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Effects of an island-wide rodent eradication programme on two threatened bird species

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ABSTRACT

Context. For the past 50 years, rodent eradications have been conducted worldwide to reverse the devastating impacts of introduced rodents on island species. However, few studies have quantitatively measured the effects of rodent eradications on native species. **Aims.** This study investigated the effects of a rodent eradication on Lord Howe Island on two native birds. **Methods.** To mitigate the risk of Lord Howe currawongs being poisoned during baiting operations, 30–40% of the population were taken into captivity during baiting, while the remaining currawongs were left in the wild. We studied currawong survival, nesting density and breeding success pre- and post-eradication to test how the baiting, a period in captivity, and the removal of rodents affected currawongs. We also investigated breeding success of white terns as they were expected to benefit from the eradication due to predator reduction. **Key results.** We found that many currawongs left in the wild disappeared during the baiting period and nesting densities in one part of the island were significantly lower after the eradication. These currawongs likely died of poisoning as they were not resighted for 2 years post-eradication. White tern breeding success did not increase after the rodent eradication, although their predators were largely eliminated. **Conclusions.** The captive management of currawongs mitigated the adverse effects of the baiting. As those currawongs that survived had high breeding success, we predict that the population will soon recover to pre-eradication size. **Implications.** Our study reinforces the necessity of integrating ecological monitoring as part of future eradications on islands.

Keywords: breeding success, captive management, common white tern, *Gygis alba*, Lord Howe currawong, Lord Howe Island, rodent eradication, *Strepera graculina crissalis*.

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Introduction

Rodents have been introduced to many islands worldwide by seafaring peoples and island colonists, resulting in severe population declines and extinctions of island species and thus altering many ecosystems permanently (Howald *et al.* 2007; Jones *et al.* 2008; Massaro *et al.* 2008). Several aspects of the biology and behaviour of rodents make them ideal invaders. Rodents can reproduce rapidly to colonise new areas or take advantage of increased food resources (Jones *et al.* 2008). Many species reach breeding age within months, have large litter sizes, and raise several litters per year (Parkes *et al.* 2007; Cory *et al.* 2011). Moreover, their varied diet allows them to survive in novel environments. They consume fruits and seeds and are also formidable predators, preying on invertebrates, reptiles and the eggs and chicks of nesting terrestrial and marine birds (Campbell and Atkinson 1999; Courchamp *et al.* 2003; Howald *et al.* 2007; Cory *et al.* 2011). Many island plant and animal species have evolved in the absence of rodents and therefore have not developed any chemical, anatomical or behavioural defences against these invaders (Blackburn *et al.* 2004; Massaro *et al.* 2008; Tershy *et al.* 2015). Hence, island plants and animals are particularly vulnerable to population declines and extinction when rodents are introduced (Campbell and Atkinson 1999; Blackburn *et al.* 2004; Howald *et al.* 2007).

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For the past 50 years, rodent eradications have been conducted worldwide to reverse the impacts of these introduced rodents, restore island ecosystems and allow the recovery of remaining island species. Islands have offered opportunities to eradicate rather than control populations of invasive rodents because their isolation limits the risk of reinvasion by rodents after an eradication attempt (Bomford and O'Brien 1995; Cromarty *et al.* 2002). Dispersal of toxic cereal-based baits by air and on the ground has been the primary strategy to eradicate rodents on islands. The most commonly used toxins are anticoagulants that affect the blood clotting mechanisms in vertebrates (Howald *et al.* 2007; Campbell *et al.* 2015). Warfarin was the most frequently used toxin, but second-generation anticoagulants such as brodifacoum have replaced it. This is primarily due to rodents developing resistance to warfarin (Billing 2000; Howald *et al.* 2007; Campbell *et al.* 2015).

Due to the non-specificity of the toxins commonly used in rodent eradications, bait application on islands poses a lethal risk to existing vertebrates (Howald *et al.* 2007; Campbell *et al.* 2015; Croll *et al.* 2016). Some species may consume the baits directly (primary poisoning), and others may be indirectly exposed by consuming poisoned rodents (secondary poisoning). Several strategies exist to reduce non-target mortalities including using vivid bait colouration, conducting baiting operations when susceptible species are absent from the island and using bait stations to exclude certain species (Howald *et al.* 2007; Campbell *et al.* 2015). Another strategy is to capture endemic or endangered species at risk of poisoning and care for the entire or a percentage of the population during the baiting operations and until the poison has disintegrated within the environment (McClelland 2002; Campbell *et al.* 2015; Herrera-Giraldo *et al.* 2019). Such captive management is very labour intensive and expensive as it requires specialist veterinary personnel and facilities. Hence, the use of captive management as a mitigation strategy to reduce non-target mortality remains uncommon. However, captive management during rodent eradications has been successfully undertaken to benefit several endemic island species, including the Henderson rail (*Porzana atra*), Seychelles magpie-robin (*Copsychus sechellarum*) and Galapagos hawk (*Buteo galapagoensis*) (Merton *et al.* 2002; Towns and Broome 2003; Brooke 2019; Rueda *et al.* 2019). Although all these mitigation measures significantly minimise the number of non-target mortalities (e.g. Brooke 2019), they are not perfect and hence it is important to measure the effects of a rodent eradication on native species and ecosystems.

The publication of quantified ecological outcomes following invasive mammal eradications, including rodents on islands, remains uncommon. This is despite the success of rodent eradications worldwide (Towns *et al.* 2006; Bellingham *et al.* 2010; Jones *et al.* 2016; Brooke *et al.* 2018). In their review of global invasive mammal eradications on islands, Jones *et al.* (2016) found that 236 native species benefitted from eradicating invasive mammals on 181 islands. However, only 22 studies of 63 species documented specific responses to eradications such as trends in abundance or reproductive success and few of these contained quantitative information (Jones *et al.* 2016). Reporting of the ecological benefits of island-wide rodent eradications is also lacking in Australia, where ecological monitoring was undertaken for less than 20% of all rodent eradications (Segal *et al.* 2021*a*). Moreover, the failure to collect pre-eradication data prevents any quantitative comparison with post-eradication data (Buxton *et al.* 2016; Croll *et al.* 2016), limiting the ability to assess the ecological benefits and consequences of eradication programmes.

