutches of North Island robins (*Petroica australis longipes*) on Tiritiri Matangi Island.

	Mean[2]	Earliest	Latest	SD[2]	*n*
1992/93	26 Oct	29 Sep	10 Dec	32.5	6
1993/94	10 Nov	28 Sept	12 Dec	21.1	9
1994/95	4 Nov	8 Sep	6 Jan	27.3	7
1995/96	16 Nov	10 Sep	26 Dec	33.5	21
1996/97	9 Nov	11 Sep	1 Jan	33.2	22
1998/99	24 Nov	1 Sep	23 Dec	33.9	25
Overall	13 Nov	1 Sep	6 Jan	29.5	97

[1] When a laying date was unknown it was estimated from the date of hatching or chick age, allowing 19 days for incubation. If eggs didn't hatch, the midpoint between the earliest and latest possible laying date was used

[2] Means and standard deviations were calculated by converting each date into the number of days after 1 January

Table 6 Mean size of North Island robin (*Petroica australis longipes*) clutches on Tiritiri Matangi Island.

	Mean	SD	*n*
1992/93	2.13	0.35	8
1993/94	2.15	0.55	13
1994/95	2.32	0.48	22
1995/96	2.38	0.49	32
1996/97	2.30	0.47	27
1998/99	2.44	0.50	32
Overall	2.33	0.48	134

two tree fern trunks, 3 were in hollows in the top of broken off trunks of dead tree ferns, and 1 was in a cavity in the side of a dead tree fern. Sixty-five nests (50%) were built in forks or branches of live trees and shrubs, including manuka (13), mapou *Myrsine australis* (9), kanuka (8), pohutukawa *Metrosideros excelsa* (7), kohekohe *Dysoxylum spectabile* (7), ti kouka *Cordyline australis* (6), mahoe *Melicytus ramiflorus* (5), *Coprosma macrocarpa* (4), hangehange *Geniostoma rupestre* (3), karo *Pittosporum crassifolium* (2), and akepiro *Olearia furfuracea* (1). Four nests were in cavities in trunks or branches of pohutukawa (2), mahoe (1), or kohekohe (1). Another 3 nests were built in the hollow of a broken-off branch of a crested wattle tree. This is the only site known to be re-used, and the nests were built by the same female over 3 different years. Three nests were built in branches of dead trees or shrubs, one was suspended in vines (species unknown), and one was in epiphytes (species unknown) on a kanuka tree. Robins have never used any of the 15 nest boxes put out for them in 1992/93. These boxes are similar to those used by black robins (*Petroica traversi*, see Butler & Merton 1992 for design), but without a hinged roof or removable nest tray. The boxes are still on the island, and have been used by saddlebacks (*Philesturnus carunculatus*) and hihi (*Notiomystis cincta*).

The mean height of the 131 nests was 3.5 m (minimum 0.9 m, maximum 10 m).

Clutch size

Only those nests inspected at least twice during incubation were included in calculations for mean clutch size (Table 6). Most clutches were of 2 or 3 eggs; 1 clutch had only 1 egg. The overall mean was 2.34 eggs (n = 127). Mean clutch size did not vary significantly among years (Kruskal-Wallis test statistic = 6.86, df = 5, P = 0.231). It did vary significantly over the course of the breeding season; 2.09 eggs in August/September (n = 33), 2.30 in October (n = 45), 2.65 in November (n = 29), and 2.33 in December/January (n = 20) (Kruskal-Wallis test statistic = 22.68, df = 3, $P < 0.001$).

Incubation and nestling stages

Only female robins incubated. Females usually received most of their food from their mates, but also foraged themselves to varying degrees. The only times when females received no food from males was when they re-nested quickly and the male was delivering all food to the fledglings. We did not check nests frequently enough to determine incubation periods precisely. Our most precise estimate for a clutch was 17-21 days, and all incubation periods could potentially have been in that range. Of 226 eggs monitored that were known to be left in nests long enough to hatch, 192 hatched (85%).

