

## Breeding biology of bellbirds (*Anthornis melanura*) on Tiritiri Matangi Island

SANDRA H. ANDERSON

School of Geography and Environmental Sciences, University of Auckland, Private Bag 92019, Auckland  
sh.anderson@auckland.ac.nz

JOHN L. CRAIG

School of Geography and Environmental Sciences, University of Auckland, Private Bag 92019, Auckland

**Abstract** Bellbird breeding activity was monitored on Tiritiri Matangi Is in 1977 and 1978. The density of bellbirds breeding within the study area was 2.13 pairs ha<sup>-1</sup>. Resighting of banded adult birds in consecutive years was 69%, and less than half the pair bonds were maintained into the following season. Breeding extended from Oct to Jan, with a peak in Nov. Most nests were built in tree ferns, and the mean clutch size was 3.6 eggs. Incubation and nestling periods were c. 12 and 14 days, respectively. The female bellbird was significantly more active than the male in care of the nestlings. Measurements of chick head and wing length were correlated with age. Nest success was 44%, and daily survival rate 97%. Predation, desertion, and exposure contributed to nest failure, and re-nesting was common. The mean number of nests female<sup>-1</sup> season<sup>-1</sup> was 1.3, while mean reproductive success was 2 chicks fledged. Young were independent 2 weeks after fledging, and moulted to adult plumage in their 1st year. The dynamics of the Tiritiri Matangi population, when compared with other populations, suggest that breeding behaviour is a flexible response to environmental factors, and will vary between populations depending on the level of predation, competition and habitat quality.

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### INTRODUCTION

The bellbird (*Anthornis melanura*) is a small honeyeater (Meliphagidae) endemic to the islands of New Zealand. Bellbirds formerly occurred throughout New Zealand, including most offshore islands from the Three Kings Islands (31°S) to the Auckland Islands (54°S), but are now rare north of 38°S. All New Zealand honeyeaters suffered a decline in the north during the 1860s (Buller 1873; Turbott 1961; Craig & Douglas 1984). The stitchbird (*Notiomystis cincta*), which is the most subordinate of the 3 species (Craig *et al.* 1981b; Craig 1984), was reduced to a single population on an offshore island. Whereas the largest and most dominant of the 3 species, the tui *Prosthemadera novaeseelandiae* (Craig *et al.* 1981a) has returned to all areas except the Three Kings Is, bellbirds have not re-established in the northern mainland. Reasons for the decline are uncertain, and although a number of attempts have been made to re-establish bellbird into northern forests all transfers have been largely unsuccessful. In contrast, on even northerly offshore islands, the bellbird is common and in the absence of introduced mammalian predators attains high densities relative to the mainland (Bartle & Sagar 1987).

The aim of this paper is to expand the baseline information on bellbird ecology, thereby increasing

the potential for successful future management of the species. The study characterises the breeding behaviour of bellbird on Tiritiri Matangi and identifies trends in the timing and duration of each breeding stage. Aspects of the population dynamics are compared with those of bellbirds on other offshore islands and the mainland of New Zealand. The role of predators, competitors, and habitat quality in the dynamics of bellbird populations is discussed. The proposal that bellbirds on the Poor Knights be classified as a distinct subspecies from bellbirds in the North Island (Bartle & Sagar 1987) is also examined.

### METHODS AND STUDY SITE

#### Study area

Bellbirds were studied on Tiritiri Matangi Island, situated in the Hauraki Gulf 25 km north of Auckland, New Zealand. At the time of study, the bellbird population was c. 150 and much of the island's 220 ha was rough pasture, with pockets of remnant forest totalling <20 ha. The study was conducted primarily in the largest (4 ha) forest patch, shortly after grazing had ceased and the island vegetation had been left to regenerate. The study forest comprised mixed coastal species, with a canopy including kohekohe (*Dysoxylum spectabile*), taraire (*Beilschmiedia tarairi*), mahoe (*Meliccytus ramiflorus*), and pohutukawa

(*Metrosideros excelsa*). Individual rewarewa (*Knightia excelsa*) and a single puriri (*Vitex lucens*) were important nectar sources. The shrubs *Coprosma rhamnoides*, *C. areolata*, and *Geniostoma ligustrifolium* provided a late season fruit source within the study forest. Bellbird activity in the coastal and valley areas adjacent to the study forest was also observed. The vegetation of these areas was dominated by New Zealand flax (*Phormium tenax*), ti (*Cordyline australis*), kanuka (*Kunzea ericoides*), manuka (*Leptospermum scoparium*), and pohutukawa.