Australia's Lord Howe Island provides an example of the devastating consequences of introduced rodents for native biota. House mice (*Mus musculus*) were introduced to Lord Howe Island in the 1860s, while black rats (*Rattus rattus*) arrived when a ship ran aground in 1918. Since then, introduced rats are thought to be responsible for the extinction of five endemic bird species, at least 13 species of endemic invertebrates and two plant species (Hutton *et al.* 2007; Wilkinson and Priddel 2011). The estimated 210 000 mice and 150 000 rats on Lord Howe Island continued to threaten the island's flora and fauna (Gillespie and Bennett 2017) and thus, to conserve the remaining native species, an island-wide rodent eradication programme was conducted in the austral winter of 2019 (Walsh *et al.* 2019; Harper *et al.* 2020). A combination of aerial bait drops on unpopulated areas and a grid of bait stations in the settled areas were used to bait the entire island (Walsh *et al.* 2019; Harper *et al.* 2020). The last rodent was detected in September 2019 and the island remained rodent free for the duration of this study.

The Lord Howe currawong (*Strepera graculina crissalis*) is a large, omnivorous, forest-dwelling bird endemic to Lord Howe Island, which is considered a subspecies of the pied currawong (*Strepera graculina*) found in eastern mainland Australia. Due to its restricted range and small population, the Lord Howe currawong is classified as vulnerable within the state of New South Wales (Office of Environment and Heritage NSW 2020*a*). The baiting programme was expected to pose a considerable risk to Lord Howe currawongs, as brodifacoum, the rodenticide used during the rodent eradication on Lord Howe Island, is also toxic to birds (Campbell *et al.* 2015; Lohr and Davis 2018). Currawongs are naturally curious and thus, were expected to consume both poison pellets and poisoned rodents. To mitigate this risk and minimise the impact of the baiting programme on the Lord Howe currawong, 129 currawongs (an estimated 30–40% of the population) were taken into captivity on the island for the duration of the baiting

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programme, while the remaining population was left in the wild.

The removal of rodents from the island was also expected to directly affect the currawongs. While rodents were not a direct threat to the currawong population, currawongs and rodents were competitors for shared food resources (seabird offspring, invertebrates and fruit). Therefore, the removal of rodents was expected to benefit the currawong population in the long term, despite rodents occasionally being part of the currawong's diet prior to the eradication (Carlile and Priddel 2007).

The population of common white terns (*Gygis alba*) on Lord Howe Island was also expected to benefit from the rodent eradication. While rodent predation of white tern nests on Lord Howe Island has not been recorded, it does occur on islands elsewhere (Grant *et al.* 1981), and thus, the removal of rodents from the island was expected to directly benefit white tern nesting success. Additionally, the poisoning of rodents on the island was expected to eliminate the population of masked owls (*Tyto novaehollandiae*) (Milledge *et al.* 2019), which are known predators of white terns on the island (Carlile and Priddel 2015). Several owl species were introduced to the island in the 1920s as an attempt to reduce rat numbers following their invasion of the island, but only the masked owl survives today (Milledge *et al.* 2019). As masked owls were expected to be eradicated during the baiting programme, white tern nesting success was expected to increase after the rodent eradication.

Finally, the island's white tern population is also affected by currawongs, which have been observed to feed on eggs and chicks of white terns. Therefore, a reduction in currawongs due to non-target mortality during the baiting programme was expected to increase tern breeding success, at least in the first few years after the rodent eradication. However, as currawongs foraged to some small extent on rodents (2.5%) prior to the eradication (Carlile and Priddel 2007), there was also the possibility that the removal of rodent prey may actually increase currawong predation of tern nests after the eradication.

This study investigated the effects of the island-wide rodent eradication programme on Lord Howe Island on the Lord Howe currawong and the common white tern. First, we measured the effect of the baiting programme on currawong survival and nesting densities. We expected currawong survival to be lower during the baiting programme (2018–2019) than before (2017–2018) or after the eradication (2019–2020). If the baiting programme had a significant effect on currawong survival, we also expected nesting densities to be lower immediately after the eradication than before the eradication. Second, we measured how the removal of rodents affected currawong breeding success. As rodents were primarily competitors for food resources, we expected currawong breeding success to increase after the rodent eradication. Third, we investigated how the captive management may have affected currawongs by comparing captive currawongs' breeding success and body condition with those of currawongs left in the wild. Finally, we investigated whether the removal and reduction of white tern predators (rodents, owls and currawongs) during the rodent eradication benefitted white tern nesting success.

Materials and methods

Study site

Lord Howe Island is located 760 km north-east of Sydney, New South Wales in the Tasman Sea between Australia and New Zealand (31.54°S, 159.08°E). Lord Howe Island was listed as a UNESCO World Heritage Site in 1982 for its spectacular natural and physical features and range of unique, endemic animals and plants (Hutton *et al.* 2007; United Nations Educational, Scientific and Cultural Organisation 2022). The island is approximately 11 km long and up to 3 km wide, rising to 875 m at its highest point, Mount Gower (Department of Environment and Climate Change (NSW) 2007). The island's 1455 ha are covered mainly by native vegetation, with approximately 75% of the island's land area inside a Permanent Park Preserve (Department of Environment and Climate Change (NSW) 2007). The island experiences a mild maritime climate, with cool, wet winters 13–18°C and drier, warmer summers 13–25°C (Department of Environment and Climate Change (NSW) 2007). The average annual rainfall is 1650 mm with high cloud cover and humidity throughout the year (>60% relative humidity) (Department of Environment and Climate Change (NSW) 2007).

The baiting programme for the eradication of rodents on Lord Howe Island consisted of three parts: (1) aerial baiting; (2) bait stations; and (3) hand-broadcasting of baits. The baits used were 2 g cereal pellets containing 0.02 g/kg of brodifacoum (Harper *et al.* 2020). Aerial baiting using a helicopter occurred over the uninhabited parts of the island on 8–12 June 2019 and 1–5 July 2019. Bait was distributed at a density of 12 kg/ha during the first baiting operation and 8 kg/ha during the second baiting operation (Lord Howe Island Board 2017; Harper *et al.* 2020). In the settled areas of the island, approximately 19 000 bait stations were deployed in a 10 × 10 m square grid between 22 May 2019 and 5 November 2019. Each bait station held a maximum of 80 g of bait (Harper *et al.* 2020). An additional 9500 hand-broadcasting points were located in the areas of overlap between the aerial application and bait station network. Bait pellets were hand-broadcast at the same time as the aerial bait drops and at the same density (Harper *et al.* 2020).

