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# RESEARCH ARTICLE

# Act for the best, prepare for the worst—Defining strategic mesopredator triggers that safeguard apex predator eradication benefits

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# Abstract

- Eradicating invasive species is critical for supporting threatened species recovery. In multi-invaded ecosystems, it may only be feasible to remove one or some of the several invasive species that are present. However, this may not deliver the desired benefits, and shifting the complement of threats in some cases can have unexpected adverse consequences. A priori evaluation of potential outcomes, and identifying critical thresholds driven by other invasives, can inform decisionmaking and decision triggers for adaptive management responses to ensure benefits are realised.
- 2. We use population viability analyses informed by field data to evaluate the potential outcomes of a single species removal from a multi-invaded ecosystem, Christmas Island. We assess whether (1) removing an invasive apex predator (cats; *Felis catus*) in isolation would allow a threatened seabird species (Indian Ocean red-tailed tropicbird; *Phaethon rubricaudra westralis*) to recover; and based on evidence that this bird species is susceptible to rat predation (2) find the nest predation threshold for a remaining invasive mesopredator (*Rattus rattus*) that should trigger complementary rat control to ensure seabird population protection.
- 3. The analyses indicate that with cat eradication, the tropicbird population is expected to recover quickly and benefit long term. The current empirical rates of nest failure due to rat predation are insufficient to cause tropicbird population decline. However, if nest failure from rat predation should exceed 40%, the tropicbird population is predicted to decline by 1% (SD $\pm$ 0.25) per year. If rat predation caused 70% or more nests to fail, the tropicbird population is predicted to decline to extinction in 17 years (~1–2 generations).
- 4. Synthesis and applications: Our results illustrate the value of PVAs as a tool for understanding potential invasive species management outcomes in multiinvaded ecosystems. Defining thresholds of ecologically significant rat impact informs the setting of decision triggers, which in combination with targeted

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monitoring, can help managers prepare to adapt to deficient or undesirable outcomes in a timely and appropriate way.

KEYWORDS

decision trigger, evidence-based conservation, feral cat, invasive rat, mesopredator release, PVA, seabird

# 1 | INTRODUCTION

Invasive mammalian predators severely impact biodiversity (Blackburn et al., 2004; Doherty et al., 2016; Szabo et al., 2012). Eradication and control programmes can reduce their impact, and where successful, provide substantial conservation gains (Augusteyn et al., 2022; Bolam et al., 2021; Jones et al., 2016). However, sometimes, these programmes can fail to deliver the intended benefits or can even lead to unwanted cascading or secondary outcomes that contribute to further biodiversity declines (Bergstrom et al., 2009; Brook et al., 2012; Dowding et al., 2009; Jones, 2010; Ortega et al., 2021; Ritchie & Johnson, 2009; Travers et al., 2021). For example, recovery rates of burrowing petrel species were less than expected following the removal of cats from Marion Island, South Africa, due to the remaining impacts of introduced mice (Mus musculus), while removal of the apex predator (cats, Felis catus) from Little Barrier Island, New Zealand coincided with reduced Cook's petrel (Pterodroma cookii) breeding success at high elevations due to increased mesopredator predation (brown rats; Rattus norvegicus; Dilley et al., 2017; Rayner et al., 2007). Outcomes are often more uncertain in multi-invaded ecosystems, due to the complexities of underlying species interactions (Baker et al., 2020; Bull & Courchamp, 2009; Courchamp et al., 2003). Multi-invaded ecosystems make up over half of the world's globally important islands for which eradications are considered feasible and that would benefit highly threatened species (Holmes et al., 2019).

To realise conservation benefits, invasive species management actions in multi-invaded ecosystems require well-informed objectives, coupled with explicit plans for adaptive management if deficient or perverse outcomes are detected (García-Díaz et al., 2021; Zavaleta et al., 2001). Monitoring species' conditions before and after invasive species removal enables the assessment of management success. It also provides valuable insights for follow-up actions or adjustments to future best practice if the desired outcomes are not achieved (Rayner et al., 2007; Simberloff et al., 2018; Zavaleta et al., 2001). However, this approach is inherently reactionary, with adaptive management decisions only able to be made once failures are detected (Bergstrom et al., 2009; Lindenmayer et al., 2013). Detecting negative outcomes may also necessitate prolonged monitoring periods, particularly for longlived species. Experimental trials, albeit expensive and sometimes impractical (McDonald-Madden et al., 2010) are an exception (Bonnaud et al., 2010; Lloyd, 2007; Oppel et al., 2014). In contrast,

a priori evaluation of potential outcomes can inform future adaptive decision-making and the setting of triggers for those decisions. When combined with targeted, cost-effective monitoring, timely, adaptive management interventions can be implemented if a system fails to shift as expected, or shifts towards a predefined undesirable state (Cook et al., 2016; de Bie et al., 2018; Lyons et al., 2008; McDonald-Madden et al., 2010).

