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To cite this article: Alexandra H. Nance, William F. Mitchell, Finella Dawlings, Carly N. Cook & Rohan H. Clarke (2023): Rodent predation and specialised avian habitat requirements drive extinction risk for endemic island songbirds in the south-west Pacific, Emu - Austral Ornithology, DOI: 10.1080/01584197.2023.2228350

To link to this article: https://doi.org/10.1080/01584197.2023.2228350

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Rodent predation and specialised avian habitat requirements drive extinction risk for endemic island songbirds in the south-west Pacific

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ABSTRACT

Island endemic birds represent approximately 90% of contemporary avian extinctions globally. Introduced predators and land-use change are key drivers of population decline in this group. Where multiple threats may compound the impacts on species, the implementation of complementary approaches to threat assessment can be especially valuable. Using Norfolk Island (NI) in the south-west Pacific as an exemplar, we assessed daily nest survival rates for five endemic songbirds (NI Robin Petroica multicolor, NI Gerygone Gerygone modesta, Slender-billed White-eye Zosterops tenuirostris, NI Whistler Pachycephala pectoralis xanthoprocta and NI Fantail Rhipidura albiscapa pezelni), monitoring 135 nests over four breeding seasons. To understand the factors associated with suitable breeding habitat, we also conducted ecological niche modelling in Maxent for all species. Depredation was the primary driver of nest failure across all species (80% of failed nests), with invasive rats (Rattus sp.) being the most common predator (61% of depredated nests) and a key predictor of nest survival. Gerygones and Fantails exhibited the highest nest survival and were also categorised as habitat generalists using ecological niche modelling. Conversely, the three species that exhibited lower nest survival (Robin, White-eye and Whistler) had specialised habitat requirements, highlighting the potential for cumulative impacts. Our data suggest that invasive rodent control within intact forested sites is a critical management action for this system, followed by strategic habitat restoration and increased connectivity. Our study provides essential ecological information for five poorly understood island songbirds and identifies key management strategies for a regional avian hotspot.

ARTICLE HISTORY
Received 29 January 2023
Accepted 17 June 2023

KEYWORDS
Ecological niche modelling; habitat suitability; island conservation; Maxent; Shaffer’s nest survival

Introduction

As hotspots of endemism and adaptive radiation, islands are centres for the generation and maintenance of global avian biodiversity (Myers et al. 2000; Kier et al. 2009; Jonsson and Holt 2015). Despite contributing to only 5% of Earth’s landmass, islands are home to nearly 20% of all bird species (Tershy et al. 2015). Alarmingly, islands have also emerged as modern hotspots of extinction (Johnson and Stattersfield 1990; Loehle and Eschenbach 2012; Leclerc et al. 2018) with more than 50% of highly threatened birds being island species (Szabo et al. 2012; Tershy et al. 2015; Spatz et al. 2017). The unique aspects of islands that drive endemism can also contribute to species’ extinction: with bounded distributions and a limited capacity to disperse, insular species are more susceptible to threatening processes (Russell and Kueffer 2019), which are often exacerbated by human visitation and settlement (Wood et al. 2017; Russell and Kueffer 2019).

The presence of humans on islands has given rise to a range of threats to island species, including habitat modification associated with land use change and the introduction of invasive species (Johnson et al. 2017; Wood et al. 2017). Habitat modification in the form of deforestation and land cultivation can reduce the already limited habitat available for island birds (Szabo et al. 2012; Leclerc et al. 2018; Russell and Kueffer 2019). Additionally, advances in global transport have created many novel vectors for exotic species introductions to, and subsequent invasions of islands (Capinha et al. 2017). The ubiquity of invasive species on islands now mirrors that of humans (Spatz et al. 2017). Together, these threatening processes have worked to rapidly and drastically reduce the abundance and diversity of island birds (Blackburn et al. 2004; Duncan and Blackburn 2007; Karels et al. 2008; Leclerc et al. 2018). In an era of ongoing biodiversity loss, assessing the threats to island birds to inform conservation action is increasingly urgent.

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Supplemental data for this article can be accessed at https://doi.org/10.1080/01584197.2023.2228350.

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Two metrics that are particularly informative in avian conservation are nest survival and habitat suitability as they each address a distinct and crucial aspect of avian ecology (Jehle et al. 2004; Elith and Leathwick 2009). Nest survival is a metric that underpins population recruitment and fecundity and is therefore critical in determining the viability and extinction risk of a population (Jehle et al. 2004; Johnson 2007). Identifying environmental correlates of nest survival (e.g. vegetation type, predator density, rainfall), informs which conditions or management actions are likely to be important for the long-term persistence of a population (Champagnon et al. 2019; Camargos de Meireles et al. 2021; Gautschi et al. 2021). Additionally, identifying distinct causes of nest failure is critical to determining appropriate strategies to mitigate the impact of nest predators. Nest survival indicators can be complemented through the use of ecological niche modelling to understand the characteristics and therefore the distribution of suitable habitat (Moreno et al. 2011). Such modelling can inform estimates of the carrying capacity of a population (Segal et al. 2021) and identify priority areas for habitat restoration and management (Duflot et al. 2018). Together, these metrics provide critical information for the evaluation of a species’ extinction risk (Owens and Bennett 2000), allowing the timely identification of meaningful management actions.

