Predicting targets and costs for feral-cat reduction on large islands using stochastic population models

Kathryn R. W. Venning[1,*], Frédérik Saltré[1], Corey J. A. Bradshaw[1]

[1]Global Ecology, College of Science and Engineering, GPO Box 2100, Flinders University, Adelaide, South Australia 5001, Australia

*Corresponding author: Global Ecology, College of Science and Engineering, Flinders University, GPO Box 2100, Adelaide, South Australia 5001, Australia; tel: +61 8 8201 2090; e-mail: kathryn.venning@flinders.edu.au

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Data availability

The R code to create the model simulations is available at https://github.com/KathrynVenning/FeralCatEradication

Declaration of interest

NIL

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Abstract

Feral cats are one of the most destructive invasive predators worldwide. Due to the high risk of feral predators pushing native species to extinction in Australia, density-reduction or eradication campaigns can improve the persistence probability and recovery of native fauna. Kangaroo Island — Australia's third-largest island — was recently nominated as a complete cat-eradication site by the federal government. Because many population density-reduction campaigns are costly and not effective in the long term, mathematical models predicting optimal culling regimes can guide management plans, especially if they include estimates of costs under different policy decisions. We constructed a stochastic population model with cost estimates to test the relative effectiveness and cost-efficiency of two main culling scenarios for Kangaroo Island to 2030: (1) constant proportional annual cull (one-phase), and (2) high initial culling followed by a constant proportional maintenance cull (two-phase). We also examined the effectiveness of a trap-neuter-release scenario to compare with the culling outcomes. We found that an average culling proportion of ≥ 0.3 would reduce the population to ≤ 0.1 of the founding population, while a two-phase cull where an initial cull of ≥ 0.6 was followed by a maintenance cull of ≥ 0.45 would reduce the final population to 0.01 of its initial size by 2030. Costs estimates varied widely depending on capture techniques used, but a combination of *Felixer*™ cat-eradication units, conventional traps, and hunting was the most cost-effective in the two-phase culling scenario when hunting is used to make up culling shortfalls (minimum costs estimated at AU$46.5 million–AU$51.6 million with an initial cull of ≥ 0.6, maintenance cull of ≥ 0.45). Trap-neuter-release was an inefficient approach compared to the culling scenarios. Our model results provided direction for the efficient eradication of feral cats on Kangaroo Island and can be transferred to feral-cat management elsewhere.

Key words: Leslie matrix, matrix population model, feral cats, invasive species, eradication costs, Kangaroo Island, culling model

Introduction

Since its domestication approximately 10,000 years ago, the common house cat *Felis catus* has spread throughout the globe and become established in most habitat types (including on most islands) (Fitzgerald et al. 1991, Medina et al. 2011, Woinarski et al. 2015), due to both accidental and deliberate human facilitation (Driscoll et al. 2007). Because they are generalist predators, feral cats are today one of the most destructive invasive mammal predators worldwide (Lowe et al. 2000, Doherty et al. 2016), contributing to many or most of the predation-induced terrestrial extinctions recorded globally (e.g., > 63 species, including 26% of bird, mammal and reptile extinctions) (Doherty et al. 2016).

Cats are also considered to be opportunistic hunters and scavengers that are able to adapt to fluctuating prey availability, switching between small invertebrates to mammals as large or even larger than themselves (Barratt 1997, Bonnaud et al. 2011, Moseby et al. 2015). They can also easily adapt to arid and hostile environments, surviving with minimal access to fresh water (Fitzgerald and Turner 2000, Medina et al. 2008, Woinarski et al. 2015). This makes feral cats particularly destructive to island ecosystems, where their prey have the added vulnerability of naivety to generalist predators for which they have evolved no or inefficient anti-predator behaviours (Close 2005, Bonnaud et al. 2011, Medina et al. 2014, Doherty et al. 2016). Australia in particular is a large island, disproportionately represented in mammal extinctions since European settlement (Abbott 2002, Abbott 2008) so that in combination with foxes (*Vulpes vulpes*), cats have become one of the most prolific killers of native species across the continent (Dickman 1996, Doherty et al. 2016).

The most effective method for reducing feral cat populations and their associated predation on native species is eradication wherever possible (Andersen et al. 2004, Schmidt et al. 2009), particularly in insular environments (Bester et al. 2002, Nogales et al. 2004, Doherty et al. 2016). Alternative non-lethal approaches (such as trap-neuter-release) also exist (Gibson et al. 2002, Wallace and Levy 2006, Longcore et al. 2009, Miller et al. 2014), and while such an approach might appeal to members of the public that do not agree with lethal control (Andersen et al. 2004), the high expense of broad-scale implementation, coupled with its low effectiveness (Longcore et al. 2009) mean it is not widely used for cat management in Australia. Despite this, the trap-neuter-release management option is commonly considered in density-control programs, or proposed by communities (Deak et al. 2019).

Most density-reduction campaigns based on direct killing have been typically implemented *ad hoc* because of the imminent menace cats pose to their prey species and the requirement to achieve outcomes quickly (Bester et al. 2002, Denny and Dickman 2010). As such, available funds or resources can be used up quickly without the benefit of long-term planning based on the projections of empirical density-reduction models (Denny and Dickman 2010), thus threatening the success of a program. As a result, inappropriate methods and poorly timed roll-out have been attributed to most island eradication failures (Campbell et al. 2011). Custom-designed culling models that plan the most efficient and cost-effective application of resources are therefore ideal precursors to any eradication program (Smith et al. 2005, McMahon et al. 2010).

Culling models are effective because of their ability to consider real-time population dynamics and resource availability to recommend feasible density-reduction plans (McMahon et al. 2010). Multiple types of culling model exist (e.g., spatially explicit, aspatial, density-driven, area-dependent) depending on the choice of scenario to reduce the population, such as a single-phase, constant proportional culling (McCarthy et al. 2013), or a two-phase cull with a high initial proportional culling rate followed by a constant proportional maintenance thereafter (a two-phase reduction model) (Campbell et al. 2011). Such models are instrumental in guiding successful eradication by providing targets and parameters that lead to efficient population reduction of the target species (Smith et al. 2005). Such two-phase eradication strategies (high initial cull followed by a consistent maintenance 'press' cull to ensure continued population decline) often still require a final 'clean up' stage where different (and usually more expensive) strategies are needed to eradicate the last surviving individuals that are difficult to detect (Bester et al. 2002, Nogales et al. 2004). High initial culls followed by maintenance culling capitalise on the notion that when densities are high, culling is more efficient, while the maintenance culling continues to reduce the population (Nogales et al. 2004, Denny and Dickman 2010).

Cat eradication is currently underway on part of Kangaroo Island, Australia's third-largest island (Fig. 1). The initial planning stages of the eradication began in 2016, with a proposed completion date of 2030. The program directors plan to use three main techniques for cat eradication: trapping, hunting, and *Felixer*™ units (a *Felixer* is an automated toxin-delivery system that uses rangefinder sensors to distinguish target cats from non-target species and spray targets with a measured dose of toxic gel; thylation.com). The social licence to apply lethal population reduction via hunting, baiting, or trapping is largely a function of the public's perception of the proposed methods (Deak et al. 2019), and relies on the co-

operation of land-owners. This applies to Kangaroo Island given it has > 4200 permanent residents spread across most of the island. Perception surveys done between 1993 and 2018 showed that > 90% of the Kangaroo Island community supported domestic and feral cat management (Berris et al. 2019). Additionally, stakeholders (community members, land owners, relevant governmental departments) are in support and are actively involved in the development and implementation of the project (Natural Resource Kangaroo Island 2015). Kangaroo Island has pre-existing community engagement for wildlife-conservation programs, and local residents are educated about the damage caused by feral cats (Berris et al. 2019). These public-information programmes improve the local public's perception of feral-animal management (Deak et al. 2019, Walsh et al. 2019).

Our aim was to design an ideal set of culling conditions that will most efficiently reduce feral cat densities on Kangaroo Island. More specifically, we (1) constructed stochastic variants of both culling and fertility-reduction (trap-neuter-release) models under different application scenarios that can be applied to guide cat eradication on Kangaroo Island, (2) estimate the relative costs of employing different combinations of the methods available, and (3) used the culling model to identify a regime that will most effectively reduce the feral cat population by the 2030 deadline. Specifically, we tested the efficacy (proportion of the population reduced, and over what time) of two culling scenarios: (*i*) constant proportional annual culling (one-phase), (*ii*) high initial culling followed by a constant maintenance cull (two-phase). We hypothesise that the two-phase culling model will reach the target population density by 2030 more efficiently than the one-phase culling model because initial effort tends to be the cheapest and most effective means of achieving high rates of reduction (Bester et al. 2002, Nogales et al. 2004, Robertson 2008, Denny and Dickman 2010). In any case, maintenance culling is required thereafter to prevent the population from recovering.

