Nest survival of birds in an urban environment in New Zealand

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Abstract: We compared nest survival of three urban bird species over two seasons in Dunedin City: silvereyes (*Zosterops lateralis*), a recent self-introduced native that is very abundant; blackbirds (*Turdus merula*), an abundant exotic species; and fantails (*Rhipidura fuliginosa*), a native species that occurs in relatively low numbers in some urban habitats. We also used artificial nests to compare nest predation rates between residential gardens and bush fragments isolated within a residential matrix. Silvereye nests had highest survival (daily survival probability = 0.98), with early nests and nests situated higher in trees having higher survival. Blackbird nest survival was lower (0.966); higher nests had better survival. Fantail nest survival varied significantly between years (0.908 in 2006–07 and 0.987 in 2007–08). Predation was a major cause of fantail nest failure, despite fantail nests being highest off the ground (mean = 4.2 m cf. 2.8 m for blackbirds and 2.2 m for silvereyes). Mortality of fantails during the week following fledging was high (41%). Low nest and juvenile survival may result in low abundance of fantails in Dunedin City. Predation of artificial nests was unaffected by nest placement (central or peripheral in the tree/shrub) and was the same in gardens as in bush fragments, with rats (*Rattus rattus*), possums (*Trichosurus vulpecula*) and possibly mice (*Mus musculus*) identified as nest predators.

Keywords: artificial nests; blackbird; fantail; silvereye; urban habitat

Introduction

Urbanisation can be one of the main causes of habitat loss and results in highly modified landscapes that support a mix of exotic and native species. The process of biotic homogenisation, whereby globally distributed exotic species replace local endemics, tends to be more pronounced in highly urbanised areas (McKinney & Lockwood 1999), which support large numbers of urban-adapted introduced species, such as house sparrows (*Passer domesticus*), starlings (*Sturnus vulgaris*) and rock pigeons (*Columba livia*) (Beissinger & Osborne 1982; Mills et al. 1989). At the other end of the urban gradient, patches of remnant habitat and low-density residential areas may support a diverse assemblage of native and exotic birds due to a greater range of resources and better quality habitat (Blair 1996; Germaine et al. 1998; Savard et al. 2000; Donnelly & Marzluff 2004; Sandström et al. 2006). Although some native species adapt to urbanised landscapes and are relatively abundant (Blair 1996; Jokimäki et al. 1996), others appear to be sensitive to environmental alterations and occur only in remnant habitat (Blair 1996). For example, native insectivores have

been identified as a vulnerable group often absent from urban assemblages, regardless of the diversity of habitat (DeGraaf & Wentworth 1986; Sewell & Catterall 1998; Hodgson et al. 2007).

For mobile species such as birds, presence is not enough to indicate sustainability, and apparently viable urban populations of native birds may in fact be functioning as population sinks, maintained through immigration from patches of better quality habitat. Populations of birds in urban areas may lack sufficient resources, and experience high levels of disturbance and high densities of predators, all of which could adversely affect nest survival, fecundity, and juvenile and adult survival. In New Zealand, nest predators are mainly a suite of introduced species, several of which can be found in urban environments. Free-ranging domestic cats (*Felis catus*) exist at high densities in residential areas (223 cats km^{-2} in Dunedin; van Heezik (unpubl. data), and rats (*Rattus* spp.) (most probably *R. rattus* rather than *R. norvegicus*; van Heezik unpubl. data) and possums (*Trichosurus vulpecula*) are present, although densities are unknown. Studies using artificial nests have documented variable predation pressure across urban gradients (Gering & Blair 1999; Matthews et al.

1999; Jokimäki & Huhta 2000; Thorington & Bowman 2003), with many factors, such as geographic differences in landscapes, fine-scale habitat attributes (Gering & Blair 1999), and housing density (Thorington & Bowman 2003), influencing rates of nest depredation. Nest survival may be higher within fragments, depending on fragment size, and the extent to which predators penetrate fragments (Wilcove 1985; Donovan et al. 1997). In New Zealand it is not known whether bush fragments in an urban landscape function as refuges from urban predators such as cats, rats and possums.

In this study we (1) compare nest survival of two native species, the recently arrived and highly abundant silvereye (*Zosterops lateralis*) and the less abundant fantail (*Rhipidura fuliginosa*), and one common exotic urban invader, the blackbird (*Turdus merula*); (2) compare nest survival of artificial nests within bush remnants and urban gardens; and (3) determine the influence on nest survival of nest placement within trees/shrubs.