Here, using Population Viability Analyses (PVA) as a predictive tool, we forecast the potential outcomes of an invasive apex predator (feral cat) eradication in isolation from a multi-invaded ecosystem (Christmas Island, Australia), for a prey species, the Indian Ocean red-tailed tropicbird (Phaethon rubricaudra westralis). The tropic ird was chosen as a model species (de Bie et al., 2018) for several reasons. First, the species is of conservation concern (DCCEEW, 2023), and like most ground nesting seabirds, is considered vulnerable to feral cat and rat predation (Fleet, 1974; Medina et al., 2011; Ringler et al., 2015). On Christmas Island, tropicbirds are an intended beneficiary of the cat eradication programme (Willacy, 2022). However, cats on Christmas Island are known to consume rats, thus, the intended benefits of a cat eradication could be compromised if significant rat impacts increase in the absence of cats (Bellard et al., 2016; Doherty et al., 2016; Dueñas et al., 2021; le Corre, 2008). Second, empirical data were available for the species describing demography, breeding behaviour and impacts; and nest success was observed to decrease as rat activity (in 15-min intervals) recorded by cameras at nests increased (Willacy et al., 2023) suggesting density-dependent rat impacts. Finally, monitoring indicators for rat impact are feasible for this species (Cook et al., 2016; Tulloch et al., 2011).

To guide decision-making that minimises the risk of insufficient or redundant investment, or unnecessary failures, we consider whether cat removal in isolation from Christmas Island will lead to population recovery for our species of concern, and, by defining thresholds of ecologically significant rat impact, determine what level of rat impact would require additional management effort. In contrast to other comparable studies, for example, Plein et al. (2022), our approach uses historic and recent field data for cat and rat impacts (Willacy et al., 2023), and empirical modelling to consider potential cat management outcomes based on the observed interactions between apex predators, mesopredators and prey. Our work informs decision triggers for rat interventions on Christmas Island, while our approach can be applied to other multi-invaded ecosystems where invasive species management actions involve the risk of deficient or adverse outcomes.

# 2 | MATERIALS AND METHODS

#### 2.1 | Study area

Christmas Island is an external Australian territory located in the Indian Ocean (10.4475°S, 105.6904°E). Since their introduction to the island over 100 years ago, feral cats and black rats, along with subsequently introduced invasive species including yellow crazy ants (Anoplolepis gracilipes), wolf snakes (Lycodon capucinus) and giant centipedes (Scolopendra subspinipes), have had a devastating impact on Christmas Island's ecosystem, contributing to the extinction of at least seven species, including the endemic Maclear's (Rattus macleari) and Bulldog rats (Rattus nativitatis; Andrew et al., 2016; Andrews, 1900), and affect many more nationally threatened species (Corbett et al., 2003; Sommerfeld et al., 2015; Tideman et al., 1994). Cats have been controlled on Christmas Island since 2010 through domestic cat management laws and stray and feral cat removals (Algar & Johnston, 2010). Removal efforts were intensified from 2017, with the goal of island-wide feral cat eradication. Rat eradication is not currently considered feasible for Christmas Island due to high levels of crab interference with traps and poison bait (Samaniego et al., 2020, 2021). However, rat control carried out at smaller scales has proven effective for lowering local rat densities for short periods (pers. comm. Parks Australia).

