

Changes in density of hihi (*Notiomystis cincta*), tīeke (*Philesturnus rufusater*) and tūī (*Prosthemadera novaeseelandiae*) on Little Barrier Island (Te Hauturu-o-Toi), Hauraki Gulf, Auckland, 2005–2013

Robin Toy^{1*}, Terry C. Greene², Brenda S. Greene³, Alicia Warren⁴ and Richard Griffiths⁵

¹78c Little Sydney Road, Motueka 7198, New Zealand

²Department of Conservation, PO Box 13049, Christchurch 8141, New Zealand

³Christchurch City Council, PO Box 73011, Christchurch 8154, New Zealand

⁴Department of Conservation, Private Bag 68908, Newton, Auckland 1145, New Zealand

⁵561 Woodcocks Rd, RD1, Warkworth 0981, New Zealand

*Author for correspondence (Email: twotoys@xtra.co.nz)

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Abstract: The hihi/stitchbird (*Notiomystis cincta*), an endangered New Zealand endemic species, has one self-sustaining population not subject to human intervention, located on Little Barrier Island (Te Hauturu-o-Toi), in the Hauraki Gulf, Auckland. All other hihi populations have been derived from Little Barrier Island and all require active management. Changes in the population of hihi on Little Barrier Island are, therefore, of great conservation interest. During 2005–2013, densities of hihi were compared using distance sampling to those of two other endemic forest birds: tūī (*Prosthemadera novaeseelandiae*) and tīeke/North Island saddleback (*Philesturnus rufusater*). Tūī has a broadly similar diet with both adapted to nectivory, and tīeke a more omnivorous diet. During 2005–2006, hihi densities were relatively high ($3.1\text{--}4.0 \text{ hihi ha}^{-1}$) but declined during 2007 (1.3 hihi ha^{-1}). Similarly, tūī had comparatively high densities during 2005–2006 ($3.0\text{--}4.4 \text{ tūī ha}^{-1}$ respectively) but declined during 2007 (1.6 tūī ha^{-1}). By 2009, hihi density increased (3.1 hihi ha^{-1}) then declined and remained at low densities during 2010–2013 ($0.8\text{--}1.1 \text{ hihi ha}^{-1}$). Tūī density also increased by 2009 (2.2 tūī ha^{-1}), but was variable during 2010–2013 ($0.7\text{--}3.3 \text{ tūī ha}^{-1}$). In contrast, tīeke densities remained relatively stable from 2005–2013 ($1.7\text{--}2.8 \text{ tīeke ha}^{-1}$). Extrapolating from 2013 estimates of 1.0 hihi ha^{-1} , 1.5 tūī ha^{-1} and $2.2 \text{ tīeke ha}^{-1}$, the island populations were about 3100 hihi (95% confidence interval (CI) 2500–3400), 4600 tūī (95% CI 4300–4900) and 6800 tīeke (95% CI 6200–7400). The variability in hihi and tūī densities suggests strong drivers of population change, perhaps availability of preferred food types. However, the comparatively constant hihi density in the latter half of the study compared to more variable tūī density suggests other factors are affecting the tūī population. The lower variability in tīeke density suggests their populations are influenced by other factors. Notwithstanding historical natural variation in hihi density, the low densities recorded during 2010–2013 are likely to have increased the risk of loss due to both short-term stochastic and long-term environmental change. We therefore recommend continued monitoring of the hihi population using distance sampling and investigation of the factors that influence hihi density.

Keywords: forest birds; distance sampling; saddleback; stitchbird

Introduction

Accurate detection and measurement of changes in a species population are central to the effective assessment of conservation status and trends. This is particularly critical for rare, endangered or range-restricted species, for which stochastic weather events, failure of food supply, disease, invasive predators or other anthropogenic threats can have a sudden and significant impact that requires immediate intervention (Festa-Bianchet et al. 2006; Hoare et al. 2007; Martin et al. 2012; Richter et al. 2003; Roberts & Kitchener 2006).

Hihi or stitchbird (*Notiomystis cincta*), the sole species in the endemic family Notiomystidae (Driskell et al. 2007), is classified as ‘nationally vulnerable’ (Robertson et al. 2017). Until the 1840s, hihi were relatively common in the North Island, including offshore islands (Heather & Robertson 2015). The last confirmed mainland sighting of hihi was in 1883 in the Tararua Ranges, Wellington (Heather & Robertson 2015). Thereafter, the population rapidly declined as a direct result of

habitat loss following European settlement, the introduction of mammalian predators, particularly rats (*Rattus spp.*) and mustelids (*Mustela spp.*) (Atkinson 1973; Empson & Miskelly 1999; Long 2003) and possibly avian disease (Department of Conservation 2005).

Hihi have been translocated to other predator-free islands and areas of the mainland where predators have been eradicated. Despite the absence of predators, none of these translocations have achieved self-sustaining populations and all require ongoing management to ensure their continued persistence (Makan et al. 2014). The only remaining natural and self-sustaining population occurs on Little Barrier Island and the status and patterns of change in this population are consequently of great conservation interest.

Tūī (*Prosthemadera novaeseelandiae*) is the largest of New Zealand’s honeyeaters and remains widespread and locally common throughout much of the North and South Islands of New Zealand including offshore islands (Higgins et al. 2001). Tūī also occurs on many offshore islands and is common on Little Barrier Island. Tūī was included in the

study as its diet is similar to that of hihi: both are adapted to nectivory (Craig et al. 1981) and may therefore be influenced by similar environmental drivers.