To gain practical insight into the conservation issues facing island endemic birds, we considered Norfolk Island as an exemplar. Norfolk Island is a remote, inhabited Australian territory in the South Pacific Ocean and is a recognised avian hotspot. The island group (Norfolk, Nepean and Phillip Islands) supports a large diversity of resident and migratory bird species including an endemic owl, parakeet and several songbirds, as well as breeding populations of 13 seabird species (Director of National Parks 2023). Historically, the island was home to 15 endemic avian species and subspecies, but human colonisation has led to the extinction of seven of these species (Garnett and Baker 2021). The likely causes of extinction include predation from invasive rodents and feral cats, hunting, and land-clearing (Garnett and Baker 2021; Director of National Parks 2023). With the exception of over-hunting, it is likely that these and other threats such as climate change continue to impose substantial pressure on many of the remaining endemic species; this is evidenced by the recent extinction of the endemic White-chested White-eye (Zosterops albogularis), which was declared extinct in 2011 (Clarke et al. 2021). Five species of endemic songbird persist on Norfolk Island: the Norfolk Robin (Petroica multicolor), Norfolk Gerygone (Gerygone modesta), Slender-billed White-eye (Zosterops tenuirostris), Norfolk Golden Whistler (Pachycephala pectoralis xanthoprocta) and Norfolk Fantail (Rhipidura albiscapa pelzelni); hereafter, Robin, Gerygone, White-eye, Whistler and Fantail respectively. Whilst reports from the 1980s and 90s provide valuable historical context, the contemporary threats to extant populations are unknown.

Understanding the impact of multiple threats on vulnerable endemic species is critical to curbing the island avian extinction crisis. This study therefore focuses on the suite of songbirds endemic to Norfolk Island, with the broad aim of generating contemporary data to assess their conservation threat status and inform appropriate management actions. Specifically, we sought to: understand threats to reproductive success by assessing nest survival rates and identifying causes of nest failure; understand habitat requirements through comprehensive species surveys and the application of ecological niche modelling; and provide practitioners with evidence-based management advice to support planning for the effective management of these unique species. In doing so, our study serves as an example where complementary approaches to understanding reproductive success and habitat suitability facilitate a deeper understanding of cumulative impacts arising from multiple threats, which has broad relevance to avian communities on islands elsewhere.

Methods

Study system

Norfolk Island (29°02’S 167°57’E) is the only inhabited island of the Norfolk Island Group, home to 2,100 residents (Australian Bureau of Statistics 2021). At least four separate human colonisation events have taken place on the island in the last 1,000 years, including Polynesian and European settlements (Gibbs et al. 2017). The Pitcairn Islanders (descendants of the infamous Bounty mutineers) permanently settled Norfolk in 1856, with their descendants making up a substantial portion of today’s population (Gibbs et al. 2017). Over the course of these settlements, many invasive plant and animal species have been introduced. Significant species introductions include the Pacific rat (Rattus exulans c. 1200s), black rat (R. rattus c. 1940s), house mouse (Mus musculus c. 1900s), feral cat (Felis catus) and around 400 exotic plants (Director of National Parks 2023).

Several forested tracts of vegetation on Norfolk Island are considered key conservation areas: the Norfolk Island National Park (NINP) and adjoining Botanic Garden (NIBG), and numerous council reserves. Collectively the NINP and NIBG protect 460 ha of native forests on Norfolk (Figure 1; Director of
National Parks 2023). The highest elevation points on the island are within the NINP: Mount Pitt (316 m) and Mount Bates (318 m; Director of National Parks 2023). The NINP and NIBG are delineated into six spatial regions according to their nearest public walking tracks (Supporting information Figure S1). There are 12 council reserves that collectively protect 224 ha of environmental and cultural assets and are mostly located on the coastal fringe (Figure 1; Norfolk Island Parks and Forestry Service 2003). Vegetation in reserves largely consists of coastal forests as well as cleared land surrounding historical monuments (Invasive Species Council and TierraMar 2021). All protected areas are actively restored and managed for invasive species (Norfolk Island Parks and Forestry Service 2003; Director of National Parks 2020). Small pockets of native forest (remnant and non-remnant) occur on private land across the island (Invasive Species Council and TierraMar 2021), with some private landholders actively pursuing habitat restoration and invasive animal management on their properties (Director of National Parks 2023).

**Study species**

The Action Plan for Australian Birds 2020 provides the latest comprehensive assessments for all species based on IUCN criteria (Garnett and Baker 2021) and lists the Robin as Endangered (Nance et al. 2021a), the White-eye as Near Threatened (Nance et al. 2021b), and the Whistler, Gerygone and Fantail as Least Concern (Nance et al. 2021c, 2021d, 2021e). Prior to the most recent Action Plan, conservation listings and management actions for these species have relied heavily on historic reports published between 1988 and 1997 (Robinson 1988, 1997; Major 1989; Bell 1990).