Methods

Study site

Located approximately 12 km south of the Fleurieu Peninsula (South Australia) at its nearest point, Kangaroo Island is Australia's third largest island (155 km long and 55 km wide), covering ~ 4400 km^2 (Masters et al. 2004, Higgins-Desbiolles 2011) (Fig. 1). The island has retained around 53% of its native vegetation, with 35% of the remaining land cover devoted to dryland agriculture (Willoughby et al. 2018). The island is uniquely absent of invasive European rabbits (*Oryctolagus cuniculus*) and is one of the few locations in Australia free of

red foxes (*Vulpes vulpes*); resident cats can therefore feed on a wider range of native species than elsewhere on mainland Australia (Bonnaud et al. 2011). For our study, we separated the island into the Dudley Peninsula (east of the narrowest point of Kangaroo Island, adjacent to Pelican Lagoon; Fig. 1) and the western side (west of the narrowest point), to reflect the management strategy for the entire island.

Feral cat densities on Kangaroo Island are thought to range from 0.15 to 2.97 cat km^{-2}, with a median of 0.7 cat km^{-2} on the western end (Hohnen et al. 2020). Taggart et al. (2019) estimated that relative feral cat densities in eastern Kangaroo Island were ~ 10 times higher than on the adjacent mainland (Kangaroo Island relative abundance = 14.6 cats camera-trap $site^{-1}$; mainland = 1.39 cats $site^{-1}$; 11 sites on both the Island and mainland).

Model

We constructed a Leslie matrix to represent age-specific fertility and survival (Caswell 2001) for the cat population. We obtained cat fertility and survival estimates from six studies of domestic, stray and feral cat population across the USA and Australia (Budke and Slater 2009) and summarised the population dynamics from a study in Western Australia done in the preliminary stages of cat eradication (Short and Turner 2005). We calculated mean and standard deviations of the age-specific demographic rates (i.e., survival, fertility) necessary for stochastic representations of the model (see below). We only used these fertility and survival estimates for females, assuming a 1:1 sex ratio (Bloomer and Bester 1991, Budke and Slater 2009).

According to demographic rates published in the peer-reviewed literature, the maximum age for feral cats ranges from 3 (Budke and Slater 2009) to 9 years (Van Aarde 1983); however, after consulting local wildlife managers, we set the maximum age for feral cats on Kangaroo Island at 6 years. We then split the initial year into two sections: pre- and post-breeding. The pre-breeding time step incorporates animals < 10 months of age, because feral cats reach sexual maturity at around 10 months (Jones and Coman 1982); this was represented as individuals in this stage having zero fertility. For all resulting predictions of changing population size, we assumed that survival was the same for males and females given no evidence to the contrary. We present all parameters and their ranges in Table 1.

We stochastically resampled the deterministic matrix **A** in all subsequent projections based on the standard deviation estimated from minimum and maximum fertility and survival values (Budke and Slater 2009), which incorporates both measurement error and inter-annual variability (process error). We assumed a Gaussian distribution around the mean of fertility

and the β distribution for survival probability, using the standard deviations for resampling of each (Table 1).

The deterministic matrix **A** is:

$$\mathbf{A} = \begin{bmatrix} f_1 & f_2 & f_3 & f_4 & f_5 & f_6 & f_7 \\ s_1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & s_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & s_4 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & s_5 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & s_6 & s_7 \end{bmatrix}$$

where f_x = age (x) -specific fertility and s_x = age-specific survival. See also Table 1 for parameter values.

Untreated (control) population

To simulate how incrementing intensities of reduction change the projected population size, we first simulated a population not exposed to any culling to represent a 'control' population. We calculated the population's stable age distribution from the base matrix **A** (Caswell 2001), and then multiplied this stable age structure by a starting population size of 3083 (approximation from density estimates on the Dudley Peninsula and western side of island) (Taggart et al. 2019, Hohnen et al. 2020). We then expressed all subsequent projections as a proportion of this founding population size to avoid the uncertainty in initial population size estimates. Kangaroo Island is insular, so there are fewer opportunities for migration into the population compared to the mainland. However, we did account for some 'leakage' into the population (domestic release or ferry stow-away) by re-running the top-performing culling scenario (initial proportional cull = 0.6, maintenance cull = 0.45 — see Results) and adding an incrementing a number of 'leaked' individuals (between 10 and 1000 cats) into the population annually to test how these additions would affect final population sizes post-culling (see Supplementary Information, Appendix A, Fig. S1).

We included a logistic compensatory density-feedback function by reducing survival when the population exceeded double the size of the current population (see below) of the form:

$$S_{\text{mod}} = \frac{\kappa}{1 + \left(\frac{N}{\tau}\right)^{\theta}}$$

where S_{mod} is the proportion of realised survival (survival modifier) as a function of the population's proximity to carrying capacity (twice the founding population size, K = 6166;

see below), N is the population size, and κ, τ and θ are constants: $\kappa = 0.998$, $\tau = 9139.11$, and $\theta = 2.835$ (see Supplementary Material, Appendix B, Fig. S2). We thus assumed that survival probability would decline as the population approached carrying capacity (double the size of the current population based on local landscape managers' recommendations), because landscape managers currently consider the population to be sub-optimal with respect to available food resources (Jones and Coman 1982, Read and Bowen 2001). While the threshold is somewhat arbitrary, it does realistically allow the population to increase if no additional mortality sources are imposed. Most research on feral cat population control does not consider the habitat's carrying capacity (Andersen et al. 2004); however, feral cats seem to maintain consistent fertility regardless of population density, although average survival tends to decrease as the population approaches carrying capacity (Courchamp and Sugihara 1999, Nutter 2006). We therefore did not adjust fertility relative to population size.

Reduction scenarios

1. Trap-neuter-release

To compare the efficacy of all proposed density control and reduction scenarios with fertility-reduction methods, we constructed a model that simulated a trap-neuter-release scenario. Although not widely implemented, the trap-neuter-release method is often suggested by a certain element of the public as a more ethical alternative to lethal control. We included this scenario here to compare its efficacy directly to the culling scenarios described below. In this model, no animals are removed from the population, but fertility is reduced to simulate sterilisation. We ran this model using the same methods for an unculled population (and over the same interval), but we reduced fertility for each iteration across a range of values (50–99%, at 1% intervals). That is, the realised fertility for each iteration varied between 50% and 1% of the 'control' model's values for the duration of the project.

2. Culling model

We built two culling models: (*i*) constant proportional annual culling (one-phase), and (*ii*) a high initial proportional cull in the first two years, followed by a constant proportional maintenance cull (two-phase). Here we consider only these phases of a strategy where the last step likely requires a 'clean-up' — the latter is difficult to consider in a model because the focus shifts to individuals. We instead defined a threshold at the end of the model, where moving to the 'clean-up' stage is deemed feasible. In each model, we removed individuals from the population vector proportional to the total culling invoked in that time step and the

stable age distribution. We ran each model for 10,000 iterations (randomly sampling 10,000 times from the stochastic survival and fertility vectors) to calculate the mean and 95% confidence bounds for minimum proportional population size. We set the projection interval to 10 years to represent the management strategy for eradication by 2030 (2020–2030).

For the one-phase scenario, we simulated constant proportional annual culling (c) (i.e., we reduced the population each year by the same proportion for the duration of the projection interval) from $c = 0.10$ to 0.90. We first determined the minimum c to provoke a population decline (this was 0.50 proportional cull), we then incremented this parameter between 0.50 and 0.99 at intervals of 0.01. For the two-phase scenario, we applied high initial culling only in the first two years of the eradication project ($c = 0.50$–0.99), with maintenance culling applied to all years thereafter ($c = 0.01$–0.50) until the end of the projection interval. For all iterations of both models, we recorded the minimum projected proportional population size (pN) for each value of c, at an incrementing proportional culling of 0.01.

Cost

Based on previous information regarding the reduction in capture efficiency as population density declines (Bloomer and Bester 1992, Nogales et al. 2004, Parkes et al. 2014), we assumed an eradication technique's efficiency (f, ranging from 0 to 1) follows a Type III functional response (i.e., sigmoidal; Nunney 1980, Denno and Lewis 2009) relative to proportional population size:

$$f = \frac{\alpha}{1 + (\beta e^{-\gamma \mathrm{p}N})}$$

where f is the relative efficiency of the culling technique, α, β and γ are constants: $\alpha = 1.01$, $\beta = 85.61$, and $\gamma = 8.86$, and pN = proportional population size (see Supplementary Material, Appendix C, Fig. S3). We assumed the same efficiency reduction across trapping, hunting and *Felixers*™ as a function of population size, such that the smaller the remaining population of cats, the less efficient each method was relative to the start of the eradication campaign. We then applied this reduction to the culling model with pre-set costs for each technique (see below), to estimate the total cost of eradication.

