Predator control improves nesting success in Waikato forest fragments

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Abstract: Predation at nests contributes importantly to current declines of New Zealand forest birds. We monitored the survival of natural and artificial arboreal nests in small forest remnants south-west of Hamilton, where ship rat (*Rattus rattus*) and possum (*Trichosurus vulpecula*) abundances were also being measured in Summer 2008/09. Artificial cup nests ($N = 77$) were placed in replicated blocks with and without pest control, in both December and January. Natural nests ($N = 11$, five bird species) were observed from 13 October to 23 December 2008 in a forest with no pest control. Digital video cameras identified ship rats, brushtail possums and harrier hawks (*Circus approximans*) as predators of eggs and chicks. There was no difference between artificial and natural nests in daily survival rates monitored in December in a block with no pest control, suggesting that artificial nests are reasonable surrogates for natural nests. Bite marks on clay eggs, other diagnostic sign, and DNA swabbed from real and clay eggs confirmed ship rats and possums were the major introduced predators at artificial nests. Bite marks also confirmed that harriers contribute to nest failure. Removal of ship rats and possums in December improved the 14-day probability of survival of artificial nests, from $P = 0.63$ (95% CI 0.45–0.77) in the non-treatment block to $P = 0.88$ (0.74–0.95) in the treatment blocks. In January, the 14-day probability of survival in all three blocks was intermediate at 0.80 (0.69–0.87), and the variation between them could not be explained by including pest control in the model. The abundance of ship rats apparently declined even in the non-treatment block over this time, for unknown reasons. Our data from tawa (*Beilschmiedia tawa*) forest remnants confirm that control of ship rats and possums alone is sufficient to improve nesting success of small arboreal birds in North Island forests.

Keywords: artificial nests; bird nest success; brushtail possum; DNA; harrier; pest control; predator identification; ship rat.

Introduction

Nest predation is the most important reason for the decline of forest birds in New Zealand, and, even more significantly, for the ongoing risk of extinctions among endemic avian species (Innes et al. 2010). Removal of predators during the nesting season is an important management tool with proven benefits in improving nesting success (Tapper et al. 1996; Innes et al. 1999; Jones et al. 2005; Starling-Windhof et al. 2011; Remeš et al. 2012), provided the predators responsible are correctly targeted. That requires identifying nest predators with certainty, and monitoring the effectiveness of pest control operations. Generalised pest control operations run the risk of expending considerable effort while failing to restore a breeding population of a target species (Coté & Sutherland 1997; Smith et al. 2010) or even of precipitating a greater danger from mesopredator release (Tompkins & Veltman 2006; Rayner et al. 2007; Sweetapple & Nugent 2007).

This study was part of a larger survey of the effects of pest control on key ecological processes in forest fragments in the Waikato Region, central North Island (Dodd et al. 2011). Lowland rural landscapes in New Zealand include many scattered, fragmented remnants of forest ecosystems that are poorly represented in the public conservation estate. Many of these fragments support a disproportionately large number of indigenous species that are unable to survive outside their native ecosystems, but which are critical for regional and national restoration (Burns et al. 2000). Introduced weeds and pests are key threats, but the ecological consequences of managing them are little understood.

The most significant pests in lowland forest fragments are two omnivorous introduced mammals, the ship rat (*Rattus rattus*) and the brushtail possum (*Trichosurus vulpecula*; hereafter referred to as possum). Both are arboreal, widespread and abundant in indigenous forests throughout the New Zealand mainland, where their browsing and predation cause widespread damage to foliage, regeneration, flowering, invertebrates and birds (Cowan 2005; Innes 2005). The aim of this study was to compare nest survival rates of birds in forest blocks with and without control targeting ship rats and possums, and to identify predators at nests. We initially intended to study only natural nests, but then deployed artificial nests when natural nests were so hard to find.