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Study species

Adult Lord Howe currawongs form breeding pairs and defend their nesting territories in forested gullies and creek lines year-round (Segal *et al.* 2021*b*). Currawongs on Lord Howe Island build their nests and raise their young between September and January each year. The female builds an open-cup nest and incubates the eggs, while both adults feed the nestlings and defend the nest. Incubation lasts for 21 days and nestlings take a further 35 days to fledge (56 days or 8 weeks in total). Juvenile currawongs stay with their parents for up to 2 months after fledging (Wood 1998). In the absence of large, resident diurnal raptors and corvids, the currawong is a significant predator of the island's vertebrates and invertebrates. Eggs and chicks of other nesting birds on the island are a considerable part of the currawong's diet, especially during the chick rearing stage. It is likely that before rodents were introduced to Lord Howe Island, invertebrates were an important part of the currawong's diet, but as many invertebrates disappeared due to the invasion of rodents (Hutton *et al.* 2007; Wilkinson and Priddel 2011), currawongs had to change their diet. Before the rodent eradication, currawongs occasionally provisioned their offspring with rodents (Carlile and Priddel 2007). However, rodents primarily competed with currawongs for food resources, rather than being an important prey item for currawongs.

White terns have a broad distribution across the Pacific and nest on many oceanic islands, from Hawai'i and the Galapagos to Micronesia and Polynesia (Higgins and Davies 1996). The species only relatively recently (in 1968) started to nest on Lord Howe Island, and due to its restricted range and small population within New South Wales, they are considered vulnerable (Carlile and Priddel 2015; Office of Environment and Heritage NSW 2020*b*). The population grew 12% per year until 2006, but growth then declined to 2.7% per year (2006–2014; Carlile and Priddel 2015). The breeding season of the common white tern on Lord Howe Island starts in September and can extend to March in the following year (Carlile and Priddel 2015). This tern species lays its single egg in a notch or depression on a horizontal branch (Hart *et al.* 2016). Incubation duties are shared between adults and lasts for around 35 days (Dorward 1963; Carlile and Priddel 2015). Both adults also provision nestlings for about 68 days, but the nestling period can range from 49 to 75 days (Hutton 1991; Carlile and Priddel 2015). Fledglings remain dependent on their parents for another 3–4 weeks (Carlile and Priddel 2015). Pairs on the island readily re-nest after losing an egg or chick (Carlile and Priddel 2015).

Currawong survival

We banded currawongs on the island between September and December each year in 2017–2020. We captured birds individually using a spring-loaded net trap on their territories, at a feeding table or where they congregated (e.g. in orchards, top of Mt Gower). Each bird was fitted with a numbered metal band and a unique combination of three coloured plastic bands. We also recorded the colour combination of all birds seen on the island throughout the breeding season each year. To estimate year-to-year survival, we conducted a Cormack-Jolly-Seber mark/recapture analysis in R (ver. 4.0.2) using RMARK ver. 2.2.7 (Laake 2013; R Core Team 2020).

Currawong nest locations and breeding success

We located currawong nests by searching the forested areas of the island systematically during the currawong breeding season (September–January) in 2017, 2018, 2019 and 2020. The three main regions searched were the Northern Hills, the Transit Hill area and the area around Intermediate Hill to the base of Mount Lidgbird. Due to the steepness of the terrain, we were only able to search a portion of the southern part of the island around Mt Lidgbird and Mt Gower. We used the island's forest walking tracks to access these areas, and any gullies or creek lines favoured by currawongs for nesting (Segal *et al.* 2021*b*) were followed from top to bottom to find currawong territories. In addition, we investigated any locations where currawongs were heard calling or seen from a distance. Once located, we followed birds displaying breeding behaviours including territorial defence, carrying nesting material or carrying food to their nest. Any nestling or fledgling begging calls heard were also investigated to locate nests. We recorded GPS locations of nests to an accuracy of less than 5 m. The areas where we found nests in 2017 were also searched for nests in subsequent years. Increased knowledge about the locations of established currawong territories from year to year and the employment of a field assistant in 2019 and 2020 allowed us to search more areas from year to year. However, this increased search effort did not influence our nest density analyses (see below), because we only included areas that were searched in all 3 years (2018, 2019 and 2020).

We estimated currawongs' nest density changes from year to year by conducting kernel density analyses using nest locations. Maps of kernel densities were generated in ArcGIS 10.7.1 using the Kernel Density tool with nests as the input and using the default cell size and search radius (ESRI Inc. 2019). The reduced sampling effort in 2017 means the nests found in that year were not a representative sample; therefore, we only produced kernel densities for 2018, 2019 and 2020, using the 2018 search area as the reference area (i.e. we excluded additional areas searched in 2019 and/or 2020). We also conducted average nearest neighbour analyses in ArcGIS 10.7.1 using the Average Nearest Neighbour tool (ESRI Inc. 2019) to test whether there was a significant difference between the

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clustering of nests each year. We again included only nests found in areas searched during all 3 years to determine whether clustering was significantly different between years (2018, 2019 and 2020).

We visited the nests every 4 days during the breeding season until the nestlings had fledged or the nests had failed. Nests were observed from a distance of 10–30 m with 10 × 42 binoculars to minimise disturbance to the nesting birds. We could not observe nest contents directly because Lord Howe currawongs vigorously defend their nests and most nests were situated very high in the forest canopy (up to 20 m). The nesting status was determined by observing the adults' behaviour at the nest (nest building, incubating, brooding, feeding nestlings) and the presence of nestlings or their begging calls.

For each year, we measured nesting success for currawongs by calculating the average number of fledglings per nest and the apparent breeding success. The apparent breeding success was the number of nests that produced at least one fledgling each year divided by the total number of nests each year, expressed as a percentage. However, the apparent breeding success underestimates failure rates because not all nests are found before they fail (Mayfield 1961; Rotella *et al.* 2004). Consequently, we also measured nesting success for each year by calculating the daily survival rate (DSR) using the modified Mayfield method (Mayfield 1961; Rotella *et al.* 2004; Shaffer 2004). We calculated DSR for the nesting period in R (ver. 4.0.2) using RMARK ver. 2.2.7 (Laake 2013) and calculated the overall nest survival for each year by raising the DSR to the power of 56, the total number of days for the nesting period. We also generated Kaplan–Meier survival curves for currawong nests in each year in R using the survival and survminer packages (Kassambara *et al.* 2021; Therneau 2021). For pairs that re-nested because their first nest failed, we used data on the nest that we monitored for the longest. Additional nests by the same pair were not considered to be independent nesting attempts. Re-nesting currawong pairs were identified by their coloured leg bands.