Tīeke or North Island saddleback (*Philesturnus rufusater*) is a species in the endemic family Callaeidae (Heather and Robertson 2015). Tīeke was formerly considered highly endangered and reduced to a single island population of around 500 birds. However, intensive management and reintroductions to islands and fenced mainland sites has resulted in the continuing recovery of the species (Hooson & Jamieson 2003). It is currently classified as 'at risk – recovering' (Robertson et al. 2017). Tīeke became extinct on Little Barrier Island soon after 1882, probably because of cat (*Felis catus*) predation (Veitch 2001). Following cat eradication between 1976–1980, tīeke were reintroduced to the island between 1984–1988, and coexisted with kiore (*Rattus exulans*) (Lovegrove 1996) until 2004 when kiore were eradicated (Howald et al. 2007). Tīeke was included in the study as its more omnivorous diet contrasts to that of hihi. Its population may therefore be influenced by different environmental drivers.

Previous counts of all three species on Little Barrier Island (Gravatt 1970a; McCallum 1982; Angehr 1984a; Girardet et al. 2001) have relied on a range of methods none of which adjusted for changes in detection probabilities, which makes temporal comparison of any relative measure of abundance problematic (Buckland 2006; Nichols et al. 2009). Accurate interpretation and assessment of long-term population trends for all these species on Little Barrier Island is, therefore, extremely difficult.

The objective of this study was to estimate the density of hihi on Little Barrier Island, to provide a baseline against which future changes can be measured. Comparison of hihi density with that of tūī, which has a broadly similar diet adapted to nectivory, and tīeke, which has a more omnivorous diet, was a secondary objective. We use distance sampling to estimate the density for all three species, discuss the underlying causes of observed population change and provide a baseline against which future changes can be measured.

Methods

Study area

Little Barrier Island (Te Hauturu-o-Toi) ($36^{\circ}12' S, 175^{\circ}05' E$) is a 3083 ha inactive volcano rising steeply to 722 m in the Hauraki Gulf, North Island, New Zealand. Since 1894 it has been managed as a nature reserve (Dodd 2007) and is currently managed by the Department of Conservation under the governance of the Ngāti Manuhiri Settlement Trust and Auckland Conservation Board. Māori cleared or burned the forest, primarily from the lower slopes in the west and south-east of the island. During the late 1800's visiting Europeans logged large areas of kauri (*Agathis australis*) (Hamilton 1961). At low altitudes, much of the vegetation is characterised by early successional vegetation dominated by kānuka (*Kunzea robusta*), particularly in formerly cleared areas. At mid-altitudes this gives way to kauri, hard beech (*Fuscospora truncata*), northern rātā (*Metrosideros robusta*), tawa (*Beilschmiedia tawa*), tawhero (*Weinmannia silvicola*) and at higher altitudes tāwheowhero (*Quintinia serrata*), tāwari (*Ixerba brexioides*) and southern rātā (*Metrosideros umbellata*) (Hamilton 1961).

Two large study areas covered a range of habitats and altitudes (Fig. 1). The south-west study area (590 ha) ranged from sea-level to over 600 m (mode 100–200 m). The north-

east study area (230 ha) was at higher altitude, 185 to 607 m (mode 400–500 m).

Sampling design and method

Bird counts were carried out in spring. Inter-annual differences in bird conspicuousness were minimized by surveying at the same time of day at the same locations in all years. In the south-west study area, 2005–2011 (except 2008), bird counts were carried out over a 6–14 day period on a grid of 98 points spaced 200 m apart, which sampled 13% of the island. Prior to sampling in 2012, a further 50 points were added to increase coverage to 19% of the island (Fig. 1). The north-east study area comprised 58 sample points covering an additional 7.5% of the island. These points were added to ensure that counts were undertaken in forest representative of the whole island. Logistical constraints imposed by topography resulted in fewer counts being undertaken in this area over a longer period of 28–38 days. Sampling in the north-east study area was not continued after 2011 due to these constraints.

Point-based distance sampling (Buckland et al. 2001) was carried out annually by a team of up to 16 volunteers. Observations were made between 0700 and 1600 but were abandoned if it was raining or wind strength persisted (> 2 hrs) at more than Beaufort Scale 3. Observers spent four minutes at each point, detecting the initial location of any hihi, tūī and tīeke seen or heard. The observation area around each point was truncated in the field at 25 m as the steep terrain and dense vegetation precluded accurate identification of birds' positions at greater distances. All observers were trained in distance sampling methods immediately prior to each year's count period. Training focused on bird identification and ensuring the principal assumptions of distance sampling were met. These are (1) birds at the sampling point are detected with certainty; (2) birds are detected at their initial locations (before they moved toward or away from observers); and (3) distance measurements are exact (Buckland et al. 2001). To meet the first assumption each count point was clearly marked to be visible from a distance, and observers were vigilant as they approached the point. To meet the second assumption, an aural detection was only recorded if there was no doubt as to the bird's location. When a bird was heard but not seen, observers recorded the direction it was heard and, at the end of the four minute observation period, moved in that direction to pinpoint the location of the bird. To meet the third assumption, considerable effort was made to measure distances accurately. Distances less than 6 m were recorded to the nearest 0.1 m using a tape measure. Observations between 6 and 25 m were measured to the nearest metre using either a tape measure or a laser range-finder (Bushnell Yardage Pro Sport 450).