Table 7 Reproductive success of North Island robins (*Petroica australis longipes*) on Tiritiri Matangi Island.

	Number of pairs[1]	Attempts recorded	Mean attempts/pair Trans	Mean attempts/pair Other	Success rate[2]	Mean fledglings/pair Trans	Mean fledglings/pair Other
1992/93	7	8	1.14		25% (8)	0.57	
1993/94	10	15	1.50	1.50	33% (12)	0.83	2.25
1994/95	14	30		2.14	36% (11)		3.00
1995/96	21	45		2.14	50% (36)		2.14
1996/97	22	36		1.64	70% (27)		2.45
1998/99	22	42		1.91	53% (32)		2.55
Overall			1.31	1.92	51% (126)	0.69	2.48

[1] Number of females that survived until the end of the year and were monitored throughout the breeding season (all females were paired but sometimes changed mates during a breeding season)

[2] Proportion of clutches found that resulted in at least one fledgling (does not include nests found after hatching)

Table 8 Circumstances of North Island robin (*Petroica australis longipes*) nest failures on Tiritiri Matangi Island.

	Frond emergence	Storm	Shell or chick pieces	Empty, disturbed	Empty, undisturbed	Egg(s) left in nest
1992/93	2		2	1	1	
1993/94	2	1	1		1	1
1994/95	2			1	2	2
1995/96	1	1		1	7	6
1996/97	2	1			2	2
1998/99	1	4		1	3	5
Total	10	7	3	4	16	16

Only females brooded nestlings. Males fed both females and young in the first few days after hatching, then both parents fed young. Nestling periods were also not determined precisely, but all could have fallen in the range of 17-21 days.

Reproductive success and nesting effort

When calculating the number of fledglings per female, we excluded females that died before the end of the year (Table 7) and females that were not monitored throughout the whole breeding season. Young were considered to have fledged if they were observed after fledging (all were checked within one week of the predicted fledging date) or had been checked when ready to fledge (within 1-2 days). The number of fledglings female^{-1} was lowest for females in their year of translocation; 0.57 in 1992 for the original 7 females, and 1.00 in 1993 for 6 females translocated that year (Table 7). Otherwise, the number of fledglings female^{-1} year^{-1} averaged 2.48, and did not vary significantly from year to year (Kruskal-Wallis test statistic = 3.033, df = 4, $P = 0.552$). The distribution of reproductive success was fairly symmetrical; most females reared 2 (33%, n = 84), 3 (15%), or 4 (15%) young year^{-1}. The maximum of 6 was achieved twice by the same female, once with 2 broods of 3 chicks each, and the other time with 3 broods of 2, 3, and 1. Productivity clearly varied among females and territories. The female just noted produced 5-6 young in each of the 4 years she has been monitored, whereas another female produced no young in 6 years.

We measured the nesting success rate as the proportion of clutches that fledged 1 or more young, counting only those nests found before or during incubation. The overall success rate by this criterion was 51%, and did not vary significantly among years ($\chi^2 = 8.73$, df = 5, $P = 0.120$). Of 56 documented nest failures, 10 nests were tipped by emerging fronds at the crown of tree ferns, 7 nests were probably damaged during high winds, and 7 nests appeared to have been disturbed by animals (Table 8). Of the latter category, 2 had pieces of eggshell in the nest and the remainder had pieces of dismembered chick. Sixteen nests were simply found empty, with no apparent disturbance, and 16 had 1 or more eggs left in them.

We recorded an average of 1.92 breeding attempts female^{-1} season^{-1}, excluding females that died before the end of the year (Table 7). This represents the minimum number of attempts because some failed attempts would not have been detected, particularly nests failing during the incubation stage. Most females had 1 (29%, n=84), 2 (51%), or 3 (15%) recorded attempts per year. As noted above, there were 3 instances in which a female had no recorded attempts. There were 2 instances of a female having 4 recorded attempts, but neither female was successful. The mean interval from fledging to laying of the next clutch was 3.9 weeks (SD = 1.8, n = 15, using cases for which we could determine the interval to within 1 week). The minimum was 10-16 days. The mean interval from nest failure to subsequent egg laying was 2.0 weeks (SD = 1.2, n = 3), with a minimum of 6-9 days. However, the sample size is small because there were few cases where we knew precisely when nests had failed. Many females had 2 successful attempts in a year, but only 1 female has had 3 successful attempts in a year. In addition to the 6 young reared over 3 broods mentioned above, the same female produced 5 young over 3 broods in another year.