Methods

Study area

Dunedin is a relatively small city (population approx. 80 000) that appears to retain a number of endemic forest bird species. The native pigeon/kererū (*Hemiphaga novaeseelandiae*) is unusually common; two honeyeaters, tūī (*Prosthemadera novaeseelandiae*) and bellbird/korimako (*Anthornis melanura*), are common; brown creeper/pīpipi (*Mohoua novaeseelandiae*) occur in some remnants; and tomtit/miromiro (*Petroica macrocephala*), fernbird/mātātā (*Bowdleria punctata*) and rifleman/tītitipounamu (*Acanthisitta chloris*) are found at or close to the city margins; van Heezik et al. 2008). A 'green belt' of about 12 bush remnants, ranging in size from 1 to 47 ha, covering a total area of about 145 ha, stretches about 6 km around the hills that frame the city. Fragments are mostly linear, with widths ranging from 135 m to 225 m. The green belt is highly disturbed, in that it is interrupted by roads and tracks, invaded by weeds, and parts have been turned into sports fields or highly manicured parks (botanic gardens, cemeteries). However, it still contains significant elements of native forest, is reasonably contiguous, and supports a greater diversity of native terrestrial bird species than other local urban habitats (van Heezik et al. 2008).

Natural nests

Nests were found in the northern fragments of Dunedin's green belt (the upper Botanic Gardens, Woodhaugh Gardens and fragments alongside Wallace St, Lachlan Avenue, and Cosey Dell Rd), except for a few blackbird nests in suburban gardens and in the Opoho playground, throughout the 2006–07 and 2007–08 breeding seasons. Nests were found either by following birds or by direct sighting. They were checked 1–2 times weekly in 2006–07

and every 2 days in 2007–08, until the nest failed or the chicks fledged. Nests were approached only when no adult bird was present, and adults were not flushed from nests to check contents.

Artificial nests

Empty natural nests were collected from parks and gardens mostly prior to breeding in 2006, and were therefore at least 8 months old but in good condition. Most were of silvereye, although three nests of fantail were used. All were small cup nests of similar size, and had natural odour of breeding birds added in the form of lining from recently used dunnock (*Prunella modularis*) or blackbird nests.

In November 2006 and January 2007, 60 nests were set out in a balanced design with two treatments: 'Habitat' (15 pairs of nests in urban gardens, 15 pairs in the green belt); and 'Placement' (30 nests on a major support stem or trunk, and 30 in the periphery of a tree/shrub, with one of each per pair of nests). Nests of a pair were placed at least 20 m apart, and pairs were at least 200 m apart. Nests in urban gardens were all placed in native or exotic trees or shrubs in the suburbs of Caversham and Roslyn, which are immediately south of the most southerly nests placed in the green belt. These suburbs contain older style, medium-density housing, with free-standing houses sitting on lots 500–1000 m^2 in size and well-established gardens containing a mix of native and exotic plantings. Pairs of nests in the green belt were placed in native shrub/tree species (exotic species of larger size were relatively rare) along a line about 4 km long, running from the Botanic Gardens (at the northern end of the city), through Woodhaugh Gardens, and south through green belt woodland.

'Placement' was modelled on silvereye nests (i.e. in the periphery of a shrub/tree offering reasonably dense vegetation) and blackbirds (on a substantial branch point on a main stem), but nests were slightly lower (1.3–2 m), slightly more peripheral in the former case and slightly more central in the latter, than natural nests. Each nest contained two artificial eggs made from Blue Tack®, which holds its shape, remains soft, and is intermediate in colour between silvereye and blackbird eggs. Eggs approximated the shape and dimensions of silvereye eggs (approx. 16 × 12 mm, Higgins et al. 2006).

Nests were checked to determine whether eggs were present and/or had tooth indentations at 2-day intervals initially (twice), then at 4-day intervals (twice), and finally after 7 days, for a total exposure period of 19 days. Eggs rasped by snails and three nests shredded by wind were replaced. The reported incubation and nestling periods for silvereyes are 11–12 days and 9–11 days respectively; for fantails 14–15 and 13–16 days respectively, and for blackbirds 14–15 days and 12–14 days, respectively (Higgins et al. 2006). Thus, exposure of artificial nests was for more than the typical incubation periods for the three species, but less than the total nesting period.

Nest success

Natural nests were considered to be successful if they fledged at least one young. Fledging was confirmed by at least two of the following criteria: fully feathered young seen in the nest; new fledglings seen or heard nearby; droppings seen around the nest or on the nest perimeter; broken down feather sheaths present in the nest; nest undisturbed and in good condition in combination with one other of the criteria. Nest loss due to predation was confirmed using any or all of the following criteria: nest disturbed (e.g. lining pulled out); no bird activity and evidence of a predator (e.g. droppings under nest); egg, chick or adult remnants found close to the nest; nest empty before chicks could possibly have fledged. In some cases, failed nests still contained eggs or dead chicks – such nests were listed as abandoned although disturbance by a predator could have been the cause.

Survival of fantails during the first week after fledging was monitored in 2007–08, where fledglings remained close to the nest. Nests were visited every day as fledging approached to determine its date and then at 2-day intervals. Fledglings are relatively easy to monitor because they are fed by both the male and the female the day after they leave the nest, and then by the male for up to 10 days while the female builds another nest.