Buckland et al. (2001) recommend a minimum of 80 observations for each species to compute robust detection functions for point count data. During 2005, the number of visits to sample points in the south-west study area did not achieve 80 observations for each species. In subsequent years, more visits were made to each point to gather more observations. In the north-east study area, 80 observations were not achieved during 2010 or 2011 because of logistical constraints of sampling within a remote and rugged area (Table 1). The impact of having fewer than 80 observations was lessened by using a pooled detection function.

Analysis

Data were analysed using DISTANCE 6.0, Release 2 (Thomas et al. 2009). Initially, radial distance measurements for each

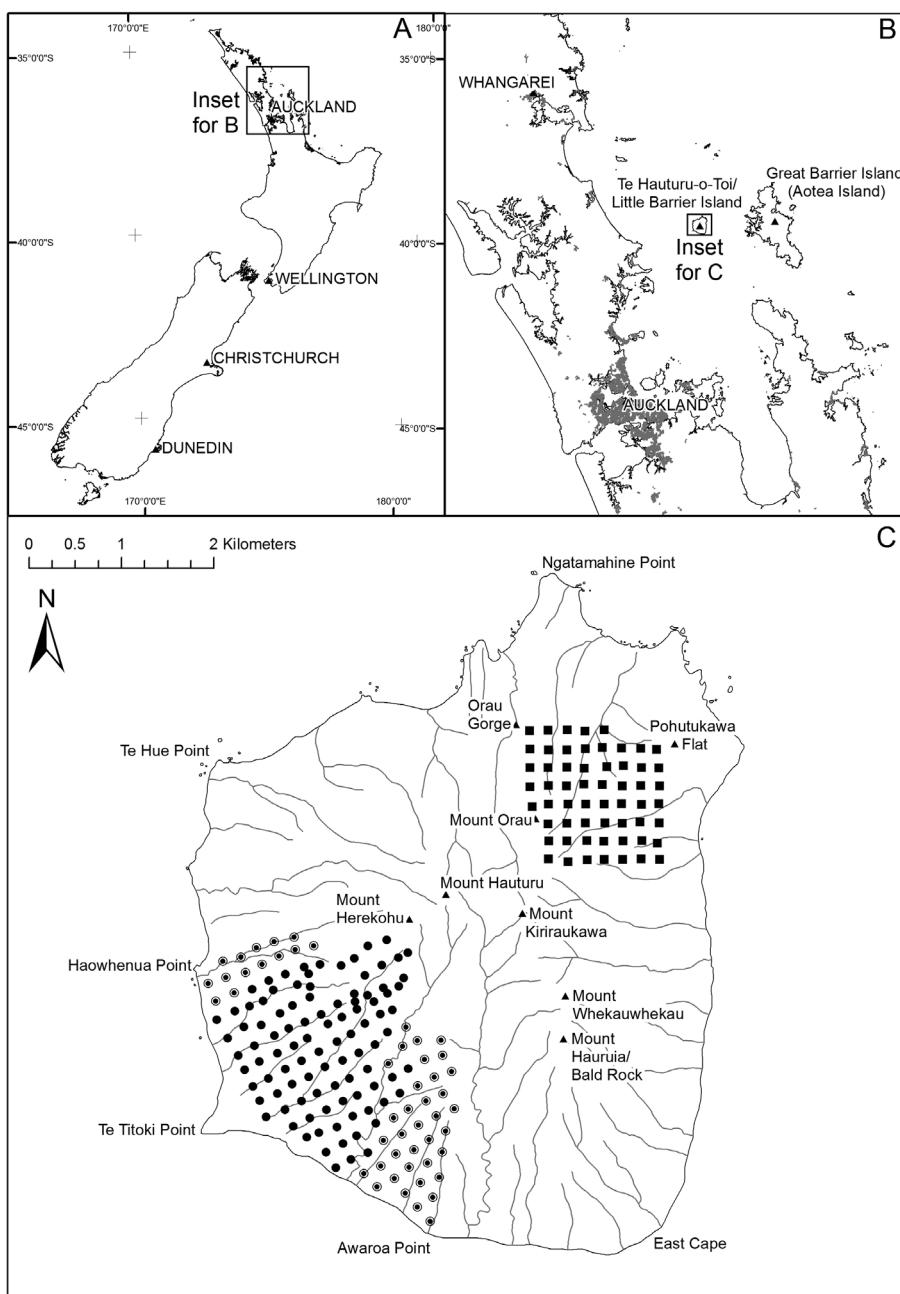


Figure 1. Little Barrier Island distance sampling observation points. Filled circles show the 2005–2011 SW sample points ($n = 98$); semi-filled circles show the 2012 additional sample points ($n = 50$); filled squares show the 2010/2011 NE sampling points ($n = 58$).

Table 1. Number of observations and sampling effort for hihi, tūī and tīeke, 2005–2013.

Study area	Year	Number of points	Number of point visits	Hihi		Tūī		Tīeke	
				n	E	n	E	n	E
SW	2005	98	264	57	22	61	23	38	14
	2006	98	623	172	28	206	33	101	16
	2007	98	1213	105	8.7	147	12	145	12
	2009	98	784	168	21	128	16	154	20
	2010	98	1078	80	7.4	145	13	177	16
	2011	98	1058	76	7.2	262	25	180	17
	2012	148	1555	86	5.5	87	5.6	184	12
	2013	148	1271	86	6.8	146	11	199	16
NE	2010	58	580	64	11	117	20	127	22
	2011	58	759	42	5.5	73	10	153	20

n, Number of observations; E, Encounter rate (100*n/Number of point visits)

species were aggregated into 1 m intervals and the resultant histograms qualitatively examined for gross errors, outliers and any issues of movement of birds towards or away from the observer prior to detection (i.e. a distinct move away from the origin) (Buckland et al 2001).