**Daily nest survival**

**Nest monitoring**

To maximise the number of nests found per species we focussed nest searches to the National Park, as previous reports and local knowledge indicated that the Robin, White-eye and Whistler predominantly occur in this area (Figure 1(a)). We conducted intensive nest searches over three breeding seasons (2018–2020) during peak breeding months (between October and January; Higgins and Peter 2002; Higgins et al. 2006). Robins were monitored for four breeding seasons (2017–2020). Nests were identified by observing nest-specific behavioural cues and following adults to active nests. We also monitored a small number of nests on private land outside of the National Park. Upon detection of each nest, we recorded the number of eggs or offspring, and, where relevant, approximate stage of hatched offspring (early, mid or late brooding), ageing nestlings based on their size
and the presence or absence of down and pin feathers (Jongsomjit et al. 2007).

Where there were sufficient nearby vegetation structures, we installed a motion-triggered camera trap (Moultrie M40i) 1–3 m from the nest for daily monitoring and to determine nest outcomes and causes of nest failure (camera monitored nests = 98 of 135 nests). We mounted cameras on structures remote from the nest tree (e.g. a nearby tree) to reduce human interaction with (and scent trails to) the nest. We conducted in-person nest checks for all nests approximately every second day to determine nest activity and contents until offspring fledged or the nest failed. In-person checks were conducted concurrent with camera monitoring. We considered a nest to have fledged if camera trap footage showed direct evidence of fledglings leaving the nest, or if we observed fledglings near the nest around the estimated time of fledging. We determined a nest to have failed if we collected evidence that met any of the following criteria:

1. Direct evidence of failure was recorded (e.g. predation, heavy winds and rain, or abandonment) via camera trap footage or in-person observations;
2. The nest was observed to be empty when fledging was implausible (i.e. the nest was still in the incubation or early to mid-brooding phase); or
3. A breeding pair was detected re-nesting within 2 weeks of a previous nest attempt with no signs of fledging care.

Wherever possible, we identified discrete causes of nest failure (e.g. depredation, abandonment, destruction from weather events).

**Predictors of nest survival**

We recorded the GPS location of each nest, along with four micro-site metrics: vegetation type, nesting tree growth form, nest height and nest ‘micro-connectivity’ (Table 1). Surrounding vegetation type was of interest due to its association with local foraging opportunity, habitat quality, and predator densities (Major 1989; Nance unpublished data). We classified vegetation type based on the dominant tree species (e.g. exotic guava forest or suite of tree species (e.g. native hardwood forest) in the nesting area. We were interested in whether structural differences of nest trees impacted nest survival, so categorised the species of nest tree based on its growth form (i.e. tree, shrub, grass tree, or vine). We were interested in nest height as a possible predictor of vulnerability to predators such as feral cats, invasive rodents and the endemic small forest owl (Ninox novaeseelandiae undulata). We measured nest height above the ground with a tape measure, or a laser range finder (Opti-Logic, model: 800LH). We developed a measure of micro-connectivity as a potential indicator of nest vulnerability to depredation by invasive arboreal rodents because previous reports suggest rodents are a key nest predator of Robins (Major 1989). We considered each nest at the centre of a circle (radius =1 m) and determined how connected the nest and nest tree were to adjacent non-nest-tree vegetation. Nests were categorised as being low (≤2 direct pathways to the nest from adjacent non-nest-tree vegetation), moderate (3 to 5 direct pathways), or highly connected (≥6 direct pathways).

We also sought to assess the association between management actions focussed on rodent control and nest survival. During the study period, rodents were controlled within the National Park via an extensive network of ground-based bait stations deployed along cleared tracks at 50–100 m intervals; the baiting network and track infrastructure has been in near-continuous use for 30 years (Director of National Parks 2020). Using GPS locations of all bait stations, we generated a raster of bait station density (cell size 1.72 × 1.72 m). All nests outside of the National Park were assigned a bait station density of 0 as there was no comparable rodent control programme occurring on associated properties at the time of this study.

To understand the relationship between nest survival and landscape-level metrics we used a LiDAR-generated digital surface model (DSM) and digital elevation model (DEM) mapped to a cell size of 1.72 × 1.72 m (Gallant

**Table 1.** Description of covariates included in global daily nest survival model for five songbirds endemic to Norfolk Island.