### Distribution

The 4 ha study forest was gridded at 15 m intervals. Adult birds using the study area had previously been captured in mistnets and individually colour-banded. Individuals were identified on sighting and their position plotted to provide an estimate of the range and core area of bellbird pairs. Nest localities were mapped to calculate the density of breeding pairs within the study area. Survivorship of individuals, as well as maintenance of pair bonds into the following season, was monitored.

### Breeding

Bellbird breeding activity was intensively monitored in Oct-Jan for 2 seasons (1977 and 1978), with additional observations made in the preceding 4 years. Information was obtained for 27 nests from 17 pairs. Nests were found by observing paired birds for signs of breeding activity. These included carrying nesting material or food, hurried feeding and 'twittering' behaviour by the female, and worn tail feathers, brood patches, and extruded cloaca in brooding females. Recorded song was also used to lure females, and the responding bird could then be followed back to a nest. Nests were described, and where possible monitored daily to assess building and laying activity. Clutch size and the hatching success of eggs were checked while the parents were absent from the nest, using a ladder and nest mirror. Head, wing, and tarsus measurements of the nestlings from a single nest were taken daily using vernier calipers to obtain a growth pattern. Nestlings were fitted with individual colour band combinations before fledging. Fledglings were monitored to independence, and the fate of juveniles recorded where possible.

### Reproductive success

To allow some comparison with the Poor Knights population, survival was calculated in the same manner as Sagar (1985). To obtain a true measure of nest success, while accounting for bias because of incomplete breeding records, Stanley's (2000) method was used to estimate stage-specific daily survival probabilities, and to calculate a point

estimate and confidence intervals for nest success of bellbirds on Tiritiri Matangi. To obtain an indication of population dynamics, the number of breeding attempts and productivity female<sup>-1</sup> were also calculated. Factors contributing to nest failure were identified where possible.

### Parental role

Active nests were observed routinely at a discrete distance for 1-h periods, to compare activity between progressive breeding stages and determine the relative role of each parent. The parent was identified at each visit to the nest, and where possible food items brought to the nest were also identified. The duration of visits to the nest, and time intervals between visits, were recorded using a stopwatch. Where duration exceeded the 60-min observation period, the minimum time was recorded. Eleven nests from 9 pairs were monitored for a total of 140 h over the course of the study.

## RESULTS

### Distribution

The average range of a bellbird pair was 201m<sup>2</sup> ( $SE_{\bar{x}} = 28, n = 9$ ) centred on the nest. Exclusiveness of the core area, and size, varied between pairs ( $\bar{x} = 139 \text{ m}^2, SE_{\bar{x}} = 22, n = 9$ ). During the breeding season, both members of the pair were typically found within the core area throughout the day. The range of most pairs overlapped at flowering resources temporarily in demand by other bellbirds. At times when no substantial nectar source occurred within the core area, the male defended feeding access within these areas of resource overlap. Important plant species during the breeding season were flowering flax, rewarewa and pohutukawa. Kanuka, manuka, ti, mahoe, hangehange, ngaio (*Myoporum laetum*), mapou (*Myrsine australis*), and the native jasmine (*Parsonsia heterophylla*) provided alternative lower reward nectar resources (Craig 1986; Anderson 1997; Castro & Robertson 1997).

Observations of territorial pairs and nests revealed 8 breeding pairs within the 4 ha study area in Nov 1977 and 9 in Nov 1978 (mean density 2.13 pairs ha<sup>-1</sup>). Numerous single birds also regularly used or resided in the same area, resulting in a higher density of individual birds. Tui held breeding territories in the study area at a similar density and competed for the same nectar resources (Stewart 1980). Dominance over the core area decreased after fledglings were independent and nesting had ceased. Although each pair remained largely site-attached throughout the year, they spent varying amounts of time away from the core area depending on food availability.

All but one of the 16 paired adults on Tiritiri Matangi in 1977 were banded, and of these 11 were

resighted the following year. Although the fate of the unbanded bird could not be certain, it was not observed with its banded mate the following year and so was presumed dead. Three of the 8 pairs remained intact and defended the same area in 1978, 1 was not observed again and the defended area taken over by neighbours, and 3 lost 1 bird of the pair. A single pair separated, each to take a new mate and become neighbouring pairs. Conversely a pair of yearlings established in 1977 persisted in the same area of forest until 1988, and a neighbouring pair formed before the study began in 1976 persisted until 1984, showing that there were also pairs which survived for many years (see also Craig & Douglas 1984).