To improve model robustness, a global detection function using data pooled across survey years, was developed for each study area. Use of this function assumes differences in detectability resulting from changes in altitude, terrain, and vegetation are accounted for by the spatial and temporal coverage in sampling points. The data were post-stratified by year to determine annual density estimates and to improve density estimates in years when numbers of observations were low. Population density was then computed using the pooling robust models recommended by Buckland et al. (2001). Model fit was examined using Q-Q plots and goodness of fit tests. For each model, aggregation of distance data improved model fit, whereas, truncation additional to that used in the field did not (Fig. 2, Table 2). Akaike's Information Criterion (AIC) was then used to select the best model and, where competing models ($\Delta AIC \leq 2$) were apparent, Akaike weights were used to calculate model averaged density estimates and associated confidence intervals. To account for the slightly clustered nature of birds during this study, the mean of the observed cluster size was used to adjust density estimates for all three species.

We investigated general patterns in density estimates within each species, including the magnitude of change between years. We then extrapolated the most recent density estimates by the total forested area to provide a population estimate for each species and compared these estimates to prior studies.

Results

Estimated density of hihi in the south-west study area was high at the beginning of the study ($3.1\text{--}4.0 \text{ hihi ha}^{-1}$), decreased to 1.3 ha^{-1} during 2007, but by 2009 had recovered to the initial 2005 density. By 2010 the population had again declined to the density seen during 2007 and remained at this lower density until 2013 (Table 3, Fig. 3). Estimated density of hihi in the north-east study area was greater at $2.0 \text{ birds ha}^{-1}$ than that in the south-west study area during 2010, and similar during 2011.

Estimated density of tūī in the south-west study area also fluctuated through the study. Initially it was comparatively high ($3.0 \text{ birds ha}^{-1}$ in 2005, $4.4 \text{ birds ha}^{-1}$ in 2006) but lower during 2007–2010 ($1.6\text{--}2.2 \text{ ha}^{-1}$). In 2011, the density of birds (3.3 ha^{-1}) had returned to the high levels seen at the start of the study, then declined during 2012 ($0.74 \text{ birds ha}^{-1}$) and 2013 (1.5 ha^{-1}) (Table 4, Fig. 4). Estimated density of tūī in the north-east study area during 2010 was higher than in the south-west study area, at $2.9 \text{ birds ha}^{-1}$, but lower during 2011 at $1.4 \text{ birds ha}^{-1}$.

Tieke populations appeared more stable than either hihi or tūī. The estimated density of tieke in the south-west study area remained relatively stable at $1.5\text{--}2.6 \text{ birds ha}^{-1}$ during 2005–2013. Estimated densities in the north-east study area were higher than in the south-west study area during both 2010, $3.6 \text{ birds ha}^{-1}$ and 2011, $3.3 \text{ birds ha}^{-1}$ (Table 5, Fig. 5).

Mean cluster size in the south-west and north-east study areas for hihi were 1.06 and $1.12 \text{ birds ha}^{-1}$ for tūī were 1.12 and $1.1 \text{ birds ha}^{-1}$ and for tieke were 1.20 and $1.25 \text{ birds ha}^{-1}$ respectively. Extrapolating from 2013 estimates of 1.0 hihi ha^{-1} ,