Study areas

We chose three remnants of indigenous forest surrounded by farmland or exotic forest, all located c. 10 km south-west of Hamilton, North Island. The first site, Kaniwhaniwha Scenic Reserve (KSR, 260 ha, 37°51′31″ S, 175°06′28″ E), is managed by the state-administered Department of Conservation, while the other two sites (Packer-Johnstone (PJ) Block, 132 ha, 37°49′51″ S, 175°06′25″ E; Hope Block, 175 ha, 37°50′10″

S, 175°04′32″ E) are privately owned. All three sites are on eastern flanks of the Kapamahunga Range, and form parts of an archipelago of forest fragments that are surrounded primarily by pasture for farming. The forest canopies[1] at all three sites are dominated by tawa (*Beilschmiedia tawa*) with abundant kāmahi (*Weinmannia racemosa*), hīnau (*Elaeocarpus dentatus*), rewarewa (*Knightia excelsa*), pukatea (*Laurelia novae-zelandiae*) and kānuka (*Kunzea ericoides)*, and an understorey with tree ferns (*Cyathea* and *Dicksonia* species), māhoe (*Melicytus ramiflorus*), pigeonwood (*Hedycarya arborea*), nīkau (*Rhopalostylus sapida*), heketara (*Olearia rani*), and kawakawa (*Macropiper excelsum*).

Methods

Pest control and nest monitoring

Ship rats and possums were targeted for removal at PJ and Hope Blocks but not at KSR. Techniques, indices of pest abundance, and outcomes of pest control are summarised in Table 1.

We monitored a small sample of natural nests from 13 October to 21 December 2008. Despite intensive searching, we found only 11 nests (fantail *Rhipidura fuliginosa* 4, tūi *Prosthemadera novaeseelandiae* 3, grey warbler *Gerygone igata* 2, eastern rosella *Platycercus eximius 1*, kererū *Hemiphaga novaeseelandiae* 1), all in the KSR block. We monitored each nest until it either fledged young or was destroyed. Video cameras recording 24 hours a day (under infrared light during darkness) were placed 1–3 m from 10 of the 11 nests, to identify predators. Sequences were digitally recorded onto hard drives placed up to 40 m away from the nest tree. We visited nest areas twice per week to check nest survival; to change the 12-volt batteries that powered the camera and recording system, and to change hard drives. Nest footage was viewed only when a predation event had been recorded.

Used, empty cup-nests of thrush (*Turdus philomelos*) and blackbird (*T. merula*), all built in late 2008, were collected from parks and gardens around Hamilton. The use of real nests helps to minimise one of the inherent disadvantages of this method (Faaborg 2004). Artificial clutches of eggs were prepared comprising two real Japanese quail (*Coturnix japonica*) eggs (30 × 24 mm; infertile; farmed for the restaurant trade) and one tethered clay egg painted to resemble a quail egg. Clay eggs with elastic tethers were made, following Boulton & Cassey (2006). No artificial nests were filmed with video cameras.

From 26 November to 9 December 2008, using both natural and artificial nests, and from 20 January to 3 February 2009, using artificial nests only, we studied predation rates in all three blocks. We set out 43 nests in the two treatment blocks (20 in P-J and 23 in Hope) and 34 in the non-treatment block (KSR). Nests were placed in forks of trees 1–3 m off the ground, 100 m apart along measured lines. The mean distance of nests to the forest edge was 200 m (range 50–600 m). They were checked four times over 14 days (maximum period between checks 5 days) before being removed. This time period was selected to mimic the mean incubation period of some common small forest birds, such as tūi, fantail and blackbird (Heather & Robertson 1996).

Damaged clay eggs were examined for incisor marks and other signs of predator identity (Boulton & Cassey 2006), under a binocular microscope. Damage to real eggs and nests was compared with literature descriptions of characteristic damage caused by various predator species (Brown et al. 1996a, 1998; Innes et al. 1996).

DNA analysis

Damaged nests and any contents were removed by fieldworkers wearing sterile gloves and placed in DNA-clean plastic or paper bags. All remains of damaged eggs, both artificial and real, were swabbed for DNA, which was extracted, amplified, sequenced, and identified to species. Swab samples from either the field or the lab were made by wiping cotton buds across the surface of damaged and artificial eggs. Sterile gloves were worn at all times when handling swabs to avoid DNA contamination. Swabs were air dried for 24 hours, placed on filter paper, and then into individual manila envelopes for transport. Swabs prepared in the lab were first dipped in Tissue Digest (DXT) before being used to wipe the surface of eggshells.

