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ARTICLE

Methods, Tools, and Technologies

Stochastic population models to identify optimal and cost-effective harvest strategies for feral pig eradication

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Abstract

Eradicating feral pigs from island ecosystems can assist in restoring damaged biodiversity values and protect commercial industries such as agriculture. Although many feral pig eradications have been attempted, management decisions are often led by practitioner experience rather than empirical evidence. Few interventions have been guided by population models to identify harvest intensity necessary to achieve eradication within a specified time frame, nor have they applied data on control effort and costs to evaluate the relative cost-effectiveness of proposed control strategies. We used effort and cost data from a feral pig-control program on Kangaroo Island, South Australia, over 17 months to derive functional-response relationships between control effort (in hours per pig) and pig abundance for four control methods: (1) ground-based shooting, (2) trapping with remote triggers, (3) poison baiting, and (4) thermal-assisted aerial culling. We developed a stochastic Leslie matrix with compensatory density feedback on survival to project population trajectories from an initial population (N_0) of 250 female pigs with an estimated island-wide carrying capacity (K) of 2500 over 3 and 10 years for populations subjected to an annual harvest of 35%–95%. We built functional-response models to calculate annual effort and cost for six cull scenarios across all harvest rates. We derived total cost and effort over 3- and 10-year projections from the sum of annual cost and effort within the projection intervals. Pig populations were reduced to <10% N_0 based on harvest rates >80% and 60% for culls of 3- and 10-year durations, respectively. In all scenarios above, the minimum required harvest rate and the total cost to reduce population to ≤10% of N_0 decreased with increasing harvest proportion, with lower total costs incurred over 3 years compared to 10 years. The simulations suggest that the most cost-effective approach for most scenarios is to maximize annual harvest and complete eradication effort over the shortest periods.

KEYWORDS
cost-effectiveness, eradication, island invasive species, Leslie matrix, marginal cost, pest species, population projection, *Sus scrofa*

INTRODUCTION

Management costs and economic losses from invasive species are conservatively estimated at US \$26.8 billion year^{-1} globally for the period 1970–2017, with costs roughly doubling every 6 years over this period and projected to continue rising as the expanding footprint of global transport, trade, and development creates opportunities for invasions (Diagne et al., 2021). Despite increasing global costs, reduction and eradication campaigns are often ad hoc (Pullin et al., 2004; Sutherland et al., 2004). While this can lead to success in some instances (Holmes et al., 2015; Parkes et al., 2010), such an approach is susceptible to bias and might lead to failure (Cook et al., 2010; McMahon et al., 2010). For successful eradication of invasive species, the rate at which individuals are removed must exceed the population's maximum rate of growth to drive the population to extinction (Bomford & O'Brien, 1995; Hone et al., 2010), yet eradication programs regularly fail to harvest sufficiently (Dana et al., 2019). Not achieving project objectives can undermine support for invasive-species management, particularly where control methods already have low social acceptability (Massei et al., 2011; Sinclair et al., 2019). To maintain social license and funding support, invasive species programs require clear, evidence-based targets to maximize probability of success.

Optimizing strategies to maximize probability of success and cost-effectiveness can improve the management of invasive species. Various methods exist for the analyses of cost-effectiveness in conservation and invasive-species management and can be applied at various scales and stages of program development or implementation—for example, to determine spatial (Bode et al., 2008; Martins et al., 2006; Wilson et al., 2006) or taxonomic targets for management (Blaalid et al., 2021), define and compare management objectives (Baxter et al., 2008), evaluate management return on investment (Murdoch et al., 2007), and compare cost-effectiveness of strategies and methods (Baxter et al., 2006; Spring & Cacho, 2015).

An inherent, but often neglected component of cost–benefit analyses applied to invasive-species management is functional responses. Functional responses typically not only describe the efficiency of predators at catching prey (Holling, 1959), but also describe changes in efficiency of methods to control invasive animals (Hone, 1990b), which are analogous to predator–prey relationships. The functional response can be inferred by observing changes in effort (e.g., in hours per pest, pests per hour) relative to abundance (Choquenot et al., 1999). If the cost per unit effort is known, functional-response relationships specific to the control method can be applied to predict the cost of invasive animal control relative to density.