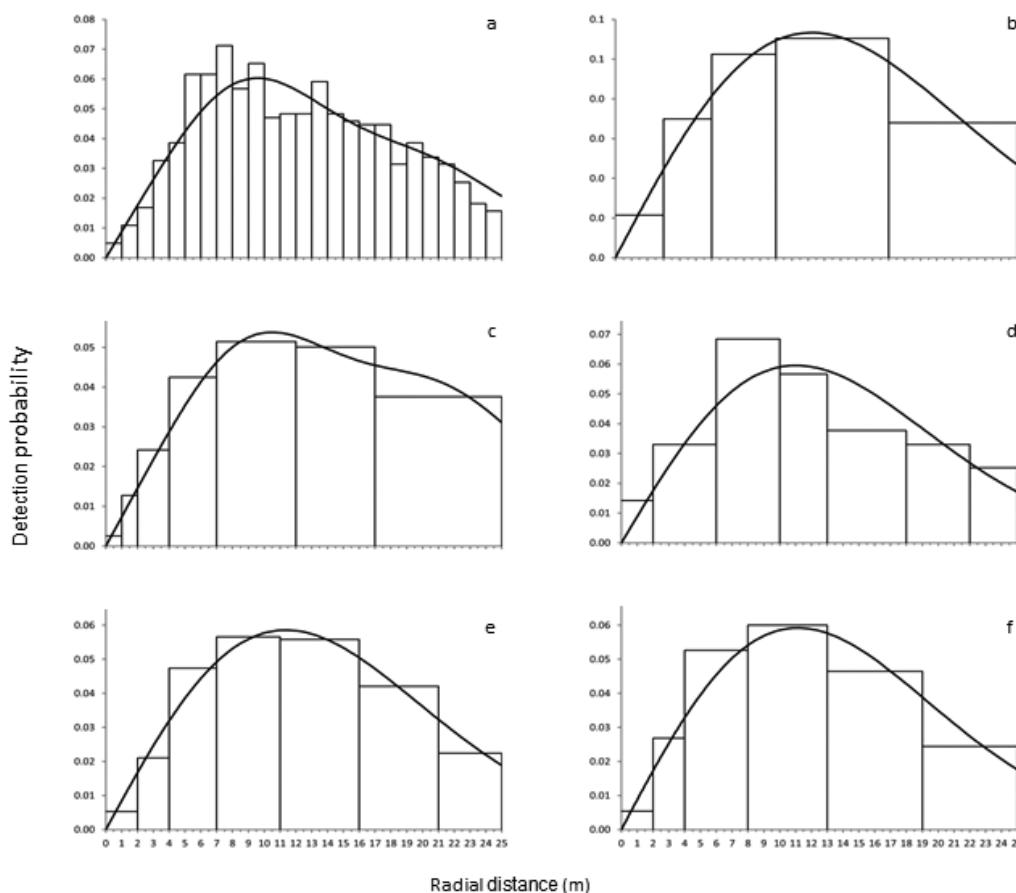


Figure 2. Global probability density graphs obtained using programme DISTANCE. The curve is the detection function (model = half normal, cosine adjusted with aggregation as used in the analysis). (a) Hihi south-west study area, 2005–2013 (b) tūī south-west study area, 2005–2013 (c) tieke south-west study area, 2005–2013 (d) hihi north-east, 2010 and 2011 (e) tūī north-east, 2010 and 2011 (f) tieke north-east, 2010 and 2011.

Table 2. Goodness of fit of population density models with $\Delta\text{AIC} \leq 2$.

Species	Study area	Cut points (m)	Model ¹	ΔAIC	Goodness of fit - P		
					χ^2	Kolmogorov-Smirnov	Cramér-von Mises (cos)
Hihi	SW	1 m intervals	Unif+poly	1.82	0.26	0.16	0.4-0.5
			Haz+poly	0.0	0.47	0.26	0.4-0.5
	NE	2,6,10,13,18, 22,25	Unif+cos	0.67	0.73	0.86	0.7-0.8
			Haz+cos	0.0	0.80	0.80	0.7-0.8
Tūī	SW	3,6,10,17,25	Unif+poly	0.0	0.22	0.027	0.2-0.3
			Unif+cos	0.25	0.92	0.33	0.5-0.6
	NE	2,4,7,11,16,21,25	Unif+poly	0.0	0.81	0.61	0.7-0.8
Tīeke	SW	1,2,4,7,12,17,25	Unif+poly	0.0	0.17	0.023	0.15-0.2
			Hnorm+cos	0.94	0.49	0.073	0.2-0.3
	NE	1,2,4,8,13,19,25	Unif+cos	1.83	0.51	0.073	0.2-0.3
			Hazrate+cos	0.0	0.42	0.26	0.3-0.4

¹ Model consisting of a key function (uniform, half-normal or hazard-rate) and an adjustment term (cosine, simple polynomial)

Table 3. Density (\widehat{D}_i) and model averaged density ($\widehat{\bar{D}}_i$) of hihi between 2005 and 2013 estimated using a global detection function.

Study area	Year	Model ¹	(\widehat{D}_i)	($\widehat{\bar{D}}_i$)	95% CI
SW	2005	Unif+poly	3.26	3.1	2.6
		Hazrate+poly	3.10		3.7
	2006	Unif+poly	4.16	4.0	3.4
		Hazrate+poly	3.97		4.7
	2007	Unif+poly	1.31	1.3	1.1
		Hazrate+poly	1.24		1.5
	2009	Unif+poly	3.23	3.1	2.6
		Hazrate+poly	3.08		3.6
	2010	Unif+poly	1.12	1.1	0.91
		Hazrate+poly	1.07		1.3
NE	2011	Unif+poly	1.08	1.0	0.88
		Hazrate+poly	1.03		1.2
	2012	Unif+poly	0.83	0.81	0.68
		Hazrate+poly	0.79		0.9
	2013	Unif+poly	1.01	1.0	0.82
		Hazrate+poly	0.96		1.1

¹ Model consisting of a key function (uniform, or hazard-rate) and a polynomial adjustment term.

1.5 tūī ha⁻¹ and 2.2 tīeke ha⁻¹, the island populations were about 3100 hihi (95% confidence interval (CI) 2500–3400, 4600 tūī (95% CI 4300–4900) and 6800 tīeke (95% CI 6200–7400).

Discussion

Several studies have shown that density estimates derived from point-transects can exceed population size derived from territory mapping (Buckland 2006; Cassey et al. 2007). This can occur when the assumptions of distance sampling are violated, particularly where there is movement toward observers (Buckland 2006; Cassey et al. 2007; Broekema & Overdyck 2012; Greene & Pryde 2012).

Table 4. Density (\widehat{D}_i) and model averaged density ($\widehat{\bar{D}}_i$) of tūī between 2005 and 2013 estimated using a global detection function.