We sourced trapping and shooting cost data from Holmes et al. (2015), with additional trapping costs from trapping supplies (traps.com.au) and *Felixer*™ data from Hodgens (2019). We summarised the catch rates and costs for each technique: (*i*) *Felixer*™ — each unit costs AU$13,000. Based on trials on part of Dudley Peninsula, 6 *Felixer*™ units over approximately 12,000 ha were successful in killing 13 cats over 38 days, which translates to

an annual kill rate of 0.080 (cats killed unit^{-1} year^{-1}). (*ii*) Traps — each trap costs between AU$157 and AU$297 (sampled uniformly). Again, based on trials on Dudley Peninsula, 40 traps over approximately 12,000 ha caught 21 cats over 148 days, which translates to an annual trap rate of 0.198 cats trap^{-1} year^{-1}. (*iii*) Shooting — from Holmes et al. (2015), we estimated a kill rate per person-hour based on 1044 kills (872 direct + 172 from wounds) over 14,725 person-hours (= 0.071 cats killed person^{-1} hour^{-1}). Ammunition and labour costs equate to AU$25.92 hour^{-1}.

To estimate total costs, we first assumed that the density of *Felixers*™ and traps applied on Dudley Peninsula (Dudley Peninsula = 37,500 ha) could be extrapolated to the much larger area of the entire island (440,500 ha). Based on these densities, we calculated the total number of units and traps required for the entire island, and then tabulated the number of cats killed by these two methods combined for the incrementing proportional cull. If the total number of cats killed by these two methods fell short of the proportional cull target in any given year and iteration, we applied three different scenarios where we varied the method used to achieve the proportional target beyond the initial roll-out of units and traps. The three different approaches to meet the shortfalls were: (*i*) increasing the number of *Felixers*™ only, (*ii*) increasing the number of traps only, or (*iii*) meeting the shortfall entirely with follow-up hunting. In each shortfall scenario, we tabulated the total costs across the projection interval and expressed these as a function of the increments in proportional culling.

Of course, this approach assumes a simultaneous roll-out of all *Felixer*™ units and traps across the entire island, when a more efficient approach might instead be to purchase a smaller number of units/traps and deploy them in a spatially sequential roll-out (i.e., a moving 'wave' of units applied to specific regions of the island in sequence). We therefore also ran a modified scenario to reflect this type of spatial pattern of application by arbitrarily assuming a smaller number of units/traps across the entire landscape. Reducing the purchase cost per unit/trap by the same arbitrary value is therefore functionally equivalent to a spatially sequential roll-out of this smaller sample of units/traps. For this example scenario, we therefore reduced the purchase cost of both *Felixers*™ and traps by two-thirds unit^{-1} (see Supplementary Material, Appendix D, Fig. S4).

Results

Untreated population

An untreated (no-cull) 'control' population is expected to increase to a median of 1.8 times the founding population (i.e., to 5525 individuals when starting with 3083) by 2030 (95% confidence limits: 1.39–2.21 times) (Fig. 2a). The instantaneous rate of change (r) from the deterministic matrix for the Kangaroo Island population is 0.167. The deterministic (mean) matrix gave a generation length of 4.7 years. The population is projected to approach carrying capacity (set arbitrarily at twice the current population size) by 2026 (Fig. 2a), at which time the population's $r = 0.0061$ (cf. initial $r = 0.190$).

Trap-neuter-release

The trap-neuter-release scenario with a fertility reduction of 80% each year reduced the population to a median proportion of 0.0754 (0.048–0.120) of its initial size by 2030 (Fig. 3), and a 50% fertility decline only reduced the population to 0.66 (0.041–0.974) of the founding population over the same timeframe.

Culling

Culling timeline 2019–2030: For the one-phase scenario, an annual proportional cull of ≥ 0.3 would reduce the population to ≤ 0.10 of its initial size. An annual cull of ≥ 0.45 would reduce the population to ≤ 0.01 of its initial size (Fig. 2b). A two-phase cull with ≥ 0.60 (initial) and ≥ 0.2 (maintenance) would reduce the population to ≤ 0.10 of its initial size. To achieve a population ≤ 0.01 of its initial size, ≥ 0.60 (initial) and ≥ 0.45 (maintenance) are required (Fig. 4). Stopping the program after the initial culling during the first two years (i.e., without any maintenance culling), the population would recover to its initial size in 15 years (range: 11–21 years; Fig. S4), whereas stopping the maintenance cull in the 9th year (i.e., a year before termination of the program) would result in population recovery to initial size in 42 years (range: 35–50 years) (Fig. S4).

Cost

To reduce the entire Kangaroo Island population to a 0.10 of its original size ($0.1N_1$) using a two-phase cull, a minimum of AU$25.0 million (AU$22.7 million–AU$26.5 million) (Fig. 5c), would be required if hunting was used to make up the yearly shortfall. In contrast, making up the shortfall with additional traps (using the same densities of traps and *Felixers*™ as on Dudley Peninsula) would increase the average costs by 112.4% to AU$53.1 million (AU$40.5 million–AU$69.1 million) for the same target (Fig. 5b). Finally, making up the shortfall with additional *Felixer*™ units would increase the average cost relative to the

hunting-shortfall scenario by > 24,000% to AU$6.1 billion (AU$5.1 billion–AU$6.8 billion) (Fig. 5a). Changing the target population size to 0.01 of the initial ($0.01N_1$), the total minimum costs would increase to AU$49.1 million (AU$46.5 million–AU$51.6 million) if the shortfall was made with hunting (96.4% more than the $0.1N_1$ hunting-shortfall scenario), AU$129.3 million (AU$94.0 million–AU$167.8 million) if the shortfall was made with traps (163.3% more than the $0.01N_1$ hunting-shortfall scenario), or AU$16.9 billion (AU$15.8 billion–AU$18.0 billion) if the shortfall was made with *Felixers*™ (> 34,000% more than the $0.01N_1$ hunting-shortfall scenario) (Fig. 5).

Assuming a two-thirds reduction in costs for *Felixer*™ and trap units (equivalent to needing only one-third of the units rolled out in a spatially sequential manner), the scenario where the shortfall is made up of additional *Felixer*™ units, the total costs for the $0.01N_1$ scenario (initial 0.6, maintenance 0.45), are reduced to AU$3.3 billion (AU$3.0 billion – AU$3.7 billion) compared to the full-cost scenario for *Felixers*™ (Supplementary Material, Appendix E, Fig. S5). The total costs for the $0.1N_1$ scenario (0.6 initial, 0.2 maintenance), are reduced to AU$2.0 billion (AU$1.7 billion–AU$2.2 billion) compared to the full-cost scenario for *Felixers*™ (Supplementary Material, Appendix E, Fig. S5). Both scenarios ($0.1N_1$ and $0.01N_1$) predictably reduce the cost of the culling scenario to ~ 30% of the full-cost scenarios.

Discussion

In each cull scenario we considered, a successful reduction of the feral cat population on Kangaroo Island to below 0.01 of its initial size by 2030 is achievable, but the minimum costs involved according to the different scenarios we ran could range from AU$46.5 million (AU$10 ha^{-1}, with hunting; Fig. 5c) to AU$18 billion (AU$40,863 ha^{-1}, with *Felixers*™; Fig. 5a) depending on the method used and the inherent uncertainty in the parameters we estimated. Simulating a spatial roll-out where one-third of the additional *Felixers*™ are required brings the maximum down to AU$3.3 billion (AU$3.0 billion – AU$3.7 billion; $0.01N_1$ *Felixer*-shortfall scenario) (Supplementary Material, Appendix E, Fig. S5). Whether these costs are a true reflection of the actual costs depends on the accurate form of the (as-yet unmeasured) functional response, and the assumed per-unit outlay of the different methods to meet the annual shortfall for the different intensities of cull. However, the lower end of our estimates for Kangaroo Island are cheaper than the costs to remove cats from Macquarie Island (AU$258 ha^{-1}), likely due to the latter's remoteness (Robinson and Copson 2014).

Cost estimates from other cat eradications on islands (e.g., Marion Island) are currently not available. Nonetheless, our comparisons do illustrate that high initial culls (> 0.45) followed by moderate maintenance culls (0.20–0.45) would be sufficient to reduce the population to 0.01–0.10 of its original size (Fig. 4), and that hunting is the most cost-effective way to meet these targets (especially if other methods are rolled out simultaneously).