All swabs were incubated at 56°C overnight in 420 µl of Tissue Digest (DXT) and 4.2 µl of DX Digest enzyme. DNA was then extracted using the Corbett X-tractor Gene (Qiagen) automated standard swab protocol, following the manufacturer's instructions. DNA was then eluted in 50 µl of elution buffer.

Polymerase chain reaction (PCR) was undertaken using universal mitochondrial DNA (mtDNA) primers CB-J-10612 and CB-N-10920, targeting a highly conserved region of the *cytochrome b* gene common across a wide range of vertebrates (Simon et al. 1994), as modified from Kocher et al. (1989). PCR amplifications were performed on a GeneAmp 9700 thermocycler (Applied Biosystems) in 25-µl reactions containing 5 µl of DNA extract, 2.5 µl of FastStart Taq DNA Polymerase PCR Buffer with $MgCl_2$, 2.5 µl of dNTPs (2 mM), 1 µl of each primer (10 pm ul^{-1}), 1 µl of BSA (10 mg ml^{-1}) and 1.5U of FastStart Taq DNA Polymerase (Roche Diagnostics). Cycles were as follows: 95°C for 4 min; 40 cycles of 94°C for 45 s, 50°C for 45 s, 72°C for 1 min; 72°C for 10 min. Amplification products were visualised under ultraviolet light, using ethidium-bromide-stained agarose gels.

Direct sequencing of purified products was carried out with BigDye™ Terminator Version 3.1 (Applied Biosystems) following the manufacturer's protocol. Sequences were analysed on an Applied Biosystems 3130xl genetic analyser using DNA Sequencing Analysis Software Version 5.3.1 (Applied Biosystems).

DNA sequences were compared and edited manually using the program SEQUENCHER 4.6 (Gene Codes). Sequence results usually consisted of mixed profiles that had to be separated to determine whether any potential predator DNA was present. The previously known 'host' *cytb* DNA sequence, which is available on GenBank, was first subtracted from the mixed profile. If a mixed profile was still evident, then another likely source of DNA contamination, human *cytb* DNA sequence, was removed. When a single profile was obtained that was neither the 'host' nor human *cytb* DNA sequence, the BLAST (Basic Local Alignment Search Tool) algorithm was used to search for the most closely matched sequences within the National Center for Biotechnology Information (NCBI) database, GenBank.

Nest survival

To calculate daily nest survival rates (DSR) of nests we used the Mayfield estimator in program MARK (White & Burnham

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[1] Plant names follow the Plant Names Database http:nzflora.landcareresearch.co.nz/

Table 1. Mean (SE) indices of abundance of ship rats and possums before and after the 2008/09 bird nesting season (September–January) at Packer-Johnstone (P-J), Hope, and Kaniwhaniwha Scenic Reserve (KSR) blocks, Waikato Region. Monitoring techniques used were standard footprint tracking tunnel indices (TTI) of ship rats (*Rattus rattus*; Gillies & Williams 2008[1], unpubl. report) and residual trap-catch (RTC) of possums (*Trichosurus vulpecula*; NPCA 2005).

Block	Pest species	Pre-breeding season index	Treatment	Early breeding season index	Post-breeding season index
P-J	Ship rat	19 June 2008: 9% TTI (SE 7)	Bait stations at 75-m spacing; cholecalciferol toxin in Feracol® baits; completed 23 Oct. 2008	28 Oct. 2008: 5% TTI (SE 2)	10 Feb. 2009: 8% TTI (SE 5)
	Possum	16–18 Jan. 2008: 11% RTC (SE 6)		28–30 Oct. 2008: 0% RTC	
Hope	Ship rat	17 June 2008: 17% TTI (SE 6)	Aerial 1080, cinnamon-lured, cereal baits. Prefed 2 kg ha^{-1}, then 2 kg ha^{-1} 0.08% 1080, 13 Oct. 2008	28 Oct. 2008: 1% TTI (SE 1)	12 Feb. 2009: 8% TTI (SE 4)
	Possum	18–20 Jan. 2008: 1% RTC (SE 1)		28–30 Oct. 2008: 0% RTC	
KSR	Ship rat		None	23 Oct. 2008: 47% TTI (SE 7)	5 Feb. 2009: 26% TTI (SE 12)

[1] Version 2.5.2 (2013) available at: http://www.doc.govt.nz/Documents/science-and-technical/inventory-monitoring/im-toolbox-animal-pests-using-tracking-tunnels-to-monitor-rodents-and-mustelids.pdf.

