

Small-scale species distribution model identifies restricted breeding habitat for an endemic island bird

R. D. Segal^{1,2} , M. Massaro^{1,2} , N. Carlile³  & R. Whitsed^{1,2} 

1 School of Environmental Sciences, Charles Sturt University, Albury, NSW, Australia

2 Institute for Land, Water and Society, Charles Sturt University, Albury, NSW, Australia

3 Department of Planning, Industry and Environment NSW, Parramatta, NSW, Australia

Keywords

breeding habitat; carrying capacity; Lord Howe currawong; Lord Howe Island; Maxent; restricted breeding range; species distribution model; *Strepera graculina crissalis*.

Correspondence

Richard D. Segal, School of Environmental Sciences, Charles Sturt University, Elizabeth Mitchell Drive, Thurgoona, Albury, New South Wales 2640, Australia.
Email: rsegal@csu.edu.au

Editor: Rahel Sollmann

Associate Editor: Philipp Boersch-Supan

Received 09 August 2020; accepted 06 April 2021

doi:10.1111/acv.12698

Abstract

Mapped geographical distributions of many birds are an overestimation of their true range and this overestimation is particularly high for threatened species. Due to their restricted ranges, specialized habitats and inability to relocate to other areas, island birds are particularly vulnerable to anthropogenic effects on their habitats, but few studies have investigated the suitability of remaining habitat for species restricted to small oceanic islands. Here, we developed a fine-scale species distribution model to investigate the breeding habitat of the Lord Howe currawong *Strepera graculina crissalis*. Using 73 nest locations as occurrence records, we found that currawongs nest preferentially near creek lines at lower elevations in the forested areas of the island (maximum elevation of 120 m). Habitat suitability decreased rapidly as the distance to creeks increased, indicating that many forested areas far from a creek line were unsuitable habitat for nesting currawongs. Using a combination of Thiessen polygons and suitable habitat to define territory boundaries, we estimated the average territory size to range between 2.48 ha and 5.23 ha. Using a conservative threshold, our model identified 195 ha of Lord Howe Island's land area as highly suitable nesting habitat for the Lord Howe currawong, while using a less conservative threshold identified a further 246 ha as medium suitable habitat (441 ha total). Hence, we estimated that the island can support a maximum number of 84 breeding territories. This study shows that the Lord Howe currawong has a narrower ecological niche than was expected, lowering the carrying capacity for this species on the island. As birds on remote islands are often unable to relocate to other suitable areas, it is important to determine the remaining habitat to ensure the continued persistence and conservation of threatened island species.

Introduction

Oceanic islands are recognized as hotspots of global biodiversity (Kier *et al.*, 2009; Myers *et al.*, 2000). While collectively small in area (5% of land area), islands provide habitat for around 15% of the world's terrestrial plant and animal species (Jones *et al.*, 2016). Many island species are endemic to particular islands or island archipelagos, and because of their restricted ranges, small populations, specialized habitats and low likelihood of recolonization, they are more vulnerable to extinction than many continental species (Auld *et al.*, 2010; Baker, Harvey & French, 2014; Tershy *et al.*, 2015). In fact, over the last 500 years, 66% of plant species extinctions and 75% of vertebrate extinctions, including 90% of all bird extinctions, have occurred on islands (Glen *et al.*, 2013; Newton, 1998; Szabo *et al.*, 2012).

The introduction of exotic predators to islands has been found to be the main cause for many population declines and extinctions of island bird species (Blackburn *et al.*, 2004; Glen *et al.*, 2013; Szabo *et al.*, 2012). However, these introductions of exotic predators often occurred concurrently with the establishment of human settlements and significant habitat alterations. In combination, the introduction of exotic predators and habitat loss has likely led to accelerated population declines and extinctions of island birds (Blackburn *et al.*, 2004; Szabo *et al.*, 2012). For remaining island birds, continued habitat destruction and deterioration due to more natural habitat being converted to agricultural land and/or the introduction and spread of exotic species (both plants and animals) have led to the reduction of already limited habitat (Blackburn *et al.*, 2004; Morris *et al.*, 2018; Szabo *et al.*, 2012). The risk of habitat loss on islands is now further

exacerbated by climate change as higher temperatures, altered rainfall patterns, sea level rise and extreme weather events are causing considerable changes to island vegetation (Ewers & Didham, 2006; Morris *et al.*, 2018). As island birds are often unable to relocate to other areas to avoid these effects on their habitats, it is important to determine the area of remaining habitat to ensure the continued persistence of threatened island species.

Mapped geographical ranges of many birds, including island species, are an overestimation of their true range and this overestimation is particularly high for threatened species (62% of species) compared to non-threatened species (37% of species) (Jetz, Sekercioglu & Watson, 2008). Even if a range of environmental conditions makes an area appear suitable for a species, the presence of predators or other cryptic barriers can prevent the existence of the species in the area (Hirzel & Le Lay, 2008; Bradie & Leung, 2017; Newton, 1998; Phillips, Anderson & Schapire, 2006). Hence, the actual area a species is occupying is often significantly smaller and more narrowly aligned with particular environmental and ecological conditions than the official mapped distribution given for a species (Jetz *et al.*, 2008; Massaro *et al.*, 2018). Determining which set of environmental and ecological parameters define a species' habitat and its quality is important for identifying and protecting remaining suitable habitat patches and restoring degraded habitat to increase its quality.

Both the reduction in habitat area and quality affects the number of individuals of a species that can exist and reproduce successfully in an area (Gill, 2007). Habitat of lower quality is expected to sustain fewer individuals of one species and may not allow individuals to breed. In contrast, higher quality habitat has theoretically the necessary resources to support higher numbers of individuals and allows those individuals to reproduce successfully. In addition, for species where individuals or breeding pairs maintain territories – areas that are actively defended – the size of the territory may provide an indication of habitat quality as territories are expected to be larger in poorer quality habitat and smaller in higher quality habitat (Adams, 2001; Lyons *et al.*, 2018). This matrix of higher and lower quality habitat patches of various sizes determines the carrying capacity, which is the maximum number of individuals of a species that can exist in an area (Armstrong & Seddon, 2008; Donovan *et al.*, 2012). However, for many species it remains unknown which environmental parameters define habitats of high and low quality (Johnson, 2007). In fact, assessing habitat quality comprehensively is challenging and time consuming because it generally not only requires quantifying resource abundance, but also determining to what degree individuals use and gain fitness advantages from those resources (Germain & Arcese, 2014; Johnson, 2007). Hence, studies assessing the suitability and quality of habitat for birds are uncommon, although these are urgently needed to determine the carrying capacity of remaining habitat for threatened species.