### Breeding

During late Aug and Sep, individuals of a pair were increasingly observed together. Courtship behaviour between male and female bellbirds included duetting and chasing, and was more frequent as nesting approached. Both birds of a pair responded to taped song within the vicinity of the core area. The earliest nestbuilding was in the 2nd week of Oct and the latest on the 19th Dec. Nesting attempts were unevenly distributed over this time (Fig. 1); most nests were started in Nov, with a peak of building in mid-Nov when 1st and 2nd nesting attempts coincided. All nests begun after Nov were 2nd or 3rd nests. All fledging had occurred by the end of Jan, indicating a breeding season for bellbirds on Tiritiri Matangi extending from Oct to Jan.

Nests were built over 3-7 days. Nests were composed of a base of twigs insulated with moss and fern scales and lined with pale feathers. The completed, lined nest was typically left vacant for 1 day before laying began. Most nests (75%,  $n = 24$ ) were situated under the hanging fronds of tree ferns (*Cyathea medullaris*, *C. dealbata*, and *Dicksonia squarrosa*). Other sites selected were under the hanging fronds of ti, in the canopy of kanuka, mapou, or totara (*Podocarpus totara*) trees, and in thickets of native jasmine or *Coprosma areolata*. All nests were built above the ground, at a height ranging from 1.5-12 m ( $\bar{x} = 4.7$ ,  $SE_{\bar{x}} = 1.1$ ,  $n = 6$ ).

Laying took place over 2-4 days depending on clutch size, with eggs laid at c. 1-day intervals until the clutch was complete. Continuous incubating began only after the last egg was laid, until which time incomplete clutches were left unattended for periods of >1 h. Eggs were short oval in shape, and pale pink in colour capped with brownish-pink splashes (Bird 1999). Measurement of a single egg gave a maximum length of 19.8 mm and a maximum width of 15.5 mm.

Clutch size was 3-4 eggs ( $\bar{x} = 3.6$ ,  $SE_{\bar{x}} = 0.1$ ,  $n = 16$ ). The hatching of clutches extended over 2-3 days, depending on clutch size. The incubation

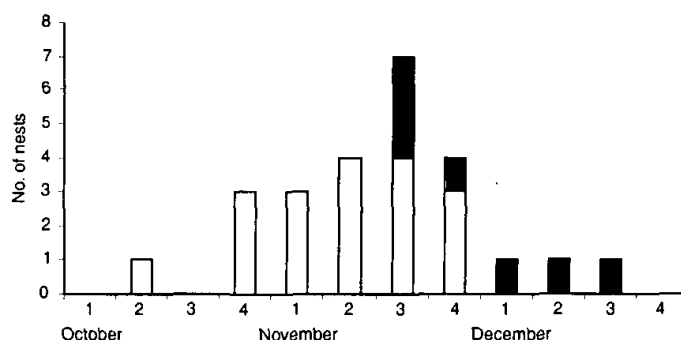


Fig. 1 Timing of nest building by bellbirds (*Anthornis melanura*) on Tiritiri Matangi Is. Open, 1st nests; filled, re-nests.

period (interval between laying and hatching of the last egg) was observed once at 12 days, although another nest was known to contain eggs for at least 13 days. The duration of the nestling period was recorded once at 14 days, although 4 other nests were known to contain chicks for at least 14 days.

For a single nest, chick wing and head length measurements were closely correlated with age (wing  $r^2 = 0.99$ ; head  $r^2 = 0.95$ ) (Fig. 2). Wing growth showed an exponential trend ( $y = 6.18e^{0.15x}$ ) while head length appeared to increase linearly ( $y = 1.59x + 13.2$ ). Tarsus growth showed a weaker correlation with age ( $r^2 = 0.77$ ) and appeared to be logarithmic, with most growth occurring by the 7th day (Fig 2).