<table>
<thead>
<tr>
<th>Covariate</th>
<th>Type</th>
<th>Possible values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>categorical</td>
<td>Robin, Gerygone, White-eye, Fantail, Whistler</td>
</tr>
<tr>
<td>Vegetation category</td>
<td>categorical</td>
<td>Native hardwood, native palm, mixed native, weed infested native, weedy forest, edge habitat, cultivated land</td>
</tr>
<tr>
<td>Nest tree growth form</td>
<td>categorical</td>
<td>Tree, tree/shrub, grass tree, climber</td>
</tr>
<tr>
<td>Micro-connectivity</td>
<td>ordinal</td>
<td>Low, moderate, high</td>
</tr>
<tr>
<td>Nest height (m)</td>
<td>continuous</td>
<td>0.95–14.7 m</td>
</tr>
<tr>
<td>Bait stations per hectare</td>
<td>continuous</td>
<td>0–13.25 bait stations per hectare</td>
</tr>
<tr>
<td>Canopy height (m)</td>
<td>continuous</td>
<td>0–50.4 m</td>
</tr>
<tr>
<td>Canopy density i.e. canopy cover (%)</td>
<td>continuous</td>
<td>0–100%</td>
</tr>
<tr>
<td>Vegetation category*micro-connectivity</td>
<td>interaction</td>
<td></td>
</tr>
<tr>
<td>Nest height*canopy height</td>
<td>interaction</td>
<td></td>
</tr>
</tbody>
</table>
Canopy height (m) was calculated by subtracting the DEM from the DSM, and canopy density (%) was calculated as a percentage of the cell that was vegetated at ≥2 m off the ground (Table 1).

We did not include camera monitoring status (nest was camera monitored Y/N) in the global model as it had no effect on daily nest survival (Shaffer’s nest survival logistic exposure GLM, $z = -1.374, p = 0.169$).

### Daily nest survival rate (DSR)

Distinct from apparent nest success, which calculates the proportion of nests that succeed or fail, we used daily nest survival (DSR) because it accounts for the positive bias associated with successful nests having a higher detection probability than failed nests (Jehle et al. 2004). We calculated DSR using Shaffer’s nest survival logistic exposure model, which is a generalised linear model with a modified link function (Shaffer 2004; Johnson 2007). The exposure function accounts for variability in the number of days between nest checks, i.e. the variability in daily exposure to failure. Because of this exposure function, Shaffer’s model is statistically robust to datasets that include nests of unknown age, unknown fate, and unknown timing of fate (Shaffer 2004; Johnson 2007).

For nests monitored with a camera trap, we considered the nest to be checked every day that the camera trap recorded activity regardless of whether the nest was checked in person. Nests that were only checked in person had fewer daily observations than nests that were monitored via camera trap. The exposure function accounts for this discrepancy: for each daily observation, the number of ‘exposure days’ (i.e. the number of days since the previous nest check) was calculated and incorporated into the survival model. In instances where nests failed due to abandonment, we considered the last day of recorded parental activity as the last survival day. Some nests were assigned an unknown fate, either because they were still active when a field season ended ($n = 12$), or because we could not confirm either failure or success ($n = 8$). An unconfirmed outcome occurred when nestlings were no longer present and had reached the approximate age for fledging but no fledglings were observed near the nest. For these nests, we excluded any nest checks with uncertain activity status from the dataset. As the model could not accommodate absent values, we excluded two nests from the survival analysis due to incomplete data (i.e. instances where micro-connectivity or nest height were not collected).

To determine important predictors of DSR, we developed a global model that incorporated all covariates and interactions of interest. To account for spatial and temporal non-independence the initial global model included a random effect where general area was grouped by year, where ‘general area’ refers to the specific regions of the National Park or island where nests were found (categorical variable with seven levels: Botanical Gardens, Captain Cook, Forestry, Mount Pitt, Palm Glen, Red Road, outside NP), and year refers to the breeding season year (ordinal variable with four levels: 2017, 2018, 2019, 2020). Ultimately, we excluded random effects from the final global model as the level of variance explained was negligible (year/general area variance = 0.05, SD = 0.23).

Model selection with subsets of the ‘global’ model was carried out using information-theoretic approaches (Burnham and Anderson 2002). The R package MuMIn (Bartoń 2020) was used to rank candidate models according to corrected Akaike Information Criterion (AICc). Models with $\Delta$AICc < 2 were selected as candidate models (Table 2, though see Supporting Information Table S1 for models $\Delta$AICc < 8). To ensure the highest ranked model ($\Delta$AICc = 0) conformed to underlying assumptions, we assessed spatial and temporal autocorrelation, goodness of fit, and residual diagnostics in the R package DHARMA (Hartig 2021). We conducted survival analyses following the approach described by Champagnon et al. (2019).

### Habitat suitability mapping

#### Species occurrence

To model the distribution of suitable breeding habitat across the island, we used the open-source maximum-entropy modelling software Maxent (Phillips et al. 2004).
To generate presence records for each species we conducted an island-wide point-count survey between 11 October and 1 November 2019. We were specifically interested in modelling breeding habitat, and as all species of interest are tree-nesting species we excluded ‘non-treed’ areas from the survey design, that is, areas that were predominately pasture, bare soil or sand, or infrastructure including roads and buildings (Figure 1 (b)). Areas that were not necessarily forested but contained suitable breeding habitat, such as residential gardens and orchards, were considered ‘treed’ areas. We recorded observations of the five endemic songbird species as well as the Silveryeye (Zosterops australis), which self-colonised in 1904 (Dutson 2013). We were interested in collecting observations of the Silveryeye as it is the only additional songbird that has colonised from nearby native populations, providing a valuable point of contrast.