Over the past 30 years, species distribution models (SDM) have provided ecologists with new techniques to combine geographical occurrence data of a particular species with

topographical, environmental and other ecological data to determine which variables define a species' habitat and its quality (Elith & Leathwick, 2009; Guisan & Zimmermann, 2000). Even based on very limited species occurrence data, these spatial models are able to predict a species' distribution by identifying areas of suitable habitat with matching environmental and ecological parameters (Franklin, 2013). Many studies using SDMs have been carried out on bird species (Kalle *et al.*, 2017; Latif *et al.*, 2015; Moradi *et al.*, 2019; Pietersen *et al.*, 2018; Tinoco *et al.*, 2009), including on islands (Massaro *et al.*, 2018; Sass, Mortensen & Reed, 2017). Maxent, a machine learning method based on the theory of maximum entropy, is one of the most commonly used algorithms in SDM (Phillips *et al.*, 2006). Maxent is often used to model distributions of species at the regional or continental scale (e.g. Elith, Kearney & Phillips, 2010; Pietersen *et al.*, 2018). In their review of over 2000 Maxent models, Bradie and Leung (2017) found that over 80% were conducted with a 1-km² resolution because climate data used in these models are typically also reported at 1-km² resolution (Hijmans *et al.*, 2005). However, data collected at this scale have only a limited ability to capture potentially significant fine-scale habitat features that may be important for habitat selection (Ko *et al.*, 2012; Latif *et al.*, 2015). This large-scale and coarse-resolution approach is especially unsuitable for species with small distributions or those species restricted to islands. In these cases, climate is much less likely to be a driving factor in species distribution, as climate varies less over small areas (Lahoz-Monfort *et al.*, 2010; Massaro *et al.*, 2018), and sufficient microclimate data for modelling are not usually available. Nevertheless, incorporating climatic data at an appropriate scale could improve the SDM of an island species, if only to illustrate the lack of influence on a species distribution. Regardless of the in- or exclusion of climatic data in SDMs, few studies have been conducted at a finer scale that is appropriate for species restricted to small oceanic islands, despite the high occurrence of threatened or endangered species on islands (but see Massaro *et al.*, 2018; Papadopulos *et al.*, 2013).

In this study, we took a fine-scale approach to investigate the breeding habitat of the Lord Howe currawong *Strepera graculina crissalis*. The Lord Howe currawong is found only on Lord Howe Island (LHI) (1455 ha), Australia, and is considered vulnerable within the state of New South Wales due to its restricted range and small population (240 individuals, O'Dwyer & Carlile, 2017; Office of Environment and Heritage NSW, 2020). We located currawong nests during two successive breeding seasons and developed a SDM using Maxent. As birds are highly mobile, nest location is a more reliable indicator of habitat suitability than presence alone (Hirzel & Le Lay, 2008; Ilera, von Wehrden & Wehner, 2010). Our objectives were to (1) identify which environmental or ecological parameters define the Lord Howe currawong's breeding habitat, (2) determine the amount of habitat suitable for currawong nesting and (3) estimate the maximum breeding population that the available habitat can support on LHI (the island's carrying capacity for Lord Howe currawong).

Materials and methods

Study site

Lord Howe Island is located in the Tasman Sea between Australia and New Zealand (31.54°S, 159.08°E), 760 km north-west of Sydney, New South Wales (Fig. 1a) [Department of Environment & Climate Change (DECC), 2007]. LHI is an eroded volcanic remnant approximately 11 km long and up to 3 km wide, rising to 875 m at its highest point, Mount Gower (DECC, 2007). The island's 1455 ha are mostly covered by native vegetation, with around 75% of the island inside a Permanent Park Preserve (DECC, 2007). The island experiences a mild maritime climate, with cool wet winters 13–18°C and drier warmer summers 13–25°C (DECC, 2007). Average annual rainfall is 1650 mm with high cloud cover and humidity throughout the year (>60% relative humidity) (DECC, 2007). The island is exposed to trade winds predominantly from the south-east and north-east (DECC, 2007; Papadopoulos *et al.*, 2013).

Study species

Approximately 60% of all Lord Howe currawongs on the island are uniquely colour banded with leg rings, allowing the identification of individual birds from a distance. Adult Lord Howe currawongs form breeding pairs and defend their nesting territories in forested areas year round (M Massaro, pers. comm.). Nevertheless, currawongs will leave their territories for short periods to forage in areas across the island, such as orchards, seabird colonies and bird feeders. Juvenile currawongs stay with their parents for up to 2 months after fledging (Wood, 1998). The sub-adults and other non-breeding currawongs often form loose groups during the breeding season.

Nest locations

The locations of currawong nests were found by searching systematically the forested areas of the island during the currawong breeding season (September–January) in 2017 and 2018. The three main areas searched were the Northern Hills, the Transit Hill area and the area around Intermediate Hill to the base of Mount Lidgbird (Fig. 1a). The island's forest walking tracks were used to access these areas and any gullies or creek lines, favoured by currawongs for nesting (Carlile & Priddel, 2007; McFarland, 1994), were followed from top to bottom to find currawong territories. In addition, any locations where currawongs were heard calling or seen from a distance were investigated. Once located, birds displaying breeding behaviours including territorial defence, carrying nesting material or carrying food were followed to their nest. Any nestling or fledgling begging calls heard were also investigated to locate nests. Due to the steepness of the terrain, we were not able to search most of the southern part of the island (southern part of Mt Lidgbird and Mt Gower). GPS locations of nests were recorded on a Garmin eTrex 30x to an accuracy of less than five metres. The areas where nests were found in 2017 were also searched for nests in 2018. Due to this previous knowledge about where territories were located and assistance with nest searching in 2018, nests were found more quickly and more of the island's forested areas could be searched in that year.

Species distribution model

Species distribution models rely on ecologically relevant environmental predictors and their relationships with species' presence (Elith & Leathwick, 2009). Maxent was chosen for this study because it can utilize presence only-data (i.e. true absences are not needed). Maxent can also model continuous

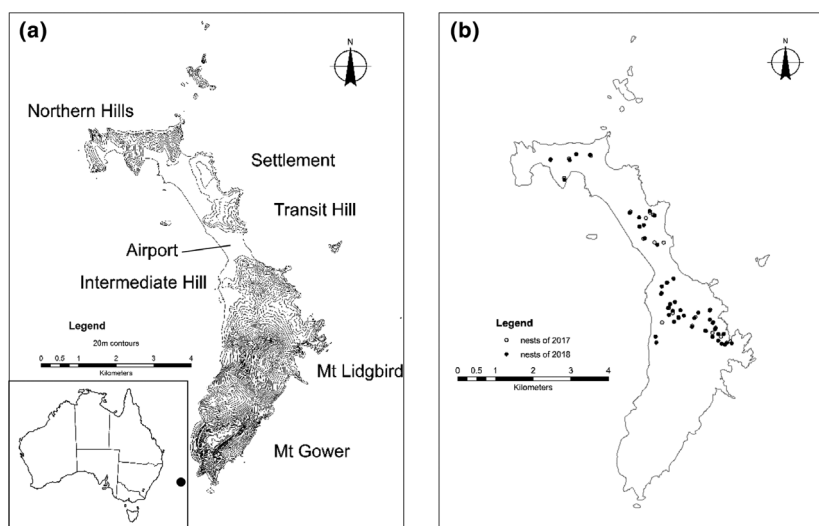


Figure 1 (a) Elevational map of Lord Howe Island, Australia and its location relative to the Australian mainland (inset) and (b) locations of currawong nests found during island surveys in 2017 and 2018.