Nesting success of natural nests from egg laying to fledging was estimated using the nest survival model in program MARK v.5.1 (White & Burnham 1999). Covariates were nest height, tree height, Visibility Index (see below), and time of season the nest was laid (i.e. early = September/October, middle = November/December, and late = January/February). Timing was therefore a fixed attribute for each nest. Program MARK also identifies whether there is a consistent change in survival among nests as a function of date, throughout the season; this is represented as 'Date' in the models. For each dataset, different time-, group- and covariate-dependent models were created and were ranked according to second-order Akaike Information Criterion (AICc) values, which are recommended when sample size is small in relation to the number of model parameters to be estimated (Anderson 2008). Delta AICc values show the magnitude of the difference in AICc between each model and the best-fitting model, and model likelihood assesses the strength of evidence between any two competing hypotheses (Anderson 2008). These values are relative and useful in comparisons only. The AIC weight value (wi) is the probability that model i is the best model (Anderson 2008). Since the Bootstrap Goodness of Fit test is not available for nest survival data, no $\hat{c}$ value could be calculated to account for over-dispersion. Success of artificial nests was calculated as a survival ratio; i.e. the proportion that survived 19 days of exposure. Survival of artificial nests was compared between habitat and placement treatments using survival analysis and Cox regression.

Nest site characteristics

Nest descriptors measured were: height of nest and tree, the ratio of nest height to tree height (NH/TH = Height Index), and visibility. Visibility was indexed using 10 separate measures addressing the following perspectives: (1) from four equally spaced points of the compass, could a predator on the ground see the nest at a distance of 10 m (indexed as visibility of nest, with 0 = very visible, 1 = quite visible, 2 = can be seen with difficulty, 3 = cannot be seen); (2) from four equally spaced points of the compass at a distance of 10 m, could a bird flying above the canopy see the nest (indexed as above); (3) visibility for a ground predator directly below (one value, indexed as above); (4) visibility from directly above (one value, indexed as above, obtained by standing directly below the nest and looking straight up). These 10 values were added together to give an overall measure of nest concealment with a maximum value of 30. Three researchers made all assessments of nest site characteristics. Two (IGM and KL) did all natural nests in 2006–07 and 2007–08 respectively, and one (SW) did all artificial nests. Before making separate assessments, they worked together testing agreement and reliability of the indexing for a large sample of natural nests.

Differences between species in nest site characteristics were tested using one-way ANOVA: nest height and tree height values were natural log transformed and Height Index values arcsin transformed to improve normality. Bonferroni post-hoc tests were used to determine where differences lay.

Predators

Predators of artificial nests were identified by comparing marks on artificial eggs to teeth impressions made using mammal skulls. Eggs bitten by small rodents (mice *Mus musculus* or young rats) were treated as predation. Large rodent teeth marks were most probably made by *Rattus rattus*, because in contrast to *R. norvegicus*, they can be arboreal (Innes 2001). Some eggs were bitten by a large native 'cricket' or weta (*Hemideina* sp.). We initially treated these nests as rodent predation and removed the nest, as attacks by weta were only recognised later. Two nests were subsequently assigned as successful (with a slightly shortened exposure period) and two were rejected from some analyses as they were removed after only 4 days. Eggs rasped by snails were replaced.

Results

Survival of natural nests

Height Index had a significant positive effect on blackbird nest survival (the higher the nest in the tree, the higher the probability of survival), although probability and likelihood values of survival functions that included tree height, or nest height and tree height, were only a

little lower (Table 1). Daily nest survival probability for blackbirds was 0.966 (CI: 0.937–0.982, SE = 0.011; Fig. 1). Because the length of laying and fledging periods can vary by a few days, the probability of nests fledging at least one young was between 37 and 41%.

The highest ranked model for fantail nest survival included the covariates year, Height Index and Visibility Index (VI): nest survival was significantly higher in the 2007–08 season than in the 2006–07 season, and the Height Index and VI both had a negative effect on nest survival (Table 2). Again, probability and likelihood values for the model containing nest height, tree height and VI were only slightly lower than those of the best ranked model. Daily nest survival probability for fantails was 0.908 (CI: 0.791–0.962, SE = 0.041) in 2006–07, and 0.987 (CI: 0.962–0.985, SE = 0.005) in 2007–08 (Fig. 1). The probability of fledging at least one young was as high as 67–70% in 2006–07 and as low as 5–7% in 2007–08. In the 2007–08 season there were 49 fledglings from 29 nests: by one week post-fledging only 20 of these had survived.

The highest ranked model for silvereye nest survival included the covariate tree height, which had a positive but barely significant effect on survival: the model without tree height also had a high level of support (Table 3). Survival was not constant throughout the breeding season, but was significantly higher during the first 35 days. Models with a different time subdivision of the breeding season (5-day intervals) were also tested and the one with a cut-off date of 35 days had the lowest AICc. Therefore, this cut-off date was included in models in Table 3. Daily nest survival probability for silvereyes was 0.980 (CI: 0.949–0.992,

SE = 0.010; Fig. 1). Probability of fledging at least one young was between 63% and 67%.

