

# Differential effects of exotic predator-control on nest success of native and introduced birds in New Zealand

Amanda Starling-Windhof · Melanie Massaro · James V. Briskie

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**Abstract** The introduction of mammalian predators has been detrimental to many native birds in New Zealand. One solution to this problem has been the creation of “mainland islands” in which exotic predators are systematically removed. Although mainland islands have been effective in increasing some native bird populations, few studies have measured the effect of predator-control on nest success nor what effect control measures have on sympatric populations of introduced birds. We measured the effect of predator-control on nest survival rates in both native and introduced passerines in a mainland island near Kaikoura, New Zealand. Nest survival was significantly higher in Waimangarara Bush (the site with experimental predator-control) than in Kowhai Bush (the site with no predator-control) and this pattern was found in both groups of birds. However, mammalian predator-control increased nest success of native species significantly more than nest success of introduced species. This suggests that native birds benefit disproportionately from control of introduced predators, most likely because they lack behavioural

defences against mammalian predators that are present among the introduced birds.

**Keywords** Nest survival · Introduced predators · New Zealand birds · Introduced birds · Mainland island · Predator-control

## Introduction

Introduced mammalian predators have been one of the main causes of bird extinctions on isolated islands (Blackburn et al. 2005). At least 42 species of native birds have become extinct in New Zealand since the arrival of humans, with most of these extinctions being attributed to the introduction of exotic mammals (Holdaway 1999). Birds on oceanic islands appear especially vulnerable to exotic mammals as they evolved in an environment where, in the case of New Zealand, the only terrestrial mammals previously present were bats (King 1984). As a result, native island birds appear to lack many of the defences that minimise predation risk from predatory mammals in continental species (Briskie et al. 1999; Lovegrove 1996; Martin 1995; Martin et al. 2000; Moors 1983). Ongoing population declines among many native birds have likewise been blamed on excessive predation from exotic mammals (Dowding and Murphy 2001; Gill and Martinson 1991; Holdaway 1999).

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M. Massaro · J. V. Briskie  
School of Biological Sciences, University of Canterbury,  
Private Bag 4800, Christchurch, New Zealand

A. Starling-Windhof (✉)  
Department of Cellular Biochemistry, Max Planck  
Institute of Biochemistry, Martinsried, Germany  
e-mail: windhof@biochem.mpg.de

Conservation in New Zealand has traditionally focused on translocating endangered birds to offshore islands free of exotic predators (Atkinson 2001; Parkes and Murphy 2003). However, attempts have recently been made to control introduced mammals on the mainland through continuous bouts of trapping and poisoning (Clout 2001). These areas are referred to as “mainland islands,” and such management has become increasingly popular as a way of controlling introduced mammal populations while conserving birds in situ (Gillies et al. 2003; Saunders and Norton 2001). The predators controlled varied from one site to another, but include mustelids (*Mustela furo*, *M. erminea*, and *M. nivalis*), rats (*Rattus rattus* and *R. norvegicus*), possums (*Trichosurus vulpecula*), and feral cats (*Felis domesticus*). The effect of predator-control is reflected in both increased nesting success and population recovery. For example, nesting success in the North Island kokako (*Callaeas cinerea wilsoni*) was significantly higher during control of ship rats and possums (Innes et al. 1999); kaka (*Nestor meridionalis*) and bellbird (*Anthornis melanura*) populations increased when stoats were controlled (Kelly et al. 2005; Moorhouse et al. 2003).

Predatory mammals were not the only introductions to New Zealand; beginning in the nineteenth century at least 30 species of mostly European birds became established through the actions of acclimatisation societies (Long 1981; Thomson 1922). In contrast to native birds, introduced European birds co-evolved with mammalian predators in their native ranges (King 1984). As a result, these continental species display a variety of life history traits that minimise the risk of predation (Briskie et al. 1999; Martin 1995; Martin et al. 2000). For example, birds subject to high predation pressure have more rapid chick development (Harfenist and Ydenberg 1995), subdued chick begging (Briskie et al. 1999), and reduced nest visitation rates (Fontaine and Martin 2006; Massaro et al. 2008). As many of the introduced predatory mammals are the same species European birds co-evolved with in their native range, it has been suggested that introduced birds should be able to cope with the pressures of high predation from mammals, and would possibly suffer less nest predation than native birds (Moors 1983). However, there is little information available at present to test this idea.