That hunting is cheaper than other methods is unsurprising given that no hardware other than rifles and ammunition are needed to be purchased outright, in contrast to the higher overheads associated with traps or *Felixer*™ units (Holmes et al. 2015, Hodgens 2019). Indeed, hunting requires many people working full time, whereas the other techniques are more passive (yet the latter also require set up, monitoring, maintenance, displacement, and removal by staff). However, approximately 500 person hours are required to equate to the current cost of a single *Felixer*™ unit (hunting ~ AU$26 per person hour^{-1} vs. AU$13,000 *Felixer*™ unit), although assuming a spatial roll-out of fewer units is functionally identical to a similar reduction in per-unit cost. Additionally, hunting is considered more humane due to the minimised contact with the animal and the instant death with a correctly executed headshot (Sharp and Saunders 2011), but access to private land and potential conflict with private landholders could complicate hunting in non-economic ways. Of course, complete eradication would necessarily entail additional costs as the final individuals were identified, hunted, and destroyed (Bester et al. 2002, Nogales et al. 2004). This would be more expensive than normal eradication efforts and would require a strategic isolation of remaining individuals, because even a few individuals remaining could conceivable seed a recovery population that could achieve initial population size in several decades (Supplementary Material, Appendix D).

Our results identify that fertility-reduction using trap-neuter-release methods are comparatively ineffective for reducing pest densities (Longcore et al. 2009). Instead, our model outputs show that a realised annual fertility equivalent to ≤ 25% of expected values (i.e., pre-fertility treatment) would reduce the population to ≤ 10%. In other words, managers would have to maintain at least 75% of the female cat population sterilised each year from 2019–2030 for the program to reduce the population to ≤ 10% of its original size. Whether this is feasible or cost-effective is beyond the scope of our study, but it does demonstrate that fertility-reduction is a much less efficient method to eradicate cats than culling. Additionally, sterilised individuals returned to the population could still continue to eat native fauna until they perished due to natural causes, so the overall ecological impact would be necessarily

414 greater than a culling-based program where individuals are removed permanently when first
415 treated.
416 We conclude that the most appropriate approach to reduce cat densities on Kangaroo
417 Island is a two-stage method, with a high initial reduction of at least 0.6—0.7 and a
418 maintenance cull of 0.45—0.65. Although a constant proportional annual cull can be
419 effective, it is generally less efficient than a two-stage approach, especially if some leakage
420 of domestic cats occurs. Indeed, our models shows that even as many as 20 cats released into
421 the population per year would see the final proportional population size increase from 0.005
422 to 0.015 at the end of the management programme (or, from 20 to ~ 45 individuals;
423 Supplementary Material, Appendix A). This is because effort is spread equally among
424 temporal windows in the constant proportional scenario, and therefore must 'catch up'
425 relative to a large, initial cull given that more surviving individuals are still breeding in the
426 former. As culling reduces density and drives the population closer to extinction, it becomes
427 progressively more difficult and expensive to cull remaining individuals (Nogales et al. 2004,
428 Parkes et al. 2014). This is because most culling methods are passive and rely on a 'non-
429 negligible probability' of the target animal encountering *Felixers*™ or traps (Moseby and Hill
430 2011). Although these techniques can be accompanied by visual, scent or sound lures, the
431 target animal still needs to be in range to be enticed by them. Thus, encounters at low
432 densities become increasingly less likely (Veitch 2001, Campbell et al. 2011), and rising per-
433 capita food abundance as the predator's population dwindles can make baits or food lures less
434 attractive (Parkes et al. 2014). Cats in particular are intelligent and can learn to avoid traps.
435 Thus, while trapping is generally considered effective for density reduction (Nogales et al.
436 2004), it is most effective in the early stages of eradication programs (Nogales et al. 2004).
437 Therefore, a two-stage approach allows for the implementation of widespread control that is
438 effective at high densities, followed by a more targeted approach through consecutive
439 maintenance as the population continues to decline.
440 Although our model is focused on Kangaroo Island, the merits of the stochastic framework
441 we developed imply that the model is transferable to other regions and even other species.
442 Altering locally measured demographic rates, population sizes, and reduction targets are
443 feasible with this approach. Our model therefore has applications for other species, including
444 European red foxes (*Vulpes vulpes*) (Edwards et al. 2004) in Australia, brush-tail possums
445 (*Trichosurus vulpecula*) and stoats (*Mustela erminea*) in New Zealand (Brown et al. 2015),
446 and racoons (*Procyon lotor*) in central Europe (Beltrán-Beck et al. 2012).

Because the Kangaroo Island trial eradication program is still in its initial stage, many of the demographic, effectiveness, and cost parameters are not yet available specifically for this region, lending further, but as yet unquantifiable, uncertainty to our conclusions. For example, we were obliged to obtain demographic rates from data published for cat populations elsewhere (Budke and Slater 2009), and we do not yet have access to spatially variable data with which to parameterise spatially explicit models that could potentially improve realism (e.g., such as variation in demographic rates among habitat types — see the following *Perspective* section) (McMahon et al. 2010). A better quantification of carrying capacity, as well as the mechanisms by which density feedback operates on the demographic rates would also improve predictive accuracy.

Many attempts to eradicate cats have been made, but they vary widely in success (Algar et al. 2002, Bester et al. 2002, Nogales et al. 2004, Algar et al. 2011, Campbell et al. 2011, Parkes et al. 2014). For effective eradication to be achieved, culling programs must be based on empirical data and ideally, directed by models like ours. Our model should allow practitioners to make their culling programs more efficient, and to allocate the resources needed to achieve their targets efficiently and cost-effectively. As more site-specific data become available, we expect the model's predictions to become ever-more realistic to identify the most plausible and cheapest pathways to eradication.

Perspective on the Kangaroo Island cat-eradication program

Poison baits (e.g., 1080 or PAPP) were not initially considered as part of the feral cat control on Kangaroo Island because of the perceived risk posed to native and domestic animals (Berris et al. 2019). However, we have confirmed that poison baits will now be used in concert with the other proposed methods, subject to land-owner consent (Natural Resource Kangaroo Island 2020). We omitted the use of baits in our model because there are insufficient data for the use and roll-out in the eradication program. That said, when more data become available, baits can be included into the model framework, which will likely decrease the cost of the other control methods we specifically modelled (Nogales et al. 2004).

Due to insufficient data for many model parameters and functions, we were obliged either to make (arguably defensible) assumptions or use data from other locations/studies (Budke and Slater 2009). Although we are confident that our results and scenarios are relevant, they will be undoubtedly be improved by the refinement of locally measured parameters such as age-specific demographic rates, updated density estimates following the 2020 bushfires, cost

data, efficiency relationships, strength of compensatory density feedback, and probability of leakage. A more detailed schedule for resource application including budget restrictions, timeline flexibility, currently available resources (to reduce initial costs via unit purchasing) and available staff would also assist in improving predicted scenario realism. Further, the *Felixer*™ is still in the initial phases of production and is not yet produced on a large commercial scale. The *Felixer*™ has many merits in regards to feral cat control because of its hazard reduction for baiting non-target species (Read et al. 2019); thus, it is likely to be increasingly applied in future management projects, especially as costs per unit decline.

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Table 1 – Mean parameter values and their standard deviations (SD) used in the stochastic model.

parameter	mean	SD
fertility (daughters)		
pre-breeding* juvenile (f_1)	0.000	—
sub-adult (f_2)	0.745	0.307
adult (f_3–f_7)	2.520	0.450
survival		
pre-breeding juvenile (s_1)	0.460	0.115
sub-adult (s_2)	0.460	0.115
adult (s_3–s_6)	0.700	0.058
senescent (s_7)	0.550	0.058

*pre-breeding juvenile: < 10 months old; not sexually mature

Figure Captions

Figure 1 – Map of Kangaroo island relative to the Australian mainland. The shortest distance from the mainland (southern tip of Fleurieu Peninsula) to Kangaroo Island is approximately 14 km.

Figure 2 – (a) Average proportion of the initial cat population (N_1) on Kangaroo Island projected from 2020–2030 for the unculled scenario. Black line indicates the median value from 10,000 iterations, along with 95% confidence intervals (grey-shaded area). (b) Minimum proportion of the Kangaroo Island feral cat population remaining after a constant proportional annual cull ranging from 0.5 to 0.9. Solid black line represents median minimum proportion of the initial population (N_1) after 10,000 iterations with 95% confidence intervals indicated as grey-shaded area.

Figure 3 – Estimated median minimum proportion of founding population remaining (founding population N_1), with decreasing fertility (fertility reduced 50–99%). Solid black line represents median minimum proportion of the initial population (N_1) remaining after fertility reduction scenarios, with 95% confidence intervals indicated as grey-shaded area.

Figure 4 –Estimated median minimum proportion of the final population remaining (relative to start population N_1) for combinations of initial proportional (i.e., *initial cull*: 0.5–0.9) and maintenance proportional (i.e., *maintenance cull*: 0.1–0.5) culling. Proportion of population remaining after culling scenarios represented by colour bar ranging from lowest (purple) to highest (yellow) remaining proportional population.