and categorical variables and is relatively insensitive to small sample sizes (Phillips *et al.*, 2006; Sass *et al.*, 2017; Syfert, Smith & Coomes, 2013). We used Maxent version 3.4.1 (Phillips, Dudík & Schapire, 2019) with combined nest locations from 2017 and 2018 as presence data, with duplicate nest locations (within the same 10-m cell) removed. The six predictor variables considered for inclusion in the model were elevation, slope, aspect, distance to coast, distance to drainage and vegetation classification. Elevation, slope and aspect are commonly used topographical variables in SDMs, while distance to coast can be an important predictor in SDMs for island species, especially for birds on oceanic islands where prevailing winds can be frequent and strong (Massaro *et al.*, 2018). Distance to drainage was included in the model because of our field observation that currawongs often nest near creek lines and gullies. Climate variables were not included in the SDM, because there is only minimal spatial variation across the island and microclimates are expected to correlate with terrain variables. Elevation, slope and aspect were derived from a 1-m digital elevation model (DEM) of the island (NSW Digital Topographical Database, 1999). The drainage layer was derived by extending an existing drainage layer with the 1-m DEM using the hydrology tools in ArcGIS. Vegetation classes were rasterized from a vegetation classification map for the island with 46 vegetation communities (Sheringham *et al.*, 2016). Vegetation classes containing no presence observations were combined into a single class (“unsuitable vegetation”), resulting in nine vegetation classes, to simplify the role and interpretation of vegetation in the model. All predictor variables were created or resampled at 10-m resolution using ArcGIS 10.5.1 (ESRI Inc., 2017). Correlation between all predictor variables was low (Pearson’s $R < 0.5$); therefore, they were all retained in the model (Elith & Leathwick, 2009).

Maxent was implemented with 10-fold cross-validation using default settings including 10 000 randomly selected background points and cloglog output (Phillips *et al.*, 2017). To account for sampling bias, a kernel bias grid of search effort was created from the nest locations and other surveyed locations (Supporting Information Figure S1a) and scaled from 1 to 20, where 1 indicated unsearched areas (Supporting Information Figure S1b) (Merow, Smith & Silander, 2013). The bias grid was used in the selection of background points used in the Maxent model and was incorporated into the model via the Advanced Settings menu in Maxent. We incorporated a sampling bias grid into our model as currawongs are not known to nest preferentially in high locations. Although there is a possibility that some nests at higher elevations were missed, nest locations at high elevation are unlikely to be highly suitable. Hence, we believe it was appropriate to allow the model to select some background points from higher elevations. Separate models were run using the different features (linear, quadratic, product, threshold and hinge and combinations of these). Maxent models are typically evaluated using the performance metric area under the curve (AUC) of receiver operating characteristic (Merow *et al.*, 2013) and the feature combination producing the highest AUC was used in the final model.

The percent contribution and percent permutation importance were used to determine the importance of the model’s environmental parameters. The percent contribution reports the gain of the model by including a particular variable and the permutation importance reports the contribution for each variable to the final model that only contained that variable. The continuous cloglog output was converted to binary presence–absence using two different thresholds. The commonly used 10th percentile training presence (including 90% of occurrences) was used as the first threshold (high suitability), resulting in a conservative estimate of suitable habitat (Liu *et al.*, 2005; Young, Carter & Evangelista, 2011). Minimum training presence (all occurrences) was used as the second threshold (medium suitability), to generate a less conservative estimate of suitable habitat (Pearson *et al.*, 2007).

Territory size and carrying capacity

Calculating territory shape and size remains problematic (Adams, 2001), particularly when nests are irregularly spaced and territory is limited by suitable habitat, as is the case here. Thiessen polygons can be used to define boundaries between territories, equidistant from nests (Adams, 2001; Paris *et al.*, 2016), assuming competition pressure is equal. Uneven topography, such as ridges and gullies, is also known to influence size and shape of territory (Adams, 2001). Hence, a combination of Thiessen polygons and suitable habitat defined by the SDM to estimate territory boundaries is a reasonable approach (Supporting Information Figure S2). The two binary suitable/unsuitable layers calculated using the two thresholds described in the previous paragraph (“conservative” and “less conservative” estimates of suitability) were intersected with Thiessen polygons generated in ArcGIS 10.5.1 (ESRI Inc., 2017) based on nest locations in 2018, due to the greater search effort that year. Where resulting polygons were discontinuous, they were either deleted (island polygons unconnected to any territory) or merged with an adjoining territory (where a territory might be closer to one nest by Euclidean distance, but continuously joined to a different territory). This process resulted in two estimates of territories, based on the two different thresholds. For each of these territory estimates, we calculated total occupied territory area and average territory size. Percentage of suitable habitat occupied was calculated as the total occupied territory divided by the total suitable habitat. Finally, an estimation of carrying capacity was determined from the total number of nesting pairs that could theoretically be present if all suitable areas were occupied.

Results

Twenty-eight nests were located during the 2017 breeding season, while 45 nests were located during the 2018 breeding season. Most nests were located in the Intermediate Hill – Mt Lidgbird forested area (Fig. 1b). Typically, nests were located under a high canopy and an open vegetation structure of palms *Howea* spp. and fork tree *Pandanus forsteri*. Nests were found in various tree species including blackbutt

Cryptocarya triplinervis, greybark *Drypetes deplanchei*, scalybark *Syzygium fullagarii*, maulwood *Olea paniculata* and Banyan *Ficus macrophylla columnaris* and various vegetation communities including greybark and blackbutt rain forest (Community 17a, 24 of 73 nests), and scalybark, curly palm *Howea belmoreana*, greybark, cedar *Guioa coriacea*, maulwood and forky tree lowland mixed forest, (Community 16a, 22 of 73 nests) (Table 1). Nest heights ranged from approximately 3 m off the ground in small trees to approximately 25 m off the ground in the forest canopy.

Nest locations were used as occurrence records, and initial models used all six predictor variables. However, as aspect and slope were found to make only a small contribution (<5% combined) to the initial model, the model was run again without including these two predictors. The hinge-only model produced the highest AUC (0.924 ± 0.032). Hinge features model processes that start or stop at a threshold and then change linearly, and produce complex, smooth response curves (Merow *et al.*, 2013). Distance to drainage had the highest percentage contribution and percentage permutation (Table 2). Elevation (DEM) had the next highest percentage contribution and percentage permutation, with vegetation class and distance to coast contributing the least to the final model (Table 2).

In the SDM, higher nesting habitat suitability (green and yellow) followed closely the Island's drainage lines (Supporting Information Figure S3). Away from the drainage lines,

habitat suitability decreased sharply, which can also be seen in the steeply negative slope of the distance to drainage response curve (Fig. 2a). Currawongs also responded strongly to elevation, avoiding the very lowest elevations and elevations greater than 200 m (Fig. 2b). The model also showed that the currawongs appeared to prefer vegetation classes 16a (scalybark, curly palm, greybark, cedar, maulwood and forky tree lowland mixed forest), 16b (curly palm closed sclerophyll forest), 17a (greybark and blackbutt rain forest) and 19 (lowland forest of maulwood, kentia palm, cottonwood and greybark) (Fig. 2c). Finally, currawongs preferred habitat at least 200 m inland from the coast (Fig. 2d).

The total suitable habitat was estimated to be between 195 ha (13.3% of total island area, conservative threshold,) and 441 ha (30.0% of total island area, less conservative threshold) (Table 3). The area of suitable habitat was naturally larger with a less conservative threshold, and the total occupied territory was also calculated as larger because more suitable habitat was included in the territory calculations. Estimation of the total area occupied by currawongs ranged from 112 ha to 235 ha, and the estimated average territory size ranged from 2.48 ha to 5.23 ha (Table 3; Fig. 3). These differences were due to more "suitable" areas being available with the less conservative threshold. The percentage of suitable habitat occupied remained consistent across all scenarios (53–57%). This resulted in a theoretical carrying capacity of 79–84 nesting pairs, if all unoccupied suitable habitat was occupied (Table 3).