1999) (http://welcome.warnercnr.colostate.edu/~gwhite/mark/mark.htm). AICc (corrected or adjusted Akaike's Information Criterion) were calculated for each model; the smaller the AICc, the more support the model has given the data.

First, in the non-treatment block (KSR) alone, we compared the three groups of nests observed (natural nests from October to December, and two separate sets of artificial nests in December and January). We estimated DSR for each group separately, and then used AICc (corrected for small sample sizes) to compare two alternative models: S(.), constant survival (assuming DSRs equal for the three groups), and S(g), the model that would best fit the data if the DSRs for the three groups were different. We used a likelihood ratio test to assess the significance of any differences in DSR between the groups, expressed as χ^2, and estimated the cumulative probability of nest survival over 14 days as DSR^{14} (± 95% confidence intervals). Second, we used the same approach to compare the DSRs of nests in managed compared with unmanaged sites, and in December compared with January.

Results

Identifying predators from video recordings

Of the 11 natural nests monitored to a conclusion in December, 4 nests fledged young and 7 were preyed on by predators, of which five were identified by the video recordings. Two nests (one each of kererū and eastern rosella) were destroyed by possums, two (both tūi) by harriers, and one (fantail) by a ship rat. None of the video records, the sign left on eggs, or the DNA results were able to identify predators at the last two nests (fantail, tūi).

Identifying predators from DNA and bite marks

We retrieved fragments of natural eggs and/or damaged artificial eggs from a total of 36 artificial and 2 natural nests (Table 2). DNA was extracted from a total of 71 swab samples (58 from artificial nests taken in the field plus 10 repeat swabs taken in the lab; 3 from natural nests). Of the 71 swab samples, 14 contained *cytb* DNA sequences that were neither the 'host' nor human, all from artificial nests. DNA provided predator identifications at 8 of the 38 nests (5 possums and 3 rats). Of the three swabs from natural nests, two identified the host bird and one gave no result.

Bite marks on the clay eggs and other signs of disturbance provided predator identifications at 19 of the 36 nests (10 rats, 5 possums, 4 harriers).

For the eight nests at which predators were identified with both techniques, there was agreement on five. In the remaining three cases, bite marks suggested harriers while DNA identified rats. Multiple traces left by visitors of different species to a given nest, both predators and scavengers, are entirely possible, and do not affect the clear result that rats, possums and harriers were the principal predatory species in these forests.

Comparing survival of natural and artificial nests in an unmanaged area

In the unmanaged area at KSR, three groups of nests (natural in December, artificial in December and January) were monitored over at least 14 days each. Their DSRs, calculated separately and pooled, are shown in Table 3.

With program MARK, we found that the best-fitting model with the lowest value of AICc was S(.), which assumes no difference in daily survival between these three groups of nests in the KSR area (Table 4). We therefore concluded that, at least at KSR, the daily survival rate of artificial nests was not different from that of natural nests observed at the same site and in the same circumstances (absence of pest control), suggesting that artificial nests were reasonable surrogates for real nests for the purposes of this experiment.

The overall survival rate of all nests at KSR measured over 14 days was 0.971 (Table 3), which means that the probability of a nest surviving for 14 days in the absence of pest management in that habitat at that time was 0.66 (0.55–0.75 95% CI), independent of whether it was a natural or an artificial nest.

Table 2. Results of predator identifications at nests in Waikato Region by three methods: DNA from eggshells, DNA from clay eggs, and bite marks on clay eggs. UID: unidentified. The number of samples is the number of examinations made, which can reach four if all three methods were tried and DNA swabs were taken twice, once in the field and once in the lab. The DNA technique does not detect all predator species equally well, or distinguish between predators and scavengers (Steffens et al. 2012), so these data are subject to an unknown degree of bias.