The objective of this study was to compare the effect of predator-control on nest survival in native and introduced birds in New Zealand. We studied nest survival of both native and introduced birds in an area where predators are controlled as well as in an area with no predator-control. Although the effects of predator-control on native species have been studied (e.g. Innes et al. 1999; Kelly et al. 2005), there is little information on how introduced birds respond to the same treatment. Given that introduced birds are often the most common species present in large parts of New Zealand, and are even more common than in their native range (Robertson et al. 2007), there is potential for mainland islands to inadvertently increase the effects of invasive birds on native ecosystems. For example, the potential for exotic birds to act as vectors or reservoirs for exotic diseases (Tompkins and Gleeson 2006) and increase the spread of invasive plants (Williams and Karl 1996) highlights the need to understand the consequences of predator-control on these non-intended targets.

## Materials and methods

The study was conducted from 2002 to 2009 at Kowhai Bush and from 2004 to 2009 at Waimangarara Bush near Kaikoura, New Zealand. Kowhai Bush is 240 ha of native woodland that we used as a non-treatment site as it has little mammalian predator-control, except for some poisoning of possums around the eastern edges where the forest is adjacent to farmland. Waimangarara Bush is 65 ha of native woodland which has been subject to continual predator-control since 2003 for possums, feral cats, mustelids, and rodents. The two sites are separated by five kilometres and experience similar climate and have similar native vegetation. The forest canopy in both sites consists mainly of kanuka (*Leptospermum ericoides*), and manuka (*L. scoparium*), with lesser abundances of *Pittosporum tenuifolium*, *Coriaria arborea*, *Phymatosorus diversifolius*, *Cytisus monspessulanus*, *Dodonaea viscosa*, *Melicactus ramiflorus*, *Clematis vitalba*, *Ribes sanguineum*, *Olearia paniculata* and *Pseudopanax arboreus* (Gill 1980). Both forests lie on the coastal plain about seven km inland, and range from 10 to 50 m above sea level. The area between the two sites has been cleared for agriculture, although both forests are connected to a larger

block of montane forest by a narrow strip of vegetation along their north-western edges. Thus, the only significant difference between the two sites is the extent of mammalian predator-control.

Differences in nest success between the two sites were compared by locating nests of each species and following their outcome. Study species were chosen based on their similarity in general life history strategies: they are all nest builders (i.e., no cavity nesters), feed primarily on invertebrates, are small to mid-sized passerines, and have clutches of three to five eggs. Furthermore, these species were selected due to their relative abundance in each study site and because their nests could be easily located and tracked. The following native bird species were included in this comparison: New Zealand fantail (*Rhipidura fuliginosa*), grey warbler (*Gerygone igata*), bellbird (*Anthornis melanura*) and the South Island robin (*Petroica australis*), while the group of introduced species included European blackbird (*Turdus merula*), song thrush (*T. philomelos*) and dunnoek (*Prunella modularis*). The silvereye (*Zosterops lateralis*) was also studied but we considered it an exotic species in the context of this study as it only colonised New Zealand (from Australia) in the early nineteenth century, and like the introduced European species, co-evolved with predatory mammals in its native range.

Nests were located by watching adults and by searching vegetation. Nests were tagged nearby with flagging tape and then visited at intervals of three to four days until they fledged or failed. A nest was considered successful if young were observed leaving the nest or if the young were ready to fledge on the previous visit (e.g., pin feathers unsheathed several centimetres). A nest was considered depredated if all eggs or young were missing (before being capable of fledging), if there were egg-shells in the nest, or if the nest was destroyed. We assumed that mammals were the main predators. Avian predators (e.g., falcons (*Falco novaeseelandiae*), moreporks (*Ninox novaeseelandiae*) and long-tailed cuckoos (*Eudynamys taitensis*)) were rare at the study sites and are more likely to prey on adults and mammals than on nests (Marchant and Higgins 1993). For example, in 12 years only one falcon and one long-tailed cuckoo were observed on the study sites, and that was only on a single occasion. Although harriers (*Circus approximans*) are common in the area, they forage