Point counts consisted of a five-minute survey whereby a single observer would arrive at a survey point and immediately begin recording species and number of focal individuals seen or heard within a 25 m radius. Individual point counts were spaced at least 100 m apart. Surveys were typically conducted between dawn and 11 am, with occasional afternoon surveys when weather conditions were favourable (mild, with little to no wind and no rain). In the National Park, we conducted surveys along ‘bait lines’ that bisect the park, which ranged from established service tracks to uncleared routes along ridgelines or through valleys. Two observers (AHN and WFM) conducted a total of 410 point counts across the three land tenures, with effort approximately proportional to the area of potential habitat: 309 point counts in the National Park and adjoining Botanical Gardens (federal land), 37 point counts across five regional reserves (local: Norfolk Island Regional Council), and 64 point counts across 22 private properties (private land).

**Model selection**

We initially considered nine candidate environmental layers associated with terrain, habitat structure and habitat quality generated from aerial Lidar data collected in 2019 (Gallant and Petheram 2020). We mapped all layers at a resolution of 30 m², which represents the average territory size of the smallest focal species, the Norfolk Gerygone (Nance unpublished data). We tested the original set of layers for collinearity using R package ENMTools (Warren et al. 2010) and removed layers with Pearson correlation coefficients >0.65 (Supporting information Table S2). The six layers used in the final models were slope, elevation above sea level, vegetation class (Table 3), binary forest status (i.e. whether the cell was classified as forested (1) or unforest (0)), forest patch size, and distance to forest edge (metres) (Supporting information Table S3). To account for bias in sampling effort, we created a bias layer by calculating two-dimensional kernel density estimates around the coordinates of all surveyed points using the R package MASS (Venables and Ripley 2002; Phillips et al. 2009). Climatic layers were not available at ecologically relevant spatial scales so were not included in any models.

‘Features’ and ‘regularisation multipliers’ are customisable features within Maxent that determine the complexity of a model, and testing variations of these two parameters has been shown to improve model fitting (Morales et al. 2017). As such, using species occurrence points and the environmental layers described above, we determined the optimal values of these two parameters for each of the six species’ habitat suitability models using R package ENMeval (Kass et al. 2021). We did this using the maxnet algorithm (Phillips et al. 2017) and tested different combinations of the five possible ‘Features’ (linear, product, quadratic, hinge, threshold) and ‘regularisation multipliers’ (between 1 and 5), using the k-fold cross-validation method with five folds (for detailed definitions of Maxent features, and how features and regularisation multipliers influence models see Elith et al. 2011; Merow et al. 2013). Because sample sizes for each species approximated a hundred presence records (as opposed to thousands), we selected the best performing model for all species based on AICc values as opposed to Area Under the Curve (AUC; Warren and Seifert 2011). To determine the predictive power of each model, we compared performance metrics (average AUC and average omission rate across folds) of the empirical model against a null model using randomly generated data in package ENMeval (Supporting Information Figure S2). We conducted all analyses in R version 4.1.1.1 (R Core Team 2021).

**Table 3. Vegetation classes and related habitat codes used in Maxent habitat suitability modelling for five songbirds endemic to Norfolk Island.**

<table>
<thead>
<tr>
<th>Habitat code</th>
<th>Vegetation type</th>
<th>Native status</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>Native Hardwood Forest</td>
<td>Native</td>
</tr>
<tr>
<td>1</td>
<td>Eucalyptus plantations</td>
<td>Non-native</td>
</tr>
<tr>
<td>2</td>
<td>Norfolk Island Pine Forest</td>
<td>Native</td>
</tr>
<tr>
<td>3</td>
<td>Moist Palm Valley</td>
<td>Native</td>
</tr>
<tr>
<td>4</td>
<td>Red Cherry Guava</td>
<td>Invasive non-native</td>
</tr>
<tr>
<td>5</td>
<td>Hawaiian Holly</td>
<td>Invasive non-native</td>
</tr>
<tr>
<td>6</td>
<td>African Olive</td>
<td>Invasive non-native</td>
</tr>
<tr>
<td>7</td>
<td>Cotoneaster</td>
<td>Invasive non-native</td>
</tr>
<tr>
<td>8</td>
<td>Cultivated lands</td>
<td>Non-native</td>
</tr>
<tr>
<td>9</td>
<td>Other woody classes on plateau</td>
<td>Mixed</td>
</tr>
</tbody>
</table>