Leslie matrix population models that project population change within discrete age-classes and time intervals (Caswell, 2001; Leslie, 1945), are one such approach that has been applied broadly to the management of threatened and invasive species (Fieberg & Ellner, 2001). Matrix population models allow the maximum rate of population growth to be determined, thereby identifying minimum harvest rates necessary to achieve population reduction within projected time frames (Venning et al., 2021). Used in combination, matrix population models and functional responses can identify minimum thresholds for effective management of invasive species, allowing comparison of the relative cost of management for scenarios that remove pests at various rates above the minimum threshold. Here, we present a case study of this approach, combining a stochastic matrix population model for feral pig population change with functional-response estimates derived from operational cost-and-effort data from a recent feral pig-eradication program on Kangaroo Island, South Australia.

Feral pigs (*Sus scrofa*) are an invasive species causing a wide range of environmental, economic, and social damages (Barrios-Garcia & Ballari, 2012; Bengsen et al., 2014; O'Bryan et al., 2022). In Australia, feral pigs occupy about 40% of the mainland and offshore islands (Lapidge et al., 2012), with a total, yet highly uncertain, population estimated at 13.5 million (95% CI from 3.5 to 23.5 million) (Choquenot, 1996; Hone, 1990a). In Australia, costs associated with direct damages, losses, and management of feral pigs since 1960 are estimated to range between US \$9.54 billion (considering all available reported costs) and US \$0.73 billion (when only highly reliable costs are considered) (Bradshaw et al., 2021). Feral pigs are recognized as a key threatening process under the *Environment Protection and Biodiversity Conservation Act 1999*, with impacts on at least 148 nationally threatened species and 8 threatened ecological communities (Commonwealth of Australia, 2017). They are a declared invasive species and are subject to control programs in all Australian jurisdictions.

On Kangaroo Island in South Australia (Australia's third-largest island at approximately 4430 km^2) (Robinson et al., 1999), feral pigs have been a hazard to threatened and endemic species (Masters et al., 2011). First introduced in 1803 (Cooper, 1954), the population grew to an estimated 5400 individuals distributed over about 1400 km^2 (31.6%) on the western end of the island (Masters et al., 2011). Despite sporadic efforts to reduce their numbers (Masters et al., 2011; Southgate & Florance, unpublished report), feral pigs persisted, costing the local economy ~US \$660,000 (AU \$1 million) year^{-1} (Primary Industries and Regions South Australia, 2020). The catastrophic bushfires of summer 2019–2020 reduced the pig population to ~500 individuals, presenting a rare opportunity to attempt eradication. The Australian and South Australian Governments allocated ~US \$1.76 million (AU \$2.66 million) over 3 years to achieve eradication (Primary Industries and Regions South Australia, 2020) using a combination of control methods including ground-based shooting, poisoning with sodium nitrite (HOGGONE), trapping, and thermal-assisted aerial culling—a novel approach to aerial culling that uses thermal imagery to improve detection (Bradshaw et al., 2023; Cox et al., 2023).

Our aim was to (1) develop a stochastic matrix population model to determine the minimum rate of pig harvest required to achieve eradication, independent of control type, and (2) use operational cost and effort observations to predict the cost of eradication under a variety of simulated culling regimes when applied at or above the minimum required rate of pig harvest. We (1) constructed a stochastic population model and applied annual harvest rates ranging from 0.2 to 0.95 to determine minimum annual harvest rates to achieve eradication with target time frames, (2) projected the reduction of the pig population based on different methods of control, and (3) estimated the relative costs and effort of employing the different methods available. We used operational cost and effort observations from pig control on Kangaroo Island to estimate functional responses for four control methods (ground shooting, trapping, poison baiting, and thermal-assisted aerial culling). We applied these functional responses to estimate the total effort and cost required to achieve population reduction to ≤0.1 of the initial population ($N_0 = 250$) for six control scenarios, including four scenarios relying on one method only, and two scenarios that applied all four control methods in fixed and varying proportions to simulate generic best practice. We applied each control scenario over time frames ranging from 1 to 10 years to identify if efficiency gains could be achieved by applying controls at lower intensity and over a longer duration. We applied all harvest scenarios to calculate cost and effort at annual harvest proportions ranging from 0.35 to 0.95. We hypothesize that if functional response theory can describe density-dependent catch–effort relationships, we can then predict the control costs by estimating the effort and cost per animal at any given population density.