Effects of the captive management on currawongs

A total of 129 currawongs were taken into captivity on the island in May 2019 (M. Shiels and F. Hulst, pers. comm.) and managed by staff from Taronga Zoo to act as insurance in the event that the wild population would decline severely due to poisoning. The remaining birds were left in the wild during the baiting programme. Before the eradication, the aim was to manage 50% of the currawong population in captivity during the baiting programme (Wilkinson and Priddel 2011), using a population estimate of 240 individuals (O'Dwyer and Carlile 2017). However, based on currawong numbers seen during this study, we now suggest that this was an underestimate of the population size of the currawongs prior to the eradication. Instead, we estimate that between 30 and 40% of the currawong population were in captivity during the baiting programme.

Of the currawongs taken into captivity during baiting, 125 were released into the wild at their capture location in September 2019. One bird was severely ill when captured and was consequently euthanised, while three further birds died in captivity. To assess the impacts of the captive management programme on the currawong population, we identified the pairs that had nested in 2018 and were subsequently taken into captivity (hereafter referred to as captive birds). We also identified those that were left in the wild during the baiting programme (hereafter referred to as wild birds). We then compared the apparent breeding success, the average number of fledglings produced and the DSR for each group after the period of captivity. The period of captive management extended into the start of the currawongs' breeding season, so we estimated the average laying dates in 2019 for the captive and wild pairs. We also compared the occupied territories in 2018 and in 2019 to assess whether any pairs were lost during the rodent eradication.

To evaluate the effects of the rodent eradication and captive management programme on the currawongs' condition, we captured 50–70 different birds annually (2018, 2019 and 2020) between October and December and weighed them using a digital balance. Using data from all 3 years, we first conducted a two-way ANOVA in R to test whether year, age or the interaction between year and age influenced currawong weights. To test whether the captive management period influenced currawong weights in 2019, we used a one-way ANOVA to compare weights of birds that had been in captivity for 4 months and those that had been left in the wild. The majority of birds weighed in 2019 were adults (93%); thus, age was not included as a predictor variable in the model. As birds were weighed several months after those birds in captivity had been released, colour combinations of leg bands of currawongs were used to determine whether birds had been in captivity during the baiting programme (n = 27) or had been left in the wild (n = 29). For both analyses, we visually inspected the residual plots to ensure the data were normally distributed and the variance across groups was homogeneous.

White tern breeding success

We located common white tern nests by searching the settlement area of the island, where they nest predominantly in Norfolk Island Pines (*Araucaria heterophylla*), during their breeding season in 2017, 2018 and 2019. We visited each nest every 4 days between October and January until the nestling had fledged or the nest had failed. Nests were observed from 5 to 20 m with 10 × 42 binoculars to minimise disturbance to the nesting

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Table 1. Survival and detection probabilities for Lord Howe currawongs on Lord Howe Island, Australia, for the years 2017–2020 using the Cormack-Jolly-Seber mark/recapture analysis.

	Survival probability (ϕ)	Detection probability (P)
2017–2018	0.6140	0.8429
2018–2019	0.2783	0.9277
2019–2020	0.8429	0.8573

birds. We measured nesting success for white terns for each year as we did for the currawongs. On some occasions, the first nest of a tern pair failed and was abandoned. For pairs that re-nested, we used data of the nest that we monitored for the longest. We assumed that a tern nest in the same location as a failed nest was a re-nesting attempt, as terns are known for their nest site fidelity (Dorward 1963; Niethammer and Patrick 1998).

Results

Currawong survival

In our population surveys during the breeding season (September–January), we recorded 228, 253, 154 and 178 currawongs in 2017, 2018, 2019 and 2020, respectively. The currawongs recorded alive in 2019 included birds that had been in captivity earlier that year and those that had remained in the wild. Currawong survival probability (ϕ) was considerably lower in the period when the baiting for rodents occurred (2018–2019) (ϕ = 0.2783, Table 1) than before the eradication (2017–2018: ϕ = 0.6140) or after the eradication (2019–2020: ϕ = 0.8429). The probability of detecting a marked currawong was high (>0.84) throughout the entire study period.

Currawong nesting density

We found 45 nests in 2018, 45 nests in 2019 and 61 nests in 2020. As some of these nests were re-nesting attempts (after the failure of the first nesting attempt), we included only one nest per pair (44, 43, 55 nests in 2018, 2019 and 2020, respectively) in further analyses. For comparing nesting densities across years, we only included nests within the areas that were searched during all 3 years (2018–2020; small square in Fig. 1). The kernel density maps of the currawong nest locations were similar across years, except for a cluster of nests on the south-eastern side of the island (Fig. 1). In 2018 (before the rodent eradication), there were 17 occupied territories in this part of the island, while there were only six occupied territories in 2019 (immediately after the rodent eradication) and seven occupied territories in 2020 in this area (Fig. 1). Across the entire island area that was searched during all 3 years (small square in Fig. 1), 17 territories occupied by currawong pairs in 2018 were not occupied in 2019, after the rodent eradication. In contrast, only one territory that was occupied by a currawong pair in 2019 was not occupied in 2020. The nearest neighbour analysis confirmed significant clustering of nests in the 2018 breeding season before the rodent eradication. Nests were