Fledgling stage

The pattern of fledgling care depended on how many chicks fledged and how quickly the female laid the next clutch. If there was only 1 fledgling, it was usually fed primarily by the male. If there were 2, each was usually fed by a different parent. If there were 3, 2 were usually fed primarily by the male, and 1 by the female. The pattern broke down as chicks approached independence, when chicks would beg from either parent and follow them. In addition, males usually fed fledglings longer than females, so chicks were fed only by the male just before independence. Females did not feed fledglings after laying the next clutch, but males sometimes fed them until the next brood had hatched.

We observed 34 sets of fledglings through to independence. That is, we observed them being fed, then observed them being chased or not fed by the parents, or dispersing from the natal territory. The latest a bird was seen being fed was 7 weeks after fledging. This involved a male who had sole care of the fledglings after the female re-nested with another male (see above). However, there were 5 other instances of fledglings being fed for at least 6 weeks. The earliest a bird was not given any food by its parents was 4.5 weeks after fledging, and the earliest a bird was chased by a parent was 4 weeks after fledging. We observed 5 instances of birds being both fed and chased by their parents at the same time (mean 5 weeks after fledging). This probably represents the point when birds become independent, as none of them was seen being fed by a parent again. The latest a bird was seen in its natal territory was 10 weeks after fledging, and the earliest a bird was seen at another location was 7.5 weeks after fledging. They would first move from the centre to an edge of the natal territory (which usually meant moving out of a gully), then begin exploring adjacent territories, and then other patches, often begging from adults they encountered.

Juveniles were sometimes chased when they encountered resident adults in other territories, but not always. We saw four different juveniles being fed by lone males in other territories. Once, the male in an adjacent territory was seen feeding the juvenile over 7 days about 4 weeks after fledging. The female also appeared to move into the male's territory at that time (chasing the juvenile several times), and mated with the resident male the next year. Three other juveniles that had dispersed from their natal patches were fed several times once or over several days. For these 3, the feeding was accompanied once by aggression, and by persistent copulation attempts for another. Lone males twice also attempted to copulate with juveniles. The juveniles responded to the attempts by turning to face the male, and gaping, the same way paired females usually respond to persistent copulation attempts by their mates. Two of the juveniles receiving food or copulation attempts turned out to be females, but did not pair with the males involved in the next breeding season. The others were of unknown sex because they died before the next breeding season.

DISCUSSION

The most important factors in the breeding biology of North Island robins on Tiritiri Matangi were probably habitat limitation and territory acquisition. Robins bred only in forest patches with a canopy of at least 6 m, the breeding population did not grow above about 65 individuals, and the proportion of juveniles surviving to breeding age declined as the population initially increased (Armstrong & Ewen, unpubl. data). These factors strongly suggest that the ability of a robin to breed on Tiritiri

Matangi depended on its ability to obtain a territory in the limited suitable habitat, in contrast to the mainland situation, where the main factor limiting reproductive success appears to be predation on nests and nesting females (Powlesland 1983; Brown 1997, Powlesland *et al.* 2000).

Habitat availability might constrain territory acquisition by both sexes, or by males only. There were always more males than females in the Tiritiri Matangi population, and all females that survived to breeding age acquired mates. We might expect that juvenile females would be welcomed into territories of lone males, and therefore that there would have been no habitat constraint on survival of juvenile females. Under this model, an equal proportion of males and females would survive to breeding age at low population density, assuming a 50:50 primary sex ratio. However, as the population reached carrying capacity, the proportion of males reaching breeding age would have decreased, but not the proportion of females reaching breeding age. Therefore, the proportion of females among recruits (birds reaching breeding age) should have become higher in later years. There was no significant change in the sex ratio of recruits among years, and the overall sex ratio of recruits was close to 50:50 (Armstrong & Ewen, unpubl. data). In addition, we observed territorial males being aggressive to young females in autumn and winter. We therefore think it is more likely that males and females both need to compete to acquire territories, and that pairing then takes place among territory holders.