Table 1 Summary of currawong nest location data for surveys conducted on Lord Howe Island, Australia in 2017 and 2018, including the number of currawong nests per vegetation community (defined by Sheringham *et al.*, 2016) and the total area, which these vegetation communities occupy on the island

Community number	Community name	2017 nests	2018 nests	Area Ha
12a	Kentia Palm forest on coral sand and calcarenite	2	0	39.2
12b	Banyan and Kentia Palm forest on coral sand and calcarenite	0	1	78.1
14	Scalybark, Blue Plum and Curly Palm closed forest of sheltered slopes or valleys	5	9	196.1
15b	Forky-tree closed forest along gullies	0	2	6.4
16a	Scalybark, Curly Palm, Greybark, Cedar, Maulwood and Forky Tree lowland mixed forest	7	15	168.0
16b	Curly Palm closed sclerophyll forest	3	3	77.8
17a	Greybark and Blackbutt rain forest	10	14	247.4
19	Maulwood, Kentia Palm, Cotton-wood and Greybark lowland forest	1	1	35.1
	All others	0	0	567.3

Discussion

Although 75% of the Island's area is forested, Lord Howe currawongs nest preferentially near creek lines or gullies at lower elevations. Previous studies have also noticed this preference of currawongs to occupy vegetated gullies (Carlile & Priddel, 2007; Knight, 1987; McFarland, 1994). Our model clearly shows that habitat suitability decreases rapidly as the distance to gullies increases, indicating that many forested areas far from a creek line were unsuitable habitat for nesting currawongs. This preference to breed in gullies may be due to their need for reliable access to water and food resources. The damp soils and leaf litter accumulation near creek lines may be ideal for the proliferation of

Table 2 The percent contribution and the percent permutation importance of each environmental variable to the Lord Howe currawong species distribution model

Variable	Percent contribution (%)	Percent permutation importance (%)
Distance to drainage (m)	64.4	54.1
Elevation (m)	24.9	38.8
Vegetation class	7.0	3.5
Distance to coast (m)	3.8	3.6

The percent contribution reports the gain of the model by including a particular variable and the permutation importance reports the contribution of each variable to the model.

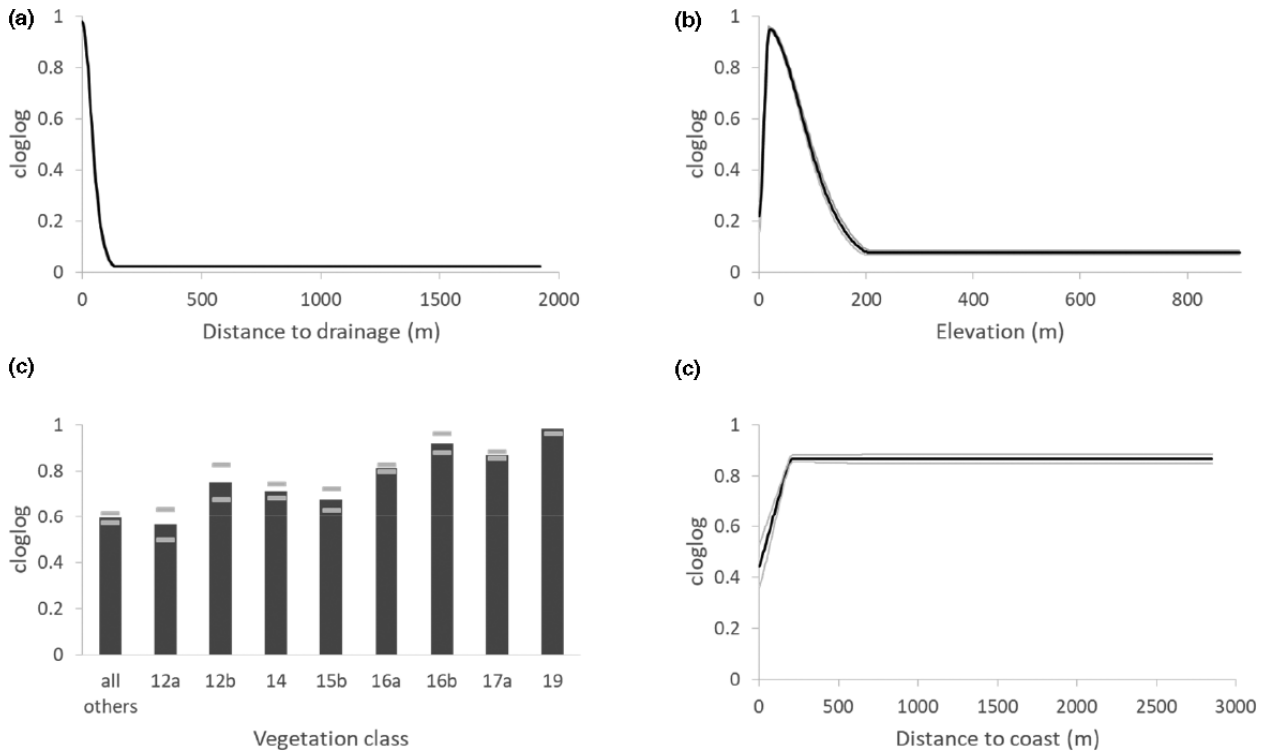


Figure 2 Model response curves for the environmental variables used in the currawong species distribution model for Lord Howe Island, Australia: (a) distance to drainage, (b) elevation, (c) vegetation class and (d) distance to coast. Black lines/bars denote mean response over 10-model runs, grey lines/bars denote 1SD. Vegetation classes (c) are defined in Table 1.

invertebrates (Frith & Frith, 1990; MacNally, Soderquist & Tzaros, 2000). As invertebrates are an important part of the currawong's diet (Carlile & Priddel, 2007; McAllan *et al.*, 2004), the dampness of the soil in gullies may provide currawongs with easy access to soil invertebrates, which may be especially important when provisioning chicks (Stone, Tasker & Maron, 2019).

Although we were able to incorporate a detailed vegetation map into our model, vegetation community did not influence where currawongs chose to nest. We believe that this is a genuine lack of preference for a particular vegetation community as currawongs nested in a variety of different tree species and their territories were located within different vegetation communities. Combining the vegetation classes in which no nests occurred into a single class made no difference to the model output because differences in preferences for vegetation classes can only arise if there were nest occurrences in these vegetation classes.

Our estimate of the average currawong territory size (2.48–5.23ha) is of the same magnitude to estimates from previous studies on LHI (5.4 ha, Carlile & Priddel, 2007; 10 ha, Knight, 1987) and mainland Australia [pied currawongs *Strepera graculina*: 7.9 ha, Prawiradilaga, 1996]. Positions of territory boundaries are resolved between contiguous neighbours through vocal displays along a boundary and, if intrusions occur, territory owners (male and female) will chase intruders out of the territory. As

neighbouring birds may differ in size and ability to defend territories, division of suitable breeding habitat, and thus resources within this habitat, may be unequal (Adams, 2001). Those individuals with access to many resources within their territory are likely to have higher breeding success, but this, in turn, may increase the overall density of birds in high-quality habitat and decrease territory sizes. Juvenile male black robins *Petroica traversi* on the Chatham Islands, New Zealand, were found to establish territories next to their parents if possible (Paris *et al.*, 2016). However, if the population density near their parent's territory was too high (>8 birds/ha), juvenile males were forced to disperse and often establish territories in lower quality habitat (Massaro *et al.*, 2018; Paris *et al.*, 2016). Similarly, on an island where all suitable habitat was occupied, male Seychelles warblers *Acrocephalus sechellensis* budded off parts of their natal territory belonging to their parents (Komdeur & Edelaar, 2001), while on an island where suitable habitat was available, offspring warblers dispersed and established their own territories until the habitat was saturated (Komdeur, 1992). It is probable that such density-dependent effects on dispersal behaviour and territory sizes are occurring in the Lord Howe currawong. The limited availability of territories on the Island may explain why currawongs occupy and defend vigorously their territories year round, and the presence of a significant number of non-breeding adults each year.