Study area	Year	Model ¹	(\widehat{D}_i)	($\widehat{\bar{D}}_i$)	95% CI
SW	2005	Unif+poly	3.0	n/a	2.8
	2006	Unif+poly	4.4	n/a	4.0
	2007	Unif+poly	1.6	n/a	1.5
	2009	Unif+poly	2.2	n/a	2.0
	2010	Unif+poly	1.8	n/a	1.6
	2011	Unif+poly	3.3	n/a	3.0
	2012	Unif+poly	0.74	n/a	0.68
	2013	Unif+poly	1.5	n/a	1.4
NE	2010	Unif+cos	3.0	2.9	2.7
		Unif+poly	2.8		3.3
	2011	Unif+cos	1.4	1.4	1.3
		Unif+poly	1.3		1.6

¹ Model consisting of a key function (uniform) and an adjustment term (cosine, simple polynomial).

n/a Model averaged density not applicable.

The first assumption, that birds will be detected at the sample point, could have been violated for hihi because of the structural complexity of the forest habitat and the occasionally cryptic behaviour exhibited. Both factors could have impaired detection at the sample point ($p < 1.0$), which would have negatively biased the density estimate. The larger size and noisy wing beats of tūī and frequent vocalisation and noisy foraging of tīeke make it less likely that they would not have been detected at or close to survey points. The second assumption, that birds are detected at their initial locations, could also have been violated for hihi since they sometimes approach observers (RT & TG pers. obs.), which would positively bias the density estimates if this was a common occurrence. Tūī rarely responded to observers and whilst tīeke sometimes did, their vocalizing

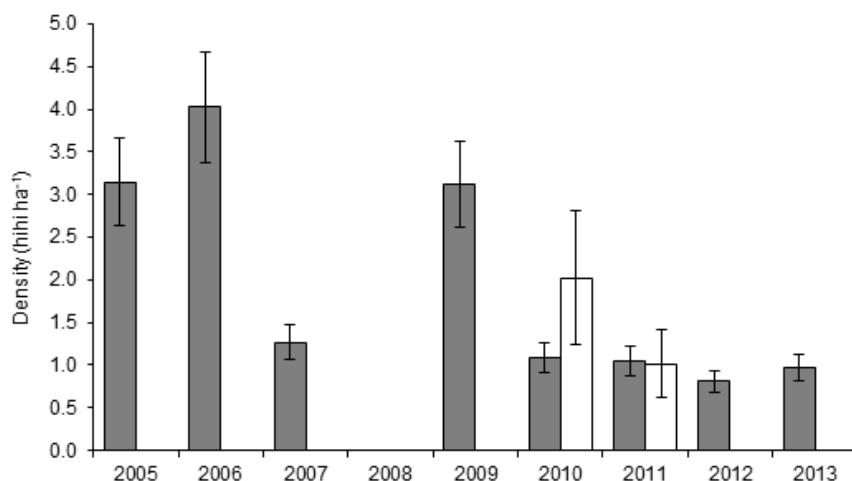


Figure 3. Model-averaged density estimates for hihi ($\text{birds ha}^{-1} \pm 95\% \text{ CI}$) between 2005 and 2013. South-west study area shaded bars, north-east study area open bars.

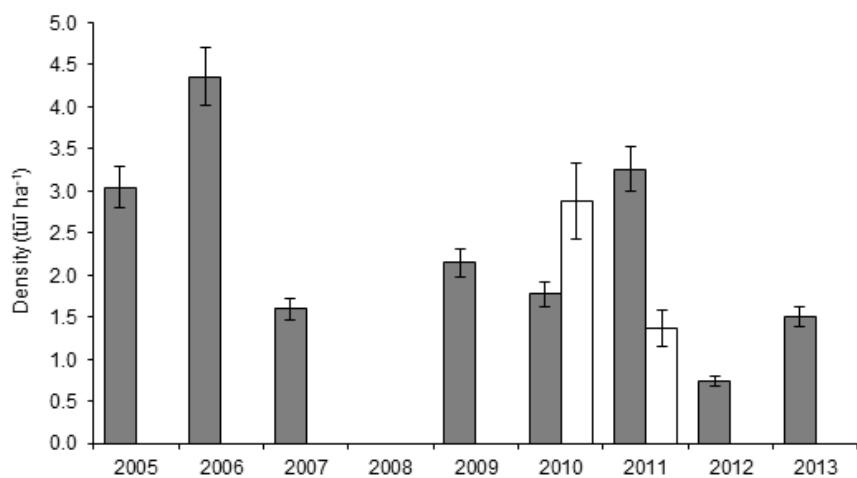


Figure 4. Density estimates for tūī ($\text{birds ha}^{-1} \pm 95\% \text{ CI}$) between 2005 and 2013. South-west study area shaded bars, north-east study area open bars.

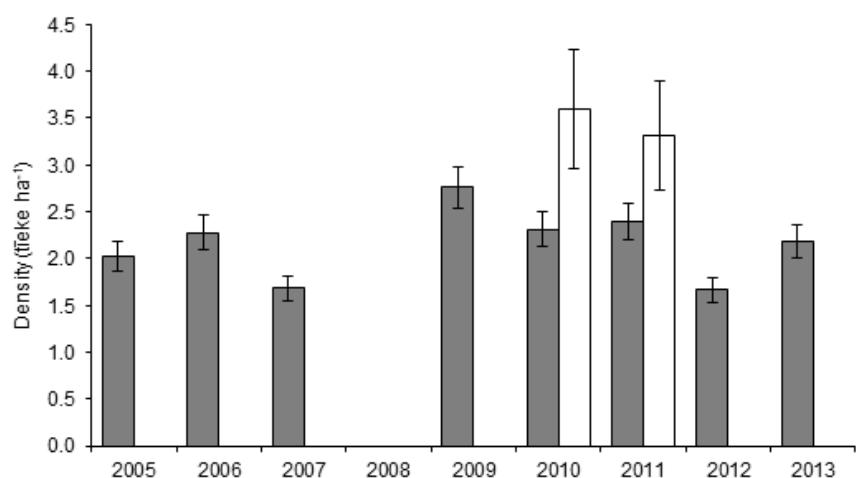


Figure 5. Density estimates for tīeke ($\text{birds ha}^{-1} \pm 95\% \text{ CI}$) between 2005 and 2013. South-west study area shaded bars, north-east study area open bars.