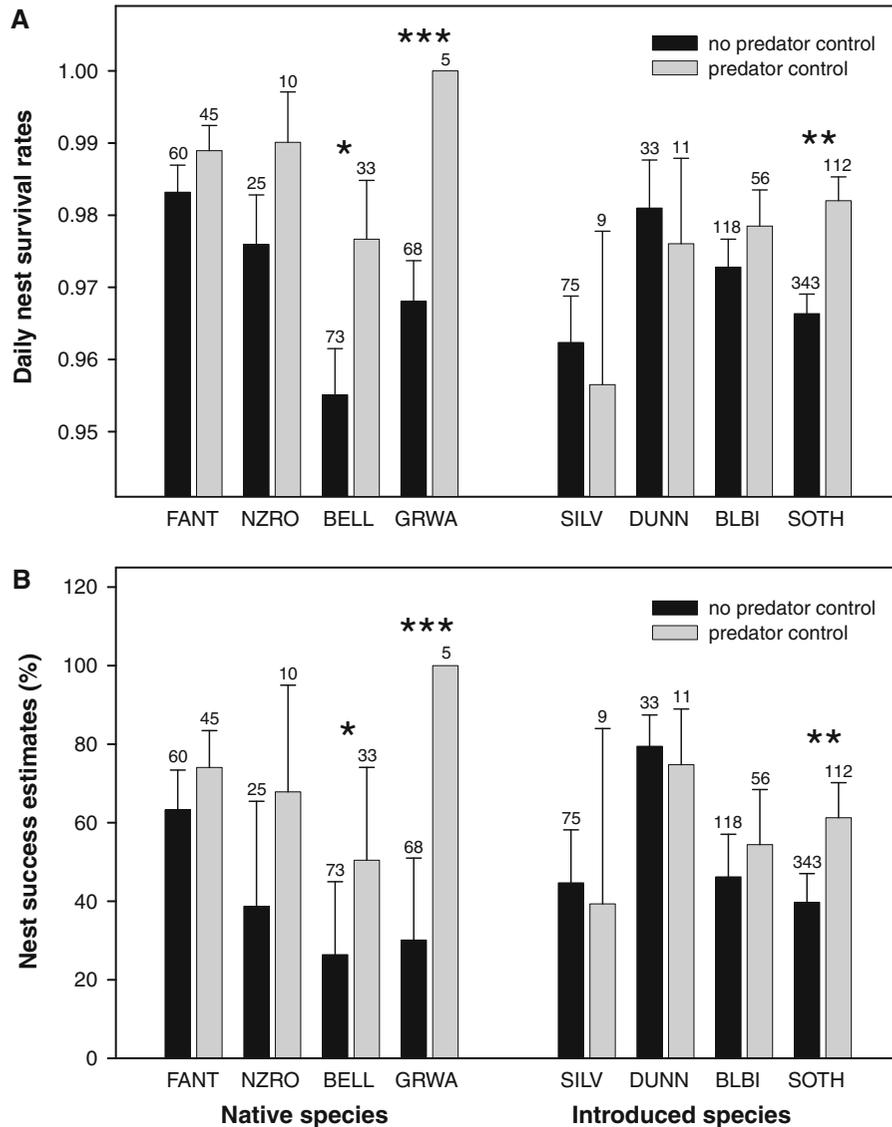
primarily over the open pastures and not in the forest canopy or under-storey. Moors (1983) also found that exotic mammals were responsible for almost all losses due to predation. Nevertheless, a few nests (less than five) at each site contained dead nestlings with peck marks. This was likely due to predation by the shining cuckoo (*Chrysococcyx lucidus*), which is common in both sites. As we were concerned primarily with the effects of introduced mammalian predators, nests that were depredated by cuckoos were excluded from any further analyses. Visits to the nests by researchers occurred with the same frequency in both study sites to control for any effect of human visitation affecting predation rates (Keedwell and Sanders 2002; Mayer-Gross et al. 1997; Verboven et al. 2001). The potential for pseudo-replication is a possible problem when data are collected in the same sites over several years. Unfortunately, we were unable to band birds to avoid re-sampling individuals, and it is possible that multiple nests of some pairs may have been included in the analysis. However, because nest searching was spread over a large area, and all species were relatively common, it is likely that any error due to pseudo-replication may be small.