# 2.2 | Study species

The Indian Ocean red-tailed tropicbird, hereafter referred to as tropicbird(s), is listed as Endangered under the *Environmental Protection and Biodiversity Conservation Act*, 1999 (DCCEEW, 2023). Christmas Island supports the largest breeding population of the species globally (>1500 breeding pairs) where they nest in high-density colonies on coastal terraces, and at lower densities scattered among inland cliffs, in rock crevices or on the ground under vegetation (*Pemphis acidula* and *Scaevola taccada*; Figure 1). Breeding pairs appear to be site-faithful (Sommerfeld et al., 2015) unless sites are overgrown or destroyed (Hennicke & Flachsbarth, 2009; Willacy et al., 2021). Most high-density colonies on Christmas Island are located directly adjacent to human



FIGURE 1 Red-tailed tropicbird breeding locations on Christmas Island (Parks Australia, *pers. comm.*), including high-density ground nesting colonies (black triangles) where nest success studies were undertaken (Table 1).

inhabited urban housing, which supported high cat densities prior to cat removal, and currently support high rat densities. Cat control since 2010 has substantially reduced cat predation of chicks, and while rat activity has slightly increased at nests, there is no evidence thus far that rat impacts have increased (Table 1; Willacy, 2022). Nonetheless, predation of eggs and nestlings by rats remains a potential threat, as does disturbance by yellow crazy ants, loss of breeding habitat due to the invasive Coral vine, *Antigonon leptopus* (Director of National Parks, 2014) and climate changedriven impacts to the regional productivity of the surrounding marine ecosystems (Bryndum-Buchholz et al., 2019).

#### 2.3 | Population viability analysis

We completed population viability analyses using the program VORTEX (Lacy & Pollak, 2023). VORTEX is one of several PVA software packages (e.g. RAMAS or ALEX); though VORTEX is endorsed by the International Union of Nature (IUCN) for species survival estimation (IUCN SSC, 2024). VORTEX uses Monte Carlo simulations to examine the impacts of predictable and random events on wildlife over a user-specified time frame (Lacy & Pollak, 2023). Each simulation iterates through a series of events that reflect the species life cycles (e.g. reproduction, mortality) and predicts probabilistic results such as the likelihood of extinction and the mean size of surviving populations (Lacy & Pollak, 2023). To account for environmental uncertainty, VORTEX samples birth rates, death rates and carrying capacity values from binomial or normal probability

TABLE 1Summary of nest survivorshipstudies completed for red-tailedtropicbirds on Christmas Island.

distributions and simulates their natural variability. VORTEX also includes catastrophe functions that allow likelihood inputs for rare events, such as natural disasters, which are simulated as stochastic pulses that temporarily decrease survival rates and/or reproductive success (Lacy & Pollak, 2023).

### 2.4 | Population viability models

We first collated demographic and life history parameters for the tropicbird, as detailed in Table 2. Many inputs were derived from empirical data sources (using methods approved by the University of Queensland NEWMA animal ethics committee [SBS/481/16], under permits granted by the Australian Government Director of National Parks [CINP\_2017\_2] and the Government of Western Australia, Department of Lands [Licence: 01506-1992\_A9991101]), while others were derived from the literature. For reproductive senescence, and the proportion of adults breeding, we assumed that reproductive effort remained constant with age, was equal for males and females, and derived the proportion of females breeding from a study of a close relative (Red-billed tropicbird, Phaethon aethereus; Sarmento et al., 2014). We assumed the sex ratio of offspring to be equal. Carrying capacity was estimated based on published population estimates (n=3350, range: 2650-3950; James & McAllen, 2014; Willacy et al., 2021) plus the estimated population loss from cat predation of nestlings and adults observed over at least the last 30 years. This estimate (n = 5250) was validated by corroboration with expert opinions (B. Tiernan, M. Holsworth, J. Sommerfeld & J. Hennicke, pers. comm.).

	Source	Years	Nests (n)	Failed (%)	Rates of predation
	Pre-cat control, average		551	69±22	
	Sommerfeld et al. (2015)	1983-1984	25	64	Unknown
		1984-1985	56	34	61% by unknown
		1985-1986	136	54	54% by unknown
	Ishii (2006)	2006	132	78	Unknown but cats, rats, goshawk or kestrel detected at nests
	Sommerfeld (2008)	2008	136	93	1% preyed upon by cats, other unknown
	Jeffery (2007)	2007	36	81	42% (35% by cats and 6% by rats)
	Lipka (2010)	2009	30	77	50% (43% by cats and 7% by rats). Also note 2x cat predation attempts on adults (3% of breeding pairs)
	Cat control, average		217	$37\pm16$	
	Algar et al. ( <mark>2012</mark> )	2011	130	21	Unknown
	Willacy et al. (2023)	2017	39	41	8% (0% by cats, 0% by rats and 8% by goshawk)
		2018	48	48	10% (2% by cats, 6% by rat, 2% by crabs and 0% by goshawk)

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#### TABLE 2 Parameters used to build models for the red-tailed tropicbird population viability analyses.