When pairing takes place, it is possible that many of the females would have had a choice of available males, given the biased sex ratio. We tested for a female preference for older males, on the assumption that females could choose among any available male with a territory in the patch she had settled in. This was probably a reasonable assumption except for the largest patch (about 400 x 100 m), where a female would typically have contact with only about one-third of the males in the patch. There was no significant preference for older males versus 1st-year males, and some females mated with 1st-year males when older males were available adjacent to them. This may not be surprising given that reproductive success does not seem to be affected by the age of either the male or the female (Armstrong & Ewen, unpubl. data).

It is interesting in this context that males have delayed plumage maturation. First-year males are similar in appearance to females and juveniles, with grey-brown feathers on the back and upper breast. They acquire the darker plumage characteristic of adult males only after their first breeding season. We have not studied moulting, but if robins follow the common passerine moult schedule, they undergo their 1st pre-basic moult soon after becoming independent from their parents (Humphrey & Parkes 1959). They probably do not moult again until their 2nd pre-basic moult, which takes place in the February after their first breeding season. It is during this 2nd pre-basic moult that males acquire dark feathers on the back and upper breast. It is probably the retention, or replacement, of lighter grey-brown feathers in the 1st pre-basic moult that results in delayed plumage maturation.

There are several functional explanations for delayed plumage maturation, some of which could potentially apply to New Zealand robins. Trivers (1972) proposed that young males use their resemblance to females to gain access to other males' mates for cuckoldry. Procter-Gray & Holmes (1981) proposed that cryptic plumage offers protection from predation to young males and their offspring. Rowher *et al.* (1980) proposed that young males that resemble females are less likely to be attacked, and therefore can obtain territories more easily. Lyon & Montgomerie (1986) proposed that dull plumage signals subordinate status, both to rival males and potential mates. Of these, we reject Trivers's (1972) hypothesis given that we have found no cuckoldry (Ardern *et al.* 1997), and reject Lyon & Montgomerie's (1986) hypothesis because it predicts that females should preferentially choose older males, which we did not find. We also find Procter-Gray & Holmes's (1981) hypothesis unlikely, given the small difference in conspicuousness of the plumage types in male robins. In contrast, Rowher *et al.*'s (1980) female mimicry hypotheses is quite feasible. Resemblance to females may reduce aggression toward juvenile males in autumn and winter, giving them a higher probability of acquiring territories. This hypothesis could be tested experimentally by dyeing the feathers of juveniles to resemble mature males, and comparing their success at acquiring territories with that of control birds.

It is also interesting that adult males sometimes feed unrelated juveniles. The only obvious adaptive explanation (cf. Emlen *et al.* 1991; Clarke 1995) is that males are courting mates for the next breeding season. We cannot reject the possibility that such feeding will increase males' chance of obtaining mates. However, none of the juveniles subsequently paired with the male, and we never observed this behaviour after the end of the breeding season. We think it is more instructive to consider the stimulus-response links that normally occur, and how they can be expressed in different contexts (Jamieson & Craig 1987; Jamieson 1991). It is not surprising that dispersing robins will beg toward unrelated adults. They have recently been begging food from their parents, and may initially use the rule "beg toward any adult". During the breeding season, adult males usually encounter begging in two contexts, from their offspring and from their mates. They respond by feeding in both contexts, hence it may not be surprising that a lone male will respond by feeding an unrelated juvenile during the breeding season (these events took place in November and December). It is also not surprising that they may attempt copulation, given that this is associated with courtship feeding during the breeding season. However, males also chase intruders from their territories, so it is also not surprising that they often respond aggressively to dispersing juveniles. What is interesting, and unknown, is the behavioural or physiological cues that determine whether an aggressive or nurturing response occurs. This is interesting not only in the context of males responding to unrelated juveniles, but also in the context of parents deciding whether to chase or feed their own young. Different responses may sometimes occur almost simultaneously, given that parents sometimes feed and chase their offspring within a matter of minutes when those offspring are approaching independence (see Results). As noted above, similar conflict of responses may exist when territory holders encounter invading birds outside the breeding season, who they can potentially repel or potentially court for the next breeding season.