Nest no.	Nest ID[1]	No. samples	Date destroyed dd/mm/yy	Result from		
				Eggshells[2] – DNA	Clay eggs – DNA[3]	Clay eggs – bite marks[3]
Natural nests						
A	KSR11 (tūi)	3	22/10/08	Tūi	-	-
B	KSR10 (fantail)	1	14/11/08	Fantail	-	-
Artificial nests (quail and clay eggs)						
1	HA5	2	28/11/08	Insect	Human	UID
2	PJC7	4	28/11/08	Quail	Human, rat	Harrier
3	HE14	2	02/12/08	Human, possum	Human, possum	Rat
4	KSRB15	4	04/12/08	Quail	Thrush, rat	Harrier
5	KSRA5	1	04/12/08	-	UID	Rat
6	KSRA1	1	04/12/08	-	Possum	Possum
7	HA13	1	05/12/08	Quail	-	-
8	KSRA7	1	04/12/08	-	Human	Rat
9	KSRD15	1	04/12/08	-	Human, possum	Possum
10	KSRB11	1	04/12/08	-	Human	Rat
11	KSRA1	1	04/12/08	Quail	-	-
12	KSRC2	2	04/12/08	Human, quail	Human	Possum
13	KSRA17	4	08/12/08	Human	Human	Possum
14	HA11	2	10/12/08	Human, quail	Possum	UID
15	KSRA11	1	12/12/08	UID	-	-
16	KSRB1	1	12/12/08	Human	-	-
17	KSRB9	2	15/12/08	Human, quail	UID	Rat
18	KSRD1	2	15/12/08	Human, quail	Human, quail	Harrier
19	KSR22	2	20/01/09	UID	-	-
20	KSR23	2	20/01/09	Human, quail	-	-
21	HA11	2	27/01/09	Human, quail	-	Possum
22	HE10	2	27/01/09	Quail	Human, quail	Rat
23	KSRB3	2	27/01/09	UID	Human	UID
24	KSRC10	3	27/01/09	Quail	UID	Possum
25	PJA9	1	27/01/09	-	UID	Harrier
26	KRSD1	2	29/01/09	Quail	UID	UID
27	KSRD9	2	29/01/09	Human, rat	UID	Rat
28	PJB12	2	29/01/09	Quail	Quail	Rat
29	HA1	2	02/02/09	-	Human, quail	Rat
30	KSRA7	3	02/02/09	UID	UID, rat	Rat
31	KSRD7	1	02/02/09	-	Human	UID
32	KSRD5	1	02/02/09	Human	-	-
33	HA3	2	04/04/09	Quail	Quail	UID
34	HA5	2	04/02/09	UID	UID	UID
35	PJC1	2	04/02/09	UID	-	UID
36	KSRD15	1	30/01/09	-	Human, possum	Rat

[1] KSR = Kaniwhaniwha Scenice Reserve, H = Hope Block, PJ = Packer-Johnstone Block.

[2] Tui (*Prosthemadera novaeseelandiae*), fantail (*Rhipidura fuliginosa*), quail (*Coturnix japonica*).

[3] Predators: ship rat (*Rattus rattus*), harrier hawk (*Circus approximans*), possum (*Trichosurus vulpecula*), thrush (*Turdus philomelos*), quail (*Coturnix japonica*).

Table 3. Daily nest survival rates (DSR and standard errors, SE) comparing three groups of nests (natural, of fantail, tūi, grey warbler, eastern rosella and kererū[1]; artificial in Dec. 2008 and Jan. 2009) at the Kaniwhaniwha Scenic Reserve non-treatment area, Waikato Region.

Group	No. nests	Nests destroyed	% success	DSR	SE	14-day survival	95% confidence intervals	
							Upper	Lower
Natural (Dec. 2008)	11	7	36	0.965	0.013	0.607	0.789	0.353
Artificial (Dec. 2008)	34	12	65	0.968	0.009	0.632	0.771	0.447
Artificial (Jan. 2009)	34	9	73	0.977	0.007	0.724	0.846	0.539
All nests	79	25	68	0.971	0.005	0.663	0.753	0.551

[1] *Rhipidura fuliginosa*, *Prosthemadera novaeseelandiae*, *Gerygone igata*, *Platycercus eximius*, *Hemiphaga novaeseelandiae*, respectively.

