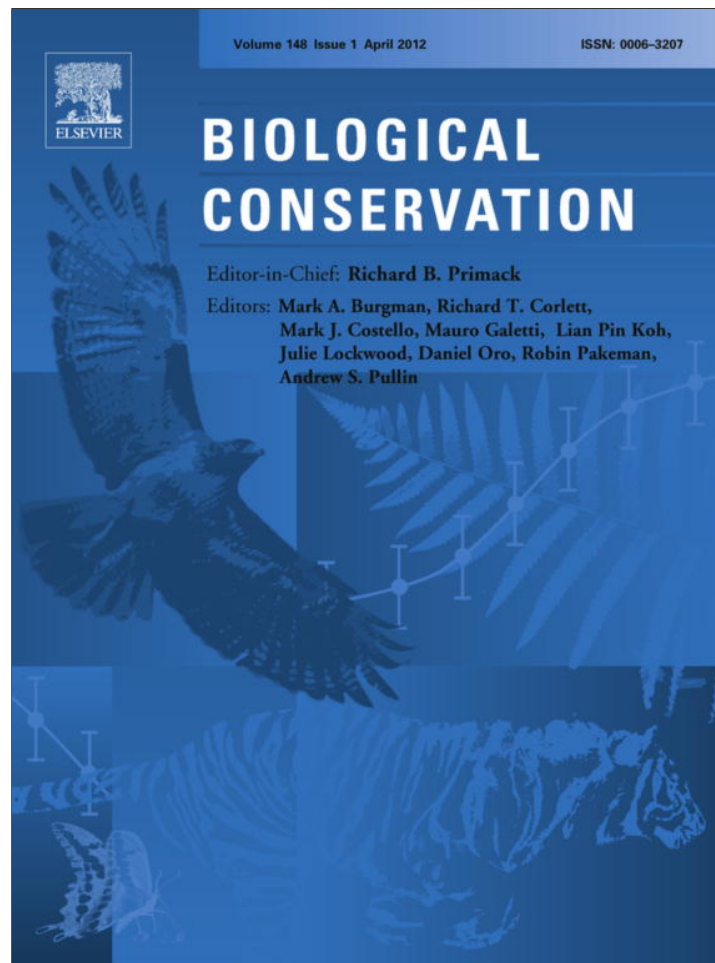


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# Nest predation in New Zealand songbirds: Exotic predators, introduced prey and long-term changes in predation risk

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## ABSTRACT

Predation is a major factor in ecology, evolution and conservation and thus its understanding is essential for insights into ecological processes and management of endangered populations of prey. Here we conducted a spatially (main island through to offshore islets) and temporally (1938–2005) extensive meta-analysis of published nest predation rates in New Zealand songbirds. We obtained information on nest predation rates from 79 populations ( $n = 4838$  nests) of 26 species of songbirds belonging to 17 families. Nest predation rates increased from southwest to northeast and also across the last 60 years (by 15–25% points in both cases). We identified a major impact of exotic mammalian predators. Nest predation was lowest in areas where no exotic predators were present (12.8%), higher in areas with ongoing predator control (33.9%), and highest in areas without control that had the full set of exotic and native nest predators (47.5%). Surprisingly, nest predation rates were higher in introduced as compared to native species. Our analyses demonstrated that human-caused factors (introduced predators and prey) overrode factors such as nest type and habitat identified as important in predicting nest predation in North America and Europe previously.

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## 1. Introduction

Predation is an important ecological factor with strong implications for conservation. For example, predation was the major cause of nest failure in dozens of bird species in Europe and North America (O'Connor, 1991; Martin, 1993; Côté and Sutherland, 1995). Moreover, the loss of at least 34 of the 110 species of birds that have become extinct since c. 1600 has been ascribed to introduced predators, such as cats, rats, mustelids, and mongooses (Groombridge, 1992). Additionally, 625 globally threatened bird species (over 50% of the total of 1226) and 99 critically endangered bird species (52% of the total of 190) are currently at risk from invasive species, especially introduced mammals (in particular rats and cats; BirdLife International, 2008a). The situation is most severe on oceanic islands where 75% of 430 globally threatened bird species are negatively affected by invasives, the most dangerous being again rats and cats (BirdLife International, 2008b). Thus, understanding factors driving predation risk is very important for effective conservation management.