Figure 5 – Estimated median total costs of feral cat eradication on Kangaroo Island for combinations of initial proportional (i.e., *initial cull*) and maintenance proportional (i.e., *maintenance cull*) culling, where the shortfall in the number of cats killed from *Felixer*™ units and traps is provided by (a) additional *Felixer*™ units, (b) traps, or (c) hunting. Cost of eradication (in AU$, adjusted for 2020) indicated by colour bar ranging from lowest (purple) to highest (yellow) costs. Contours and white values indicate cost in $AU millions or billions accordingly. Note different *z*-axis (contour) scales in a, b, and c.

Figure 1

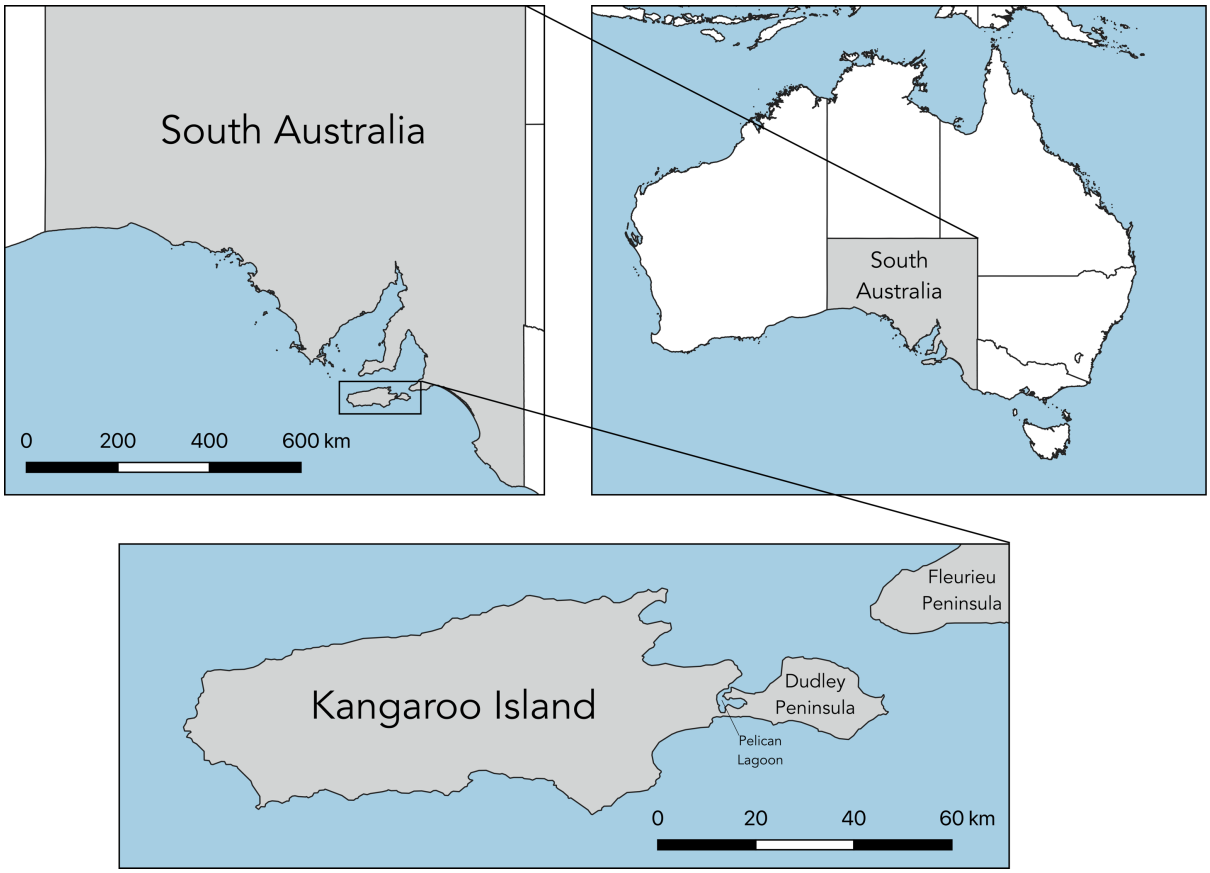
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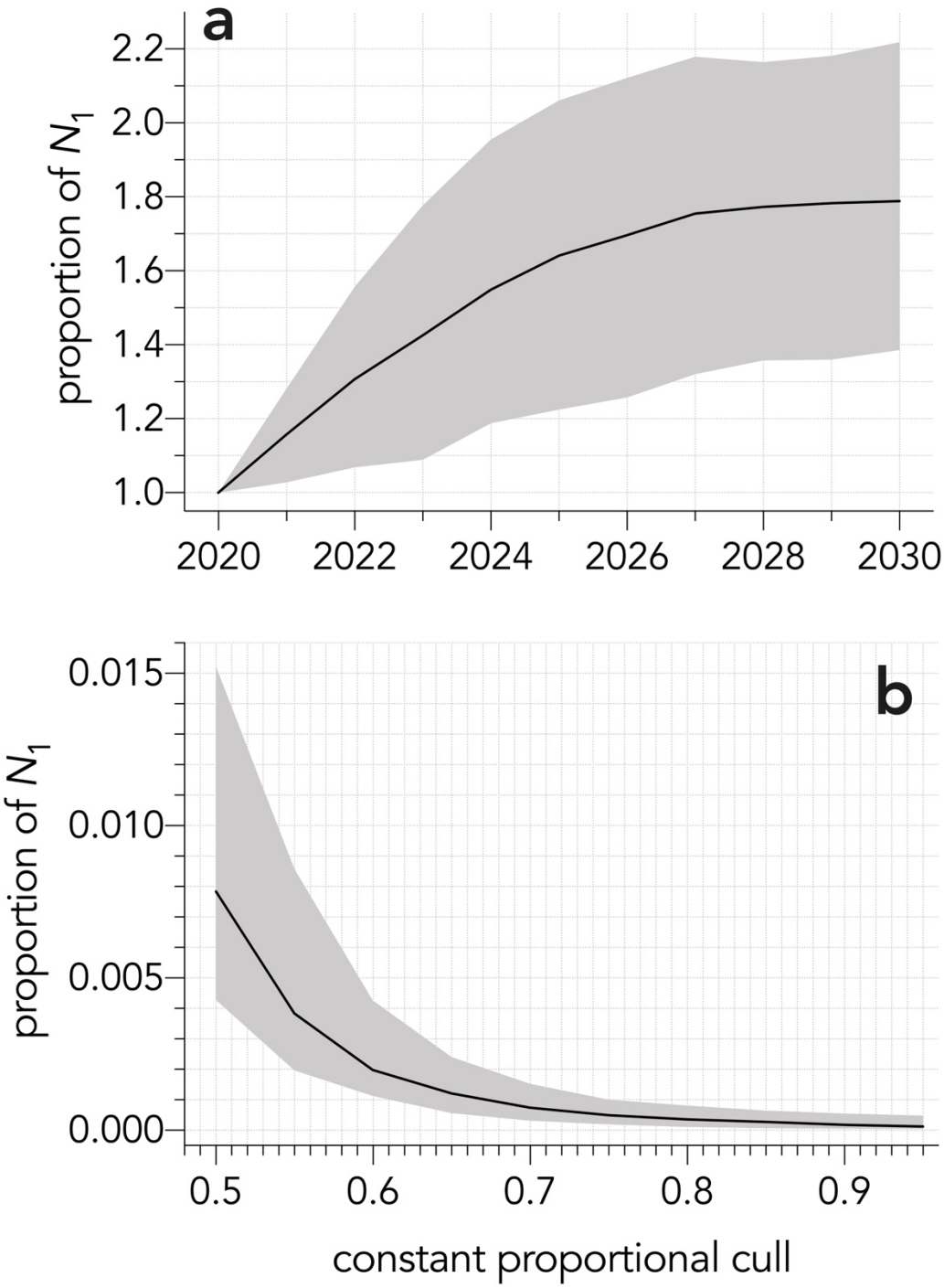
Figure 2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679 **Figure 3**