(Continued)
Results

Nest survival

Nest survival analysis included 1,535 daily observations from the 133 nests for which we had complete data across 4 years (Supporting Information Table S4). Five candidate models were identified from 400 automatically generated additive and multiplicative models. Of these five candidate models, none included interaction terms (Table 2). All models included ‘species’ as a main effect, driven largely by Fantails and Gerygones, which exhibited significantly higher nest survival than other species (Fantail DSR model estimate 0.88, \( z = 2.129, p = 0.03 \); Gerygone DSR model estimate 1.25, \( z = 1.99, p = 0.047 \); Figure 2(a)). Bait station density was also positively correlated with DSR in all candidate models, indicating nest survival was higher in areas with more intensive baiting, although effect sizes were small (best model: \( z = 1.95, p = 0.05 \); Figure 2(b)). Four of the five models included the effect of micro-connectivity, indicating lower DSR for moderately and highly connected nests, although this difference was only significant for moderately connected nests (best model: \( z = -2.338, p = 0.02 \); Figure 2(c)). One model included the effect of nest height off the ground and indicated that DSR was not correlated with nest height (candidate model 2: \( z = 0.915, p = 0.36 \); Supporting information Figure S3).

Nest outcome

Of the 135 nests assessed for nesting outcome, 20 had an unknown fate. Of the remaining 115 nests, 48% \( (n = 55) \) of nests failed. While nest failure was attributed to a range of causes, the most common cause of failure was predation \( (n = 44 \) or 80% of failed nests). Other causes of failure recorded were abandonment (during incubation \( n = 4 \), at late brooding stage \( n = 1 \)), destruction by high winds \( (n = 1) \), and non-parental infanticide from a conspecific Robin pair \( (n = 1) \). Four nests failed for unknown reasons. We did not observe any instances of gradual brood reduction in nests where the number of hatchlings was known. Each species experienced varying levels of nest predation, with White-eyes exhibiting the highest rate of predation \( (56\% \) of nests with a known outcome), followed by Whistlers \( (50\% \) of nests), Robins \( (39\% \) of nests), Gerygones \( (30\% \) of nests) and Fantails \( (26\% \) of nests).

Invasive rats \( (Rattus \text{ sp.}) \) were the most common predator identified \( (61.4\% \) of all nest failures), though the Pacific Long-tailed Cuckoo \( (LTC; \text{ Urodynamis tai-tensis}) \), a scarce migrant, accounted for four nest failures \( (7.3\% \) of all nest failures; Nance and Clarke 2019). There was no direct evidence of other predators (e.g. house mice \( \text{Mus musculus} \) or feral cats \( \text{Felis catus} \)) causing nest failure. We found evidence of invasive rats preying on eggs and chicks of all five focal nesting species at nest heights ranging from 1.3 to 8.3 m above the ground. LTCs were only recorded killing (and likely preying upon) chicks from Whistler \( (n = 3) \) and Robin \( (n = 1) \) nests, with no evidence that they preyed upon eggs or subsequently parasitised nests i.e. we made no observations of LTC hatchlings in the nests of study species, though attempted brood parasitism cannot be ruled out for abandoned nests or those that failed for unknown reasons. We were unable to identify the predator for 30% \( (n = 13) \) of predation events due to camera trap failures or the absence of camera trap monitoring. We classified these nests as being preyed upon based on the presence of egg fragments or nestling remains at or near the nest, or if the nest was intact but its contents had been removed prior to plausible fledging (Robinson 1988; Major 1989).

Habitat suitability

Modelling presence records against environmental variables indicated that suitable habitat for Robins, Whistlers and White-eyes was largely restricted to the National Park and surrounding properties (Figure 3(a–c); Supporting Information Figure S4). Comparatively, suitable habitat for Gerygones and Fantails had a wider distribution, with (at minimum) moderately suitable habitat extending to most regions across the island despite highly suitable habitat being largely limited to the National Park (Figure 3(d,e)). Silvereyes had the largest area of highly suitable habitat across the island, though habitat suitability in the central regions of the National Park was distinctly lower (Figure 3(f)).

The distribution of suitable habitat and the factors that influence habitat suitability varied across species (Figure 4). While Robins, Whistlers, and White-eyes could persist in most treed vegetation types, ‘cultivated land’ was highly unsuitable for all three species (Figures 4(a–c)). Forest patch size and distance from the edge were key factors for Whistlers and White-eyes: both required larger interior forested patches (Figure 4(a, c)). Robins also required large patches but appeared to be less affected by edges (Figure 4(b)). Nevertheless, Robins were heavily influenced by forest cover with non-forested areas being highly unsuitable (Figure 4(b)). Fantails and Gerygones had more generalised habitat requirements and were less influenced by patch size, forest cover and vegetation type. There was no measurable difference in habitat suitability between smaller and larger habitat patches for these species, nor were there differences between non-forested and forested habitat
Vegetation type had little effect on habitat suitability for Gerygones and Silvereyes (Figure 4(d, f)), though Fantails exhibited more variation in response to vegetation type (Figure 4(e)). Spatial partitioning was evident between the endemic songbirds and the Silvereye: the central region of the National Park, with high elevation native hardwood forest, was highly suitable habitat for all five endemic species.
including the congeneric Slender-billed White-eye, yet this area was found to be unsuitable for the non-endemic Silvereye (Figures 3(f) and 4(f)).