Insular faunas have peculiar historical and evolutionary trajectories due to the interplay between contingency and determinism

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in colonization of islands and subsequent speciation and adaptation (Losos and Ricklefs, 2009). For example, most of New Zealand's biota results from overwater colonization, rather than survival since New Zealand separated from Australia (Goldberg et al., 2008). The accidental happenstance of colonization greatly influenced the course of subsequent evolutionary diversification, because it occurred in the almost complete absence of terrestrial mammals. Consequently, New Zealand birds are expected to be vulnerable to exotic predators, as is generally the case in insular avifaunas (Blackburn et al., 2004) that are under strong pressure from exotic mammals (Phillips, 2010). Confirming this claim, exotic mammalian predators have caused many extinctions and severe declines among New Zealand's endemic avifauna (Dowding and Murphy, 2001; Duncan and Blackburn, 2004; Tennyson, 2010) and are believed to be the main cause of ongoing population declines of several species (e.g. O'Donnell, 1996; Innes et al., 2010).

Previous large-scale studies of nest predation in birds have been limited to continental settings (O'Connor, 1991; Martin, 1993; Côté and Sutherland, 1995; Chamberlain et al., 2009). These studies revealed several correlates of nest predation risk, including nest type, habitat, and geographical context (Thompson, 2007). However, due to the location of their interest, which included North America and Europe, these studies were not able to separate effects of exotic predators and introduced prey. Yet, we know that exotic predators can have disproportionately strong effects on native prey (Salo

et al., 2007) and introduced prey can lack anti-predator defenses to native predators that might make them more vulnerable (Barrio et al., 2010). Islands, including New Zealand, are plagued by exotic predators, which have been confirmed as important nest predators of many native bird species (Keedwell and Sanders, 2002; Sanders and Maloney, 2002; Poirot, 2004, Table 1.1). New Zealand also has many introduced bird species mostly from Europe (Blackburn et al., 2009), allowing the dissection of the relative importance of species origin. Thus, New Zealand birds provide a unique opportunity for obtaining novel insights into the factors driving rates of nest depredation.

Here, we modeled effects of exotic predator presence (exotic predators controlled, not controlled, not present) and the origin of prey (exotic vs. native) on nest predation rates in New Zealand songbirds. We used a database built by an exhaustive literature search that spans the whole country and several decades. We also used the long-term nature of our database to analyze whether nest predation rates have changed over time. We adjusted our analyses for factors that had been shown to be important predictors of nest predation rates in other areas, including geography, life history, and habitat characteristics.

## 2. Material and methods

### 2.1. Building the data set

We collected data for this study from the literature, where we focused on intensive field studies of a single or several species of New Zealand songbirds (see Appendix S1). From the resulting articles we extracted where possible the number of nests destroyed by predators, number of failed nests, number of nests studied, and when and where the study was done. An obvious constraint on the data is that it is not always possible to assign a particular nest loss to predation without direct evidence obtained by video-taping. Here we relied on two approaches to identify nest losses caused by predators. First, if the author(s) explicitly stated how many nests were taken by predators, we accepted this claim. Second, if nests lost to predators were not explicitly enumerated, we assigned a loss to nest predation if the total clutch or brood disappeared suddenly without other obvious reasons (e.g. storm or human interference). We only included partial losses if losses were reported as the total number of eggs or nestlings lost, instead of whether some loss occurred from the whole nest. In these latter cases, there was no way of teasing apart partial and total losses. We calculated the number of nests studied as the number of eggs divided by clutch size reported for that particular study. Because this method includes partial predation, total losses are slightly overestimated in these populations ( $n = 4$  populations).