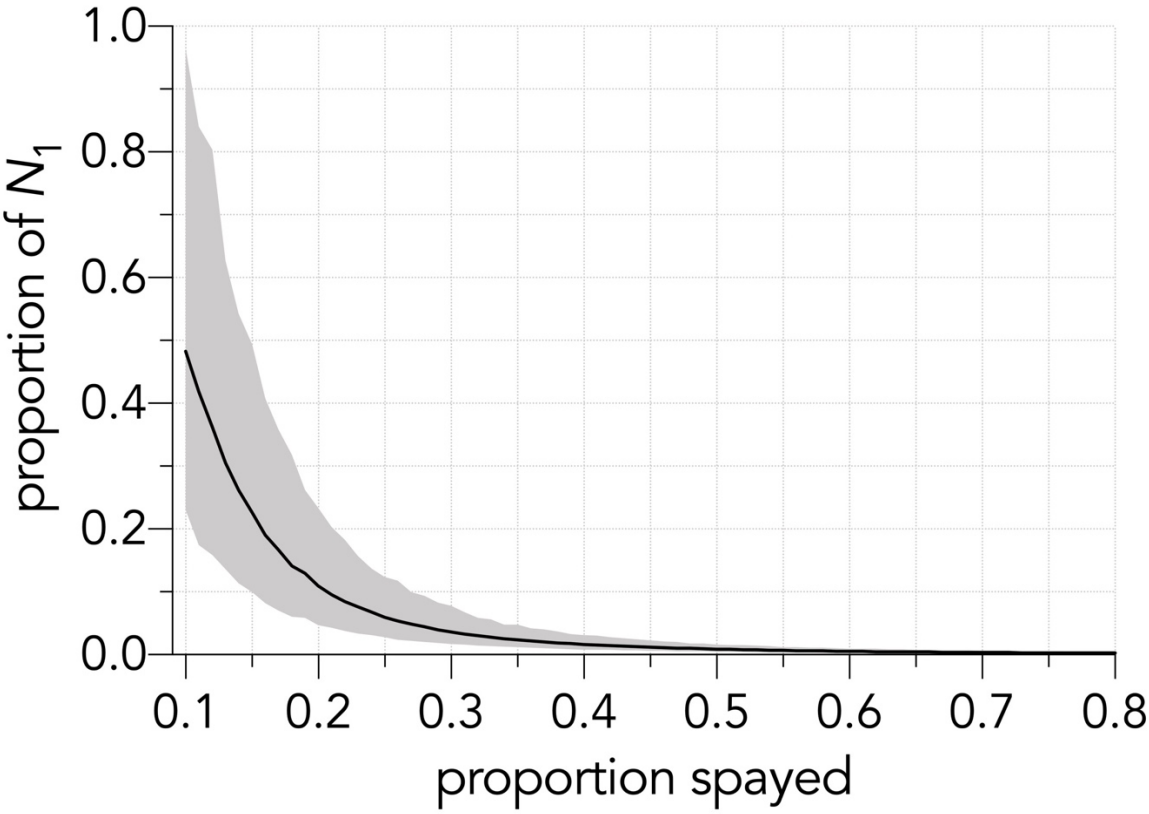

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Figure 4

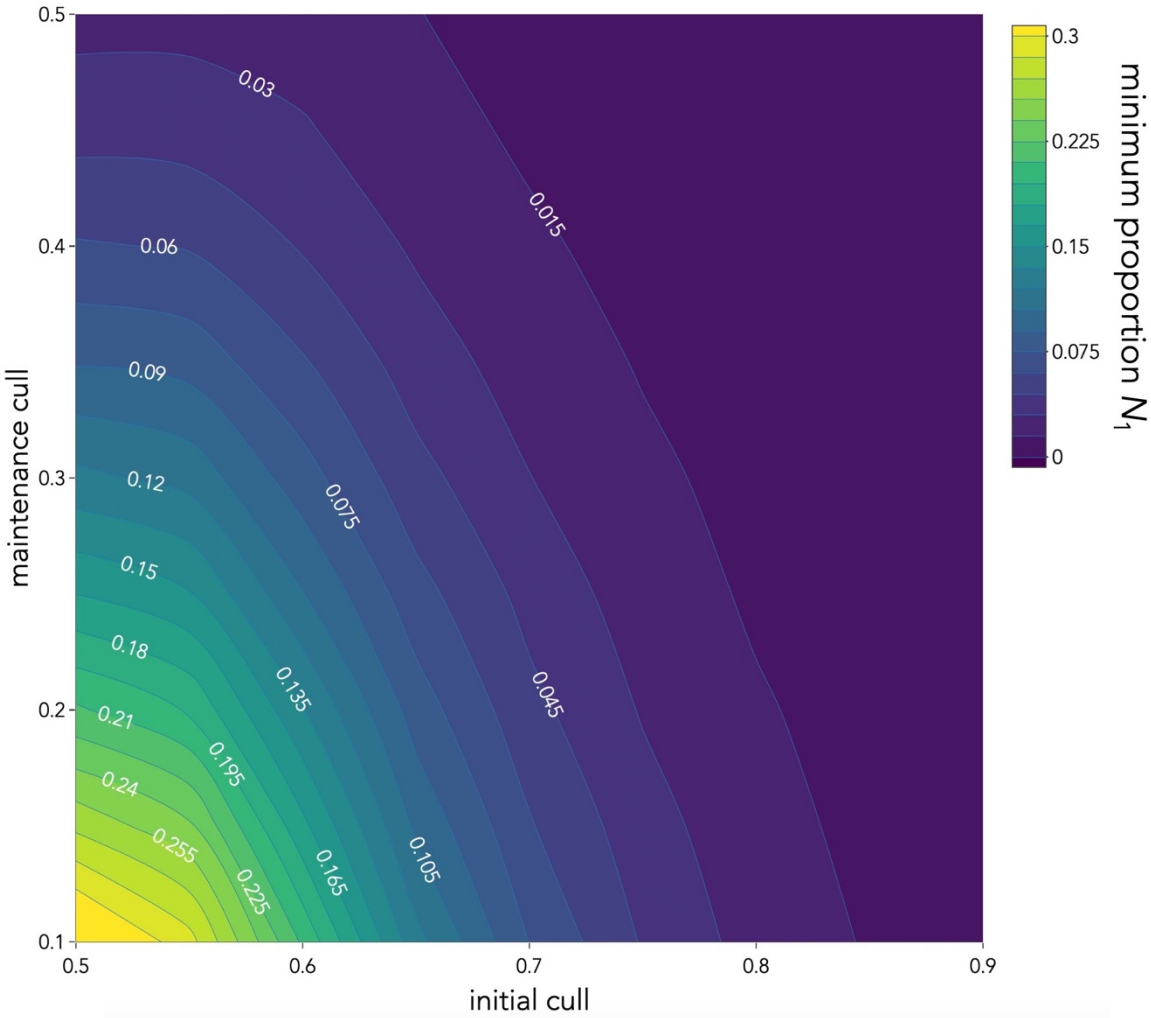
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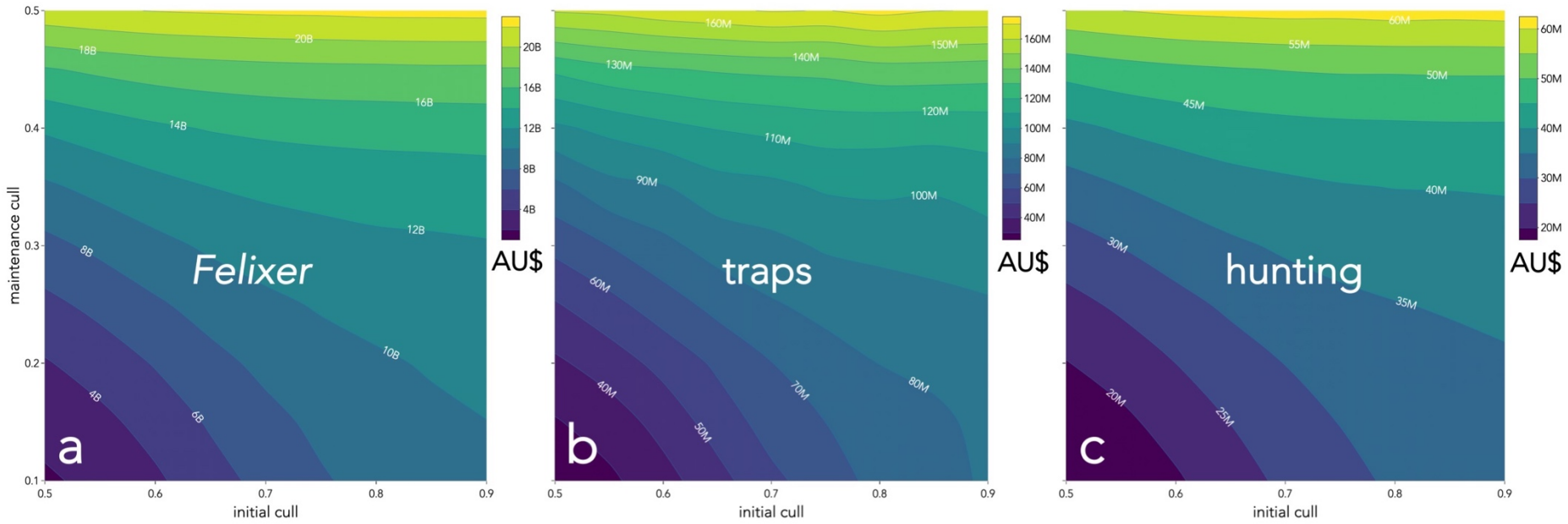
Figure 5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SUPPLEMENTARY MATERIAL

Predicting targets and costs for feral-cat reduction on large islands using stochastic population models

Kathryn R. W. Venning, Frédérik Saltré, Corey J. A. Bradshaw

The following supplementary material includes figures, methods, results and further contextualisation for information given in the main text.