Experimental predator-control at Waimangarara Bush involved systematic attempts to control all introduced predators through traps and poison. Fenn traps were set for mustelids, while leg hold traps were set to catch feral cats (Blair 2002). The anti-coagulant brodifacoum was used to poison rodents and possums. Poison bait stations began operation in late winter each year, before the breeding season of the birds, and were restocked at weekly intervals throughout the spring and summer. It is important to have continual poisoning throughout the breeding season because rat populations can recover quickly after an initial poisoning (Innes et al. 1995). Both the traps and bait stations were positioned along trails throughout the study area. The distance between traps and bait stations averaged about 50 m, which is similar to that used in other mainland island projects in New Zealand (e.g. Kelly et al. 2005; Moorhouse et al. 2003; Saunders and Norton 2001). As the monitoring of mammalian populations before and after the implementation of predator-control was beyond the scope of this study, we made the assumption that the predator-control measures we used would reduce the density of introduced predators to a level that reduced the probability of nest predation.

**Statistical treatment**

A total of 1,076 nests of eight species were used for these analyses. This included a sample of 757 nests of four introduced species and 319 nests of four native species. This was divided between 795 nests in Kowhai Bush and 281 nests in Waimangarara Bush. Exact nest numbers for each species in Kowhai and Waimangarara Bush are given in Fig. 1. We only

included nests in this study that were still active at the time they were found (i.e., eggs were warm or chicks alive), because for nests that failed before they were found it is impossible to distinguish whether they failed due to a predation event or whether the predation event occurred after abandonment of the nest. To compare the probability of nest success (raising at least one chick until fledging) between predator treatments (Kowhai or Waimangarara bushes) and species groups



**Fig. 1** Daily nest survival rates (a) and overall nest success estimates (b) of native and introduced species of New Zealand birds in a site with no predator-control and a site with predator-control. FANT = fantail, NZRO = New Zealand robin, BELL = bellbird, GRWA = grey warbler, SILV = silveryeye,

DUNN = dunnock, BLBI = blackbird, and SOTH = song thrush. Sample sizes of nests that were monitored are above the bars. Stars indicate level of significance of differences within species ( $P < 0.05 = *$ ,  $P < 0.001 = **$ ,  $P < 0.0001 = ***$ )

(native or introduced), we used a generalised linear mixed model (GLMM), with a binomial error and fit by the Laplace approximation. The model was conducted in the lme4 package in R v. 2.9.1 (Bates and Maechler 2009; R Development Core Team 2009). The binomial response variable was “outcome” (success 1, or failure due to predation 0). The predictor variables were “species status” (i.e., whether the species was native or introduced) and “predator treatment” (i.e., predators controlled for all nests from Waimangarara Bush, but predators not controlled for nests in Kowhai Bush). In this analysis, differences among species were accounted for by including species per predator treatment as a random effect. We conducted likelihood ratio tests to calculate more conservative *P*-values.

For graphical and further analyses we also calculated daily nest survival rates for each species per predator treatment using the Mayfield Method (Mayfield 1961; 1975). We followed Hensler and Nichols (1981) to calculate standard errors for Mayfield’s daily survival probabilities and the program CONTRAST was used to analyse the intra-species differences in daily nest survival rates (Sauer and Williams 1989). To calculate overall nest survival estimates for the entire nesting period for each species, daily nest survival rates were raised to the exponent of the number of days between first egg laying and fledging. We obtained data on overall nesting period length for each species from Heather and Robertson (1996).