The average AUC values for all species models were relatively low (AUC range = 0.64–0.71; Supporting Information Table S5) indicating there may be other covariates (e.g. climatic variables) not considered here that would improve model performance. However, null model comparisons indicated that all empirical models performed significantly better than models generated from random data (Supporting information Figure S2). This suggests that habitat suitability predictions generated from presented models are reliable despite yielding lower AUC values.

Discussion

Our study is the first to provide a comprehensive estimate of nest survival and habitat requirements for Norfolk Island’s endemic songbirds. These findings are vital for understanding the extinction risk of these species, and the development and implementation of meaningful management actions (Owens and Bennett 2000). Importantly, we found evidence for two distinct groups: the vulnerable and the resilient. Robins, Whistlers and White-eyes experienced threats associated with lowered nesting success, which is compounded by the independent process of more restrictive habitat requirements, making them particularly vulnerable. Conversely, Fantails and Gerygones exhibited higher nest survival, and, along with the Silvereye, could more readily persist in modified habitats, making them more resilient. Our results conform to broader ecological patterns associated with habitat specialists and generalists, in that habitat specialists (in this system Robins, Whistlers, and White-eyes) are more vulnerable to both disturbance and predation pressure compared to generalists (Fantails and Gerygones; Low 2002).

Nest survival

Invasive rodents are key drivers of decline for many island endemic species (Harper and Bunbury 2015) and our findings confirm they are a key threat to island songbirds in the present study. That rodents present as a key threatening process is further supported by measures of nest vulnerability to rodents (i.e. in areas of lower bait density and higher nest connectivity) which were key predictors of daily nest survival. Our findings provide strong evidence that invasive rodents are an important driver of decline for island endemic species and are a particular threat to tree-nesting birds (Brown 1997; Szabo et al. 2012; Duron et al. 2017). Importantly, there was little evidence that nests built higher above the ground were less susceptible to predation, indicating that rodents are not limited by vertical movement. Instead, nests that were more connected to surrounding vegetation were more likely to fail, regardless of nest height. This suggests that rodents are more likely limited by the connectedness of above-ground vegetation.
Figure 4. Response curves of four key environmental variables generated from Maxent habitat suitability models for (a) Norfolk Golden Whistler, (b) Norfolk Robin, (c) Slender-billed White-eye, (d) Norfolk Gerygone, (e) Norfolk Fantail, and (f) Silvereye. For each 4-plot species panel, from top left to bottom right: habitat suitability (y-axis; 0 = highly unsuitable habitat and 1 = highly suitable habitat) is predicted against patch area i.e. size of forested patch (m²), distance from the forest edge (m), forested (1) versus non-forested habitat (0), and ten different vegetation categories (0 = Native hardwood, 1 = non-native Eucalyptus plantation, 2 = native Pine forest, 3 = native Palm valley, 4 = invasive red guava, 5 = invasive Hawai’ian Holly, 6 = invasive African Olive, 7 = invasive Cotoneaster, 8 = non-native cultivated lands, 9 = other woody classes). Bird images reproduced from Menkhorst et al. (2017) with permission from CSIRO Publishing. Artists: Peter Marsack and Kim Franklin.
Further, while nest survival was positively correlated with bait station density, the conservation benefit did not appear to be commensurate with effort. While baiting can be an effective rodent control strategy, all bait stations in the network were deployed at the ground level, and it remains unclear to what level arboreal rodents are targeted by or interact with bait stations on the ground (Nance unpublished data). Together, these results indicate the importance of considering a rodent control strategy that targets rodents where they are most active.

Rodent pests are present across the entire island, thus a coordinated island-wide rodent control programme incorporating all land tenures may provide ecological and social benefits. This could involve collaborative baiting and trapping efforts across private, local and federal land tenures, or identifying priority areas within which to conduct intensive baiting. Indeed, a community initiative led by the Norfolk Island Regional Council has recently begun in the north-west of the island that extends the National Park baiting network into neighbouring regional reserves and private properties (L-U King, pers. comm.). With additional and ongoing support, such initiatives could extend further across the island resulting in improved outcomes for endemic species and the wider island community.