Besides analyzing proportion of nests lost to predators, we also transformed these data to daily predation rates (DPR) by the method of Ricklefs (1969). To validate the values thus obtained, we also calculated daily failure rates by two other approaches (Beintema, 1996; V. Remeš, unpublished data), which were based on the nest survival model of Mayfield (1975). Estimates produced by all three methods were highly correlated ( $r = 0.99$ – $1.00$ ,  $n = 78$ ) and we use the method of Ricklefs (1969) in all statistical analyses. For all these estimates, length of the nest cycle was calculated as the sum of the length of incubation and nestling periods (in days), and clutch size (number of eggs). Clutch size was added because eggs are laid daily and the nest is exposed to the risk of depredation from the laying of the first egg. None of these methods estimates true daily predation rates that can be obtained by applying the Mayfield method (Mayfield, 1975) on original data sets – these are obviously not available when working with literature data. However, we included the best available estimates of

DPR into our analyses, because overall proportion of depredated nests is a product of daily predation rate and the length of exposure. Thus, excluding daily rates could lead to biased results (see Remeš and Martin, 2002).

From each study we extracted broad habitat category (forest vs. open) and whether it was conducted in a rural or urban area. For each species we also obtained its nest type (open vs. closed, which included domed and cavity nests), average adult body mass (g), and whether the species is native or introduced, based on a general reference (Higgins et al., 2001, 2006; Higgins and Peter, 2002). For each study we also extracted information on predator control. We categorized our studies into three groups. First, there were studies on populations with no predator control that were exposed to the whole suite of native and exotic predators ( $n = 58$ ). Second, there were studies where exotic mammalian predators were controlled ( $n = 17$ ). Predator control was conducted by means of various traps, bait stations or aerial 1080 poisoning (sodium monofluoroacetate), and targeted the following exotic mammals: mustelids (stoat [*Mustela erminea*], weasel [*M. nivalis*], and ferret [*M. furo*]), cats (*Felis catus*), rats (*Rattus rattus* and *R. norvegicus*), possums (*Trichosurus vulpecula*), and hedgehogs (*Erinaceus europaeus*). Third, there were studies from islands with no exotic mammalian predators present ( $n = 4$ ). These included islands where no exotic predators were ever present (Aorangi Island and Snares Island), or where predators had been eradicated (cats on Cuvier Island in 1960s, on Tiritiri Matangi in 1972, on Little Barrier Island in 1980; kiore [*Rattus exulans*] on Cuvier Island and Tiritiri Matangi in 1993, on Little Barrier Island in 2004; Lovegrove, 1996; Veitch, 2001; Poirot, 2004; Massaro et al., 2008). However, there are reasons to treat kiore separately from newly introduced mammalian predators. First, it was introduced to New Zealand by Maori starting ca. 1000 years ago (Atkinson, 2001), allowing for microevolutionary response in its prey (Stockwell et al., 2003). Second, based on some accounts, it is not so dangerous and destructive as other rat species (e.g. ship rats [*Rattus rattus*]; Lovegrove, 1996). Thus, we also categorized studies where kiore was present as having no exotic predators and re-run the analyses. Sample size of studies with no exotic predators present increased to  $n = 8$  and that of studies with all predators present decreased to  $n = 54$ . Potential native predators on the islands without exotic predators included moreporks (an owl *Ninox novaezeelandiae*), Australasian harriers (*Circus approximans*), long-tailed cuckoos (*Eudynamis taitensis*), shining bronze-cuckoos (*Chrysococcyx lucidus*) and perhaps the large Duvaucel's geckos (*Hoplodactylus duvaucelii*). Introduced Indian mynas (*Acridotheres tristis*) might have played a role as nest predators at Tiritiri Matangi Island (Sagar, 1985; Lovegrove, 1996; Armstrong et al., 2000; Anderson and Craig, 2003; Rayner et al., 2007; Massaro et al., 2008).