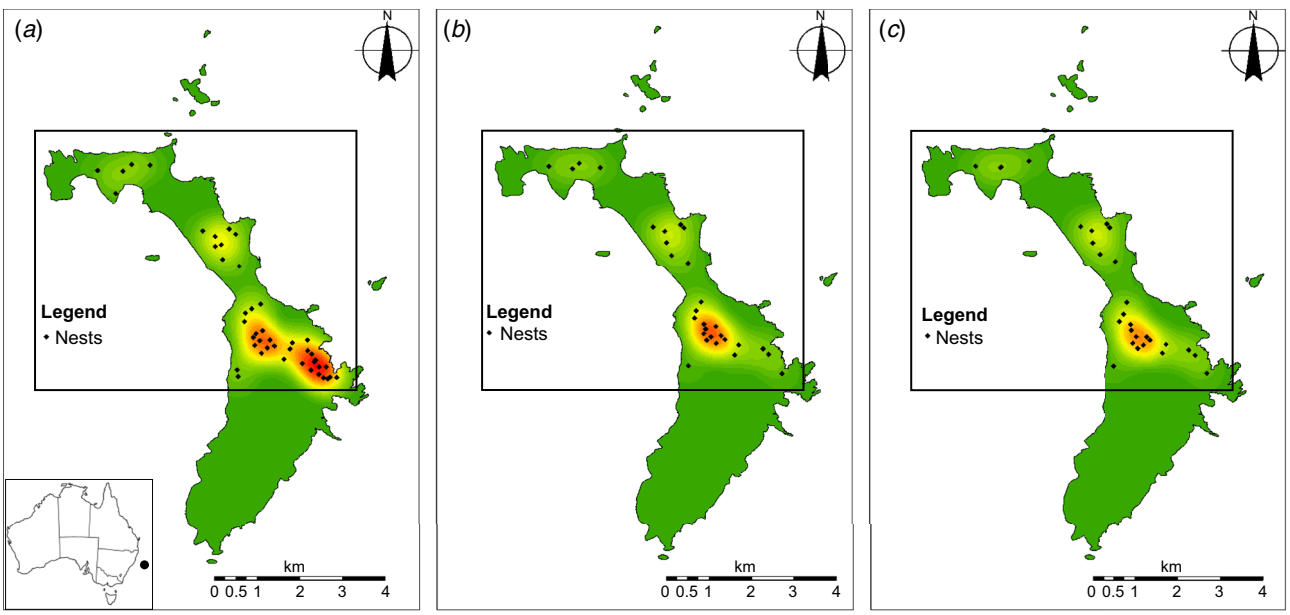


Fig. 1. Map of kernel density of Lord Howe currawong nests in (*a*) 2018, (*b*) 2019 and (*c*) 2020 on Lord Howe Island, Australia. To facilitate comparison between years, nests found outside the rectangle in 2019 and 2020 were excluded. Red areas represent the highest densities and green areas represent the lowest densities.

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more dispersed and less significantly clustered in 2019 and 2020 (post eradication) (Table 2).

Currawong breeding success

In total, 48, 71, 75 and 96 fledglings were raised by 28, 44, 43 and 55 currawong pairs in 2017, 2018, 2019 and 2020, respectively (Table 3). Despite a number of empty territories in 2019, we found a similar number of nests in 2019 than in 2018, because we searched extensively other areas of the island in 2019 that we did not search in 2018. There was no significant difference in the number of fledglings raised per nest between years (F = 0.39, P = 0.76, d.f. = 3) and the apparent breeding success was also similar across years (Table 3). Nest survival probability of currawongs was very high (>0.83) before and after the rodent eradication (Fig. 2*a*) and there was no significant difference in nest survival among years (χ^2 = 1.9, P = 0.6, d.f. = 3) (Fig. 2*a*).

Effects of captive management on currawongs

Of the 125 currawongs taken into captivity for the duration of the baiting operations and released, at least 55% were adult birds, while the remainder were juveniles. Of the adult birds taken into captivity, 16 pairs had nested in 2018 before the captive period (Fig. 3*b*). After release from captivity, 26 pairs from captivity nested in 2019 (Fig. 3*c*): the remaining, previously captive adults may have bred in locations not surveyed in 2019. Six nesting pairs from 2018 that were not taken into captivity were found to be nesting in the same locations in 2019. No pairs from the Rocky Run and Boat Harbour areas of the island were taken into captivity and 70% of the territories in this area of the island were unoccupied in 2019.

The last captive currawongs were released on 24 September 2019, several weeks into their usual breeding season. As a result, the estimated average laying date for birds that had been in captivity was 15 October 2019. This date was 3 weeks later than the estimated average laying date of those breeding birds that had not been in captivity (24 September 2019) and slightly later than in 2018 (10 October 2018) and 2020 (3 October 2020). Additionally, for breeding birds that had been in captivity, the average number of fledglings per nest (1.61 ± 1.01), the apparent breeding success (83.3%) and the DSR for nests (0.99638 ± 0.00181) was lower than for those breeding birds that had remained in the wild during baiting operations (1.84 ± 0.60; 100%; 1.000 ± 0.000, respectively). However, the average number of fledglings per nest was not statistically significantly different between birds that were in captivity and those left in the wild (F = 1.007, P = 0.322, d.f. = 1).

Currawongs were significantly heavier before the rodent eradication in 2018 than those weighed after the rodent eradication in 2019 and 2020 (F = 15.811, P < 0.001, d.f. = 2, Fig. 4*a*). Juveniles were also significantly heavier than adults as we weighed birds during the breeding season

Table 2. Observed distances, expected distances and nearest neighbour ratios between Lord Howe currawong nests on Lord Howe Island, Australia, in 2018, 2019 and 2020.

	Observed distance (m)	Expected distance (m)	Nearest neighbour ratio	*Z*-score	*P*-value	Significance
2018	185.2	250.8	0.7386	−3.3540	0.00080	***
2019	234.1	300.3	0.7795	−2.2071	0.02124	*
2020	228.9	304.8	0.7508	−2.5231	0.01163	*

Within the same area on Lord Howe Island, currawong nests were significantly more clustered in 2018 (before the rodent eradication) than in 2019 and 2020 (after the rodent eradication).
*P < 0.05; ***P < 0.001.

Table 3. Number of nests, number of fledglings, average number of fledglings per nest, apparent breeding success, daily nest survival rates (DSR) and Kaplan–Meier nest survival estimates for the Lord Howe currawong on Lord Howe Island, Australia, in 2017, 2018, 2019 and 2020.

	Number of nests	Number of fledglings	Average number of fledglings per nest (±s.d.)	Apparent breeding success (%)	DSR (±s.e.)	DSR nest survival estimate	Kaplan–Meier nest survival estimate
2017	28	48	1.71 (±0.897)	92.9	0.99516 (±0.00342)	0.762	0.909
2018	44	71	1.61 (±0.895)	86.4	0.99444 (±0.00226)	0.732	0.838
2019	43	75	1.74 (±0.875)	90.7	0.99735 (±0.00132)	0.862	0.921
2020	55	96	1.81 (±0.942)	88.7	0.99654 (±0.00141)	0.824	0.848