Table of contents

Appendix A – Leakage into the population

Appendix B – Survival modifier

Appendix C – Type III functional response

Appendix D – Stopping culling prematurely

Appendix E – Reduced initial costs of *Felixer*™ units

Appendix A – Leakage into the population

Background

The opportunities for immigration of cats to this island population are low because of strict controls on cat ownership and importation. However, accidental or deliberate releases, or domestic cats breeding with feral animals, are still plausible. All domestic cats on Kangaroo Island must be de-sexed, registered and microchipped by law (Natural Resource Kangaroo Island 2015), which greatly reduces the possibility of a domestic-feral breeding. Nonetheless, we considered a hypothetical scenario of 'leakage' of domestic cats into the population on Kangaroo Island to explore this phenomenon's effects on eradication efficiency.

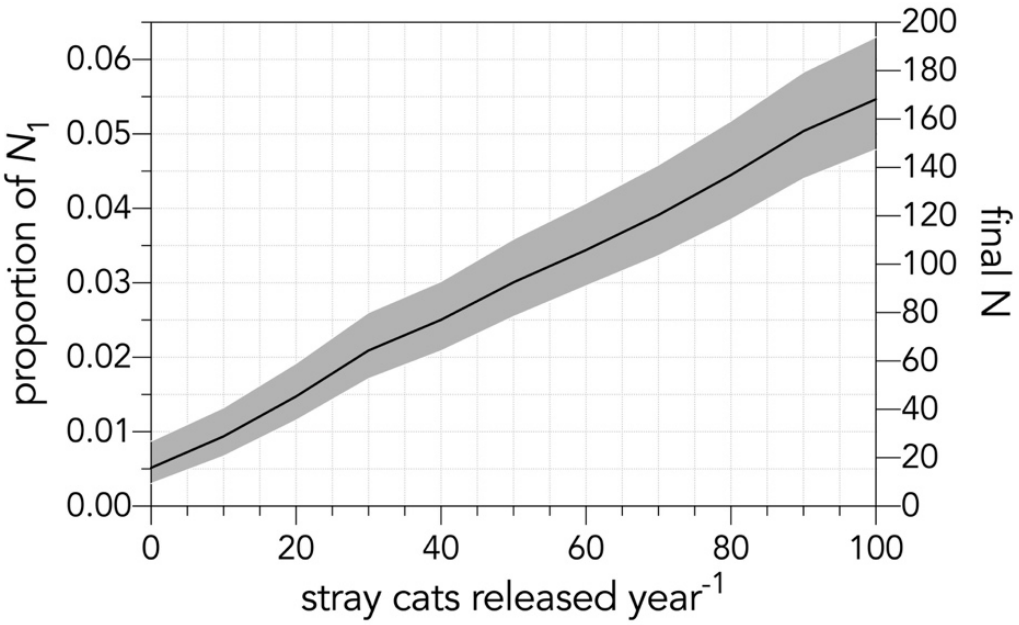
Approach

We used the optimal-culling scenario (two-phase; initial 0.6, maintenance 0.45) to identify how leakage would affect the population at the end of the culling scenario. To achieve this, we added an incrementing number of individuals (between 10 and 100, in intervals of 10) annually to the population vector, while simultaneously running the culling scenario. We ran each leakage scenario for 10,000 iterations (randomly sampling 10,000 times from the stochastic survival and fertility vectors) to calculate the mean and 95% confidence limits for minimum population size.

Results

If no cats are leaked into the Kangaroo Island population (i.e., baseline expectation), the final population at the completion of culling would be 16 cats (range: 9–27, 95% confidence intervals). This would increase by a factor of 1.8 (i.e., 29 cats; range: 21–41) if 10 cats were added annually (Fig. S1). If 50 cats were added annually, the final population would increase to 93 cats (79–111) (Fig. S1).

Figure S1. Final population (*N*) at completion of the ideal culling scenario (two-phase; initial 0.60, maintenance 0.45), adding 10–100 cats annually into the population. Solid black line represents mean population after stochastic resampling. Grey shaded area represents 95% confidence bounds for minimum population size.

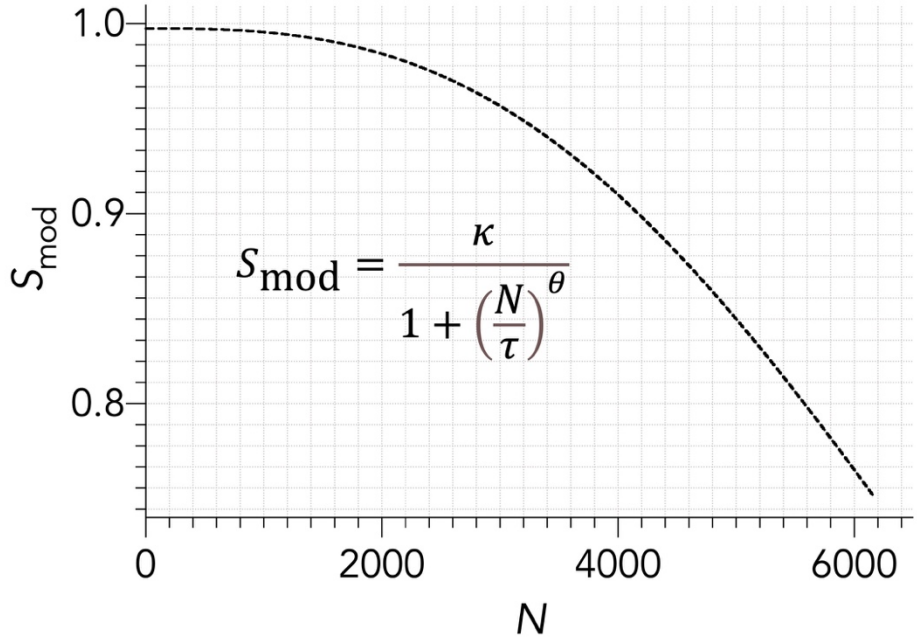


Implications

There are currently 244 registered domestic cats on Kangaroo Island, including a single breeder cat (presuming all cat owners follow the by-laws, this equates to only one domestic cat able to reproduce; Natural Resource Kangaroo Island 2015). It is therefore highly unlikely that 100 cats are leaked into the population annually. However, it is possible that a few cats (1–5) are accidently released annually. Likewise, it is possible some cat owners do not register their pets or accommodate 'stray' cats (provide food and/or water, but no direct ownership). Based on our simulation, leakage to this extent is unlikely to reduce overall eradication efficiency, particularly if owners abide by the by-laws, and with > 90% public approval for eradication (Natural Resource Kangaroo Island 2015) compliance with existing by-laws will be high. Regardless, even an annual leakage of 10 cats could increase the final population after the culling scenario to 1.8 times compared to the baseline scenario (Fig. S1). As such, wildlife practitioners and council members should continue community engagement and to enforce cat ownership by-laws.

Appendix B – Survival modifier (compensatory density-feedback mechanism)

Figure S2. Reduction in probability of survival relative to population size (*N*), with carry capacity (*K)* set to twice the size of the founding population (6,166). κ, τ and θ are constants ($\kappa = 0.998$, $\tau = 9139.109$ and $\theta = 2.835$).



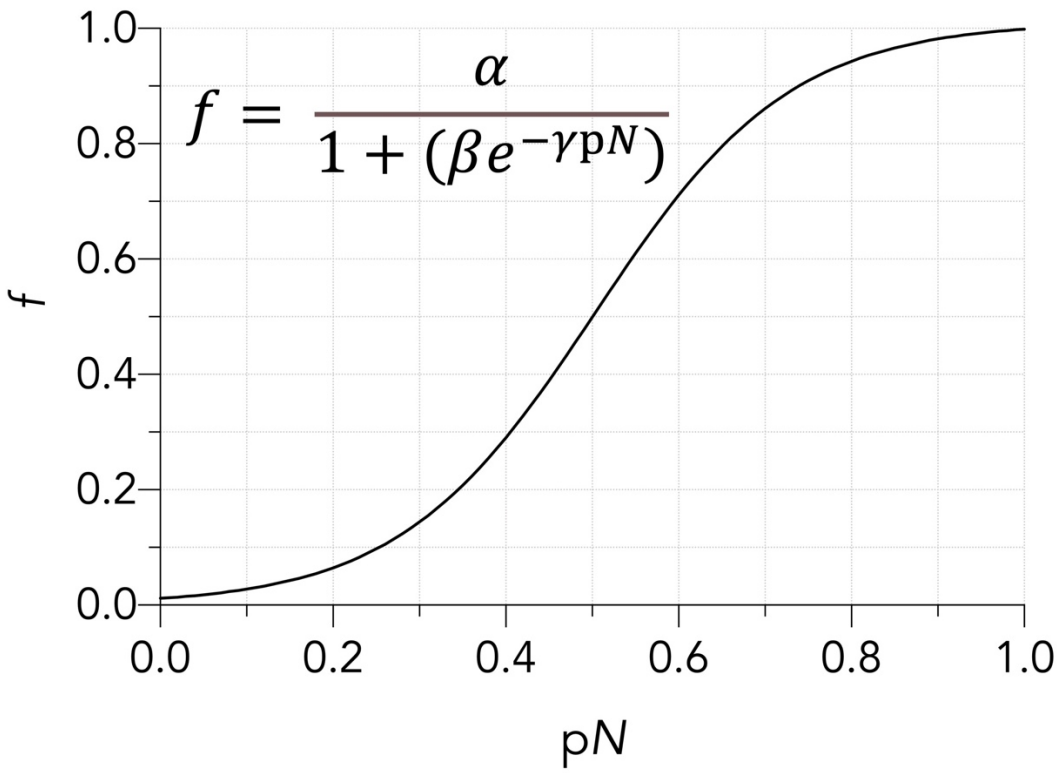
Appendix C – Type III functional response