	Models			Range explored for sensitivity analysis		
Parameters	(i) pre-control	(ii) cat control	(iii) eradication with simulation	Perturbation (range and increments)	Conventional	Regression
Reproductive system	Monogamy			_	_	-
Age at reproduction	3			-	-	-
Maximum age of reproduction (years)	17			_	_	-
Maximum age (both sexes)	17			_	-	-
Maximum number of clutches per year	2			_	_	-
One clutch: Two clutches:	97 3			-	-	-
Clutch size	1					
Sex ratio at births	1:1			_	-	-
% breeding (both sexes) $\pm$ EV	0.79±20			0-1, 0.1	±10% (EV ±10%)	0.69-0.99
Mortality						
Brood (egg- age 1) $\pm$ EV	$0.69 \pm 0.22$	$0.37 \pm 0.16$	0.37+ <sup>a</sup>	0-1, 0.1	+10% (EV ±10%)	0.21-0.53
Cat predation	$0.39 \pm 0.07$	$0.01 \pm 0.01$	0	-	-	-
Rat predation	$0.05 \pm 0.03$	$0.03 \pm 0.03$	0.05+ <sup>a</sup>	-	-	-
Goshawk predation	-	$0.03 \pm 0.03$	$0.03 \pm 0.03$	_	-	-
Crab predation	-	$0.01 \pm 0.02$	$0.01 \pm 0.02$	-	-	-
Abandonment	-	$0.14 \pm 0.01$	$0.14 \pm 0.01$	-	-	-
Intraspecific competition	-	$0.01 \pm 0.01$	$0.01 \pm 0.01$	_	-	-
Unknown	$0.25 \pm 0.12$	$0.14 \pm 0.04$	$0.14 \pm 0.04$	-	-	-
Juvenile (age 1–2) $\pm$ EV	$0.14 \pm 0.05$			0-1, 0.1	±10%(EV ±10%)	0.04-0.24
Adult (age 3+) $\pm$ EV	$0.17 \pm 0.05$	$0.14 \pm 0.05$	$0.14 \pm 0.05$	_ 0-1, 0.1	— ±10% (EV ±10%)	 0.04-0.24
Initial population size	$5250\pm500$	3350	3350	-	-	-
Carrying capacity $\pm$ EV	$5250\pm500$			3350-6500	±10% (EV ±10%)	3500-8000

*Note*: Environmental Variation (EV) is the annual variation in the probabilities of reproduction and survival that arise from random variation in environmental conditions. EV is derived from the standard deviation of the range of estimated values for that parameter. <sup>a</sup>Simulated increases of 10% were added to these values.

We next simulated three management scenarios aimed at forecasting cat control outcomes. They were (i) pre-cat control, (ii) cat control and (iii) cat eradication (Table 3). For each scenario, rates of mortality varied for three age classes, the brood-nest establishment to 1 year, juveniles—ages 1-3 years and adults—3 years and above. The brood age class is the most vulnerable to all causes of mortality including predation by cats, rats, goshawks and crabs, particularly from the time of hatching to approximately 14 days old (Fleet, 1972, 1974). Adults are vulnerable to cat impacts only while incubating eggs or tending young chicks during the breeding season and are not considered vulnerable to rat impacts unless they are already experiencing mortal stress. Juveniles spend their time foraging at sea before reaching breeding age (Sommerfeld et al., 2015) and therefore are not vulnerable to cat or rat predation impacts. Mortality rates for each age class in each management scenario were informed by empirical studies completed on Christmas Island (Tables 1 and 2).

Population viability was modelled for 100 years to align with assessments of extinction risk as outlined by the IUCN Red List Guidelines (IUCN, 2017; O'Grady et al., 2008; Reed & McCoy, 2014). This represented approximately eight generations based on the generation time of 10.9–12.1 years (Bird et al., 2020). Each model was run for 1000 iterations, and extinction was defined as the complete removal of at least one sex. For each ecosystem state, (a) the probability of extinction at 100 years; (b) the mean population size of extant populations at 100 years; and (c) the deterministic and stochastic population growth rates were recorded. Inbreeding depression had no effect on population size or probability of extinction so was excluded from analyses (data not shown).