### 2.2. Statistical analyses

We assessed potential taxonomic and spatial effects in our data and found that including taxonomic information is not required and that including latitude and longitude is enough to model spatial effects (see Appendix S2). Due to the shape of New Zealand, latitude and longitude are correlated ( $r = 0.78$ ,  $n = 79$ ) and thus we reduced them into one variable using a Principal Components Analysis, yielding a variable we call “Geography”. Geography incorporated 89% of the variation associated with latitude and longitude and its values increased from southwest to northeast. Besides latitude and longitude (in the form of “Geography”), we included as covariates adult body mass, nest type (open vs. closed), habitat category (forest vs. open), and rural vs. urban area (see above and O'Connor, 1991; Martin, 1993; Côté and Sutherland, 1995; Thompson, 2007; Chamberlain et al., 2009). As the main predictor variables of interest, we included predator control, native vs.

introduced status of the avian prey, and the midpoint of the study period (see above).

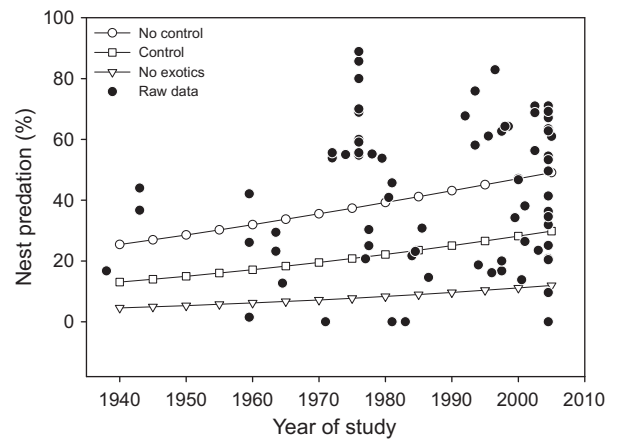
We used SAS procedure Genmod with binomial distribution and logit link to model the number of depredated nests out of the number of nests studied (i.e., binomial proportion; GLM). We used SAS procedure Glim to model daily mortality rates, weighed by square root of sample size (LM). All tests were two-tailed. In GLM, we checked for potential overdispersion of the data. As the data were overdispersed, we assumed that the dispersion parameter is given by Pearson's  $\chi^2/df$ , and all statistics were adjusted accordingly. In LM, we checked residuals for any deviations from normality, equal variance, and linearity. Residuals always conformed to all these requirements. We calculated pseudo- $R^2$  value for the GLM model as:  $(\text{null deviance} - \text{residual deviance})/\text{null deviance}$ . This value is analogous to the classic  $R^2$  value from linear models (Hagle and Mitchell, 1992). Adult body mass was  $\log_{10}$  transformed and daily predation rates were square root transformed. Besides tests of significance we always report parameter estimates for use in potential future meta-analyses and for judging biological significance of our results (see Tables 1 and 2).

### 3. Results

We obtained information on nest predation rates from 79 populations ( $n = 4\,838$  nests; see Appendix S3 for a map with study sites) of 26 species of songbirds belonging to 17 families. The most frequently represented families were Turdidae (18 studies), Meliphagidae (11 studies), and Petroicidae (11 studies), while five families had only one study each. Our sample of species included members of most of the 22 songbird families living in New Zealand, but there were no data for representatives of two native and three introduced families. Our data cover 70% of the 37 breeding species of New Zealand songbirds (excluding Chatham Islands). Studies differed considerably in sample size (Table 1). The number of nests studied did not change with the midpoint of the study ( $r = -0.09$ ,  $p = 0.429$ ,  $n = 79$ ). Two earliest studies had midpoint in 1938 and 1943, respectively; however, all other studies had a midpoint after 1960 and the number of studies per year increased until the present. More studies were conducted on native species ( $n = 52$ ) than on introduced species ( $n = 27$ ).