METHODS

Study site

Feral pigs were distributed over approximately 1400 km^2 (31.6%) on the western end of Kangaroo Island (Masters et al., 2011) (Figure 1). Large tracts of native forest and shrubland remain, particularly in the west and south of the island, at the coastal fringe, and on roadsides, accounting for approximately 53% of total landcover (Willoughby et al., 2018). Approximately 68% of remaining natural vegetation is protected within Conservation Reserves and Wilderness Protection Areas, accounting for around 32% of the island's area (Robinson et al., 1999). Dryland agriculture and plantation forestry account for 35% and 3% of landcover, respectively, and are major components of the Kangaroo Island economy (O'Neil et al., 2017; Willoughby et al., 2018).

Stochastic population model

We constructed a female-only, post-breeding Leslie (age-structured) matrix model in R (R Core Team, 2022) to project annual population growth (Caswell, 2001). The model assumes a sex ratio of 1:1 (Snow et al., 2019) and equal probability of survival between males and females. In Australia, few pigs are suspected to live beyond 5 years (Choquenot, 1996), although longevity up to 12–14 years has been reported (Snow et al., 2019). We set the maximum age at 14 years, although the probability of survival in age class is $n_{14} > 0$ (see Table 1), allowing individuals to live beyond 14 years in some instances.

Given a maximum age of 14 years, the deterministic matrix **A** is:

$$\mathbf{A} = \begin{bmatrix} f_1 & f_2 & f_3 & \dots & f_{13} & f_{14} \\ s_1 & 0 & 0 & \dots & 0 & 0 \\ 0 & s_2 & 0 & \dots & 0 & 0 \\ 0 & 0 & s_3 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & s_{13} & s_{14} \end{bmatrix},$$

where f_x = age specific fertility (the number of female offspring per individual per year in age class x) and s_x = age specific survival (the probability of surviving from age t to $t+1$). For an initial population N:

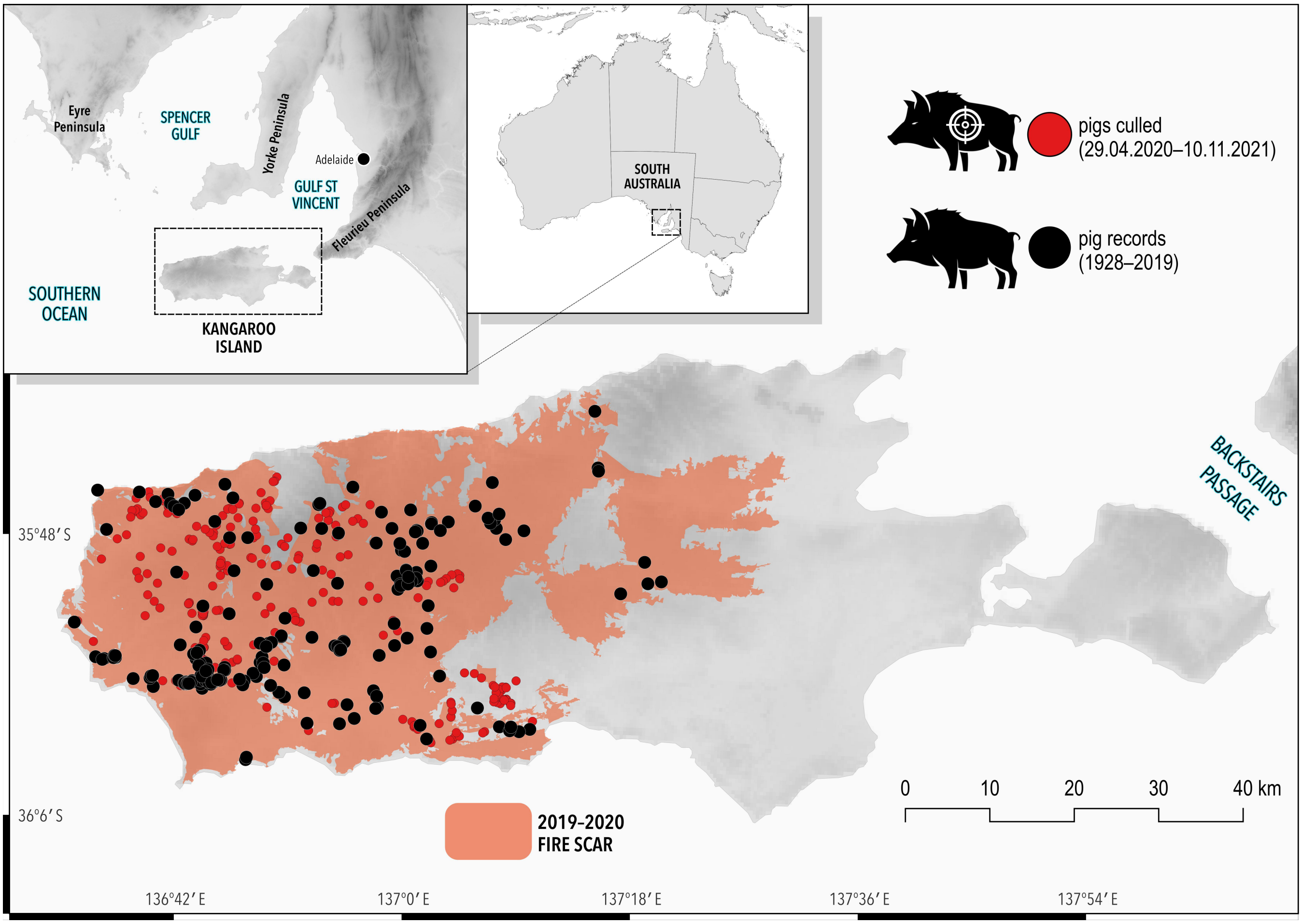

FIGURE 1 Kangaroo Island, showing its location relative to the Australian mainland. The orange area indicates the extent of the 2019–2020 bushfires. Black dots indicate the location of pig records 1928–2019 (ALA.org, 2024), and red dots indicate the location of pig culling events recorded after the 2019–2020 bushfires.

TABLE 1 Fertility and survival values (mean and SD) for all age classes used in the stochastic model.

Vital rate	Mean	SD
Fertility (daughters)		
Juvenile (f_1)	0.79	0.099
Adult ($f_{2–14}$)	2.38	0.089
Survival		
Juvenile (s_1)	0.45	0.203
Adult ($s_{2–14}$)	0.675	0.310

$$N_t = \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ \vdots \\ n_{14} \end{bmatrix},$$

where n_x = number of females in age class x at time t, population growth can be projected as:

$$N_{t+1} = \mathbf{A}N_t. \tag{1}$$

The mean and SD of age-specific vital rates (survival and fertility) are required to project stochastic population growth. These are unreported for the Kangaroo Island pig population, and data are insufficient to calculate these from harvest records (e.g., Skalski et al., 2005). In lieu of available local estimates, we used ranges for survival and fertility reported for Australian pig populations (Choquenot, 1996). We approximated SD for each range under the assumptions of the Student's t distribution as (Appendix S2: Table S1):

$$\mathrm{SD} = \frac{\text{high range value} - \text{low range value}}{2(1.96)}. \tag{2}$$

At each time-step and for each age class, we accounted for stochastic variation in the model by randomly resampling from Gaussian and beta distributions around the means of fertility and survival probabilities, respectively (Table 1).

Population projections

To produce a vector of females per age class (N_0), we calculated the population's stable stage distribution from the deterministic matrix **A** (Caswell, 2001) and multiplied this by the initial population size of 250 (females only). We used N_0 as the initial population in all simulations. We assumed that the carrying capacity (K) was 5000 individuals. Because the Leslie matrix projects change in the number of females only, we adopted $K = 2500$ for the female-only model. Systematic estimates of the Kangaroo Island pig population have not been reported but, prior to the 2019–2020 bushfires, the population was estimated at 675 and 5400 individuals occupying an area of 140,000 ha (31.6%) of Kangaroo Island (Masters et al., 2011) based on densities of 0.5 to 4 pigs km^{-2} observed elsewhere in Australia (Choquenot, 1996). Monitoring over the period 2009 to 2018 estimated a stable population (Masters et al., 2011; Primary Industries and Regions South Australia, 2020; Southgate, unpublished report; Southgate & Florance, unpublished report), and discussions with local wildlife managers on Kangaroo Island supported the estimated K and pre-bushfire population of ~5000.