Nest descriptors

Fantail nests were highest off the ground, followed by blackbirds', followed by silvereyes' ($F = 27.68$ df = 2, $P < 0.01$; fantails vs blackbirds $P < 0.001$ and silvereyes $P < 0.001$; blackbird vs silvereyes $P = 0.039$; Fig. 2). Fantails also nested in higher trees than blackbirds and silvereyes ($F = 10.727$, d.f. = 2, $P < 0.001$; fantail vs blackbirds $P = 0.009$ and silvereyes $P < 0.001$; Fig. 2). There was no difference between species in Visibility Index ($F = 2.871$, d.f. = 2, $P = 0.061$) or in Height Index values ($F = 0.443$, d.f. = 2, $P = 0.643$; Fig. 2).

Causes of nest failure

Of the 113 nests monitored in both seasons, 40% failed (Table 4). Predation accounted for at least 29% of failures, adverse weather 18% and unknown causes 53% (Table 4).

Artificial nests

A total of 21% of nests (25 of 120 nests) were visited by predators. Predators identified on the basis of teeth marks on artificial eggs were rats (3 nests) and possums (2 nests). Teeth marks of mice or young rats were also found (7 nests). Thirteen nests suffered some interference: in seven cases the eggs disappeared completely, and in six cases the nest was interfered with but the eggs remained intact.

Placement in the centre or periphery of a tree, or nesting in different urban habitats (urban gardens vs green

Table 1. Nest survival models for blackbirds in urban Dunedin, using Program MARK (White & Burnham 1999). NH = nest height; TH = tree height; VI = Visibility Index; AICc = second-order Akaike Information Criterion values; Delta AICc shows the magnitude of the difference in AICc between each model and the best-fitting model; model likelihood assesses the strength of evidence for models relative to each other; (wi) is the probability that model *i* is the best model; K = number of parameters.

| Model	AICc	Delta AICc	wi	Model Likelihood	K
{S = S(Const+NH/TH)}	67.88	0.00	0.18	1.00	2
{S = S(Const+TH)}	68.51	0.63	0.13	0.73	2
{S = S(Const+NH,TH)}	68.53	0.65	0.13	0.72	3
{S = Constant}	68.84	0.96	0.11	0.62	1
{S = S(Const+NH, NH/TH)}	69.49	1.62	0.08	0.45	3
{S = S(Const+NH)}	69.58	1.71	0.08	0.43	2
{S = S(Const+Year+NH/TH)}	69.66	1.78	0.07	0.41	3
{S = S(Const+TH,NH/TH)}	69.80	1.92	0.07	0.38	3
{S = S(Const+NH,TH,VI)}	70.54	2.67	0.05	0.26	4
{S = S(Const+NH,TH,NH/TH)}	70.57	2.69	0.05	0.26	4
{S = S(Const+TH,VI)}	70.82	2.94	0.04	0.23	2
{S = S(Year)}	70.86	2.98	0.04	0.23	2
{S = S(Const+NH,VI)}	71.56	3.68	0.03	0.16	3
{S = S(Time)}	311.84	243.96	0.00	0.00	93
{S = S(Time*Year)}	453.99	386.11	0.00	0.00	122
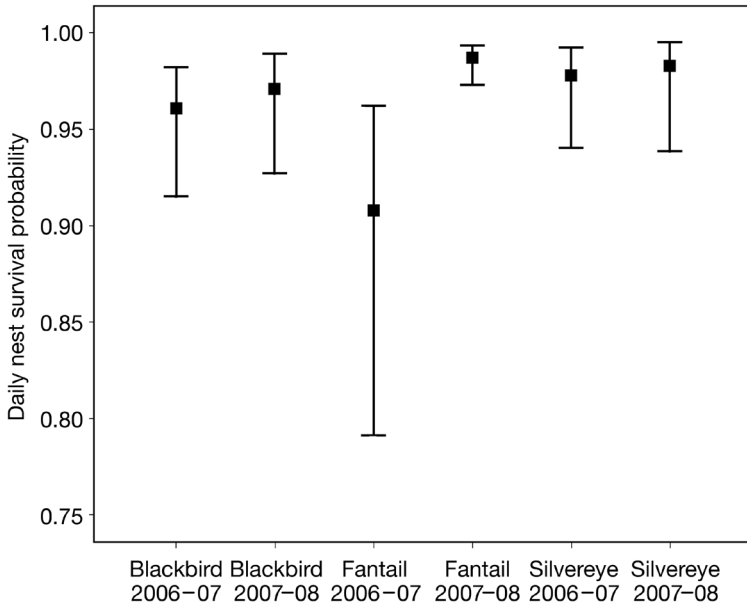
Figure 1. Daily nest survival probabilities (and 95% confidence intervals) for blackbirds, fantails and silvereyes during two seasons in urban Dunedin.