Once robins did acquire mates, they usually stayed in the same pairs in the same territories until 1 of the pair died, the longest pair bond lasting 6 years. However, there were several cases of mate switching, both within and between breeding seasons. Of the 12 switches discussed, 8 of these left the original male unpaired and are therefore assumed to have been initiated by the female. In most instances, the previous pair had had poor reproductive success or the female re-nested with a new male while her previous mate cared for the fledglings from the previous clutch. The latter can be considered sequential polyandry (Davies 1991), and was also reported by Powlesland *et al.* (2000). Sequential polyandry is an effective strategy for increasing reproductive output in a male-biased population, hence it is interesting that more females did not adopt this strategy, particularly in the first few years when most females had adjacent lone males. In general, robins appear to be strongly socially monogamous, regardless of sex ratio. Analysis of minisatellite DNA from this population in the first three years also showed that all pairs were sexually monogamous (Ardern *et al.* 1997). However, that male robins have large cloacal protruberances for their size (Isabel Castro, pers. comm.), which is usually a characteristic of polygynous birds (Birkhead *et al.* 1993).

The breeding season was mostly from September to February, although eggs were laid in August in one year, and a few young did not become independent until March. Based on the same criteria, Powlesland *et al.* (2000) found the breeding season at Pureora to be from September to March in the two years of their study, and a higher proportion of clutches were laid in December and January in their population. Powlesland *et al.* (2000) noted that although the breeding season was just long enough to rear three broods, few pairs did. This is consistent with our results on Tiritiri Matangi.

Powlesland *et al.* (2000) noted that robin breeding seasons are not correlated with altitude. They also do not appear to be correlated with latitude or climate in general. Tiritiri Matangi has a milder climate than Pureora, which is further south, inland and at higher altitude. Powlesland *et al.* (2000) suggest that robin density, possibly in combination with prey availability, determines the timing and duration of the breeding season. They noted that when robins were translocated from Chetwode Island to Motuara Island, where they were initially less crowded, their breeding season was longer. We agree that food supply may influence the breeding season, but the breeding season on Tiritiri Matangi was shortest in the first two years, when population density was lowest. There is no reason to believe that food supply was worse in those years. We suspect that the effect resulted from translocation, as most females breeding in those years had been released recently (there were translocations in both years).

Details of nest building, incubation and nestling care were similar to those described by Powlesland *et al.* (2000). Mean nest height was lower on Tiritiri Matangi (3.5 m) than at Pureora (5.3 m), which probably just reflects the higher canopy at Pureora. Similarly, differences in nest sites probably reflect differences in forest composition. For example, a large proportion (34%) of nests at Pureora were on tawa (*Beilschmiedia tawa*) trees or dead trunks, whereas tawa are rare on Tiritiri Matangi and there are few dead trunks. Similarly, many nests at Pureora were built in epiphytes or covered by epiphytes, a situation which was less common on Tiri where the forest is younger and has fewer epiphytes. There were more nests on tree ferns on Tiritiri Matangi (40%) than at Pureora (19%).