## Results

The comparison of daily nest survival rates and overall nest success estimates within species (Fig. 1) showed that all of the native species had higher survival rates in Waimangarara Bush (mammalian predator-control) compared to Kowhai Bush (no mammalian predator-control). Of the four native species, the bellbird and the grey warbler benefited significantly from the predator-control in Waimangarara Bush (Fig. 1; bellbird, Chi-square = 4.33, *df* = 1, *P* = 0.037; grey warbler, Chi-square = 32.05, *df* = 1, *P* < 0.0001), while differences in daily survival rates between Waimangarara Bush (mammalian predator-control) and Kowhai Bush (no mammalian predator-control) were not significant for the fantail (Chi-square = 1.26, *df* = 1, *P* = 0.26)

**Table 1** Parameter estimates ( $\pm 1$  SE), *z* statistics and *P*-values of a generalized linear mixed model testing whether predator-control affects the probability of nest success in native New Zealand birds and introduced birds differently. Species per predator treatment was included as a random effect (variance =  $0.033 \pm 0.182$ )

Fixed effects	Estimate	Std. error	<i>z</i> value	<i>P</i> *
Intercept	0.3878	0.1355	2.861	0.004
Species status	-0.3212	0.2125	-1.511	0.131
Predator treatment	0.4591	0.2400	1.913	0.056
Species status $\times$ predator treatment	0.7896	0.4006	1.971	0.049

\**P*-values presented here are not the same than those presented in the text. In the text, *P*-values of the more conservative likelihood ratio test are presented

and the New Zealand Robin (Chi-square = 2.10, *df* = 1, *P* = 0.15).

In comparison, predator-control in Waimangarara Bush influenced nest survival of introduced species differently (Fig. 1). Two of the four introduced species had lower daily nest survival rates in the predator-controlled Waimangarara Bush than in Kowhai Bush with no predator-control, but these differences were not significant (silveryeye, Chi-square = 0.069, *df* = 1, *P* = 0.79; dunnoek, Chi-square = 0.13, *df* = 1, *P* = 0.72). Blackbirds and song thrushes had increased daily survival rate in Waimangarara Bush compared to Kowhai bush, however only in the song thrush was this difference significant (song thrush, Chi-square = 13.34, *df* = 1, *P* = 0.0003; blackbird, Chi-square = 0.81, *df* = 1, *P* = 0.37).

When we tested whether predator-control affects the probability of nest success differently in native species than introduced species, this analysis confirmed that overall probability of nest success was higher in the predator-controlled Waimangarara Bush (Chi-square = 5.79, *df* = 1, *P* = 0.016) than in Kowhai Bush (site with no predator-control), but it also showed that native species benefited significantly more from predator-control than introduced species (Chi-square = 3.87, *df* = 1, *P* = 0.049; Table 1).

## Discussion

We found that the control of exotic mammalian predators during the breeding season increased nest survival in both native and introduced species of

passerine birds in a lowland New Zealand forest environment. Moreover, predator-control affected nest success of native New Zealand birds and introduced birds differently: native species benefited more from control of exotic predators than introduced species. The vulnerability of many native New Zealand birds to introduced mammalian predators is well documented (Dowding and Murphy 2001; Innes et al. 2010; Sanders and Maloney 2002), and our study confirms the positive effects of predator-control on nest survival that have been found in other native species (e.g. Innes et al. 1999). However, most studies of predator-control have focused on a few target species, typically endangered native birds (e.g. Kelly et al. 2005; Moorhouse et al. 2003). Our results indicate that one cannot extrapolate these results to all other species within the community, as predator-control can disproportionately increase nest survival rates of some species while providing seemingly little benefit to other species.