Table 2. Nest survival models for fantails in urban Dunedin, using Program MARK (White & Burnham 1999). NH = nest height; TH = tree height; VI = Visibility Index; Timing = early season, middle season or late season, except in models that have the suffix '2', where Timing is early season or middle+late season; see Table 1 for definitions of AICc, Delta AICc, model likelihood, *wi* and K.

| Model	AICc	Delta AICc	*wi*	Model Likelihood	K
{S = S(Const+Year + NH/TH,VI)}	123.80	0.00	0.17	1.00	4
{S = S(Const+Year +NH,TH,VI)}	124.13	0.34	0.15	0.85	5
{S = S(Const+Year +First40Days+NH/TH,VI)}	124.35	0.56	0.13	0.76	5
{S = S(Const+Year +Timing+ NH/TH,VI)} 2}	124.40	0.60	0.13	0.74	5
{S = S(Const+Year +NH/TH,TH,VI)}	125.04	1.25	0.09	0.54	5
{S = S(Const+Year +NH,NH/TH,VI)}	125.72	1.92	0.07	0.38	5
{S = S(Const+Year +TH,VI)}	125.97	2.17	0.06	0.34	4
{S = S(Const+Year + NH/TH)}	125.98	2.19	0.06	0.34	3
{S = S(Const+Year +Timing+Year*Timing)} 2}	126.75	2.95	0.04	0.23	3
{S = S(Const+Year+NH,TH)}	127.03	3.23	0.03	0.20	4
{S = S(Year)}	128.14	4.34	0.02	0.11	2
{S = S(Const+Year +Timing+Year*Timing)}	128.48	4.68	0.02	0.10	4
{S = S(Const+Year+VI)}	129.40	5.60	0.01	0.06	3
{S = Constant)}	129.49	5.69	0.01	0.06	1
{S = S(Const+Year+Timing)} 2}	129.91	6.11	0.01	0.05	3
{S = S(Const+ NH/TH,VI)}	130.21	6.41	0.01	0.04	3
{S = S(Const+Year+NH,VI)}	130.93	7.13	0.00	0.03	4
{S = S(Const+Year+Timing)}	131.81	8.01	0.00	0.02	4
{S = S(Time)}	453.82	330.02	0.00	0.00	148
{S = S(Time*Year)}	466.54	342.74	0.00	0.00	157
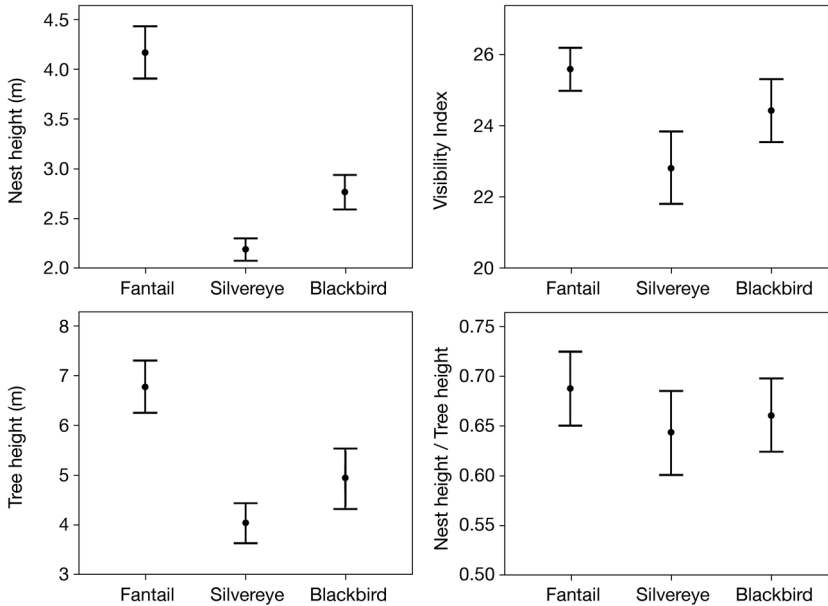
Figure 2. Mean nest heights, tree heights, Height Index (nest height: tree height) and Visibility Index values (+ SE) for natural nests of fantails ($n = 38$), silvereyes ($n = 34$) and blackbirds ($n = 32$ for nest height and 33 for the others) in urban Dunedin (2006–08).

Table 3. Nest survival models for silvereyes in urban Dunedin, using Program MARK (White & Burnham 1999). NH = nest height, TH = tree height, VI = Visibility Index, Timing = early season, middle season or late season, except in models that have the suffix '2', where Timing is early season or middle+late season; see Table 1 for definitions of AICc, Delta AICc, model likelihood, *wi* and K.