At each time increment of the projection, survival probabilities in all age classes were recalculated using a modifier to simulate compensatory density feedback. We modified survival (S_{mod}) as:

$$S_{mod} = \frac{\kappa}{1 + \left(\frac{N}{\tau}\right)^{\theta}}, \tag{3}$$

where N = population size, and κ, τ, and θ are constants ($\kappa = 1$, $\tau = 2500$, $\theta = 3$) such that applied survival probabilities decrease as the population approaches K. We defined these constants arbitrarily through iterative changes to the modifiers until the population projection returned the expected response (Figure 2).

Constant proportional cull

We first simulated a "baseline" stochastic projection (1000 simulations) to examine median projected growth in an unmanaged population, that is, a population not subjected to any density-reduction measures. We projected population growth from N_0 over 100 years (approximately 40 generations) to test the stability of the unmanaged population (Frankham et al., 2014), incorporating annual stochasticity and density feedback on survival as described above. We then built a constant proportional cull model to examine the influence of annual harvest rate on the proportion of population remaining over two different projection intervals—3 and 10 years.

While the Kangaroo Island Feral Pig Eradication Program seeks to achieve complete eradication, we modeled costs based on a population reduction target >0 because data were not available for pig control effort below an estimated population size <200. We expect that eradication costs will increase substantially as pig density approaches zero (Choquenot, 1996), but we could not infer the true rate of change reliably from the available data, and cost estimates would become increasingly imprecise as simulated population size approached zero. In lieu of these data, we applied a target population threshold of $N_0 \leq 0.1$ (≤25 females; 1% of K) based on the lower end of the "50/500" rule where <50 N_e (effective population size) is considered prone to inbreeding depression and extinction (Frankham et al., 2014).

We selected the 3-year projection interval to align with the Government of South Australia's target time frame for the eradication of feral pigs from Kangaroo Island (Primary Industries and Regions South Australia, 2020). We also selected a 10-year projection interval arbitrarily (but conceivably within a management-relevant time frame) for comparison. For each year of the projection interval, the constant proportional cull model reduced the population by the same proportion, from 0.2 to 0.95 in increments of 0.05. For each harvest proportion, we repeated the model over 1000 simulations, incorporating stochastic variation in fertility and survival as described above. For all simulations and harvest rates, we recorded the minimum projected proportional population size after each time increment. From these, we calculated median minimum proportional population size and 2.5th and 97.5th percentiles for all harvest rates at both projection intervals.

Pig-control data

The Government of South Australia Department of Primary Industries and Regions provided pig-control data from 29 April 2020 to 7 December 2021. These data included outcomes from pig control completed by a range of control actors, including government employees (Primary Industries and Regions, South Australia, Kangaroo Island Landscapes Board and National Parks and Wildlife Service, South Australia), pest-control contractors, non-government organizations, and members of