#### 2.5 | Sensitivity analyses

Manual perturbation, relative sensitivity and regression sensitivity analyses were used to assess the robustness of the PVA models and model responses to input parameter uncertainty (Mortensen & Reed, 2016). Manual perturbations demonstrated where populations TABLE 3 Cat management scenarios on Christmas Island that were modelled using population viability analyses.

(i) Pre-cat control	Scenario	Mortality of tropicbird chicks was high, and largely attributed to cat predation, while rat predation was between 6% and 7% (Table 1). Cat predation of sitting adults also occurs (Lipka, 2010)
	Model parameters	Brood mortality equates to the average proportion of failed nests observed across studies (Table 1). The rate of adult mortality equates to the cat predation rate (Lipka, 2010), subtracted from the natural adult background rate of mortality (Bird et al., 2020). Juvenile mortality equates to the natural background rate of mortality (Bird et al., 2020)
(ii) Cat control	Scenario	Cat control began in 2010. By 2018, the domestic cat population in urban areas, directly adjacent to tropicbird breeding colonies, had diminished by ~70% to 40 individuals (Parks Australia, pers. comm.). Cat densities had also been substantially reduced Island-wide (by 80%; McGregor & Potts, 2019). Following cat control, nest success increased, and cat predation events were rare (chicks and adults). Rat activity observed at nests using cameras increased slightly, but there was no evidence that rat impacts increased (Willacy, 2022). Year to year rat predation variation was in the range of 0%–7%. Loss of shore terrace nesting habitat caused by the invasive Coral vine (Willacy et al., 2021) potentially limits tropicbird population recovery (Director of National Parks, 2014)
	Model parameters	Brood mortality equates to the average proportion of failed nests observed across studies (Table 1). Adult and juvenile mortality equate to the natural background rate (Bird et al., 2020). Carrying capacity is varied by -10% and -20% to model weed impacts
(iii) Eradication, with rat predation	Scenario	Cat predation impacts are absent. Rat predation (eggs/chicks) increases (in increments to find the breeding success threshold [1- brood mortality rate] at which rat predation becomes meaningful)
simulations	Model parameters	Brood mortality as for (ii) minus cat depredation, with incremental increases (+10%) representing increased rat depredation. Adult and juvenile mortality as for (ii)

crashed within the possible range of parameter values, and how close model inputs were to those values; relative sensitivity or 'elasticity' analyses showed how small changes in parameter estimates affected deterministic population growth; while a global sensitivity analysis (regression analysis) was used to determine which parameter explained the most variability in changes to population growth and extinction risk.

For manual perturbation, we varied the mortality rates for all age classes from 0 to 1, in increments of 0.1, while holding all other parameters constant, to determine at what point mortality begins to contribute to population decline. For relative sensitivity, changes in input values, including the mortality rates of all age classes, the proportion of adults breeding and carrying capacity were calculated using the equation  $(\lambda + -\lambda -)/(0.2^{-}\lambda 0)$ , where  $\lambda$ + and  $\lambda$ - are the output from the adjusted parameter values,  $\lambda 0$  is the baseline model output and 0.2 is the total perturbation of the parameter values  $\pm 10\%$  (Mortensen & Reed, 2016).

For the regression method, multiple parameters including the mortality rates for all age classes, % breeding (both sexes) and carrying capacity were varied simultaneously to more fully sample the parameter space. Latin hypercube sampling in VORTEX was used to create 1000 parameter sets with input values chosen from uniform distributions of empirically observed parameter ranges. Ten iterations of each parameter set were run, resulting in a dataset of 10,000 populations of varying abundances. The VORTEX simulation results were analysed in R (R Core Team, 2023). To allow for direct comparisons between each parameter on stochastic population growth rate, all predictor variables were scaled and centred using *z*-transformation. We then used a generalised linear model (family=Gaussian, link=identity) with stochastic growth rate as the response, and all parameters as predictor variables. Assumptions

of the linear relationship between each predictor were checked by visual inspection of the residual plots, and no substantial deviations from a linear trend were found. Finally, each main effect was plotted against the growth rate. See Supporting Information (Table S1 and Figure S1) for these results.