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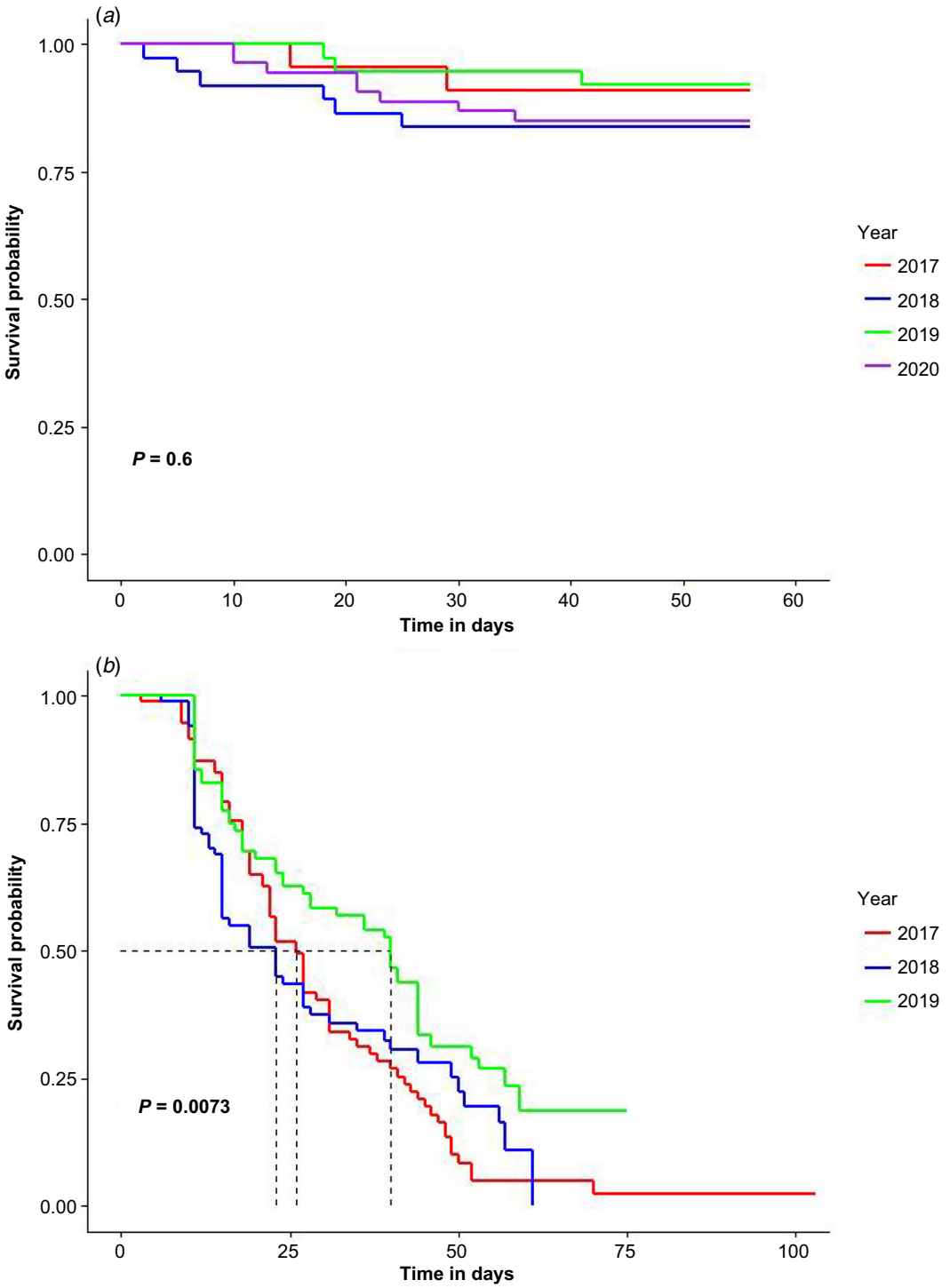


Fig. 2. Kaplan–Meier survival rate curves of offspring in (*a*) Lord Howe currawong nests in 2017, 2018, 2019 and 2020 and (*b*) white tern nests in 2017, 2018 and 2019 on Lord Howe Island, Australia.

when adults are busy with parental care duties ($F = 5.278$, $P = 0.023$, d.f. = 1). However, the interaction between year and age was not significant ($F = 1.283$, $P = 0.280$, d.f. = 2). Of the currawongs weighed during the breeding season in 2019, those birds that had not been in captivity ($n = 29$) were significantly heavier than those in captivity ($n = 27$) ($F = 4.675$, $P = 0.0351$, d.f. = 1, Fig. 4*b*). As most of the birds weighed in 2019 were adults, the significant difference in weight between captive and wild birds was not due to age.

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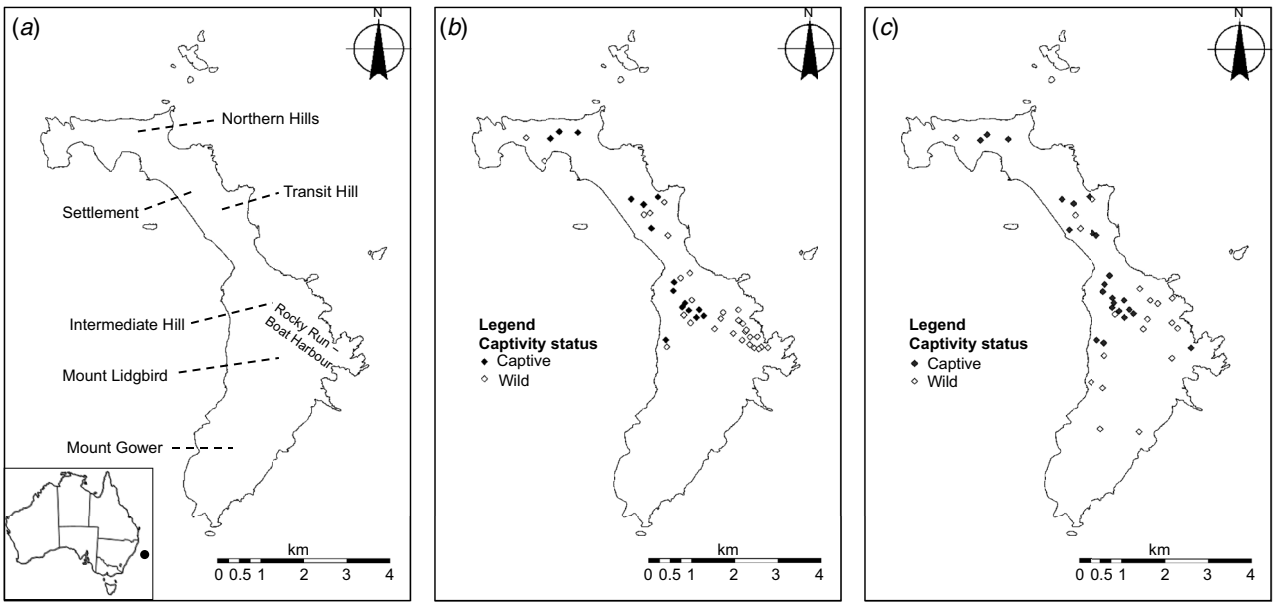


Fig. 3. (*a*) Map of Lord Howe Island, Australia, including locations referred to in the manuscript, (*b*) locations of currawong pairs that nested in 2018 that were subsequently taken into captivity and (*c*) locations of currawong pairs that nested in 2019 that had previously been in captivity. Of the 16 pairs that nested in 2018 and were subsequently taken into captivity, 14 pairs nested in the same location in 2019.