Table 4. AICc models assuming equal S(.) or different S(g) daily nest survival rates for three groups of unmanaged nests (natural, of fantail, tūi, grey warbler, eastern rosella and kererū[1], in Dec. 2008; artificial in Dec. 2008 and Jan. 2009) at the Kaniwhaniwha Scenic Reserve non-treatment area, Waikato Region.

Model	AICc	Delta AICc	AICc weight	Model likelihood	No. of parameters	Deviance
S(.)	205.089	0	0.822	1.00	1	203.08
S(g)	208.154	3.065	0.178	0.22	3	202.13

[1] *Rhipidura fuliginosa*, *Prosthemadera novaeseelandiae*, *Gerygone igata*, *Platycercus eximius*, *Hemiphaga novaeseelandiae*, respectively.

Table 5. Daily nest survival rates (DSR, and standard errors, SE) comparing artificial nests at managed (Packer-Johnstone and Hope sites pooled) and natural plus artificial nests at the unmanaged Kaniwhaniwha Scenic Reserve site, Waikato Region.

Month	Group	No. nests	Nests destroyed	% success	DSR	SE	14-day survival	95% confidence intervals	
								Upper	Lower
December 2008	Managed	43	5	88	0.991	0.000	0.882	0.949	0.739
	Unmanaged	45	12	65	0.968	0.009	0.632	0.771	0.447
	Overall	88	17	81	0.982	0.004	0.772	0.852	0.660
January 2009	Managed	43	8	81	0.989	0.004	0.858	0.934	0.711
	Unmanaged	34	9	73	0.977	0.007	0.724	0.846	0.539
	Overall	77	17	78	0.984	0.004	0.799	0.874	0.690

Table 6. AICc models including the effect of pest control, S(management), or not, S(.), on the survival of artificial nests in pest-managed (Packer-Johnstone and Hope sites pooled) and unmanaged (Kaniwhaniwha Scenic Reserve) sites, Waikato Region.

Month	Model	AICc	Delta AICc	AICc weight	Model likelihood	# parameters	Deviance
December 2008	S(management)	127.170	0	0.909	1.000	2	123.16
	S(.)	131.777	4.601	0.091	0.099	1	129.77
January 2009	S(management)	125.724	0	0.505	1.000	2	121.71
	S(.)	125.766	0.042	0.495	0.979	1	123.76

Comparing managed and unmanaged sites

To explore the possible effect of predator control on the survival of artificial nests, we pooled the data for the two managed sites (P-J and Hope) and compared them with those for the unmanaged site (KSR). Because the previous test showed no difference between artificial and natural nests at KSR, we included the natural nests in this comparison. The estimated daily survival rate in managed areas was higher than in unmanaged areas in December 2008 (0.991 compared with 0.968; Table 5).

A model of nesting success including the effect of management had greater support (a reduction in AICc value by 4.6 in December; Table 6) than the null model. Program MARK found a significant improvement in model fit when 'management regime' (pest control) was included ($\chi^2_1 = 6.62$, $P = 0.01$). The 14-day nest survival for these December artificial nests was 0.88 (0.74–0.95, 95% CI) at treatment sites and 0.63 (0.45–0.77) at non-treatment sites (Table 5).

We repeated the same analysis for the second replicate set of observations of artificial nests set out in the same areas in January 2009. The two models appeared to have almost equal support: the difference in AICc value is 0.04 (Table 6). There was no significant improvement in model fit when pest control was included ($\chi^2_1 = 2.05$, $P = 0.15$). For the simplest

Table 7. AICc models including the effect of month of observation, S(month), or not, S(.), on the survival of artificial nests in pest-managed (Packer-Johnstone and Hope sites pooled) and unmanaged (Kaniwhaniwha Scenic Reserve) sites, Waikato Region, in December 2008 and January 2009.

Model	AICc	Delta AICc	AICc weight	Model likelihood	# parameters	Deviance
S(.)	262.938	0	0.727	1.0	1	260.94
S(month)	264.894	1.96	0.273	0.376	2	260.89

model, having a single DSR for the managed and unmanaged groups in January, the overall 14-day nest survival was 0.80 (0.69–0.87, 95% CI; Table 5).