The fledged young remained in the vicinity of the nest for 2 weeks. At 12 days post-fledging the young were foraging independently, though with supplementary feeding by the parents. Thereafter the fledglings dispersed throughout the study area. Juveniles were evident in numbers by Feb, feeding individually or converging in areas where food resources (especially *Coprosma* berries) were concentrated. Interactions within these loose juvenile feeding flocks were high, and sibling bellbirds were frequently sighted together. Juveniles moulted to adult plumage in the autumn of their 1st year, although males retained an indistinct facial stripe throughout the 1st year. While some bellbirds were observed breeding at 1 year of age, it is not known whether others delayed nesting until older.

### Reproductive success

Breeding success on Tiritiri Matangi appeared lower at all stages compared with the Poor Knights population (Table 1), although these calculations may be biased by variation in monitoring regimes (Armstrong *et al.* 2002). Nest success on Tiritiri Matangi, calculated from data for all 1st nests ( $n = 17$ ) and corrected to take into account the time-span of observation for each nest using

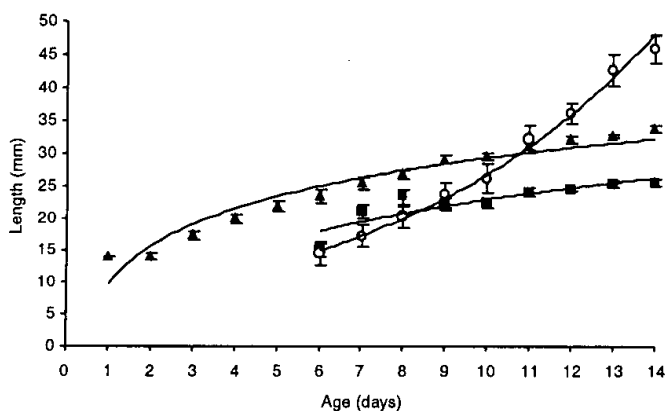


Fig. 2 Mean growth rates of 3 bellbird (*Anthornis melanura*) chicks from a single nest on Tiritiri Matangi Is. Solid triangle, head; solid square, tarsus; open circle, wing. Error bars,  $\pm 1 SE_{\bar{x}}$ .

Table 1 Comparison of apparent breeding success of bellbirds (*Anthornis melanura*) on Tiritiri Matangi Is and Poor Knights Is. No. of nests in parentheses.

	% eggs hatched	% chicks fledged	% overall success
Poor Knights Is	87 (42)	95 (8)	83 (?)
Tiritiri Matangi Is	70 (16)	68 (16)	49 (12)

Stanley's (2000) method, was 44%. The combined survival rate model was used since this had the lowest value for Akaike's Information Criterion (AIC) (Burnham & Anderson 1988), and so offered the best compromise between fit to the data and simplicity (Armstrong *et al.* 2002). Daily survival rate, assuming an incubation period of 12 days and a nestling period of 14 days (with log-odds transformed 95% confidence intervals), was 97% during the incubation stage (88-99) and 97% during the nestling period (91-99).

Since only 1st nests were used to estimate nest success, but re-nesting was common, an indication of population dynamics was obtained by calculating the number of breeding attempts, and productivity (young fledged), per female. The mean number of nests female<sup>-1</sup> season<sup>-1</sup> was 1.3 ( $SE_{\bar{x}} = 0.17$ ,  $n = 16$ ), while average minimum female productivity per season was 2.0 ( $SE_{\bar{x}} = 0.6$ ,  $n = 13$ ). Pairs with a clutch of 4 eggs were significantly more likely to fledge young successfully when compared with 3-egg clutches (Fisher's exact,  $P = 0.01$ ,  $n = 12$ ). The age of pairs was not known for sufficient nests to consider parent age as a potential variable determining success.

Re-nesting was more common following initial nest failure (55%,  $n = 9$ ) than following successful nests (29%,  $n = 7$ ). Factors associated with nest failure were predation, desertion, and storm damage. Predators present on the island were kiore

(*Rattus exulans*), ruru (*Ninox novaeseelandia*), and the Australasian harrier (*Circus approximans*). Four of the failed nests had been depredated. One of these was a confirmed kiore predation, whereas 2 other nests showed signs of kiore predation (empty nest with shell underneath). The latter were repeat nests at the same site. The 4th predation was by a harrier on a nest on the exposed lower edge of the bush patch. Three other failed nests were deserted. In one of these the nest had been exposed by a fallen trunk and contained a dead chick, another contained a chick c. 1 day old and a broken egg, and the 3rd contained a chick c. 9 days old and a cold egg. Storm damage accounted for 2 failed nests, 1 of which was exposed on the outer fringe of the bush patch. Five nests contained an infertile egg, and hatching success (excluding eggs that failed because of predation, weather, or desertion), was 75% (41/55 eggs,  $n = 16$ ).