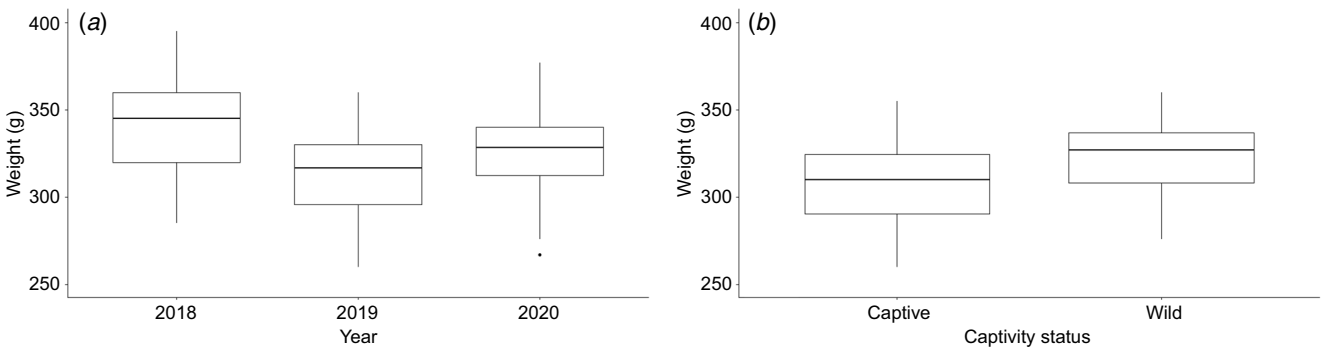


Fig. 4. Weights of Lord Howe currawong sampled during the breeding seasons in 2018 (n = 65), 2019 (n = 56) and 2020 (n = 66). (*a*) Currawongs were significantly heavier in 2018 than in 2019 and in 2020. (*b*) Weights of currawongs post-release in 2019 differed significantly between birds that had been in captivity (n = 27) and those that had been left in the wild (n = 29).

White tern nesting success

We located 77, 68 and 57 common white tern nests during the 2017, 2018 and 2019 breeding seasons, respectively (111, 116 and 111 nests, respectively, including re-nesting attempts and nests not followed to completion). In these nests, we observed that 17, 5 and 10 nestlings hatched in 2017, 2018 and 2019, respectively. However, only one nestling survived until fledging in all three breeding seasons (Table 4). We assume that the other hatched nestlings were predated, abandoned or had fallen from their nest tree. The DSR for each year were similar but there was a significant difference between the nest survival curves (χ^2 = 9.8, P = 0.007, d.f. = 2) (Table 4, Fig. 2*b*). The highest nest survival probability occurred after the rodent eradication (0.188).

Discussion

This study has shown that the baiting operations during the island-wide rodent eradication immediately affected the Lord Howe currawong population. A significant number of currawongs that were not taken into captivity for the baiting period disappeared and were not resighted after the rodent eradication in 2019 or 2020. Our analysis clearly showed that survival rates of currawongs was significantly

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Table 4. Number of nests, number of fledglings, average number of fledglings per nest, apparent breeding success, daily nest survival rates (DSR) and Kaplan–Meier nest survival estimates for the common white tern on Lord Howe Island, Australia, in 2017, 2018 and 2019.

	Number of nests	Number of fledglings	Average number of fledglings per nest	Apparent breeding success (%)	DSR (±s.e.)	DSR nest survival estimate	Kaplan–Meier nest survival estimate
2017	77	1	0.013	1.3	0.95950 (±0.00456)	0.014	0.025
2018	68	0	0	0	0.95048 (±0.00586)	0.005	0.000
2019	57	0	0	0	0.95779 (±0.00548)	0.012	0.188

lower when the baiting occurred (from 2018 to 2019) than in the period before (2017–2018) or after the rodent eradication (2019–2020). Furthermore, we identified 11 and 10 unoccupied nesting territories on the island's south eastern side (Rocky Run and Boat Harbour area) in 2019 and 2020, respectively, and this resulted in an overall lower nesting density in this area after the rodent eradication. None of the birds nesting in this area in 2018 were taken into captivity during the baiting programme. As birds from those territories were not resighted in 2019 or 2020, despite considerable searching effort, we conclude that these missing birds died from primary or secondary poisoning. Moreover, 25 currawongs were found dead in the forest during and shortly after the baiting programme and necropsies of 15 of those birds showed evidence of poisoning in all those currawongs (R. Segal, N. Carlile, pers. obs.). The remaining 10 birds were too decomposed (only bones remained) to conduct necropsies. There were likely more currawong deaths but due to the terrain and density of the forest, their carcases were not found before complete decomposition.

The captive management of the currawongs clearly mitigated the adverse effects of the baiting programme on the Lord Howe currawong population. Of the 125 currawongs that were in captivity during the baiting programme, 44 and 60 bred and raised offspring successfully in 2019 and 2020, respectively. As around 45% of the captive birds were juveniles, some of these juveniles only reached maturity and started to breed in 2020. The period in captivity delayed egg laying for those birds in 2019 and breeding success was slightly lower in captive currawongs than wild birds. The lower breeding success and weights of captive versus wild birds in 2019 may indicate that there were considerable energetic costs placed on released captive birds to re-establish their territories, many of which were filled during their absence. Overall, breeding success was as high in 2019 and 2020 as prior to the rodent eradication (2017 and 2018). Furthermore, several pairs of currawongs were observed raising second broods in the 2019 breeding season (L. Brice, pers. comm.) after we had left the island. The consistently high currawong breeding success after the eradication will over time compensate for the immediate loss of individuals during the eradication.