Model	AICc	Delta AICc	*wi*	Model Likelihood	K
{S=S(Const+First35days+TH)}	57.35	0.00	0.14	1.00	3
{S=S(Const+First35days)}	57.43	0.08	0.13	0.96	2
{S=S(Const+FirstMonth+Year +Year*FirstMonth+TH)}	57.79	0.44	0.11	0.80	4
{S=S(Const+Year*FirstMonth+TH)}	57.88	0.54	0.11	0.76	2
{S=S(Const+FirstMonth +Year*FirstMonth+TH)}	58.07	0.72	0.10	0.70	3
{S=S(Const+First35days+VI)}	58.92	1.58	0.06	0.45	4
{S=S(Const+FirstMonth+Year+TH)}	59.11	1.76	0.06	0.41	4
{S=S(Const+First35days+VI)}	59.11	1.77	0.06	0.41	3
{S=S(Const+First35days+NH)}	59.19	1.84	0.05	0.40	3
{S=S(Const+First35days+NH,TH)}	59.29	1.95	0.05	0.38	4
{S=S(Const+First35days+NH,VI)}	60.66	3.31	0.03	0.19	4
{S=S(Const+First35days+NH,TH,VI)}	60.66	3.32	0.03	0.19	5
{S=S(Const+First35days+NH/TH,VI)}	60.85	3.50	0.02	0.17	4
{S=S(Const+Oct,Nov)}	62.02	4.68	0.01	0.10	3
{S=S(Const+Oct)}	62.18	4.84	0.01	0.09	2
{S=S(const+Time)}	62.24	4.90	0.01	0.09	2
{S=S(c+Timing)}	63.07	5.73	0.01	0.06	2
{S=S(Const+Oct,Nov,Dec)}	64.06	6.71	0.00	0.03	4
{S=S(c+Timing)} 2}	64.20	6.86	0.00	0.03	2
{S=S(Const+TH)}	65.53	8.18	0.00	0.02	2
{S=S(Constant+Year+TH)}	67.44	10.09	0.00	0.01	3
{S=Constant}	67.56	10.22	0.00	0.01	1
{S=S(Year)}	69.21	11.86	0.00	0.00	2
{S=S(Time)}	274.17	216.82	0.00	0.00	93
{S=S(Time*Year)}	430.61	373.26	0.00	0.00	130

Table 4. Causes of nest failure for fantail, silvereye and blackbird nests in urban Dunedin, over the 2006–07 and 2007–08 seasons. The unknown category includes nest abandonment.

	Predation	Weather	Unknown	Total failed	Total nests
Fantails	7	4	7	18	38
Blackbirds	4	2	10	16	39
Silvereyes	2	2	7	11	36
Total	13	8	24	45	113

belt), had no effect on the overall probability of artificial nest survival during the 19-day period (Cox regression: $\chi^2_2 = 0.16$, $P = 0.9$). Nests in urban gardens were only 1.1 (95% CI 0.5–2.5) times more likely to fail than nests in the green belt, and central nests were only 1.1 (95% CI 0.5–2.4) times more likely to fail than peripheral nests. None of the nest descriptors demonstrated any predictive power in determining artificial nest success.

Discussion

Silvereyes were the most abundant and ubiquitous of the three species studied within both the urban environment and surrounding native peri-urban habitats. Blackbirds are among the most abundant of urban-adapted exotic species, whereas fantails can be found in low numbers in some urban habitats, such as bush fragments and residential areas with complex and mature garden vegetation (van Heezik et al. 2008). Nest survival of these three species tended to reflect their relative abundances. The blackbird is one of the few exotic urban birds that can be found in native bush; however, numbers decline with distance from the edge (Wilson et al. 1988), and urban populations are highly likely to be self-sustaining. In contrast, it is unclear whether the urban fantail populations in Dunedin are self-sustaining or sink populations, maintained through immigration from peri-urban sources.

Average survival of silvereye nests from laying to fledging was about 63–67%; higher than the 50.3% and 51.3% recorded in Australia (Higgins et al. 2006) but lower than the 86% reported in urban Dunedin several decades ago (Kikkawa 1966). Survival of silvereye nests was higher during the first 35 days of the breeding season. It is possible that food supply and weather conditions were optimal during this period. Whereas tree height appeared to have a positive effect on survival, this effect was barely significant and model likelihood and probability values were not much higher than for the next ranked model, which did not include this parameter. Silvereye nests were located lowest among the three species (2–2.5 m), and in the lowest trees (mean height = 4.0 m). Nesting closest to the ground did not appear to render them more vulnerable to nest loss from predators.

Values for blackbird nest survival obtained in this study (37–41%) fell within the range of values obtained at other localities in New Zealand: 22% and 46% (Higgins et al. 2006); 46.6% of 88 nests monitored in urban Dunedin (Kikkawa 1966); 33% (Niethammer 1970); and 33% in a mix of native and exotic trees and shrubs in an agricultural landscape (Boulton & Cassey 2006). Survival in this study was similar to values from urban areas in the UK (33%) and Australia (44.9%; Kentish et al. 1995), but lower than values reported for urban gardens in Oxford, UK (50%), and an urban area in Czechoslovakia (62.5%; reviewed in Kentish et al. 1995). Greater nest success in urban than woodland habitats in Australian and European studies has been attributed to a reduced diversity of predators, human presence and activity reducing predation, and possibly dominance by cats that may exclude other predators (reviewed in Kentish et al. 1995). However, survival of blackbird nests in urban Dunedin in this study was low compared with other urban areas, even though there were relatively few predators. Causes of many of the failures are unknown. In a study using artificial clay eggs, Boulton & Cassey (2006) reported no predator imprints for 37% of predator events; it would be useful in future to invest more effort into identifying why nests fail.