### Parental role

Differential status between the sexes (Craig 1986) reversed with the onset of nesting. The female became more dominant in the vicinity of the nest, and where visits coincided at the nest the female displaced the male.

Only the female undertook nest-building, but she was often accompanied by the male. The female was also solely responsible for incubation, while the male visited occasionally and fed her or called her off the nest to feed. Incubation bouts were often longer than 1 h, while intervals off the nest were less than 15 min (Table 2). The male guarded the nest area and also actively defended a nectar source in which the female was able to feed.

Both parents cared for the nestlings, bringing in food and disposing of faecal sacs, although the female visited significantly more often (Wilcoxon signed rank test,  $S = 37.5$ ,  $P \leq 0.05$ ,  $n = 15$ ) and spent significantly longer intervals at the nest (Wilcoxon signed rank test,  $S = 60$ ,  $P \leq 0.01$ ,  $n = 15$ ) than the male (Tables 2, 3). Time spent brooding the young decreased over the nestling period (Table 2). Food brought to the nest consisted mainly of insects, acquired by hawking, foraging in litter and gleaning tree surfaces, although fruit was observed carried to a late (Jan) nest. Tree species which were preferred foraging locations of bellbirds included kohekohe, manuka, kanuka, and pohutukawa.

The fledged young were cared for by both parents, unless the female re-nested in which case the male assumed custody. There was no significant difference between the parents in either frequency or duration of visits to young fledged from the nest (Wilcoxon signed rank test) (Tables 2, 3). Feeding rates decreased as the fledglings approached independence and their diet shifted to available fruit. Adult time spent with the fledglings was minimal (Table 2).

**Table 2** Time (min) at and away from eggs or young by female and male bellbirds (*Anthornis melanura*) during breeding ( $\bar{x}$   $\pm$   $SE_{\bar{x}}$   $n$  = no. of nests).

		Interval on nest		Interval off nest	
		Female	Male	Female	Male
Incubation	Early (day 1-4) $n = 5$	46.2 $\pm$ 11.7	0.2	9.1 $\pm$ 3.1	49.9 $\pm$ 12.6
	Mid (day 5-8) $n = 4$	22.9 $\pm$ 6.2	0.1 $\pm$ 0.1	4.3 $\pm$ 1.3	38.0 $\pm$ 11.5
	Late (day 9+) $n = 6$	31.7 $\pm$ 8.7	1.4 $\pm$ 0.2	7.0 $\pm$ 1.7	.
Nestling	Early (day 1-5) $n = 7$	6.0 $\pm$ 1.1	0.9 $\pm$ 0.2	4.6 $\pm$ 1.4	182.1 $\pm$ 163.8
	Mid (day 6-10) $n = 5$	2.2 $\pm$ 0.8	0.4 $\pm$ 0.1	6.2 $\pm$ 1.1	30.8 $\pm$ 18.6
	Late (day 11+) $n = 3$	1.2 $\pm$ 0.2	0.2 $\pm$ 0.1	6.1 $\pm$ 2.1	14.9 $\pm$ 3.8
Fledgling	Early (day 1-5) $n = 1$	0.2	0.1	4.9	21.2
	Late (day 6+) $n = 4$	0.1	0.1	29.9 $\pm$ 2.8	9.6 $\pm$ 2

The brood was attended for proportionally less time as breeding advanced (Fig. 3), and from mid-nestling was more often unattended than attended.

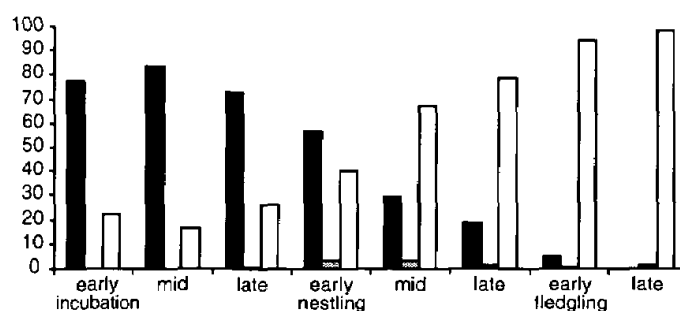
**Table 3** Visitation rate (visits  $h^{-1}$ ) to eggs/young by female and male bellbirds during breeding ( $\bar{x}$   $\pm$   $SE_{\bar{x}}$   $n$  = no. nests)