Both the proportion of depredated nests and daily predation rates increased with the year of study (Fig. 1) and increased from the southwest to the northeast of New Zealand, although the strength of the latter relationship depended on data partitioning (Table 2, Appendix S4). Our models predicted an increase in the proportion of depredated nests by 15–25% points both across the length of New Zealand (ca. 13 geographical degrees or 1500 km, Appendix S3) and over the last 60 years. The strength of increase over time was the same for native vs. exotic species, open habitats vs. forests, and urban vs. rural areas, because all interactions of these factors with year were non-significant (all  $p$ -values  $> 0.16$ ).

Daily predation rates were higher in introduced species (LS mean from the model in Table 2: 1.03%, 95% CI = 0.51–1.72) as compared to native species (0.46%, CI = 0.19–0.83). By contrast,



**Fig. 1.** Nest predation rate (raw, unadjusted data) in relation to the year of study (midpoint year). Depicted are also predictions (from Table 2) separately for the three categories of studies based on the presence of nest predators (see Methods). Note that the prediction for “No exotics” is based on a very limited sample of studies. Predictions are made for a native species with an open nest, living in a forested, rural habitat, with average body mass and geographic location.

there was no difference in the proportion of depredated nests between these two categories (Table 2). This seeming paradox arose because the proportion depredated is a product of daily predation rates and exposure time. Native species had longer breeding cycle than introduced species (sum of egg plus nestling stage [days]: native mean = 40.7, SE = 1.8,  $n = 17$ ; introduced mean = 29.7, SE = 1.3,  $n = 9$ ) and thus the lower daily predation rate accumulated over a longer time period with the resulting similar proportion of depredated nests. It is worth mentioning that although native species live predominantly in forest and exotic species in open country (e.g. farmland), the difference in daily nest predation rates was not caused by these habitat differences, because the analysis was controlled for both habitat type and urbanization (see Table 2).

Predation was lowest in areas where no exotic predators were present, highest in areas with no predator control and intermediate in areas with ongoing control of exotic nest predators (Table 2). Overall failure differed in the same way between populations where exotic predators were controlled compared to populations without control (Fig. 2). Consequently, the proportion of failed nests that failed due to depredation was similar (73.6% [in both cases] vs. 70.3% [72.5% if kiore is treated as a non-exotic species]). However, nest predation was much lower in populations without exotic predators but overall failure was comparatively high; consequently, the proportion of failed nests that failed due to predation was quite low here (13.7% [33.0% if kiore is treated as a non-exotic species]; Fig. 2).

### 4. Discussion

Based on spatially and temporally extensive dataset on nest depredation in New Zealand songbirds we showed that nest preda-

**Table 1**  
Descriptive characteristics of nest predation and failure data in New Zealand songbirds.

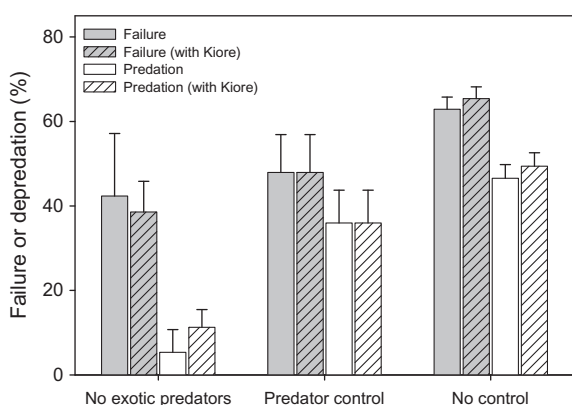
	Mean	SD	Median	Range	No. studies
No of studied nests	61.2	70.9	43.0	5–521	79
Length of the study (years)	2.3	1.6	2.0	1–9	79
Nests destroyed by predators (%)	42.8	22.9	44.0	0–88.9	79
Nests that failed (%)	59.6	21.8	63.3	8.8–93.1	59
Failed nests that failed due to predation (%)	68.0	25.0	72.5	0–100	59
Daily predation rate ( $\text{day}^{-1}$ )	0.019	0.013	0.018	0–0.058	79
Daily failure rate ( $\text{day}^{-1}$ )	0.031	0.018	0.028	0.004–0.075	59

**Table 2**

Results of generalized linear models (GLM) of the proportion of depredated nests (response variable: No. depredated/No. studied;  $n = 79$ ), and of linear models (LM) of daily predation rates (square root transformed,  $n = 79$ ). Kiore was treated as an exotic species. In GLM, Pearson's  $\chi^2/df = 7.2$ .