Comparing artificial nests in December vs January

There was no monthly effect on nest survival (Table 7). A model including such an effect, S(month), had almost equal support with the null model (the difference in AICc was only 1.96). There was no improvement in model fit when the management regime was included ($\chi^2_1 = 0.05$, $P = 0.83$). The probability of nest survival over 14 days for the simplest model (the one assuming a single DSR of 0.982 for both the managed and unmanaged groups) was 0.78 (0.71–0.84, 95% CI). The poorer nest survival in managed areas in January was not, therefore, simply a temporal slackening in reproductive effort attributable to the birds rather than to predators.

Discussion

The use of an innovative combination of methods (video recording at natural nests, plus amplification of forensic DNA and identification of sign at artificial nests) increased our chances of identifying all the predators that visited the damaged nests. We found that examining bite marks on clay eggs was the simplest and most productive method. We confirmed that ship rats, possums and harriers together constituted the primary guild of predators preying on small forest birds in North Island podocarp–broadleaved forest.

The same three predator species have been recorded during previous studies of predation in this habitat at the nests of birds, such as robins (*Petroica australis longipes*) and tomtits (*P. macrocephala toitoi*) at Kaharoa near Rotorua (Brown 1997); North Island kōkako (*Callaeas cinerea wilsoni*) at Rotoehu, Bay of Plenty (Innes et al. 1996) and at Mapara Wildlife Management Reserve, King Country (Flux et al. 2006); kererū at Motatau, Northland (Innes et al. 2004); various passerines at Benneydale and Hamilton, central North Island (Boulton & Cassey 2006); and tūi in the Waikato (Innes et al. unpubl. data). Magpies (*Gymnorhina tibicen*) and stoats (*Mustela erminea*) are much less often identified as predators at nests of small forest birds in North Island forest (Morgan et al. 2006), although stoats are key predators of some other larger forest birds, e.g. juvenile kiwi (*Apteryx mantelli*; Robertson & de Monchy 2012) and (especially in beech (*Fuscospora* spp. and *Lophozonia* sp.) forest after a masting year) kākā (*Nestor meridionalis septentrionalis*; Moorhouse et al. 2003), and whio (*Hymenolaimus malacorhynchos*; Whitehead et al. 2008).

Control of introduced mammals to protect native birds is done routinely in New Zealand, but harriers are usually regarded as part of the native guild of avian predators natural to New Zealand's historical (especially prehuman) ecology. Predatory birds, primarily harriers, still account for a substantial proportion of attacks on songbird nests in contemporary New Zealand forests (Innes et al. 1999; Boulton & Cassey 2006; Flux et al. 2006; Morgan et al. 2006), especially where there are few mammalian predators (Lewis et al. 2009). However, harriers colonised New Zealand only after human invasion in the 13th century, and they have probably benefitted greatly from human activities, especially large-scale forest clearance and the introduction of many small mammal and other bird species as additional prey (Heather & Robertson 1996), so it is debatable whether their contribution to predation of contemporary forest birds is still 'natural'.

Steffens et al. (2012) showed that predators at black-fronted tern (*Chlidonias albostriatus*) nests were not equally detectable by DNA because many eggs were completely removed and because some predators (e.g. hedgehogs *Erinaceus europaeus occidentalis*) did not leave detectable DNA on eggshells. We did not use video cameras at artificial nests, and extracted eggshells from only two videoed nests. Our DNA results are few, but consistent with expectations based on other signs, video records, and the literature. None of these methods are fully representative, and all are likely to underestimate visits by predators to nests in different ways.

The question of whether use of artificial nests is a valid technique 'to achieve…adequate sample sizes of nests distributed across the landscape in a way that minimized statistical biases' (Faaborg 2004) in studies of nest predation has been controversial (Ortega et al. 1998; Zanette 2002; Berry & Lill 2003; Mezquida & Marone 2003; Moore & Robinson 2004). We used artificial nests only after failing to find enough real nests, and our objectives for both nest types included accurate identification of nest predators, as Faaborg (2004) recommended. We used natural nests baited with real (quail) and clay eggs and placed them in realistic positions in a simple trial design as recommended by Major and Kendal (1996), but even then, artificial nests do not necessarily survive at the same rate as natural nests (King et al. 1999; Robel et al. 2003; Burke et al. 2004; Thompson & Burhans 2004; Robinson et al. 2005).