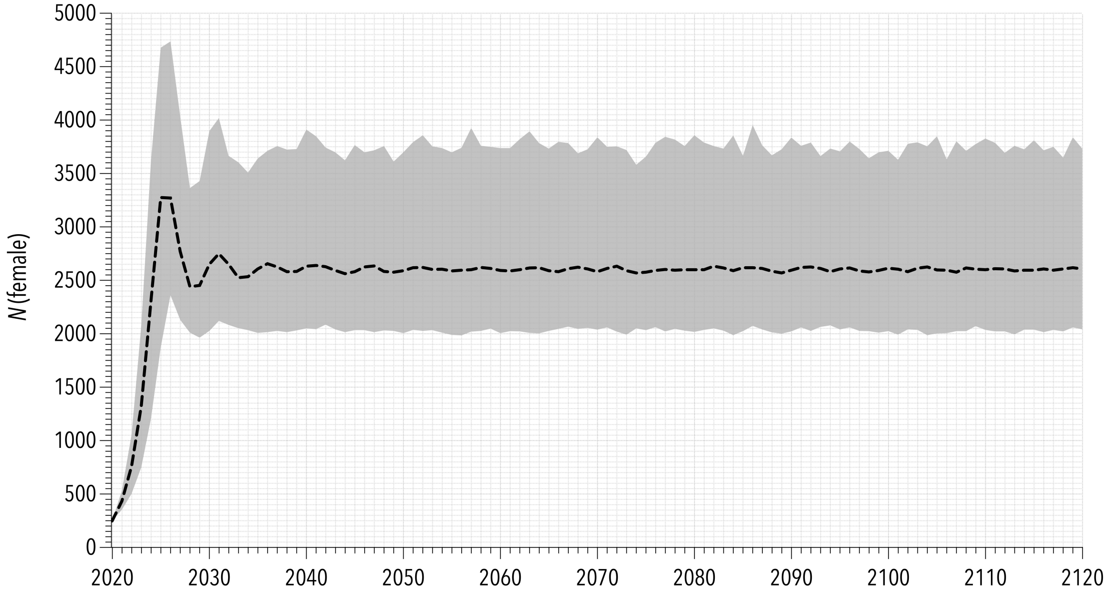

FIGURE 2 Stochastic population growth in an unmanaged population from an initial population (N_0) of 250 females over 10-year projection interval with compensatory density feedback applied to survival. Black dashed line indicates median population growth from 1000 simulations; gray-shaded area indicates 2.5th and 97.5th percentiles.

the public. Each record included the date, time, geographic coordinates, number of pigs killed, and the control method used. Most records included the amount of effort (in hours) expended per event and name of the individual or organization who did the control. Of the 757 pigs killed, sex was only reported for adult pigs, which were identified as either sows ($n = 145$) or boars ($n = 111$), or was unreported for the remaining pigs ($n = 501$). This gave an observed adult sex ratio of 1.31:1 (female: male) (95% CI: 1.11:1–1.54:1), but because the non-adult sex ratio was not known, we assumed a sex ratio of 1:1 (Snow et al., 2019). Age was reported using broad life stages, for example, adult ($n = 256$, 34%), porker ($n = 163$, 22%), piglet ($n = 173$, 23%), and unspecified ($n = 165$, 22%).

Pig-control methods

The data included four main pig-control methods: (1) shooting, (2) thermal-assisted aerial culling, (3) trapping, and (4) poison baiting. Additional causes of death were reported including vehicle strike ($n = 2$), dogs ($n = 2$), and unspecified ($n = 20$). Ground shooting was done through active searching (e.g., tracking, spotlighting, thermal imagery), opportunistic encounters, and shooting at sites where feed had been deployed as an attractant. Shooting records did not specify the approach taken, but we inferred this from knowledge of the preferred method of individual pig controllers through discussion with project staff (M. Korcz, Kingscote, South Australia, personal observation) and estimated that 58.8% of total shooting effort included free feeding. Using this estimate, we assigned free-feeding costs proportionately to the total estimate of shooting effort (see *Costs* below).

Thermal-assisted aerial culling data were collected during two culls done from 18 to 30 March 2021 and 20 August 2021–24 September 2021. HeliSurveys (helisurveys.com.au) was engaged to provide the helicopter, pilot, and thermal camera operator, while the marksman was a Government of South Australia employee. The helicopter traveled at a height of 50–100 m above ground and at between 15 and 25 knots ground speed while searching.

Trapping was done using the MINE (manually initiated nuisance elimination) Trapping System (Jager Pro, 2022), a remotely triggered, corral-style trap (diameter ~10.5 m, height ~1.7 m). The traps are connected to the mobile communication network and use motion-sensing cameras to detect movement within the trap. Operators are notified by text or email when motion is detected, real-time images are reviewed, and a decision made either to trigger the trap or wait. To minimize neophobic avoidance behavior, trap deployment and activation occurred in a staged manner over several days, including delivery of trap components to the site, gradual assembly of the corral, and deployment of grain (attractant).