Predictor variable	GLM: proportion depredated			LM: daily predation rates		
	F	p	Estimate (SE)	F	p	Estimate (SE)
Intercept			−34.7 (10.7)			−1.80 (0.60)
Geography	3.7	0.055	0.149 (0.079)	2.4	0.127	0.0057 (0.0037)
Nest type (open) <sup>a</sup>	5.1	0.025	Closed: −0.59 (0.27)	5.4	0.023	Closed: −0.031 (0.013)
Log body mass	0.4	0.539	0.15 (0.25)	1.6	0.211	−0.017 (0.013)
Habitat (open) <sup>a</sup>	0.6	0.449	Forest: 0.20 (0.27)	0.9	0.341	Forest: 0.013 (0.014)
Urban vs. rural (urban) <sup>a</sup>	0.4	0.536	Rural: 0.20 (0.32)	0.5	0.485	Rural: 0.011 (0.016)
Predator control (no exotics) <sup>a</sup>	27.4	<0.001	Control: 1.14 (0.52) No control: 1.96 (0.49)	12.3	<0.001	Control: 0.049 (0.022) No control: 0.089 (0.020)
Native vs. Introduced (native)	0.1	0.800	Introduced: 0.062 (0.246)	7.0	0.010	Introduced: 0.034 (0.013)
Year	9.3	0.002	0.016 (0.0054)	9.5	0.003	0.00093 (0.00030)
	Pseudo- $R^2 = 0.38$			$R^2 = 0.44$		

<sup>a</sup> Reference levels of categorical variables are given in brackets.



**Fig. 2.** Failure and predation rates (mean + 1SE) for populations of New Zealand songbirds with no exotic predators present ( $n = 3$ ;  $n = 7$  when Kiore is treated as a non-exotic predator [always hatched bars]), where exotic predators were controlled ( $n = 9$  in both cases), and where all native and exotic predators were present (i.e., no predator control was in place;  $n = 47$ ;  $n = 43$  when Kiore is treated as a non-exotic predator). Depicted are raw data for populations where both predation and failure rates are known.

tion intensity increased with the year of study (between 1938 and 2005), from the southwest to the northeast of the island, and was higher in introduced as compared to native species. It was strongly affected by the presence of exotic predators and whether they were controlled or not.

#### 4.1. Exotic predator control

Nest predation rates were lowest in areas with no exotic predators present, intermediate in areas with ongoing predator control, and highest in areas with all exotic and native predators present (Table 2, Fig. 2, Appendix S4; see also Lewis et al., 2009 for similar results with artificial clutches). This agrees with previous findings that exotic predators have a strong negative effect on both native (extinctions, Blackburn et al., 2004) and introduced birds (establishment success, Cassey et al., 2005). Predator control has been shown to generally benefit bird populations (Côté and Sutherland, 1997; Heath et al., 2008; Holt et al., 2008; Smith et al., 2010, 2011). However, there has also been substantial heterogeneity in effect sizes among individual studies depending on how well the predators were controlled (Smith et al., 2010), how well they have been monitored (Nicoll and Norris, 2010), whether mammalian or avian predators were removed (larger effects in mammalian removals,

Holt et al., 2008) or whether the controlled predators actually had much impact on nest success (Bodey et al., 2011).