and noisy foraging meant their initial positions were easier to identify than those of hihi and tūī. Despite these possibilities for detection bias, detection functions showed little evidence that it occurred (Fig. 2). Violation of the third assumption, that measurements were exact, was reduced through training, and using tape measures and laser range-finders.

Ninety-five percent confidence limits for the density estimates were generally small, especially in the south-west study area, giving confidence in interpretation of results. Ninety-five percent confidence limits are greater in the

north-east study area probably due to the smaller number of observations.

Marked inter-annual variation in density estimates for both hihi and tūī was observed. Variation in timing of hihi breeding will affect conspicuousness since male hihi increase their call rate as females prepare to lay and often stop calling once eggs are laid (Taylor & Castro 2000). However, nest monitoring performed on Hauturu 2005 to 2008 showed that 93% of nests under construction were discovered after this study was completed (Baptist et al 2007, Cross 2008, Waite

Table 5. Density (\widehat{D}_i) and model averaged density ($\widehat{\bar{D}}_i$) of tīeke between 2005 and 2013 estimated using a global detection function.

Study area	Year	Model ¹	(\widehat{D}_i)	($\widehat{\bar{D}}_i$)	95% CI
SW	2005	Unif+poly	2.0	n/a	1.9 2.2
	2006	Unif+poly	2.3	n/a	2.1 2.5
	2007	Unif+poly	1.7	n/a	1.6 1.82
	2009	Unif+poly	2.8	n/a	2.6 3.0
	2010	Unif+poly	2.3	n/a	2.1 2.5
	2011	Unif+poly	2.4	n/a	2.2 2.6
	2012	Unif+poly	1.7	n/a	1.5 1.8
	2013	Unif+poly	2.2	n/a	2.0 2.4
NE	2010	Hnorm+cos	3.8	3.6	3.0 4.2
		Unif+cos	3.8		
		Hazrate+cos	3.4		
	2011	Hnorm+cos	3.5	3.3	2.7 3.9
		Unif+cos	3.5		
		Hazrate+cos	3.1		

¹ Model consisting of a key function (uniform, half-normal or hazard-rate) and an adjustment term (cosine, simple polynomial); n/a Model averaged density not applicable.

2009). Variation in timing of breeding is therefore unlikely to have affected conspicuousness of hihi.

Hihi and tūī feed largely on nectar (Higgins et al. 2001). Variation in timing of flowering of particular nectar sources could also affect hihi conspicuousness since birds feeding in the understorey are more conspicuous than those feeding in the canopy. When it is flowering, a high percentage of hihi feeding observations can be on toropapa (*Alseuosmia macrophylla*) a seasonally-significant, nectar-producing, understorey shrub (unpubl. data, Angehr 1984a, Gravatt 1970b). It is therefore likely that marked differences in the abundance and/or timing of toropapa flowering would affect the conspicuousness of hihi and positively bias density estimates. Variation in timing or abundance of flowering of other significant species such as haekaro (*Pittosporum umbellatum*) could similarly affect conspicuousness of hihi and tūī. Tīeke have a cosmopolitan diet with a far greater reliance on invertebrates (Heather & Robertson 2015) and as such their conspicuousness is less likely to be affected by phenological variations in nectar producing plants, so density estimates are less likely to be biased. The detailed phenological data needed to quantify inter-annual variation in flower abundance are not available.

The study area covered as large an area and diversity of habitats as was logistically practical, but hihi and tūī movement within the island may have contributed to the inter-annual differences in density. Angehr (1984a) noted individual birds moving 500 m from nesting sites to feed and movements of up to 3 km, which could have been in response to availability of food sources. Hihi fly 2 km on Tiritiri Matangi Island (R. Renwick pers. comm.) and 2–3 km at Maungatautari Ecological Island (K. Richardson pers. comm.) to visit artificial feeders. Tūī are known to fly long-distances to food sources (Heather & Robertson 2015) and have been seen flying to and from Little Barrier Island to other islands and the mainland (RT & TG pers. obs.). Tīeke, in contrast, hold territories throughout the year and, given the size of the sample area, bias caused by birds' movement is unlikely to have significantly affected

density estimates.

Given the lack of systematic bias in the detection functions, the consistent commencement of surveys prior to the initiation of breeding activity and the large spatial coverage of the study, we feel reasonably confident that estimates reflect actual variation in density. However, in the absence of a double-sampling method by which to compare density estimates to an absolute count of abundance in part of the survey area (Hutto & Young 2003, Bart et al. 2004), these estimates are best viewed as indicative measures of abundance, particularly for hihi, with an unknown level of systematic bias.