To force the model to adjust the efficacy of the different culling methods according to the number of individuals in the population, we constructed an arbitrary Type III functional response of the form:

$$f = \frac{\alpha}{1 + (\beta e^{-\gamma \mathrm{p}N})}$$

where f is the relative efficiency of the culling technique, α, β and γ are constants: $\alpha = 1.01$, $\beta = 85.61$, and $\gamma = 8.86$, and pN = proportional population size (Fig. S3). There is no empirical basis for these particular parameter values; instead, we wanted to demonstrate a generic sigmoidal function to alter the efficiency of each culling method.

Figure S3. Reduction in the efficiency of a culling method (f) as the proportion of the remaining population size declines (pN). Here, α, β and γ are constants ($\alpha = 1.01$, $\beta = 85.61$ and $\gamma = 8.86$).



Appendix D – Stopping culling prematurely

Background

Following eradications to completion are essential to achieve density-reduction or eradication goals, but due to funding limitations or unforeseen circumstances, such programs are sometimes cancelled or stopped prematurely (Keitt et al. 2011, Capizzi 2020). Depending on at what stage of eradication a program is stopped, the remaining population can rebuild to its pre-management densities or beyond (Armstrong et al. 2001, Bradshaw et al. 2007).

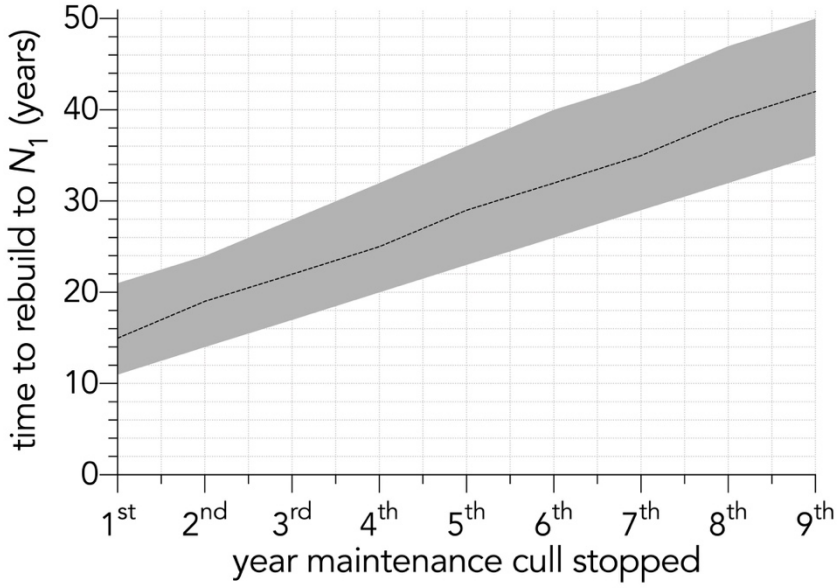
Approach

To examine how quickly the Kangaroo Island cat population would recover to initial population size (N_1 = 3083) relative to variation in the premature stopping of the culling program, we stopped the optimal management cull (0.45 proportionate annual cull) at yearly values following the initial cull (0.60 proportionate cull for first two years). We then allowed the population to rebuild using the same methods as in the untreated population (see main text *Methods*). We then recorded the time it took for the rebuilding population to equate to N_1. We ran each stoppage scenario for 10,000 iterations (randomly sampling 10,000 times from the stochastic survival and fertility vectors) to calculate the mean and 95% confidence limits for population size.

Results

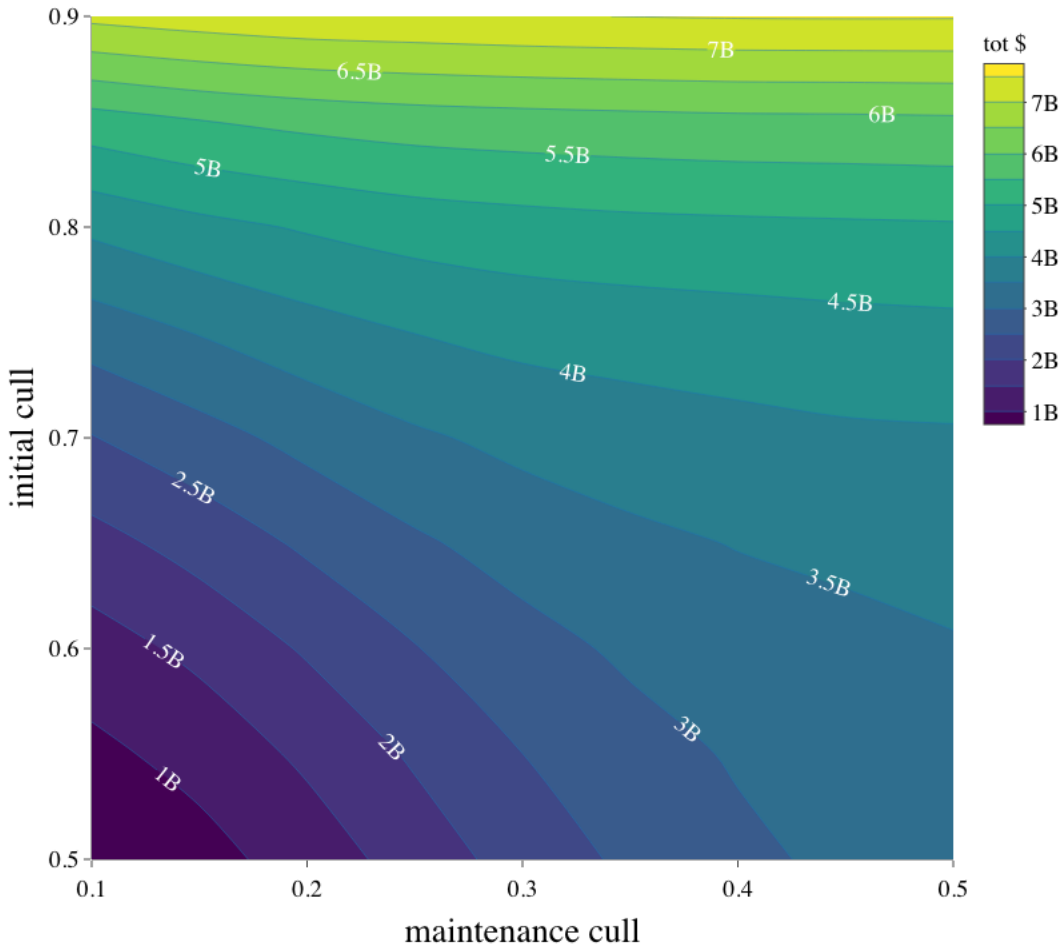
Without a maintenance cull (i.e., only two years with 0.6 proportional cull applied), the population recovers to its initial size in 15 years (range: 11–21 years) (Fig. S4). Stopping culling prior to the end of the targeted duration of the 10-year culling program (i.e., 9th year) results in population recovery to initial size in 42 years (range: 35–50 years) (Fig. S4).

Figure S4. Years required for population to rebuild to founding population size (N_1) when the maintenance cull is stopped prematurely (year maintenance cull stopped). Initial culling of 0.60 for two years is followed by maintenance culling (0.45) for the years indicated. Solid black line represents the median time to rebuild to founding population (years), and the grey area represents the 95% confidence interval.



Appendix E – Reduced initial cost of *Felixer*™ units

Figure S5. Estimated median total cost of feral cat eradication on Kangaroo Island for combinations of two-phase cull (high initial proportional cull followed by steady maintenance proportional cull), where shortfall is made up by *Felixer*™ units. Here, we reduced the initial cost of *Felixer*™ units by 2/3 to simulated resource sharing and/or reduced initial costs. Costs of eradication (in AU$, adjusted for 2020) indicated by colour bar ranging from lowest (purple) to highest (yellow). Contours and white values indicate cost in $AU billions.



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