Typical blackbird nests tended to be placed about two-thirds of the way up trees about 5 m high, and therefore were 2.5–3 m off the ground. Increasing tree and nest height, and the ratio of nest height to tree height, in the Dunedin study all had a significant positive effect on blackbird nest survival. However, while higher placed nests were more likely to survive, most nests were not higher than 3 m off the ground. This apparent selection for lowish shrubby plants was also noted in an Australian study (Kentish et al. 1995), and the suggestion that this might be attributed to ease of detection and monitoring by observers rather than a preference by the bird might also apply to this study. Failure of nests in the Australian study was more likely to occur at lower strata (<1 m) due to ground predators, and above 5 m, due to inclement weather, which resulted in starvation of chicks. Nest height was suggested as the result of a compromise between these conflicting demands.

Common causes of nest failure of New Zealand blackbird nests include predation, desertion, and human interference (Higgins et al. 2006). In our study predation accounted for most known causes of mortality, followed by adverse weather. While blackbird nest survival seems relatively low, the abundance of this urban-adapted species

suggests it is sufficiently high, and if combined with high fecundity and/or survival of juveniles and adults may result in urban populations that can be sustained without immigration.

Fantail nest survival varied significantly between years: in a good year (67–70%, 2007–08) it was as high as silvereye nest survival, and better than nest survival of fantails in non-urban areas (48% on Tiritiri Mātangi – McLean 1984; 37% on Cuvier Island – McLean & Jenkins 1980), but in a bad year it was very low (5–7%, 2006–07). Nest survival values recorded in Australia were 41%, 48% and 59% (Higgins et al. 2006). Mortality of fledglings after they have left the nest is usually high; in our study 41% of fledglings had died by the end of the first week. At Cuvier Island only 19% of fledglings had survived after about 6 months (McLean & Jenkins 1980), and Powlesland (1982) reported high mortality of immatures over winter. Although none of the other studies reported annual differences in nest survival, it is possible that in urban areas survival is much more variable, and during bad years may result in virtually no recruitment to the population. Therefore, the viability of the urban fantail population could depend, at least in part, on the frequency of bad years. The low abundance of fantails in most urban habitats suggests either very poor juvenile or adult survival, and/or reasonably frequent years of low nest survival.

Fantail nests in Dunedin were situated highest of all three species, typically between 4 and 4.5 m off the ground, about two-thirds of the way up trees about 6–7 m high. Being situated higher off the ground did not seem to confer an advantage, because the lower nests were more likely to survive, possibly because lower nests were more sheltered from the weather. Nests at non-urban locations tended to be situated closer to the ground. McLean and Jenkins (1980) noted that nests on Cuvier Island were lower (mean = 1.68 m, range: 0.8–3.2 m) than nests on the mainland (mean = 3.7 m, range = 0.7–24 m) and attributed this to a lack of introduced predators on the island, or regenerating island vegetation. Most nests on Tiritiri Mātangi were built in the lowest 3 m of forest (mean = 1.9 m) and at Kowhai Bush, near Kaikoura, a mainland locality, between 1 and 5 m (mean = 2.9 m; Powlesland 1982).

The negative relationship between the Visibility Index and nest survival in fantails, i.e. more concealed nests were less likely to survive, is most likely related to nest placement. Nests with more cover were more likely to be in the periphery of trees where weather effects (primarily wind) are stronger; e.g. all four natural nests destroyed by wind in 2006–07 were at or near the periphery of trees on the windward side. Predation resulted in the failure of at least 39% of fantail nests in this study, and was identified as the main cause of failure to hatch and a significant cause of nestling mortality of fantails in Kowhai Bush, where the main predators were rats and mustelids (Powlesland 1982). The suite of predators in urban environments is

likely to be different from that in native bush, but very little is known about the occurrence of mammalian predators across the urban gradient in Dunedin. Domestic cats exist at high densities in Dunedin, and possums and ship rats are certainly present, but mustelids are probably less abundant. The higher nest placement by fantails found in the present study could be a response to predation by cats, and may result in nests being more vulnerable to storms and high winds. However, by selecting trees 6–7 m high, fantails are effectively placing restrictive limits on the amount of habitat available to them for breeding, since the largest urban green space, residential gardens, is characterised by very little vegetative cover above 5 m (van Heezik, unpubl. data).