Large inter-annual changes in hihi and tūī density are likely to reflect real change in population abundance. In July 2007 a storm caused widespread defoliation on Little Barrier Island (AW pers. obs.) and may have reduced food available to nectivorous birds. This could be the reason for the lower hihi and tūī densities seen in 2007 compared to 2006. Such severe stochastic environmental events could explain density decreases observed between other years. Recovery rates from such events are likely to be high as hihi commonly produce four eggs per clutch and may produce two broods per year, and tūī produce two to four eggs per clutch and up to two broods per year (Heather & Robertson 2015).

In contrast, the absence of significant inter-annual variation for tīeke suggests that stochastic events, that affect hihi and tūī, have a lesser impact on species that have a more cosmopolitan diet with a far greater reliance on invertebrates. Our estimated island population of 6800 tīeke is similar to Hooson & Jamieson's (2003) estimate of the carrying capacity of the island (about 8000 birds), which was based on territory size and mapping available habitat.

Comparison of the results of our study with earlier counts is complicated by the use of different methods. Between 1975 and 1989, hihi were counted on transects as part of general forest bird surveys (Girardet et al. 2001). Observations were truncated at 10 m either side of three, 500 m walked transects (1 ha plots), without correcting for detection probability. The transects covered an altitudinal range but not the range of slopes, stream-beds and ridges utilised by hihi. Each transect was walked eight to 12 times in March to May each year and will have included juveniles from that year's breeding. Annual counts averaged 1.0 hihi per transect (0.32, 0.72, 2.1 on the three transects) and as in our study, there were marked year-on-year changes spanning a 55% decline to a 360% increase.

At six-weekly intervals throughout 1982 to 1984, Angehr (1984a) counted all birds seen or heard along three, 500 m long transects with observations made 15 m either side of the walked route (1.5 ha transects). Detection probability was not considered in calculating density, but counts were related to vegetation type and normalised by the area of habitat on the island to derive a conservative island estimate of 5545 hihi (1.8 hihi ha^{-1}). This island estimate is very similar to the average density from 2005–2013 (1.9 hihi ha^{-1}). Some of the 1982–1984 counts will have included juvenile hihi, which the 2005 to 2013 counts will not due to these counts only being undertaken in spring.

The use of different methods precludes formal comparison of density estimates from this study and earlier work. However, the inter-annual variability in density estimates seen in this study is similar to that in Girardet et al (2001). Historical accounts also suggest rapid changes in hihi abundance. Between 1880 and 1984, records of hihi on Little Barrier Island appear to show the population fluctuating markedly, for example, Reischek recorded hihi as rare in 1882 but abundant in 1883 (Angehr

1984b). Despite such accounts of periodic rarity, there is no evidence of a genetic bottleneck (Brekke et al. 2011).

Tūī are common on Little Barrier Island (Gravatt 1970a; McCallum 1982; Girardet et al. 2001). Like hihi, tūī density estimates were variable, but in the latter four years of the study tūī density continued to vary, while hihi density estimates varied little. This may arise since tūī numbers will comprise residents and transient birds coming to the island to feed, whereas hihi are all resident.

Kiore were introduced to the island by early Māori and eradicated in 2004 (Howald et al. 2007). Cats were present from about 1870 until 1976–1980 (Veitch 2001). Although there are no estimates of hihi density prior to these introductions, anecdotal evidence suggests any impact of these predators is likely to have been relatively minor. Kiore are known to feed in trees and prey on passerine birds and the eggs of smaller ground nesting petrels and shearwaters (Campbell et al. 1984, Booth et al. 1996; Rayner et al. 2007). However, hihi had co-existed with kiore for many centuries (Veitch 2001), and while there is one record of kiore predation of a hihi on a nest (Guthrie-Smith 1925) there is no evidence they were a major predator of hihi. During the 1975–1989 forest bird surveys, that covered the period of cat eradication (1976–1980), the relationship between cat density and hihi relative density was not significant (Girardet et al. 2001). Hihi feed within 1 m of the ground 6.4% of the time (Angehr, 1984a), so spend most of the time at heights at which they are less susceptible to cat predation.

The impact of native predators such as ruru (morepork, *Ninox novaeseelandiae*), kookoē (long-tailed cuckoo, *Eudynamys taitensis*), and historically kārearea (New Zealand falcon, *Falco novaeseelandiae*) and whēkau (laughing owl, *Sceloglaux albifacies*) (Low 2010; Rasch 1985) on forest bird populations is unknown.

Tieke were introduced to Little Barrier Island between 1984 and 1988 following the eradication of cats. Hooson & Jamieson (2003) used the average territory size of tieke and the area of Hauturu to estimate the island could support 8000 tieke. The difference between this and our estimate of 6800 tieke most likely arises from topographical or vegetation differences between Hauturu and the islands used by Hooson & Jamieson (2003) to derive tieke average territory size.

Large fluctuations in hihi and tūī density appear to be common. Although explicit underlying causes remain uncertain, the most likely reasons are food availability and seasonal movements of birds to patchy resources (Heather & Robertson, 2015). Despite lack of current significant predation pressure and a high diversity and abundance of food sources the low densities of hihi recorded during 2010–2013 (0.83–1.1 hihi ha⁻¹) are of considerable concern. Little Barrier Island supports the only self-sustaining population of hihi and a low-density population is at risk of significant loss due to short-term stochastic events such as storms, moderate-term threats due to invasion of predators or disease and longer-term gradual changes occurring through climate change (Correia et al. 2015). We therefore recommend continued population monitoring of the hihi population using distance sampling and investigation of the environmental factors that determine population density.

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