



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.

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