Exotic mammalian predators are the single most important factor limiting populations of New Zealand songbirds and a serious threat to the survival of many bird populations (Innes et al., 2010). Our study has two important implications for exotic predator control. First, populations with no exotic predators experienced lower nest predation rates compared to populations with exotic predator control (Table 2, Fig. 2, Appendix S4). This observation confirms that (i) the control never completely removes the targeted predator species, and (ii) the more species of predators are controlled, the more is nest depredation rate depressed (see also Smith et al., 2010). This latter effect might be caused by prey switching by the remaining, uncontrolled predator species in populations with (partial) exotic predator control. For example, poisoning of rats (*Rattus rattus*) can cause a switch to alternative food (birds) by a generalist predator (stoat, *Mustela erminea*, Murphy and Bradfield, 1992). Additionally, incomplete predator removal leaves space for mesopredator release where the niche left by one predator species is filled by others sharing the same diet (Côté and Sutherland, 1997; Rayner et al., 2007). Of course, these processes potentially hold also for native predators after the removal of their potential prey or competitors (i.e., exotic predators).

Second, nest mortality in populations with no exotic predators was partly compensatory. These populations experienced much lower predation rates as compared to populations with exotic predator control, but this was partly outweighed by much higher share of non-predatory nest mortality (Fig. 2) leading to similar overall nest failure rates (42% with no exotic predators [39% if kiore is treated as a non-exotic species] vs. 48% with exotic predator control [in both cases]). Lower predation rates mean that nests are on average exposed to other risks for longer. This simple effect might have accounted for higher share of non-predatory nest mortality in populations with no exotic predators. Alternatively, these populations might have low success due to detrimental genetic effects including inbreeding, because all these populations are isolated on offshore islands (Jamieson and Ryan, 1999) and have been presumably severely bottlenecked (Briskie and Mackintosh, 2004).

#### 4.2. Introduced vs. native prey species

Higher nest predation rates in introduced species were not predicted. Indeed, it has been suggested that introduced birds should be able to cope with exotic predator pressure better and would consequently suffer less predation than native species, because introduced predatory mammals in New Zealand are the same species European birds coevolved with in their native range (Moors,

1983; Starling-Windhof et al., 2010). For example, in line with this argument, in an experimental study rabbits in Australia avoided fox (*Vulpes vulpes*) and ferret (*Mustela furo*) of European origin, but not a native marsupial predator, the spotted-tailed quoll (*Dasyurus maculatus*; Barrio et al., 2010). However, this logic rests on the assumption that breeding birds can decrease nest depredation probability by their behavior (inconspicuousness, defense etc.), which might not be true, especially in small songbirds. Then, higher nest predation intensity might stem from high densities and thus nest availability of introduced species of songbirds (MacLeod et al., 2005).

Alternatively, higher nest depredation rates in introduced species might be the result of simple sampling effects. First, species that have been introduced and established in New Zealand, and indeed elsewhere worldwide, are a non-random sample of available species in terms of phylogenetic position and distributional, ecological and life-history characteristics (reviewed in Blackburn et al., 2009). Abundant, widespread, and resident species were disproportionately more often introduced into New Zealand from Britain (Blackburn and Duncan, 2001). Such species are also distinct in terms of their life-history characteristics (Blackburn et al., 1996), which might have predisposed them to high nest predation risk identified here. Second, many of the native species have already disappeared from much of the New Zealand mainland under pressure from predators. This extinction filter might have biased our estimates of depredation rates in native species downwards. Thus, higher nest depredation rates in introduced songbirds in New Zealand might be the result of historical contingencies of the introduction and extinction processes rather than any specific predator–prey interactions.

On the other side, despite historical contingencies, ecological patterns can be replicated across native and exotic ranges. For example, ecogeographic rules might be replicated in introduced birds as compared to their native ranges, suggesting common ecological processes generating these rules. For instance, there is a positive correlation between abundance and range size in 12 songbirds both in Britain (their native range) and New Zealand, where they were introduced from Britain (Blackburn et al., 2001). Moreover, range sizes and abundances correlate positively between Britain and New Zealand for the same 12 species (Blackburn et al., 2001). However, replication of biotic interactions can be less probable because of differing communities of potential predators or parasites. No study has yet evaluated the difference in predation pressure between native and introduced populations of exotic birds (Blackburn et al., 2009). Surprisingly, we found quite high correlations between New Zealand and Europe in both proportion of depredated nests (nonparametric Spearman's  $r = 0.50$ ) and daily predation rates ( $r = 0.74$ ,  $n = 8$ ; data for Europe from Perrins, 1998). At the same time, average values were similar and did not differ significantly between the regions, which agrees with previous analyses of single species (e.g. yellowhammer, MacLeod et al., 2005). These results demonstrate a surprisingly high repeatability of predator–prey interactions across continents with widely differing environments, predator communities, and the history of human impact.