Nest survival and predator abundance have been shown to vary across urban gradients: some studies have found increased nest predation in more urbanised areas where there are more generalist predators, both avian and mammalian (Jokimäki & Huhta 2000; Thorington & Bowman 2003), whereas others reported decreased nest predation and declining predator abundance with increasing human housing density (Wilcove 1985; Donovan et al. 1997; Gering & Blair 1999; Haskell et al. 2001). The value of native habitat fragments as refuges from nest predators may depend on the landscape the patches are in and the size of a fragment relative to its edge (Wilcove 1985; Donovan et al. 1997; Thorington & Bowman 2003). Native bush fragments in Dunedin that are surrounded by residential areas appear to support a greater diversity and relative abundance of bush birds than are found in most residential areas (van Heezik et al. 2008). Despite this, rates of interference of artificial eggs by potential nest predators were the same in gardens and the green belt, suggesting that these bush fragments do not provide refuges from predation for breeding birds. Wilcove (1985) found nest predation was particularly intense in woodlots near suburban neighbourhoods, compared with woodlots in isolated rural areas, and in small woodlots as opposed to larger ones. The small size and linear shape of the fragments in this study mean that edge effects, which can result in higher nest predation up to 50 m inside a fragment (Batáry & Báldi 2004), prevailed throughout the fragment. The value of fragments may lie in the greater range of resources they contain, compared with residential areas (Germaine et al. 1998; Donnelly & Marzluff 2004).

Rodents and possums were identified as the main predators of artificial nests in gardens and bush fragments, but cats were not identified as nest predators in this study. Cats take natural eggs from nests (Morgan et al. 2006), but might not bite artificial eggs. Large mammals such as cats were also reported by Wilson et al. (1998) to be uncommon predators of artificial nests. Thus, the absence of attacks by cats on artificial nests may give little information about their potential role as nest predators. The abundance of rodents in New Zealand residential

areas is unknown. Although resources are abundant (fruit, compost, garbage, pet food, bird feeders, etc.) their numbers may be suppressed by domestic cat predation. Such resources also attract possums, which are found in residential areas but are more likely to be abundant in bush fragments. Stoats (*Mustela erminea*) eat artificial eggs (Smith et al. 2008) and are common predators of birds (King & Moody 1982). The absence of attacks on artificial nests by stoats suggests they are not important nest predators in Dunedin. Artificial eggs also showed evidence of interference by mice in our study. Although some doubt has been expressed as to whether small-mouthed predators can predate nests defended by adult birds several times the size of the predators (Haskell 1995), mice and possibly shrews successfully preyed upon eggs in natural nests defended by adult birds in several video camera studies (King & DeGraaf 2006 and references therein).

None of the variables concerning nest placement and visibility influenced artificial nest predation. The degree of concealment from above is more likely to influence nest predation by avian predators, but they do not appear to be abundant in the Dunedin area (van Heezik et al. 2008) and were not recorded as predators of artificial eggs. Rodents and possums are mainly nocturnal foragers for which visual cues are probably less important. All the nests monitored in this study were below 2 m in height: within this vertical stratum all nests appeared to be equally likely to be encountered by possums and rodents.

The use of artificial nests in predation studies is contentious, with some authors concluding that artificial nest studies should be abandoned in response to evidence that neither absolute rates nor spatial patterns of predation on artificial nests mimic those of natural nests (Major & Kendal 1996; Zanette 2002; Burke et al. 2004). Artificial nests may be predated by different predators than natural nests, and these may be predators that adult birds might normally be able to deter (Zanette 2002; Burke et al. 2004; Thompson & Burhans 2004; King & DeGraaf 2006). Supporters of artificial nest studies emphasise improved techniques with respect to nest design and placement and egg design, restricting comparisons to local sites where the predator community is the same and a more realistic assessment of the questions being addressed (Faaborg 2004). Artificial nest experiments have limitations, but research on natural nests can also have limitations (Villard & Pärt 2004), and there are situations where artificial nests can be used to address important conservation questions, particularly when used in conjunction with natural nests (Wilson et al. 1998). A common feature of most studies is the diverse array of nest predators, including several mammalian and avian species (Jokimäki & Huhta 2000; Zanette 2002; Thorington & Bowman 2003; Thompson & Burhans 2004; King & DeGraaf 2006).

We did not compare survival rates of artificial and natural nests, but used artificial nests to compare rates of interference with eggs in different urban habitats, and to identify the predators that interfered with artificial eggs. Compared with most northern-temperate artificial nest experiments, Dunedin has a limited suite of predators, which simplifies the complexity that routinely confounds interpretation of results from artificial nest experiments elsewhere. Predators identified from attacks on artificial eggs in this study are well-known predators of natural nests, with cats being the only likely predator missing from the artificial nest study. We believe that the simplicity of the situation in Dunedin, combined with our use of realistic nests and odour, addresses most of the standard reservations with respect to the use of artificial nests.

Conclusions

Nest survival figures provide only one piece of the puzzle with regard to understanding the viability of urban bird populations. Information on the number of clutches laid each season, fledgling, juvenile and adult mortality, and emigration and immigration rates is necessary before conclusions can be drawn confidently about whether populations are self-sustaining within the urban environment. Variable fantail nest survival and low survival of fledglings and juveniles may contribute to their relatively low abundance in the urban environment. Preference shown by fantails for nesting at heights that are unavailable in most residential gardens must also limit their distribution in suburban areas. Artificial nests confirmed the expected suite of predators, with the exception of domestic cats, and suggest that the small fragments that make up the green belt confer no protection against nest predators.

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