		Female	Male
Incubation	Early (day 1-4) $n = 5$	1.8 $\pm$ 0.4	2.0
	Mid (day 5-8) $n = 4$	3.0 $\pm$ 0.7	0.5 $\pm$ 0.8
	Late (day 9+) $n = 6$	6.0 $\pm$ 2.0	5.0
Nestling	Early (day 1-5) $n = 7$	23.6 $\pm$ 14.1	9.3 $\pm$ 4.8
	Mid (day 6-10) $n = 5$	40.6 $\pm$ 16.6	25 $\pm$ 7.8
	Late (day 11+) $n = 3$	11.0 $\pm$ 4.0	6.3 $\pm$ 4.8
Fledgling	Early (day 1-5) $n = 1$	41.0	6.0
	Late (day 6+) $n = 4$	2.7 $\pm$ 0.3	12.5 $\pm$ 5.2

## DISCUSSION

Bellbird population dynamics have been little studied, although some information is available from individual reports (Oliver 1955), nest records of the Ornithological Society of New Zealand, notes from Stewart Is (Guthrie-Smith 1914) and Kapiti Is (Wilkinson & Wilkinson 1952), and a detailed account of the breeding population on the Poor Knights Is (Sagar 1985). Despite the paucity of comparative behavioural information, differences in the Poor Knights population in timing of breeding, and clutch number and size, were used to substantiate weak differences in plumage and morphometric characters and warrant subspecific status (Bartle & Sagar 1987).

The population density of bellbirds recorded on Tiritiri Matangi was low compared with offshore islands free of mammalian predators (Turbott & Bull 1954; Sagar 1985). Resighting of adult birds in consecutive seasons on Tiritiri Matangi was 69%, and less than half the pairs remained intact into the following season. This suggests that turnover of adults may have been higher than originally thought (Craig & Douglas 1984). Adult turnover and low density on Tiritiri Matangi may be causally related to the presence of competitors and predators, as well as habitat modification. Tui and

**Fig. 3** Proportion of time eggs or young were attended by male and female bellbirds (*Anthornis melanura*) over the breeding period on Tiritiri Matangi Is. Filled, female; shaded, male; open, unattended.

silvereve (*Zosterops lateralis*), both nectar-feeding species, were present on the island. Tui are known to displace bellbirds at resources (Craig *et al.* 1981a), while silvereys feed on many of the same plant species, suggesting inter-specific competition may have contributed to lowering bellbird density. In addition the predators Australasian harrier, ruru, Indian myna (*Acridotheres tristis*) and kiore also occurred on Tiritiri Matangi, and nest predation was common. Habitat modification may have further limited bellbird population numbers, because farming reduced and fragmented the forests, and regeneration of the shrub layers was limited by more than a hundred years of clearing, browsing and trampling by domestic stock, along with seed predation by kiore (Esler 1978). Density estimates of bellbirds on Cuvier Is, where kiore were also present (Blackburn 1967), and Little Ohena Is, which is limited to 5.5 ha (Blackburn 1970), were similar to those for Tiritiri Matangi. In contrast on the Poor Knights Is, where other honeyeaters were absent, the forest unmodified, and predation by harriers (the sole predator) negligible, bellbirds attained a density 10-fold higher than on Tiritiri Matangi (Sagar 1985).

The nesting period on Tiritiri Matangi was extended relative to the single laying peak on the Poor Knights. Sagar (1985) proposed sharp seasonal variation in food availability on islands as the cause of the contracted season on the Poor

Knights, although pohutukawa was the main nectar supply on both Tiritiri Matangi and the Poor Knights Is. Similarity between the nesting period on Tiritiri Matangi and breeding reports for the mainland (Oliver 1955) suggests breeding season duration may reflect more than physical differences between islands and the mainland. Bellbirds on the Poor Knights are only reported to have single clutches, while on Tiritiri Matangi 6 of 17 pairs laid more than 1 clutch and up to 3 clutches were laid season<sup>-1</sup>. Most repeat nests on Tiritiri Matangi were in response to nest failure and as such were replacement clutches rather than true 2nd broods. On Tiritiri Matangi all nesting after November was replacement clutches. Thus, the most likely cause of a prolonged breeding season on Tiritiri Matangi, and the mainland, is low population density and the low success of early broods.