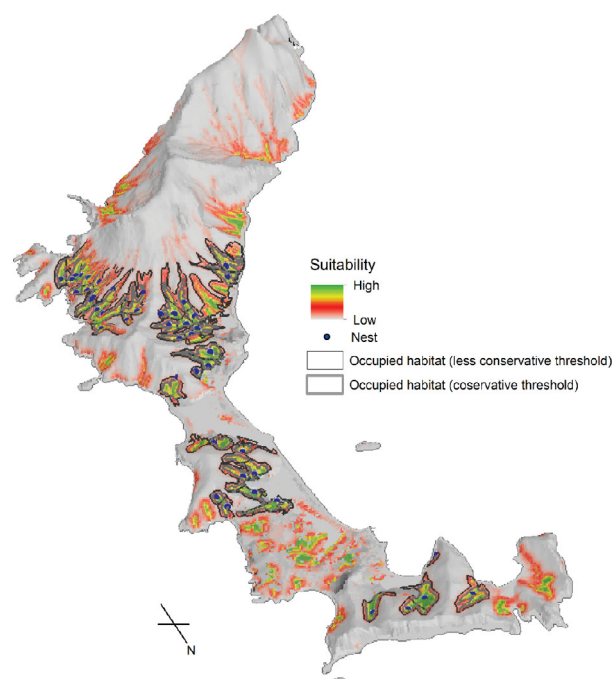


Figure 3 3D view of suitable and occupied habitat for currawongs on Lord Howe Island, Australia derived from Maxent species distribution model based on nest locations in 2018. View is from the north of the island towards Mounts Gower and Lidgbird.

Table 3 The area of total suitable habitat for nesting currawongs on Lord Howe Island, Australia estimated from the 2018 Maxent model

	Conservative (10th percentile training presence threshold)	Less conservative (minimum training presence threshold)
Total suitable habitat (ha)	195	441
Total occupied area (ha)	112	235
Average territory size (\pm SE) (ha)	2.48 (\pm 0.19)	5.23 (\pm 0.41)
Percentage of suitable habitat occupied (%)	57	53
Number of nesting pairs	45	45
Theoretical carrying capacity (pairs)	79	84

The total occupied area and average territory size were derived from intersection of Thiessen polygons around currawong nests and suitable habitat using conservative and less conservative thresholds. The carrying capacity was determined by dividing the total suitable habitat by the average territory size.

Based on our estimate of territory size in 2018, we estimated that the island can support a maximum number of 84 breeding territories. Estimating carrying capacity is an inexact science as it is necessarily based on assumptions about

minimum territory size, minimum distance between nests and habitat suitability (Chapman & Byron, 2018; Glenn *et al.*, 2017). In many instances, it is assumed that the vegetated area of an island represents available habitat, which is then divided by average territory area (e.g. Paris *et al.*, 2016; Ryan & Jamieson, 1998). In the case of LHI, this would result in an overestimation of the carrying capacity, as the suitable habitat for currawongs is more narrowly defined due to the importance of gullies and elevation. By defining suitable habitat more accurately using a SDM, and using this as a basis for defining plausible territories, we have been able to estimate both current shapes and sizes of territories and the theoretical number of nesting pairs that the island could support. It is possible that this number is an overestimate, because a proportion of areas which were identified as suitable habitat is not contiguous, and therefore too small to form a territory. However, this overestimation is in contrast to existing large territories attributed to a single pair that could contract to allow additional nesting pairs to establish. It is also possible that we underestimated our mean territory size because territory holders may defend larger areas than was considered suitable habitat by the SDM using nest records as occurrence data. In this case, our estimations of total territory size would be underestimated at the outer boundaries for those territories with no contiguous neighbours and explain why our average territory size estimates are smaller than those reported in previous studies. Further ground-truthing in future years could eliminate these uncertainties and increase the accuracy of our territory size estimates. But regardless of these uncertainties, our technique of defining territory boundaries by using a combination of Thiessen polygons and suitable habitat defined by the SDM is an improved approach for estimating carrying capacity more accurately.

Any significant changes in resource availability may decrease or increase habitat suitability, resulting in lower or higher limits in carrying capacity (Chapman & Byron, 2018). A significant change in resource availability has recently occurred on LHI. Until recently, there were up to 210 000 house mice *Mus musculus* and 150 000 ship rats *Rattus rattus* on LHI (Lord Howe Island Board, 2017). As currawongs forage on a wide variety of fruit, invertebrates and vertebrates from the forest canopy, understorey and forest floor (Carlile & Priddel, 2007; McAllan *et al.*, 2004), both rodent species are competitors for food resources. Rodents also forage on seeds and seedlings, reducing plant recruitment and fruit availability (Broome *et al.*, 2019; Campbell & Atkinson, 1999; Priddel *et al.*, 2011; Sinclair *et al.*, 2005; Springer, 2016). With the completion of an island-wide rodent eradication in 2019, the removal of these invasive species is likely to increase food availability for the currawongs. There is some evidence that the abundance of invertebrates increased following the rodent eradications on Macquarie Island and Antipodes Island in Australia and New Zealand respectively (Horn, Greene & Elliot, 2019; Springer, 2012, 2016). This increased food availability may allow currawongs to breed at higher densities in suitable habitat or establish territories in previously unsuitable areas. To test

whether the removal of rodents influences habitat quality and currawong nesting densities, a study comparing the nesting densities and habitat selection before and after the rodent eradication is necessary.

Specialist species with narrow habitat requirements or specialized diets have been identified as being more likely to be subject to range overestimation (Jetz *et al.*, 2008). This would include the Lord Howe currawong, despite its high mobility and omnivorous diet. Although currawongs roam across LHI, their nesting habitat is confined to a narrow ecological niche. While most studies use presence data of individuals of a species, we used nest location as occurrence data in this study, allowing us to clearly identify what habitat is suitable for currawongs to reproduce and not only to exist. Thus, the use of nest location as occurrence data in SDMs may prevent or at least reduce range overestimation found for many species.

As the nesting habitat of the Lord Howe currawong is confined to a narrow ecological niche, any changes to rainfall and temperature patterns due to climate change that lead to drier gullies and soils may result in a reduction of the breeding population that the island can support. Small populations are especially vulnerable to extinction due to random effects (demographic and environmental stochasticity, genetic drift) and inbreeding (Ballou *et al.*, 2010; Caughley, 1994). Genetic diversity provides the basis for adaptation to environmental change (Ballou *et al.*, 2010; Jamieson, 2010). Given the small population size of the Lord Howe currawong and its limitations to grow substantially due to the restricted breeding habitat, its current conservation status (Vulnerable, Office of Environment and Heritage NSW, 2020) may need to be reconsidered.