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# 3 | RESULTS

# 3.1 | Cat control improved red-tailed tropicbird population outcomes

The population viability analyses indicate that cat control implemented to date has improved outcomes for the tropicbird population. Prior to cat control, the population had declined to an adjusted carrying capacity (n=2749, with a growth rate of 0.01; Table 4), with no extinction vulnerability over a 100-year time frame ( $P_e=0$ ; Figure 2). Sensitivity analyses show that the decline was largely caused by cat predation of the brood age class (chicks) rather than adult birds, as breeding success was close to—and in some years below—the critical threshold required for population persistence (30%; Figure 3). Only a small number of breeding adult tropicbirds were preyed upon by cats per year (3%), well below the critical threshold of 50%.

In the relative sensitivity analysis, models were most sensitive to changes in adult mortality, followed by juvenile and brood mortality. Though none of the vital rates we varied had a disproportionate effect on population growth rate. Regression analysis showed that four of the five parameters we varied had a significant effect on stochastic growth rates. Adult mortality ( $x^2$ =179,559; p <0.001), juvenile mortality ( $x^2$ =101,656; p <0.001), fledgling mortality ( $x^2$ =47,731; p <0.001) and % females breeding ( $x^2$ =7141; p <0.001), all significantly modified

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Scenario	Probability of extinction	Stochastic population growth rate (r)	Population size
Pre-cat control	0	0.01 (SD±0.19)	2749 (SD±2449)
Cat control	0	0.15 (SD±0.12)	5045 (SD±466)
Rat predation simulations			
Current = $0.37 \pm 0.16$ (0.02 ± 0.02)	0	0.15 (SD±0.12)	5094 (SD±478)
$10\% \!=\! 0.45 \!\pm\! 0.14$	0	0.13 (SD±0.12)	5036 (SD±468)
$20\% \!=\! 0.55 \!\pm\! 0.18$	0	0.09 (SD±0.14)	4837 (SD±549)
$30\% = 0.65 \pm 0.24$	0	0.05 (SD±0.19)	4192 (SD $\pm$ 1035)
$40\% = 0.75 \pm 0.30$	0.64	-0.01 (SD±0.25)	717 (SD±1122)
$50\% = 0.85 \pm 0.36$	1	-0.10 (SD±0.29)	0
$60\%\!=\!0.95\!\pm\!0.42$	1	-0.21 (SD±0.23)	0
$70\% = 105 \pm 0.48$	1	-0.15 (SD±0.05)	0

TABLE 4 Comparison of red-tailed

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tropicbird population variability measures.

*Note*: Parameters used in models are shown in Table 2. All model scenarios were run using a 100-year time frame. Values are means and standard deviations.



FIGURE 2 The probability of survival and change in tropicbird populations following cat control, with variations to carrying capacity (K) made to simulate the impact of weeds on potential population size (reductions of 10% and 20% to available nesting habitat). In the pre-cat control scenario, carrying capacity relates to 5250 given in Table 2, whereas the cat control scenario relates to the initial population size of 3350.

the red-tailed tropicbird population growth rate; however, adult mortality and juvenile mortality accounted for 51% and 31% of the total deviance, respectively. Carrying capacity had no effect on the stochastic growth rate (see Table S1 and Figure S1).

Importantly, these analyses show that tropicbird populations are very sensitive to small changes in adult and juvenile survival and are less sensitive to changes in brood mortality. Hence with current cat control measures reducing cat predation of adults and chicks, the tropicbird population is predicted to recover and stabilise at the island's carrying capacity. Simulated reductions in carrying capacity, for example, if weed expansion reduced breeding site availability, do not affect the rates of recovery that would be gained with cat control, but as expected, reduce the population size that can be attained (Figure 3).

# 3.2 | What rate of nest predation by rats affects population persistence?

After cats were controlled (by ~70%-80%), field data showed that annual observed rat predation contributed between 0% and 6% to

overall nesting failure rates (eggs/chicks), which was equivalent to pre-cat control levels (Table 1). This rate of predation did not affect tropicbird population persistence (Figure 4). The simulated rat predation of nests (eggs/chicks) became ecologically important once rat predation rates exceeded 40% (Figure 4). When rat predation of nests reached 50%, the tropicbird population declined by  $0.10 \pm CI$  0.30% per year to less than 50 individuals within 66 years. Extinction was highly probable within 100 years ( $P_e$ =0.91). When simulated rat predation rates increased above 60%, rates of decline per year more than doubled (0.21 ± CI 0.23%), and the population declined to less than 50 individuals within 25 years. Extinction was highly likely within 100 years ( $P_e$ =1). Above 70%, tropicbird populations declined to less than 50 individuals within 17 years.