The high breeding success after the rodent eradication suggests that currawongs did not suffer from a food shortage due to the loss of rodents from their diet. The reduced competition with rodents for other food resources, such as native fruits, invertebrates and vertebrates, may have compensated for any loss of rodent prey that the currawongs may have experienced. Details of how the composition of the currawongs' diet has changed following the removal of rodents as prey and competitors requires further investigation. Regardless of these detailed changes in diet composition, the higher amount of food resources available to currawongs after the rodent eradication is likely to affect other aspects of the currawongs' ecology. For example, prior to the rodent eradication, suitable breeding habitat for currawongs was limited to creek lines within the forest. This restricted habitat prevented many currawongs from breeding (Segal *et al.* 2021*b*). Based on spatial modelling before the rodent eradication, we estimated that the island can support a maximum of 84 breeding pairs (Segal *et al.* 2021*b*). Due to the difficult terrain on Lord Howe Island, the number of breeding pairs we found during each of our annual surveys was lower than the estimated carrying capacity. Increased food resources resulting from reduced competition with rodents may have the effect of upgrading marginal habitat to suitable habitat. Several species of terrestrial birds have expanded their range following rodent eradications on islands, including kaka (*Nestor meridionalis*) and bellbirds (*Anthornis melanura*) on Great Mercury Island, New Zealand, and pipits (*Anthus novaeseelandiae aucklandicus*) on Campbell Island, New Zealand (Bellingham *et al.* 2010; Towns *et al.* 2018). An increase in the amount of habitat suitable for breeding currawongs, in turn, would allow more currawongs to breed each year. Alternatively, increased resources after the rodent eradication may enable currawongs to breed successfully on smaller territories and thus, in higher densities (Adams 2001; Segal *et al.* 2021*b*). Many populations of invertebrate and vertebrate prey species have been found to increase on islands elsewhere following rodent eradications (Bellingham *et al.* 2010;

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Priddel *et al.* 2011). Regardless of the mechanisms, overall, the rodent eradication is likely to benefit the currawong population in the long-term.

Although the captive management of currawongs was a success, there was a clear bias from which locations currawongs were taken into captivity. All juveniles and some adult currawongs were captured at a site where they have been fed prior to the rodent eradication. Other adults were taken from territories if their territories could be easily accessed on foot (northern hills, Transit Hill and Intermediate Hill areas). Adults from more remote areas (Rocky Run, Boat Harbour and Erskine Valley) were not captured, due to the long transportation times from the point of capture to the captive facility. The omission of birds from these areas may have long-term implications for the genetic diversity of the island's currawong population for two reasons. First, despite their small distribution, bird populations on small islands can host genetically distinct subpopulations, as has been recently shown to be the case in the endemic Lord Howe woodhen (*Hypotaenidia sylvestris*) (Major *et al.* 2021). In this flightless species, woodhens from Mt Gower are genetically distinct from the lowland population (Major *et al.* 2021). Genetic distinction at a 1 km scale is uncommon in birds, however it has been observed at a 6–10 km scale in other island bird species (white-breasted thrasher, *Ramphocinclus brachyurus* (Temple *et al.* 2006); Réunion grey white-eye, *Zosterops borbonicus* (Bertrand *et al.* 2014)). Second, the loss of a significant number of currawongs during the rodent eradication has reduced an already small population further, making this population even more susceptible to the loss of allelic diversity through genetic drift (Ballou *et al.* 2010). In combination, genetic drift and inbreeding can lead to small island populations becoming genetically different in relatively short time periods (Funk *et al.* 2016; Forsdick *et al.* 2017). Two island populations of black robins were found to be genetically different after only 26 years apart because they had lost different alleles during this period (Forsdick *et al.* 2017). Similarly, the sub-populations of the Lord Howe woodhen are genetically different because of a loss of allelic richness in the lowland subpopulation from inbreeding following a severe population bottleneck in the 1980s and subsequent genetic drift (Major *et al.* 2021). The loss of a significant number of currawongs combined with the location bias when currawongs were captured may have implications for the genetic health of the currawong population in the future. Further research is underway to test whether genetic diversity has been lost in the currawong population due to the rodent eradication.

The island's common white terns have not benefitted from the rodent eradication as was expected. Although rodents were removed entirely from the island, introduced masked owls were almost completely eliminated from the island (H. Bower, pers. comm.) and the currawong population was considerably reduced (shown here), white tern nesting success remained zero after the rodent eradication. Our nest survival curves show that white tern offspring survived for longer in the nest after the rodent eradication (Fig. 2*b*), but regardless of this initial increased survival of offspring in the nest, we did not observe a single chick that survived until fledging in 2019. On other islands in the Pacific, white tern breeding success ranged widely, from 9% on Christmas Island to 74% in Hawai'i (Ashmole 1968; VanderWerf 2003). On Lord Howe Island, it is possible that some 'rogue' currawongs were responsible for the high nest failure in white terns. On Big South Cape Island, New Zealand, a few weka (*Gallirallus australis*) were responsible for killing a large number of sooty shearwater (*Ardenna griseus*) chicks at one site, while other sites remained unaffected (Harper 2007). The loss of eggs and chicks due to poor weather, such as strong winds and heavy rain, may also be a contributing cause for the low breeding success of white terns on Lord Howe Island.

Globally, many different species of seabirds have been the greatest beneficiaries of rodent eradications on islands due to reduced predation of eggs and chicks (e.g. Lavers *et al.* 2010; Springer 2012; Croll *et al.* 2016). Rodents have the greatest impact on ground- and burrow-nesting seabirds (Jones *et al.* 2008; Lavers *et al.* 2010). For example, the nests of black-winged petrels (*Pterodroma nigripennis*) were heavily predated by rats on Lord Howe Island prior to the rodent eradication (T. O'Dwyer, pers. comm.). It is likely that ground-nesting seabirds have benefitted considerably more from the rodent eradication than white terns on Lord Howe Island.

This study is one of few that assessed quantitatively the ecological effects of an island-wide rodent eradication on native birds, including one terrestrial bird species, using pre- and post-eradication data (Jones *et al.* 2016; Segal *et al.* 2021*a*). As well as informing stakeholders and demonstrating a return on investment for funding bodies, measuring the ecological benefits and consequences of rodent eradications may contribute to the planning and management of future eradications. Results of this study highlight the importance of carefully planned and executed captive management of threatened native species and the necessity of integrating ecological monitoring as part of future rodent eradications on islands.

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Data availability. The data used in this study is not currently available to other parties.

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