Given the disproportionate number of threatened island endemics, considerable amounts of funding and resources have been invested globally into island species conservation. Therefore, there is a need for evidence-based approaches to efficiently use these resources. SDMs provide a rapid assessment technique to measure habitat suitability and availability for endangered species where time is of critical importance. Spatially referenced environmental variables are now more readily available and are available at scales small enough to be ecologically relevant to range-restricted species, such as those on small oceanic islands. The SDM approach taken here operates at a scale that is relevant to the on-ground conservation management of species and allows the estimation of carrying capacity. While climatic variables do not necessarily need to be included in the models due to the minimal spatial variation at these smaller scales, it may be useful to include other environmental variables such as vegetation structure [e.g. from LIDAR surveys (Huber *et al.*, 2016; Singh *et al.*, 2017)], prey abundance and presence of predators (Hirzel & Le Lay, 2008; Pearson *et al.*, 2007; Pietersen *et al.*, 2018). Changes to a species' distribution and territory size may indicate changes in the quality of remaining habitat patches, allowing the intervention by conservation practitioners. Hence, we encourage the increased use of SDMs for species restricted to islands.

Acknowledgements

This study was conducted under Charles Sturt University animal ethics permits A17066 and A18047 and New South Wales scientific licences SL101935 and SL102102. R.D.S. was supported financially by an Australian Research Training Program and Institute for Land, Water and Society scholarship. R.D.S. was funded by the Lord Howe Island Board and Office of Environment and Heritage NSW for the 2017 field season. M.M. was supported by an Australia & Pacific Science Foundation grant (18/4) and a grant by the Australian Research Council (DP200101281). Island accommodation was provided for a reduced cost by the Lord Howe Island Board. We would like to thank Terry O'Dwyer, Bruce and Fiona Robertson and Jaclyn Pearson for their assistance in nest searching. We would also like to thank the following LHIB staff for their assistance during our time on the island: Hank and Sue Bower, Andrew Walsh and Darcie Bellanto. We also thank Leon Brice and Ian Fitzgerald for their support during our work on the island and for allowing access to their properties for nest searches. We also thank Deanna Duffy (SPAN, CSU) for assistance with spatial data and analysis and two anonymous reviewers for their comments that greatly improved the paper.

Conflicts of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

- Adams, E.S. (2001). Approaches to the study of territory size and shape. *Annu. Rev. Ecol. Syst.* **32**, 277–303.
- Armstrong, D.P. & Seddon, P.J. (2008). Directions in reintroduction biology. *Trends Ecol. Evol.* **23**, 20–25.
- Auld, T.D., Hutton, I., Ooi, M. & Denham, A.J. (2010). Disruption of recruitment in two endemic palms on Lord Howe Island by invasive rats. *Biol. Invasions* **12**, 3351–3361. <https://doi.org/10.1007/s10530-010-9728-5>
- Baker, J., Harvey, K.J. & French, K. (2014). Threats from introduced birds to native birds. *Emu* **114**, 1–12. <https://doi.org/10.1071/MU12122>
- Ballou, J.D., Lees, C., Faust, L.J., Long, S., Lynch, C., Bingaman Lackey, L. & Foose, T.J. (2010). Demographic and genetic management of captive populations. In *Wild mammals in captivity: principles and techniques for zoo management*: 219–252. Kleiman, D.G., Thompson, K.V. & Baer, C.K. (Eds.). Chicago: University of Chicago Press.
- Blackburn, T.M., Cassey, P., Duncan, R.P., Evans, K.L. & Gaston, K.J. (2004). Avian extinction and mammalian introductions on oceanic islands. *Science* **305**, 1955–1958.
- Bradie, J. & Leung, B. (2017). A quantitative synthesis of the importance of variables used in MaxEnt species distribution models. *J. Biogeogr.* **44**, 1344–1361. <https://doi.org/10.1111/jbi.12894>

- Broome, K., Brown, D., Brown, K., Murphy, E., Birmingham, C., Golding, C., Corso, P., Cox, A. & Griffiths, R. (2019) House mice on islands: management and lessons from New Zealand. In *Island invasives: scaling up to meet the challenge*. 100–107. Veitch, C.R., Clout, M.N., Martin, A.R., Russell, J.C. & West, C.J. (Eds). Gland, Switzerland: IUCN.
- Campbell, D.J. & Atkinson, I.A.E. (1999). Effects of kiore (*Rattus exulans* Peale) on recruitment of indigenous coastal trees on northern offshore islands of New Zealand. *J. R. Soc. N. Z.* **29**, 265–290. <https://doi.org/10.1080/03014223.1999.9517597>
- Carlile, N. & Priddel, D. (2007). *Population size and distribution of the Lord Howe Currawong (Strepera graculina crissalis)*. Hurstville, NSW: Department of Environment and Climate Change.
- Caughley, G. (1994). Directions in conservation biology. *J. Anim. Ecol.* **63**, 215–244.
- Chapman, E.J. & Byron, C.J. (2018). The flexible application of carrying capacity in ecology. *Glob. Ecol. Conserv.* **13**, e00365. <https://doi.org/10.1016/j.gecco.2017.e00365>
- Department of Environment and Climate Change (NSW). (2007). *Lord Howe Island biodiversity management plan*. Sydney, Australia: Department of Environment and Climate Change (NSW).
- Donovan, T.M., Warrington, G.S., Schwenk, W.S. & Dinitz, J.H. (2012). Estimating landscape carrying capacity through maximum clique analysis. *Ecol. Appl.* **22**, 2265–2276.
- Elith, J., Kearney, M. & Phillips, S. (2010). The art of modelling range-shifting species. *Methods Ecol. Evol.* **1**, 330–342.
- Elith, J. & Leathwick, J.R. (2009). Species distribution models: ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Evol. Syst.* **40**, 677–697.
- ESRI Inc. (2017). *ArcGIS Desktop 10.5.1*. Redlands, California: ESRI.
- Ewers, R.M. & Didham, R.K. (2006). Confounding factors in the detection of species responses to habitat fragmentation. *Biol. Rev. Camb. Philos. Soc.* **81**, 117–142. <https://doi.org/10.1017/S1464793105006949>
- Franklin, J. (2013). Species distribution models in conservation biogeography: developments and challenges. *Divers. Distrib.* **19**, 1217–1223. <https://doi.org/10.1111/ddi.12125>
- Frith, D. & Frith, C. (1990). Seasonality of litter invertebrate populations in an Australian upland tropical rain forest. *Biotropica* **22**, 181–190.
- Germain, R.R. & Arcese, P. (2014). Distinguishing individual quality from habitat preference in a territorial passerine. *Ecology* **95**, 436–445.
- Gill, F.B. (2007). *Ornithology*. New York: W.H. Freeman and Company.
- Glen, A.S., Atkinson, R., Campbell, K.J., Hagen, E., Holmes, N.D., Keitt, B.S., Parkes, J.P., Saunders, A., Sawyer, J. & Torres, H. (2013). Eradicating multiple invasive species on inhabited islands: the next big step in island restoration? *Biol. Invasions* **15**, 2589–2603. <https://doi.org/10.1007/s10530-013-0495-y>
- Glenn, E.M., Lesmeister, D.B., Davis, R.J., Hollen, B. & Poopatananpong, A. (2017). Estimating density of a territorial species in a dynamic landscape. *Landsc. Ecol.* **32**, 563–579. <https://doi.org/10.1007/s10980-016-0467-6>
- Guisan, A. & Zimmermann, N.E. (2000). Predictive habitat distribution models in ecology. *Ecol. Model.* **135**, 147–186. [https://doi.org/10.1016/S0304-3800\(00\)00354-9](https://doi.org/10.1016/S0304-3800(00)00354-9)
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965–1978. <https://doi.org/10.1002/joc.1276>
- Hirzel, A.H. & Le Lay, G. (2008). Habitat suitability modelling and niche theory. *J. Appl. Ecol.* **45**, 1372–1381.
- Horn, S., Greene, T. & Elliot, G. (2019). Eradication of mice from Antipodes Island, New Zealand. In *Island invasives: scaling up to meet the challenge*: 131–137. Veitch, C.R., Clout, M.N., Martin, A.R., Russell, J.C. & West, C.J. (Eds). Gland, Switzerland: IUCN.
- Huber, N., Kienast, F., Ginzler, C. & Pasinelli, G. (2016). Using remote-sensing data to assess habitat selection of a declining passerine at two spatial scales. *Landsc. Ecol.* **31**, 1919–1937. <https://doi.org/10.1007/s10980-016-0370-1>
- Ilera, J.C., von Wehrden, H. & Wehner, J. (2010). Nest site selection and the effects of land use in a multi-scale approach on the distribution of a passerine in an island arid environment. *J. Arid Environ.* **74**, 1408–1412.
- Jamieson, I.G. (2010). Founder effects, inbreeding, and loss of genetic diversity in four avian reintroduction programs. *Conserv. Biol.* **25**, 115–123. <https://doi.org/10.1111/j.1523-1739.2010.01574.x>
- Jetz, W., Sekercioglu, C.H. & Watson, J.E.M. (2008). Ecological correlates and conservation implications of overestimating species geographic ranges. *Conserv. Biol.* **22**, 110–119. <https://doi.org/10.1111/j.1523-1739.2007.00847.x>
- Johnson, M.D. (2007). Measuring habitat quality: a review. *Condor* **109**, 489–504.
- Jones, H.P., Holmes, N.D., Butchart, S.H.M., Tershy, B.R., Kappes, P.J., Corkery, I., Aguirre-Muñoz, A., Armstrong, D.P., Bonnaud, E., Burbidge, A.A., Campbell, K., Courchamp, F., Cowan, P.E., Cuthbert, R.J., Ebbert, S., Genovesi, P., Howald, G.R., Keitt, B.S., Kress, S.W., Miskelly, C.M., Oppel, S., Poncet, S., Rauzon, M.J., Rocamora, G., Russell, J.C., Samaniego-Herrera, A., Seddon, P.J., Spatz, D.R., Towns, D.R. & Croll, D.A. (2016). Invasive mammal eradications on islands results in substantial conservation gains. *Proc. Natl. Acad. Sci. USA* **113**, 4033–4038. <https://doi.org/10.1073/pnas.1521179113>
- Kalle, R., Combrink, L., Ramesh, T. & Downs, C.T. (2017). Re-establishing the pecking order: Niche models reliably predict suitable habitats for the reintroduction of red-billed oxpeckers. *Ecol. Evol.* **7**, 1974–1983. <https://doi.org/10.1002/ece3.2787>
- Kier, G., Kreft, H., Lee, T.M., Jetz, W., Ibisch, P.L., Nowicki, C., Mutke, J., Barthlott, W. & Crane, P.R. (2009). A global assessment of endemism and species richness across island