**Distribution of suitable habitat**

Our findings corroborate and are broadly consistent with historical reports of songbird threats on Norfolk Island, as they demonstrate that Robins, Whistlers and White-eyes exhibit a more restricted distribution than other songbirds. Notably, the type of forest (native versus exotic) was less relevant to suitability than the presence or absence of the forest itself. Most forested vegetation types were moderately or highly suitable for these species with the exception of more extensive stands of the invasive Hawai’ian Holly (*Schinus terebinthifolius*), which was associated with very low habitat suitability values for Robins. Further, cultivated land (e.g. private orchards and gardens) was highly unsuitable for all three species, providing compelling evidence for the importance of forested habitat on Norfolk Island. As habitat suitability consistently increased with increasing patch size for these three species, expanding forested areas (and thus forest patch size) through restoration activities would be particularly relevant to their management. Given the National Park is almost exclusively forested, expanding forested areas would require collaboration with other land-owning stakeholders on the island. Collaborating with private landholders to maintain patches of forest on their land may provide a temporary avenue for range expansion. This could be combined with the gradual restoration of invasive forests to native forests, and the creation of ecological corridors between private, council and National Park lands as a long-term goal. Restoration of forested habitats on the nearby satellite island of Phillip Island (190 ha) may also present as a particularly effective strategy to increase the total area of suitable habitat for the endemic songbirds of Norfolk Island. This is especially so given the observed cumulative impacts of habitat loss and elevated nest predation rates, because Phillip Island is not occupied by rodents and was cleared of all other invasive mammals (notably European Rabbit, feral goats and feral pigs) by 1988 (Director of National Parks 2023).

A necessary consideration when interpreting modelling results from this system is the intrinsic spatial bias associated with the National Park. The National Park covers the island’s highest elevation forests (which proved to be highly suitable habitat for all endemic species), is the largest contiguous patch of forest, and is intensively managed. All other forest patches are at lower elevations, are substantially smaller and embedded within a rural matrix, and have experienced varying levels of management. As such, it is not possible to disentangle responses to patch size and elevation in this study system. Nevertheless, with a maximum elevation of just 319 m, it is unlikely to be more important to songbird persistence than direct availability of forest habitat in this system.

**Long-term monitoring**

The populations considered in this study represent the global distributions of all five focal songbirds, with available breeding habitat making up considerably less than the 36 km² land area of Norfolk Island. Small populations are sensitive to environmental fluctuations and generally have a lowered capacity to adapt to change (Lacy 2000; Willi et al. 2006). The recent extinction of the White-chested White-eye (c. 2011) highlights the very real threat of ongoing loss in this system. There is a long history of habitat clearance and invasive predator introductions on Norfolk Island; the further range restrictions and dominant cause of nest predation documented in this study may be indicative of an extinction debt that is yet to be fully realised. Timely identification of and response to population declines is necessary to ensure the long-term persistence of these species, and this can only be achieved through consistent long-term monitoring (White 2018). As such,
monitoring that is linked to management triggers should be considered for this suite of species (Hilton et al. 2022). Where possible, monitoring that incorporates nest survival and other important demographic measures will enable more accurate predictions of population trajectories under various scenarios (Mitchell, Nance and Clarke In Review).

To improve our understanding of habitat requirements for these species, it will be necessary to regularly update and fine-tune models of this system using empirical data. Relevant methods could include regular and repeated surveys across seasons, and searches for nesting activity in areas of habitat identified as being highly suitable. Exploring additional variables such as nest position in relation to surrounding vegetation may yield further information on susceptibility to nest predation by various predators. Such data would allow managers to test and update models to improve their predictive power, which would in turn aid in the implementation of precise and targeted management actions. Finally, further research on threats to fledglings and adult birds (e.g. depredation by feral cats or avian predators) will be important to address life-stage-specific threats.

Conclusions

The global trend of avian extinction is driven by substantially higher extinction rates of island endemics. Assessing the ecological and conservation requirements of extant island species allows researchers and managers to better evaluate the progress made and identify critical next steps in preventing further extinctions. We consider our findings a necessary foundation for designing an evidence-based strategy for managing songbirds on Norfolk Island, and a blueprint for understanding threats to songbirds more broadly. Our study provides a timely assessment of the state of the endemic songbirds on Norfolk Island and demonstrates that some species exhibit higher susceptibility to the threats of invasive rodents and habitat modification. We identify the need for island-wide management strategies and community-wide collaborative efforts to improve the population trajectories of these biologically and culturally significant species.

Acknowledgments

We thank the management team of Norfolk Island National Park for their knowledge contributions and dedicated support throughout this project: Nigel Greenup, Melinda Wilson, Joel Christian, Ken Christian, James Donaldson and Ross Quintal. Nicholas MacGregor at Parks Australia is also thanked for his support. We thank Neil Symington and Shaun Levick for generating and providing access to LiDAR-derived environmental layers. We are grateful to local field volunteers for their generous contributions, particularly Mark Hallam, Judith Andersen, Daniela Cristofaro, Dee Duncanson and Snowy Tavener. We thank Margaret Christian for generously sharing her time and knowledge. We thank Benjamin Viola and Jessica Zhou for their administrative support throughout this project. All research was conducted under an approved Parks Australia Management Plan, Norfolk Island Regional Council research permit 41/2019, and Monash University Animal Ethics approval 2021-14636. Authors AN and WM were supported by an Australian Government Research Training Programme Scholarship.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This research was supported by the Australia and Pacific Science Foundation under grant (APSF19017); and the Royal Zoological Society of New South Wales [Ethel Mary Read Research Grant 2019].

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