Poison baiting was done using HOGGONE meSN microencapsulated sodium nitrite bait (Animal Control

Technologies Australia, 2020). Baiting involves a staged process, like that used for trapping, whereby free feeding encourages pigs to congregate at the bait site over several days before placebo baits are introduced to train feeding from the bait dispenser and ultimate deployment of toxic bait.

Sex ratios with 95% CI were calculated for all control methods. However, due to the large number of records for which the sex of killed pigs was not reported, we assumed all control methods had the same effect on males and females.

Efficiency

To estimate changes in efficiency of control methods relative to proportion of pigs remaining, we calculated specific relationships between the proportion of pigs remaining after each control event and efficiency for individual control methods. Efficiency (in hours per pig) of the ith event (E_i) is:

$$E_i = \frac{f_i}{n_i}, \tag{4}$$

where n_i = number of pigs killed in the ith event and f_i = effort (in hours) expended in the ith event. For thermal-assisted aerial culling, multiple kill events were often recorded per flight (e.g., several distinct groups of pigs encountered during the flight), but the effort was only recorded as total flight time per outing. As such, we counted each flight outing as a unique event and calculated efficiency as the total number of pigs killed per flight divided by the flight duration. We could not calculate event-specific efficiency for events where effort was not reported, nor could we calculate it for events where cause of death was reported as anything other than by using one of the four main control methods.

Because we do not know the true number of pigs in the total population, we calculated change in proportion of pigs remaining relative to the total number of pigs killed during the study period (29 April 2020 to 7 December 2021), plus the estimated number remaining on Kangaroo Island ($n = 200$) at the end of the study period (Primary Industries and Regions South Australia, 2021). Therefore, the proportion of the feral pig population remaining ($N_{p,i}$) after the ith event was:

$$N_{p,i} = \frac{(n_{\text{total}} + 200) - n_{i,\text{total}}}{(n_{\text{total}} + 200)}, \tag{5}$$

where n_{total} = total number of pigs killed during the collection period ($n = 757$) and $n_{i,\text{total}}$ = total number of pigs killed up to and including the ith event. We included all reported pig kills in the total number killed, including events where effort was unreported or cause of death was reported as anything other than one of the four main control methods, to allow calculation of proportional population change over time.

Functional responses

To compare model performance, we fitted logarithmic, exponential, and linear models to the relationship between proportion of pig population remaining and effort per pig for each control method. We assumed that the efficiency of all control methods decreases as population density declines, following a Type II functional response (Choquenot et al., 1999; Hone, 1990b) resulting from decreasing probability of "capture" (detection/destruction) (Caley & Ottley, 1995). Contrary to this assumption, raw data for trapping and shooting exhibited trends of increasing efficiency with decreasing proportion of pigs remaining, and the efficiency of poisoning only declined weakly as the proportion of pigs remaining declined (Appendix S1: Figure S1). Because we did not know the underlying error structure, we could not do a formal outlier analysis. However, we attempted two methods to obtain functional response models that satisfied the expected Type II functional response for shooting, poisoning, and trapping.

First, we stratified control data according to the contributing individual, or organization/group, where details of individual contributors were not provided. For each control method, we analyzed records for each individual or organization/group to see if functional responses could be observed. Shooting records ($n = 82$) could be attributed to between 8 and 25 operators. Only three individual operators were identified, "BF" ($n = 60$), "DJ" ($n = 9$), and "PJ" ($n = 8$), with the remaining records identified by contributing organization only. Single records were contributed by unidentified operators from both Kangaroo Island Landscape Board ($n = 1$) and South Australian Department of Primary Industries and Resources ($n = 1$), while the remaining records were contributed by organizations/groups identified as South Australian National Parks and Wildlife Service ($n = 5$), farmers ($n = 7$), and "other" ($n = 9$). In the cases of South Australian National Parks and Wildlife Service, farmers, and "other," we could not determine if these were contributed by the same or different individuals. Satisfactory model fit was not achieved for any of the individuals or organizations/groups (Appendix S1: Figure S2).