- and mainland regions. *Proc. Natl. Acad. Sci. USA* **106**, 9322–9327. <https://doi.org/10.1073/pnas.0810306106>
- Knight, B.J. (1987). A population study of the Lord Howe Island currawong. *Austr Birds* **21**, 28–29.
- Ko, C.-Y., Root, T.L., Lin, S.H., Schneider, S.H. & Lee, P.-F. (2012). Global change projections for Taiwan island birds: linking current and future distributions. *Nat. Conserv.* **2**, 21–40. <https://doi.org/10.3897/natureconservation.2.2351>
- Komdeur, J. (1992). Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature* **358**, 493–495.
- Komdeur, J. & Edelaar, P. (2001). Male Seychelles warblers use territory budding to maximize lifetime fitness in a saturated environment. *Behav. Ecol.* **12**, 706–715.
- Lahoz-Monfort, J.J., Guillera-Arroita, G., Milner-Gulland, E.J., Young, R.P. & Nicholson, E. (2010). Satellite imagery as a single source of predictor variables for habitat suitability modelling: how Landsat can inform the conservation of a critically endangered lemur. *J. Appl. Ecol.* **47**, 1094–1102.
- Latif, Q.S., Saab, V.A., Mellen-McLean, K. & Dudley, J.G. (2015). Evaluating habitat suitability models for nesting white-headed woodpeckers in unburned forests. *J. Wildl. Manag.* **79**, 263–273. <https://doi.org/10.1002/jwmg.842>
- Liu, C., Berry, P.M., Dawson, T.P. & Pearson, R.G. (2005). Selecting thresholds of occurrences in the prediction of species distributions. *Ecography* **28**, 385–393.
- Lord Howe Island Board. (2017). *Lord Howe Island rodent eradication project – NSW species impact statement*. Lord Howe Island, Australia: Lord Howe Island Board.
- Lyons, A.L., Gaines, W.L., Singleton, P.H., Kasworm, W.F., Proctor, M.F. & Begley, J. (2018). Spatially explicit carrying capacity estimates to inform species specific recovery objectives: Grizzly bear (*Ursus arctos*) recovery in the North Cascades. *Biol. Conserv.* **222**, 21–32.
- MacNally, R., Soderquist, T.R. & Tzaros, C. (2000). The conservation value of mesic gullies in dry forest landscapes: avian assemblages in the box- ironbark ecosystem of southern Australia. *Biol. Conserv.* **93**, 293–302.
- Massaro, M., Chick, A., Kennedy, E.S. & Whitsed, R. (2018). Post-reintroduction distribution and habitat preferences of a spatially limited island bird species. *Anim. Conserv.* **21**, 54–64. <https://doi.org/10.1111/acv.12364>
- McAllan, I.A.W., Curtis, B.R., Hutton, I. & Cooper, R.M. (2004). The birds of the Lord Howe Island group: a review of records. *Aust. Field Ornithol.* **21**, 1–82.
- McFarland, D.C. (1994). Notes on the Lord Howe currawong *Strepera graculina crissalis*. *Australian Bird Watcher* **15**, 310–313.
- Merow, C., Smith, M.J. & Silander, J.A. (2013). A practical guide to MaxEnt for modelling species' distributions: what it does, and why inputs and settings matter. *Ecography* **36**, 1058–1069. <https://doi.org/10.1111/j.1600-0587.2013.07872.x>
- Moradi, S., Ilanloo, S.S., Kafash, A. & Yousefi, M. (2019). Identifying high-priority conservation areas for avian biodiversity using species distribution modelling. *Ecol. Ind.* **97**, 159–164. <https://doi.org/10.1016/j.ecolind.2018.10.003>
- Morris, K., Algar, D., Armstrong, D., Ball, D., Bryant, S.L., Canty, P., Copley, P.B., Dickman, C., Fisher, A., Gillespie, G.R., Johnston, M. & Kelly, D. (2018). Values of islands across Australia's states and territories. In *Australian Island Arks: conservation, management and opportunities*: 11–43. Moro, D., Ball, D. & Bryant, S. (Eds). Clayton South, Victoria, Australia: CSIRO Publishing.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858.
- New South Wales Digital Topographical Database. (1999). *ANZLIC ANZNS0404001262*. Bathurst, New South Wales, Australia: Department of Information Technology and Management (LPI).
- Newton, I. (1998). *Population limitation in birds*. San Diego: Academic Press.
- O'Dwyer, T. & Carlile, N. (2017). *Draft assessment of Lord Howe currawong *Strepera graculina crissalis* population numbers in preparation for proposed rodent eradication program*. Hurstville, NSW: Office of Environment and Heritage.
- Office of Environment and Heritage NSW. (2020). Pied Currawong (Lord Howe Is. subsp.) – profile. <https://www.environment.nsw.gov.au/threatenedspeciesapp/profile.aspx?id=10897>
- Papadopulos, A.S.T., Price, Z., Devaux, C., Hipperson, H., Smadja, C.M., Hutton, I., Baker, W.J., Butlin, R.K. & Savolainen, V. (2013). A comparative analysis of the mechanisms underlying speciation on Lord Howe Island. *J. Evol. Biol.* **26**, 733–745. <https://doi.org/10.1111/jeb.12071>
- Paris, D., Nicholls, A.O., Hall, A., Harvey, A. & Massaro, M. (2016). Female-biased dispersal in a spatially restricted endemic island bird. *Behav. Ecol. Sociobiol.* **70**, 2061–2069. <https://doi.org/10.1007/s00265-016-2210-3>
- Pearson, R.G., Raxworthy, C.J., Nakamura, M. & Peterson, A.T. (2007). Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *J. Biogeogr.* **34**, 102–117. <https://doi.org/10.1111/j.1365-2699.2006.01594.x>
- Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E. & Blair, M.E. (2017). Opening the black box—an open source release of Maxent. *Ecography* **40**, 887–893. <https://doi.org/10.1111/ecog.03049>
- Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006). Maximum entropy modelling of species geographic distributions. *Ecol. Model.* **190**, 231–259. <https://doi.org/10.1016/j.ecolmodel.2005.03.026>
- Phillips, S.J., Dudík, M. & Schapire, R.E. (2019). Maxent software for modelling species niches and distributions (Version 3.4.1). Available from http://biodiversityinformatics.amnh.org/open_source/maxent/. Accessed on 2019-5-02.
- Pietersen, D.W., Little, I.T., Jansen, R. & McKechnie, A.E. (2018). Predicting the distribution of the vulnerable yellow-