The seasonal pattern in clutch size was the same at Tiritiri Matangi and Pureora, with clutch sizes highest in November and smallest at the beginning and end of the breeding season. South Island robins at Kowhai Bush showed a similar pattern (Flack 1979; Powlesland 1983). While the seasonal pattern was the same at Tiritiri Matangi and Pureora, the mean clutch size was 10% smaller on Tiritiri Matangi (2.34 versus 2.60) and this was consistent for all months. We might expect birds to evolve smaller clutches on islands because of lower predation risk, but not within 7 years of reintroduction from the mainland. If the difference was genetic, it may have reflected a difference between robins at the Mamaku Plateau (the source area for the Tiritiri Matangi robins) and Pureora. Alternatively, the slightly smaller clutch size and slightly shorter breeding season on Tiritiri Matangi could both result from resource limitation. Pureora robins may have greater resources because their population density is kept low by predation. Under this resource limitation hypothesis, we would have expected to see a decrease in per capita reproductive output as the population increased, as happened with saddlebacks (*Philesturnus carunculatus rufusater*) over their first five years after reintroduction to Mokoia Island (Davidson 1999). The pattern may have been prevented by the effects of translocation on reproductive output. The longest breeding season and highest reproductive output were in the 3rd year of the study on Tiritiri Matangi (1994/95), when no birds had been recently translocated but the population had yet to reach carrying capacity. It was also an El Niño year, which may have affected the weather and food availability but no data are available.

Powlesland *et al.* (1999) experimentally tested the effect of exotic mammals on reproductive success of robins at Pureora. They found that robins had an average of 3.8 fledglings female^{-1} in seasons after 1080 poisoning took place, whereas they had 1.5 and 0.4 fledglings female^{-1} in the same areas in the previous or following season. The higher number of fledglings was attributable mainly to an increase in the proportion of clutches that produced fledglings, from 11-30% to about 70%. The values for Tiritiri Matangi were intermediate, with 2.48 fledglings female^{-1} year^{-1} and a 51% nesting success rate. Given that Tiritiri Matangi had no exotic mammals (except for kiore in the first year), it is not surprising that reproductive success was higher than that at Pureora without management. However, it is interesting that reproductive success was 35% lower than the level achieved at Pureora after mammal control.

The lower reproductive success was partially accounted for by the 10% difference in clutch size, but resulted mainly from a higher rate of nest failure on Tiritiri Matangi. Nesting success rate, like clutch size, can be influenced by resource abundance, but we saw no evidence of chicks starving to death. We suspect that the higher nest failure rate on Tiritiri Matangi resulted from more predation by birds, particularly Indian mynas (*Acridotheres tristis*), moreporks (*Ninox novaeseelandiae*), or harriers (*Circus approximans*). Seven nests appear to have been disturbed by predators, including 4 nests after kiore had been eradicated (Table 8). The contents of another 16 nests simply disappeared, and these losses were also most easily attributed to avian predation. Assuming that young would have fledged from these 23 nests in the absence of predation, the predator-free nest success rate would have been about 71%, with about 3.5 fledglings female^{-1}. There are no mynas at Pureora (R.G. Powlesland, pers. comm.), which may account for the difference. The lower canopy on Tiritiri Matangi may also have made nests more vulnerable, particularly to harriers. It is possible that the avian predation rate was unusually low after the 1080 poisoning operation as a result of birds being killed by the 1080, but only 1 of 6 radio-tagged moreporks was found to have died shortly after the operation (Powlesland *et al.* 1998). Another factor was that robins nested more frequently in tree fern crowns on Tiritiri Matangi, hence more nests were tipped by emerging fronds.

While reproductive success on Tiritiri Matangi was lower than that at Purerora after mammal control, this was irrelevant to the population's dynamics. The number of juveniles produced was far greater than the number needed to replace the adults that died, and population modelling suggests that reproductive success would need to have been reduced to 0.8 fledglings female^{-1} before it affected the population's viability (Armstrong & Ewen unpubl. data). It is the subsequent survival of juveniles that limits the population, and juvenile survival appears to have been constrained by habitat availability. The key difference between the two populations was that, in the absence of management, reproductive success was low enough at Pureora that the population probably never reached densities where juveniles could not obtain territories. The population density can be changed with managment. With the intensive bait-station operation in the Waipapa Ecological Area at Pureora, robin densities now seem to have reached a level where juvenile survival is also limited by habitat availability.

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