# 4 | DISCUSSION

To reduce uncertainty around invasive species management actions in complex, multi-invaded ecosystems, a priori consideration of potential outcomes, that supports future adaptive decision-making, FIGURE 3 Results of perturbation sensitivity analyses for the baseline model vital rates over 100 years, including breeding success, juvenile mortality and adult mortality. The brood mortality rate is also referred to as breeding success (1- brood mortality). The (i) pre- and (ii) post-cat control average mortality rates are shown by red and blue dotted lines, respectively. Juvenile mortality rates are the same for both scenarios and are shown in blue only.



is valuable. Here, using population viability analyses, we assessed whether removing cats in isolation from Christmas Island would allow a threatened ground-nesting seabird, the Indian Ocean redtailed tropicbird, to recover; and based on evidence that this bird species is susceptible to rat predation, found the nest predation threshold from a remaining invasive mesopredator that should trigger complementary rat control. We found that cat control implemented to date has improved red-tailed tropicbird population outcomes. Current observed rates of nest predation by rats, and modest increases in that rate, are unlikely to affect tropicbird population persistence in the short or long term. However, if ongoing cat control leads to a substantial increase in rat density or activity, and concurrently nest predation rates, then the tropicbird population will begin to decline when rat-induced nest failures increase above 40%. As rat-induced nest failure rates increase, the tropicbird population decline accelerates, and at 60% nest failure, population extinction is expected with high likelihood within 100 years. These thresholds can be used to inform a management trigger. Because rat

predation rates are currently so low ( $\overline{x} = 3\%$  of chicks for 2017 and 2018, range = 0%-6%), rat density would need to change by an order of magnitude to reach this level of impact. Alternatively, changes to rat behaviour, adult defence of nests or background rates of nest predation and mortality could also contribute to closing that gap.

# 4.1 | Cat control improves outcomes for red-tailed tropicbirds

Seabird populations are considered extremely vulnerable to cat impacts because their ground-nesting behaviour makes incubating adults and their chicks susceptible to predators (Woinarski et al., 2017). On Christmas Island, before cat control began, cats caused the failure of a substantial proportion of nests (39%; Sommerfeld et al., 2015). However, observed cat predation rates of adults were low, possibly due to their size (600–800g; Lipka, 2010). Because tropicbirds are long-lived, have low reproductive output



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**FIGURE 4** Nest failure scenarios for fledgling mortality that represent the effect of incremental changes to rat predation on extant population abundance and the probability of survival, assuming all other rates of failure remain constant.

(e.g. one chick per breeding pair per year) and have delayed onset of reproductive maturity, they are particularly vulnerable to changes in adult survival, but less affected by breeding failure (le Corre, 2008), unless complete predation of offspring is sustained over an adult's lifetime (Jones et al., 2008; Sandvik & Erikstad, 2008). Although empirical evidence shows that removing cats from Christmas Island increases tropicbird nesting success, the model results show that the conservation benefit gained for the population is relative to the amount of suitable breeding habitat available for the increased population to expand into.

# 4.2 | Rat predation ≥40% of nests would cause tropicbird decline

A setting where rat impacts exceed background background mortality rates (historic  $0.69 \pm$  SD 0.22, or current  $0.37 \pm$  SD 0.16) through mesopredator release would be a poor management outcome. Such an increase could occur if the rat population increased substantially. Plein et al. (2022) also suggest that rat populations would need to substantially increase before their impact became equivalent to the impact previously delivered by cats. Rat densities on Christmas Island are low compared to tropical islands elsewhere (Harper & Bunbury, 2015), which may partly explain their low level of impact. On other islands with higher rat densities, rats are known to substantially affect tropicbird nesting success (Fleet, 1974; Ringler et al., 2015). Europa, located in the Western Indian Ocean, had high levels of rat predation on tropicbird nests that contributed, along with predation by land crabs, pied crows (Corvus albus) and barn owls (Tyto alba), to annual tropicbird (Phaethon rubricauda and Phaethon lepturus europae) breeding success rates of less than <10% (M. le Corre, pers. comm.; Ringler et al., 2015). On Kure Atoll, Pacific rats (*Rattus exulans*) occur in high densities and impact tropicbird (*Phaethon rubricauda*) breeding success, causing between 89% and 100% of annual nestling losses (Fleet, 1972). Note that neither of these islands had feral cats present.