Moors (1983) also compared predation rates of introduced birds with those of native birds in New Zealand and found little difference, but his study was based on a small number of nests and his estimates did not control for observation biases (e.g. Mayfield 1961, 1975). Our study suggests that introduced birds, whose populations flourish in New Zealand, may inherently cope better with high levels of nest predation than native birds. Introduced birds co-evolved with mammalian predators in their native range and are likely to have a suite of adaptations that minimise the risk of nest predation. For example, incubation and nestling periods are usually considerably shorter in introduced species (e.g., 13–14 days in song thrush, *Turdus philomelos*; Cramp 1988) than in native New Zealand birds (e.g., 20 days in rifleman, *Acanthisitta chloris*; Higgins et al. 2001), reducing the period in which introduced birds are at risk. Furthermore, birds that evolved with mammalian predators can re-nest quickly to accommodate multiple-brooding (Burley 1980), and they decrease their levels of activity around the nest to minimise the risk of attracting the attention of predators (Martin et al. 2000; Skutch 1949). In contrast, birds that evolved on islands have a number of life history traits that appear to make them particularly susceptible to nest predation from introduced mammals (Franklin and Wilson 2003; Massaro et al. 2008; Trevelyan and Read 1989). For example, bellbirds on the Poor

Knights Islands have never been exposed to introduced mammalian predators and show higher levels of activity around the nest than bellbirds on the New Zealand mainland (Massaro et al. 2008). Such lack of defences against exotic predators may mean that nest survival rates of native birds are more likely to directly track predator density, while introduced species are likely to cope with all but the highest levels of predation risk. Determining which traits place native birds at increased predation risk would be worth further study.

Although the full range of introduced mammalian predators were targeted for control at the Waimangarara Bush site, it was not possible to completely remove all individuals and eliminate nest predation by non-native animals, and we assumed that the control measures implemented resulted in a reduction of introduced predator populations. This assumption is reasonable given that the predator-control methods were similar to that used in other mainland island projects in which predator numbers are shown to be effectively reduced (Gillies et al. 2003; Kelly et al. 2005; Saunders and Norton 2001). The decrease in nest predation rate we detected in Waimangarara Bush also suggests a significant effect of predator-control on predation rate. Given the broad and indiscriminate nature of predator-control used, we were also unable to attribute the change in nest success to a particular predator (e.g., rats). Nevertheless, as the objective of many mainland island projects is to restore a wide range of ecological processes, and not just reduce nest predation on native birds, our results confirm that such comprehensive predator-control programmes are likely to increase the nest success of a range of native birds.

One weakness of our study was the lack of replicate predator-control and non-treatment sites. With only one site subject to predator-control, and one non-treatment site, it is possible that the nest survival differences we found were the result of other differences between sites. Although the two sites were similar in climate, elevation, vegetation structure and avifaunal composition, additional replicate sites would be needed to confirm the pattern we found. Unfortunately, controlling the full range of exotic mammalian predators present on the New Zealand mainland is expensive and time-consuming at the scale needed to encompass a representative sample of the avifauna, and at least in our study area,

there are few other additional areas of native woodland remaining that could be used as replicate sites. However, it may be possible to expand our study by a meta-analysis of nest success of birds in other mainland island sites across New Zealand. Nest success is being monitored at many of these sites by other researchers, but as far as we know, only native species are targeted and there is little information to assess the effect of predator-control on introduced birds. The results of our study suggest the inclusion of introduced birds at other mainland island projects would be valuable for understanding the effect of predator-control on the entire avian community.

Although mammalian predator-control can aid in the recovery of endangered native species, there is concern over the risk of secondary poisoning to native fauna and the persistence of poisons in the environment (Innes and Barker 1999; Lloyd and McQueen 2000). One mooted solution to the problem has been the creation of fenced reserves that prevent the re-invasion of predators after they have been eliminated. A number of fenced mainland islands have now been built in New Zealand (e.g. Clapperton and Day 2001), but we know of no published study that has compared nest success of native and introduced birds within these areas. With the complete elimination of all non-native predators in fenced areas, it is possible that the nest success of introduced birds could increase in the same manner that we observed among native species with our less complete effort of predator-control. If the complete removal of exotic predators eliminates the differential in nest success between native and introduced birds, it is possible that the differential benefit of predator-control to native species that we found also disappears. Clearly, there is a need to monitor changes in the populations of introduced birds in any area of predator-control (fenced or otherwise) to determine if native birds that benefit from predator-control on the one hand then suffer on the other hand from increased numbers of introduced birds.

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