Bellbird nests on Tiritiri Matangi were built typically well above the ground, perhaps in response to ground predators, and were often in tree ferns. Both tui (Stewart 1980) and New Zealand robin (*Petroica australis*) (Armstrong *et al.* 2000) were also monitored on the island and both nested within the same height range and preferentially used tree ferns as nest sites. Contrastingly, on the Poor Knights, in the absence of rodents, nests built at ground level were common (21%,  $n = 70$ ) (Sagar, 1985). Incubation and nestling periods in the Tiritiri Matangi population also appeared to be shorter (12-13 and 14 days, respectively, as against 14.5-15.5 and 19 days) than on the Poor Knights Is, but similar to those reported for the mainland (Wilkinson & Wilkinson 1952) although low sample sizes limit interpretation of these results. Lack (1968) suggests that security from predators allows birds to spend longer raising a brood. An inverse relationship between predation level and brooding period for the 2 islands supports this theory.

The clutch size on Tiritiri Matangi ( $\bar{x} = 3.6$ ,  $SE_{\bar{x}} = 0.1$ ) is similar to that reported by Oliver (1955) for mainland populations, and larger than that reported for the Poor Knights ( $\bar{x} = 2.9$ ,  $SE_{\bar{x}} = 0.1$ ) (Sagar 1985). Difference in clutch size is probably related to differences in population density and breeding success (Sagar 1985). Larger clutch size in the Tiritiri Matangi population may be a response to the seasonal population change, which would result in fluctuating food supply and allow exploitation of oncoming food in spring (Lack 1968). Conversely the inability of individuals on the Poor Knights to consistently lay a large clutch may be a result of resource limitation at high density (Lack 1968), and low population turnover (Sagar 1985).

Bellbird nestling growth was rapid, and closely resembled the pattern reported by Stewart (1980)

for tui. A precise fit between length and age for both wing and head growth in chicks provides a useful management tool for breeding bellbirds, especially in situations where nests can only be monitored intermittently. Rate of tarsus growth indicates that nestlings can be banded safely from the 7th day.

Nest success on Tiritiri Matangi, calculated for all first nests using Stanley's (2000) method, was relatively low. Survival rate did not differ between egg and chick nest stages. The high rate of bellbird nest failure on Tiritiri Matangi was similar to that for North Island robin monitored on the island for 6 seasons, including one before kiore were eradicated from the island (Armstrong *et al.* 2000). This suggests that although kiore predation was a factor in bellbird nest failure, and was also identified for tui nests (Stewart 1980), other factors are also significant. Predation by Australasian harriers was confirmed in at least 1 instance in the present study, and loss of robin nests to morepork, hawks, and myna was significant (Armstrong *et al.* 2000). The relatively low canopy on Tiritiri Matangi and the large edge of the bush fragment may expose nesting passerines to increased avian predation, especially where suitable nesting habitat is limiting. Loss of bellbird nests to storm damage may also have been a result of marginal habitat use. In all instances of nest desertion in bellbird only 1 chick remained in the nest, and there were no instances of nests fledging single chicks. This may mean that re-nesting, rather than raising a single chick, offered a better investment for bellbird parents. The tendency for bellbird to abandon single-chick nests would also effectively protect them from parasitism by cuckoos. Alternatively, begging by a single chick may not have been sufficient to stimulate the parents to continue feeding. One of the suggestions why Chatham robin (*Petroica traversi*) chicks fostered to warbler nests failed to survive the nestling period was that they did not call frequently enough to stimulate the foster parents to bring sufficient food (Butler & Merton 1992).

Although bellbird nest success was low, female reproductive success season<sup>-1</sup> was higher as a consequence of re-nesting. Insufficient data on the age of birds were available to determine whether this was a factor in female productivity and nest success. However, Stewart (1980) reported that in tui breeding on the island, 1st-year females were responsible for the extremes in clutch size, while older males were able to defend areas adjacent to richer nectar supplies and the broods of older parents grew faster.

The female of a pair was primarily involved in nest care, including nest-building, brooding and feeding the offspring. While males contributed to

feeding their incubating mate and the young, most time was spent defending the core area and access to a food supply. Male bellbirds on the Poor Knights may have been more involved in feeding young than their Tiritiri Matangi counterparts, at least during the early nestling period (Sagar 1985). Because males are dominant over females (Craig & Douglas 1984; Craig 1986), they would have a greater ability to obtain food in the high-density population of the Poor Knights. On Tiritiri Matangi, where bellbird densities were lower, males may have been more effective defending a food source for the female and offspring, or females may have required less male help where resources were higher. Stewart (1980) found that in tui, the ability of the male to defend a quality territory had implications for the pair in maintaining an efficient feeding regime for themselves and their progeny.