#### 4.3. Long-term and large-scale trends

We detected a significant increase in nest predation rates with time. Several factors might have been responsible. First, it could have been caused by habitat fragmentation as a key finding in many fragmentation studies has been the reduction in nest survival in small forest fragments due to an increased rate of nest predation (Stephens et al., 2003). However, although not representative of the whole country, the only study from New Zealand did not find any detrimental effects of fragmentation on nest

survival (Boulton et al., 2008). Fragmentation is also not expected to have the effects on nest survival observed elsewhere because the exotic mammals that do most of the predation are if anything more abundant in the interior than at edges (e.g. King et al., 1996). Second, increasing levels of nest predators could elevate nest depredation rates. However, good data on long-term changes in densities of exotic mammalian predators in New Zealand are lacking. Third, substantial, often irreversible, changes in vegetation structure caused by exotic mammalian herbivores (Coomes et al., 2003; Husheer et al., 2003) might have reduced the availability of safe nest sites. Fourth, food shortage caused by fragmentation (Zanette et al., 2000) or exotic rodent species (St Clair, 2011) might have led to poorer nest vigilance with resulting high nest predation rates. Whatever is the reason for the increase in nest predation rates in New Zealand, however, it is potentially of considerable conservation interest as nest predators can limit populations of songbirds in New Zealand way below the level dictated by other limiting factors (Innes et al., 2010).

It has been commonly assumed that nest predation rates increase towards the equator (Martin, 1996). However, recent work challenged this traditional view (e.g. Brawn et al., 2011). Our analyses produced somewhat ambivalent results with respect to geography. After accounting for other relevant factors, nest predation rates increased from southwestern to northeastern New Zealand, but the significance of this relationship depended on the treatment of kiore (compare Table 2 and Appendix S4). It should be also noted that the north–south gradient in New Zealand is confounded with human population density, land modification, and the timing of exotic predators being introduced (earlier in the north). Thus, it is not clear whether our data have a significant bearing on the traditional question of temperate vs. tropical comparisons. However, from an applied point of view, our model (Table 2, Appendix S4) predicted an increase in the proportion of depredated nests by 15–25% points towards the equator, which is quite a substantial change with potential implications in population management and conservation (Smith et al., 2010).

## 5. Conclusions

Nest predation rates in New Zealand songbirds varied on large spatial and temporal scales, but were mainly affected by the presence of exotic mammalian predators introduced historically by humans. Thus, this human-caused factor overrode other correlates of nest depredation identified in North America and Europe (e.g. nest type, habitat, or urbanization; O'Connor, 1991; Martin, 1993; Côté and Sutherland, 1995; Thompson, 2007; Chamberlain et al., 2009). Island populations are at greater risk of serious population decline than mainland populations due to slow life-histories and consequent low population growth potential of island-inhabiting species (Murray, 2001). Thus, management of exotic predators is the key prerequisite for the maintenance of bird populations on the New Zealand mainland and offshore islands (Innes et al., 2010) as is also the case in other severely transformed areas (e.g. Hawaii; Banko et al., 2001). This conclusion is strengthened by the observation that exotic predator control can have positive effects beyond increasing nest success. These include benefiting non-target species (Baber et al., 2009) and possibly increasing the quality of young through removing indirect detrimental effects of predator presence (Dunn et al., 2010), although the latter has not been investigated experimentally.

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### Data accessibility

The data supporting all analyses and results of this paper have been deposited in Dryad Repository under doi:10.5061/dryad.6q81t4m4.

### Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2012.01.063.

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