Alternatively, rat predation rates on tropicbird nests could increase if rat behaviour changed so that they targeted bird nests more often. For example, changes to the availability of resources, such as prolonged dry season conditions, which results in lower invertebrate productivity and biomass, may lead to resource restrictions and encourage rats to focus on higher risk prey such as eggs and chicks of large bird species, as observed on Kure Atoll in response to Scaevola taccada fruit availability (Fleet, 1974). Rat predation rates could also increase if adult tropicbirds were less able to defend their nests. Declines in regional marine productivity in the near to medium term due to climate change (Bryndum-Buchholz et al., 2019) may cause adults to leave nests unattended for longer, leading to more opportunities for rats to prey upon nests. Unattended nests are also vulnerable to other causes of failure, such as predation by native species (land crabs or goshawks, Accipiter fasciatus natalis) and nestling dehydration or starvation (Sommerfeld et al., 2015). If nest failure due to other causes increases, including breeding habitat loss from weed expansion, the rate of rat predation that leads to tropicbird population decline will be lower than indicated by the PVA. The impact threshold should therefore be revised with any new knowledge of shifting carrying capacity caused by changing circumstances (Potgieter et al., 2022). Furthermore, to account for ecosystem state uncertainty, Type I or II error, or the predictive capacity of a PVA if there is uncertainty around input parameters, a buffer could be added to the decision trigger's impact threshold (Cook et al., 2016; de Bie et al., 2018).

#### 4.3 | Monitoring and management implications

The current rate of rat predation on tropicbird nests is far below the ecologically significant impact threshold identified in our modelling. If ongoing cat control causes nest predation by rats to increase close to a decision trigger (e.g. of 40%-70%), either because of a numerical response by rats, or behavioural changes in rats or tropicbirds, then complementary rat control should be carried out. The population of our species of concern is large (>3500), adults are long-lived and rats prey on eggs and nestlings only. Therefore, if rat predation did increase, even to above the management trigger, tropicbird population extinction would not occur for more than 15 years. This time frame allows a window to detect, respond to and mitigate rat impacts. Thus, the decision for rat control could be triggered when the chosen cost-effective monitoring indicator signals that average rat predation is consistently above 40%, for example, for 5 years, or following a single increase to 60% depending on the risk tolerance of managers (Addison et al., 2015). Monitoring indicators of rat impact (e.g. rat populations, rat impact, nest success) as cat eradication progresses should be evaluated against this threshold, with targeted rat control occurring once thresholds are breached.

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This study represents a novel use of population viability analysis to understand the relationships between key demographic variables in a network of species, and to set decision triggers based on impact thresholds that can prepare managers to adapt in a timely and appropriate way to the potential outcomes of removing a single species from a multi-invaded ecosystem. This approach can be applied to multiple and complementary (Bal et al., 2021; Tulloch et al., 2013) native species for a more thorough ecosystem-wide adaptive management strategy, and to complex, multi-invaded ecosystems elsewhere to inform monitoring and management priorities that deliver conservation benefits.

#### AUTHOR CONTRIBUTIONS

Eve McDonald-Madden, Sarah Legge and Rosalie Willacy conceived the ideas and designed methodology; Rosalie Willacy collected the data; Rosalie Willacy analysed the data; Rosalie Willacy, Eve McDonald-Madden and Sarah Legge led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. Whenever possible, our research was discussed with local stakeholders to seek feedback on the questions to be tackled and the approach to be considered. Whenever relevant, literature published by scientists from the region was cited.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

#### DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository https://doi.org/ 10.5061/dryad.9kd51c5tr (Willacy et al., 2024).

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# SUPPORTING INFORMATION

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

**Table S1.** Results of relative sensitivity and regression analyses(deviance table from generalized linear model).

Figure S1. Results of regression analysis.

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