Fledglings on Tiritiri Matangi became independent 2-3 weeks after leaving the nest. In contrast Poor Knights fledglings are attended for up to 6 weeks (Sagar 1985). Where there is intense competition among con-specifics for food, and juveniles have lower foraging or competitive ability, there is often extended parental care (Trivers 1972; Clutton-Brock 1991). The relatively high frequency of re-nesting on Tiritiri Matangi may have also contributed to early fledgling independence. Birds on Tiritiri Matangi were in adult plumage and breeding within their 1st year (pers. obs.) as on the mainland, and in contrast with the Poor Knights where they did not breed in their 1st year (Sagar 1985). The low population turnover and high population density recorded for the Poor Knights would make it difficult for 1-year-old birds to breed (Sagar 1985).

Both K- and *r*-selected characteristics have been ascribed to bellbird populations (Sagar 1985). However the information from Tiritiri Matangi suggests the populations are not *r*- or K-selected, but respond appropriately to immediate ecological conditions. Thus features such as length of breeding season and clutch size are flexible behavioural responses to differing environmental factors, and are not reliable evidence for heritable subspecific differences between insular and mainland populations. Population characteristics probably differ significantly among islands, between islands and the mainland, and between different parts of the mainland. Additional differences in plumage and growth characteristics in the Poor Knights population were weak (Bartle & Sagar 1987), and may also be environmental responses, since a certain degree (20%) of variability in growth patterns, related to geographic locality and season, is expected within a species (Ricklefs 1973). Given this, there appears to be

little support for the subspecific status of the Poor Knights population.

Analysis of the Tiritiri Matangi and Poor Knights bellbird populations provides insights for the management of this and other honeyeaters. In the absence of predators and competitors, relatively high but stable densities of bellbirds may be expected. Habitat modification and the presence of even minor predators, and competitors, appear to reduce life expectancy and breeding success, resulting in lower densities. Re-nesting may occur as a response to nest failure, and larger clutch size as well as breeding in the 1st year may be a consequence of higher population turnover. On the mainland where a more effective and wider variety of predators occur (ship rats *Rattus rattus*, Norway rats *Rattus norvegicus*, stoats *Mustela erminea*, cats *Felis catus*), and habitat modification is widespread, bellbird densities and breeding success are likely to be still lower, and large clutch size, re-nesting, and prolonged breeding more common (Potts 1884; Sparrow 1982). In this situation, bellbird numbers may decline gradually until only the more dominant and non-incubating males are present (Craig & Douglas 1984), followed by local extinction. Given the importance of this honeyeater in the pollination and seed dispersal of a range of native plant species, the implications for forest regeneration may be serious (Castro & Robertson 1997; Anderson, in press).

Tiritiri Matangi Island has undergone a series of changes since this study, including the eradication of kiore, planting of native vegetation cover over much of the island, and introduction of the endemic nectar-feeding stitchbird (*Notiomystis cincta*). Variation in bellbird breeding ecology in response to these environmental changes might be predicted. Graham (2002) reported a 90.6% increase in bellbird numbers on the island following kiore eradication, probably as a direct result of increased food availability and release from predation. Neither tui nor silvereyes showed a significant increase for the same period (1990-1998). A higher nesting success and a lower incidence of re-nesting for bellbirds might therefore be predicted. Any increase in bellbird density and nest success should be reflected in breeding season duration and clutch size. Preliminary results from a recent comparative study of bellbird breeding ecology on Tiritiri Matangi confirm that both clutch size and breeding success appear to have increased in response to changed ecological conditions, while nest height has decreased (Oron 2002). A full study of the Tiritiri Matangi population would provide a useful test of these results. In addition, attention to the dynamics of bellbird populations on the mainland is recommended. Predators, especially ship rats (Atkinson 1973), as well as competitors and the introduction of

avian disease (Myers 1923; Turbott 1961; Bartle & Sagar 1987) have been implicated as possible factors in the initial decline of bellbirds on the mainland. Population variables of bellbirds in areas with and without predator control should be compared.

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