In artificial-nest studies, a mismatch between the size of natural eggs used and the capabilities of predators in the study area will result in misleading data on predation rates (Coppedge et al. 2007; Oliviera et al. 2013), and clay or plasticine eggs can be more readily marked by small predators than real eggs that are too large (Bayne et al. 1997; Maier & Degraaf 2001). In our study, predators were all large enough to open quail eggs. Mice (*Mus musculus*) struggle to break quail egg shells (unpubl. data) but no mice were detected at nests in our study.

We accept that specific monitoring devices such as tracking tunnels are better ways to index the abundance of one particular predator (e.g. ship rat) than are artificial nests (Getzlaff et al. 2013).This was not our objective, and our potential predator suite was very broad, including large mammals (possums) and birds (potentially harriers and ruru *Ninox novaeseelandiae*).

Lewis et al. (2009) comment that their use of artificial nests may have missed an entire predator group, the mustelids, that were tracked in their study areas but never detected by marks on clay eggs. We accept this potential error, even though stoats are known to relish eggs and do leave very distinctive tooth marks (King & Moody 1982); but we doubt that it could be important. Individual mustelids are potentially at least as damaging to individual birds as are rats, but rats are more often recorded visiting nests (Table 2), as expected because they are far more abundant. For example, North Island forests in January typically support an average of up to about 600 ship rats per100 ha (Hooker & Innes 1995; Brown et al. 1996b), whereas the normal range of densities for stoats in comparable forest around Lake Waikaremoana is about 2–10 per 100 ha (Basse et al. 1999). The sheer numbers and wide distribution of rats (King et al. 1996), and their agility in reaching arboreal nests (Foster et al. 2011), make rats the most significant predator of small songbirds in North Island mixed forest. Also, we did not film mustelids at any natural nests in this study.

Without denying the importance of these issues, several authors have pointed out the advantages of using artificial nests that make them worth considering in the New Zealand context (Smith et al. 2008; van Heezik et al. 2008; Lewis et al. 2009; King & Scurr 2013). These include avoidance of the time and cost, plus the possible risk of searching bias, inherent in the task of finding enough natural nests, especially of endangered species; full or partial control over confounding variables; minimal risk of attracting predators to natural nests by human activity; and the potential to employ tethered clay eggs, a simple and relatively reliable way to identify nest predators and to test the effectiveness of a management programme. The need to make conservation decisions for New Zealand bird species is becoming increasingly urgent, while budget and logistics often enforce a choice between information from artificial nests or no information at all (Smith et al. 2008). These considerations strengthen the case for using artificial nests, provided the sources of variability are minimised as far as possible (Lewis et al. 2009).

In our study, a comparison between daily survival rates of natural and artificial nests in an unmanaged area (KSR) detected no differences that would argue against use of artificial nests to estimate predation on natural nests (Tables 3 and 4). In December, but not in January, the higher probability of survival of artificial nests in managed areas was consistent with previous studies finding that routine pest control assists nesting birds during the peak of the season (Tables 5 and 6). For example, fantail success would be 76% in a pest-managed site compared with 37% with no pest management after 30 days (total fantail nesting duration); tūi success would be 73% compared with 32% after 35 days; kererū success would be 62% compared with 17% after 53 days (Heather & Robertson 1996).

There are two possible reasons why the addition of pest control significantly improved the model only in December: (1) the January DSR could have decreased in the treatment blocks, or (2) it could have increased in the non-treatment block. Both are potential explanations, because as Table 1 shows, the rat tracking index increased over the summer (as it usually does, with the dispersal of young rats) in the treatment blocks, whereas it decreased at KSR even in the absence of pest control. This is not unknown (Innes et al. 2004), but is unusual.

On the other hand, such a small difference in DSR may mean nothing in the long term, since even a large increase in nesting success does not in itself guarantee an increase in the population of the protected species (Coté & Sutherland 1997; Keedwell et al. 2002; Smith et al. 2010). However, effective control of ship rats and possums in large forest fragments of the central Waikato since 2007 (the 'Hamilton Halo' project of Waikato Regional Council and Landcare Research) has significantly increased the numbers of tūi in nearby Hamilton City (Fitzgerald & Innes 2013) and substantially in the forest sites themselves (Innes et al. 2013 unpubl. 2012 bird count report).

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