- breasted pipit (*Anthus chloris*) using species distribution monitoring. *Emu* **118**, 166–172. <https://doi.org/10.1080/01584197.2017.1372689>
- Prawiradilaga, D.M. (1996). *Foraging ecology of pied currawongs *Strepera graculina* in recently colonised areas of their range*. Unpublished PhD thesis, Australian National University, Canberra, Australia.
- Priddel, D., Carlile, N., Wilkinson, I. & Wheeler, R. (2011) Eradication of exotic mammals from offshore islands in New South Wales, Australia. In *Island invasives: eradication and management*: 337–344. Veitch, C.R., Clout, M.N. & Towns, D.R. (Eds). Gland, Switzerland: IUCN.
- Ryan, C.J. & Jamieson, I.G. (1998). Estimating the home range and carrying capacity for takahe (*Porphyrio mantelli*) on predator-free offshore islands: implications for future management. *N. Z. J. Ecol.* **22**, 17–24.
- Sass, E.M., Mortensen, J.L. & Reed, J.M. (2017). Habitat suitability models indicate the White-breasted Thrasher *Ramphocinclus brachyurus* occupies all suitable habitat in Saint Lucia. *Bird Conserv. Int.* **27**, 96–110. <https://doi.org/10.1017/S0959270915000374>
- Sheringham, P., Richards, P., Gilmour, P. & Kemmerer, E. (2016). *A systematic flora survey, floristic classification and high-resolution vegetation map of Lord Howe Island*. Lord Howe Island, NSW: Lord Howe Island Board. Available from <https://datasets.seed.nsw.gov.au/dataset/lordhoweislandveg2016-vis4450>.
- Sinclair, L., McCartney, J., Godfrey, J., Pledger, S., Wakelin, M. & Sherley, G. (2005). How did invertebrates respond to eradication of rats from Kapiti Island, New Zealand? *N. Z. J. Zool.* **32**, 293–315.
- Singh, M., Tokola, T., Hou, Z. & Notarnicola, C. (2017). Remote sensing-based landscape indicators for the evaluation of threatened-bird habitats in a tropical forest. *Ecol. Evol.* **7**, 4552–4567. <https://doi.org/10.1002/ece3.2970>
- Springer, K. (2012). Ecological restoration of sub-Antarctic Macquarie Island. *Proc. Vertebrate Pest Conf.* **25**, 34–37.
- Springer, K. (2016). Methodology and challenges of a complex multi-species eradication in the sub-Antarctic and immediate effects of invasive species removal. *N. Z. J. Ecol.* **40**, 273–278.
- Stone, Z.L., Tasker, E. & Maron, M. (2019). Patterns of invertebrate food availability and the persistence of an avian insectivore on the brink. *Austral. Ecol.* **44**, 680–690. <https://doi.org/10.1111/aec.12713>
- Syfert, M.M., Smith, M.J. & Coomes, D.A. (2013). The effects of sampling bias and model complexity on the predictive performance of Maxent species distribution models. *PLoS One* **8**, e55158. <https://doi.org/10.1371/journal.pone.0055158>
- Szabo, J.K., Khwaja, N., Garnett, S.T. & Butchart, S.H.M. (2012). Global patterns and drivers of avian extinctions at the species and subspecies level. *PLoS One* **7**, e47080. <https://doi.org/10.1371/journal.pone.0047080>
- Tershy, B.R., Shen, K.-W., Newton, K.M., Holmes, N.D. & Croll, D.A. (2015). The importance of islands for the protection of biological and linguistic diversity. *Bioscience* **65**, 592–597. <https://doi.org/10.1093/biosci/biv031>
- Tinoco, B.A., Astudillo, P.X., Latta, S.C. & Graham, C.H. (2009). Distribution, ecology and conservation of an endangered Andean hummingbird: the violet-throated metaltail (*Metallura baroni*). *Bird Conserv. Int.* **19**, 63–76. <https://doi.org/10.1017/S0959270908007703>
- Wood, K.A. (1998). Seasonal changes in diet of pied currawongs *Strepera graculina* at Wollongong, New South Wales. *Emu* **98**, 157–170. <https://doi.org/10.1071/MU98023>
- Young, N., Carter, L. & Evangelista, P.A. (2011). MaxEnt Model v3.3.3e Tutorial (ArcGIS v10). Natural Resource Ecology Laboratory, Colorado State University. Available from <https://www.coloradoview.org/wp-content/coloradoviewData/trainingData/a-maxent-model-v8.pdf>

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Areas of Lord Howe Island, Australia that were (a) searched for currawong nests in 2017 and 2018 and (b) kernel density bias map of areas on Lord Howe Island that were searched.

Figure S2. Schematic diagram of the process for estimating currawong territories on Lord Howe Island, Australia.

Figure S3. The Maxent species distribution model for the Lord Howe currawong on Lord Howe Island, Australia based on the locations of the nests found in 2017 and 2018.