Records for trapping ($n = 10$) and poisoning ($n = 18$) could not be attributed to individual operators and so we instead attributed them to the contributing organization only. Trapping records were contributed by South Australian National Parks and Wildlife Service ($n = 4$), South Australian Department of Primary Industries and Resources ($n = 3$), and South Australian Department of Environment and Water ($n = 2$) to which we were able to fit logarithmic and exponential functional response curves to data provided by South Australian National Parks and Wildlife Service and South Australian Department of Primary Industries and Regions (Appendix S1: Figure S3).

Poisoning records were contributed by South Australian National Parks and Wildlife Service ($n = 6$), South Australian Department of Environment and Water ($n = 5$), Kangaroo Island Landscape Board ($n = 5$), and "other" ($n = 2$), to which we fit the logarithmic and exponential functional response curves to records contributed by each organization (Appendix S1: Figure S4). However, due to few records for both trapping and poisoning, we applied the functional responses derived from the combined datasets to produce our cost estimates.

Our second method for achieving model fit in keeping with the expected Type II functional response involved visually inspecting plots of effort per kill (in hours per pig) relative to proportion of pigs remaining to identify obvious outliers (Appendix S1: Figure S1). We then removed all records contributed by the individual or organization responsible for the outliers. We then refit the models, resulting in satisfactory relationships in the expected direction.

We used Akaike's information criterion weights (w_i) and the information-theoretic evidence ratio to compare model performance to identify which model (logarithmic, exponential, linear) best fit the abundance-efficiency functional response. Differences between model performances were negligible across all control methods (Table 2). We chose the exponential model to apply in the subsequent stages of effort and cost estimation (see below) because it conforms best to the expected Type II functional response for species reduction.

Costs

We describe costs below (summarized in Table 3). Generic costs that were applicable to more than one control method included: (1) Labor—US \$24.33 (AU \$36.87) person^{-1} h^{-1}, based on South Australia Public Sector Award OPS4 classification (Commissioner for Public Sector Employment, 2017). (2) Ammunition—US \$2.64 (AU \$4.00) pig^{-1} based on US \$1.32 (AU \$2.00) bullet^{-1} at a rate of 2 bullets pig^{-1} allowing for misses and sight zeroing. (3) Feed grain—US \$9.24 (AU \$14.00) day^{-1} site^{-1} based on deployment of 10 kg grain at US \$0.92 (AU \$1.4) kg^{-1} and assuming grain-deployment effort of 1 h day^{-1}. We assumed the same effort rate for deployment of placebo bait and toxic bait. (4) Vehicles—costs associated with vehicle use, for example, annual lease, fuel, mileage, and maintenance were not reported and are expected to vary based on the type of vehicle used, distances traveled, fluctuation in fuel cost over time, and whether the vehicle was leased or owned, etc. In lieu of accurate vehicle costs, we assigned generic vehicle costs of US \$6.6 (AU \$10) h^{-1} for each hour of labor required for shooting, trapping, and baiting. Although arbitrary, this allowed the inclusion of a vehicle-cost component proportional to the effort required for each of these control methods. Vehicle costs were not included in thermal-assisted aerial culling cost estimates. We excluded several generic costs from the cost calculations, including general administrative overheads (office space and equipment, project administration, office-based staff, community/stakeholder engagement, etc.), and costs associated with deploying and maintaining trail cameras for monitoring pig activity because these are assumed to be constant for the pig-eradication project, independent of control method. We did not include cost of firearms in the method-specific costs assuming firearms can be employed across multiple control methods, for example, destruction of pigs caught in traps, ground-based and aerial shooting.

We summarized method-specific costs as

1. Thermal-assisted aerial cull—Project initialisation cost US \$8016.36 (AU \$12,146.00), including crew mobilization (pilot and camera operator) and helicopter from Jindabyne, New South Wales, project data management, and initial fuel delivery. Crew and helicopter flight time, including wages, fuel, and maintenance, cost US \$1638.56 (AU \$2482.66) day^{-1}, with average flight effort of 3.7 h day^{-1}. Additional daily costs include helicopter crew meals and accommodation, and government marksman labor, meals, and accommodation. Helicopter crew meals and accommodation cost US \$277.2 (AU \$420) day^{-1} crew^{-1}. Government marksman labor cost assumed the marksman was engaged in cull-related activities on a full-time basis for the duration of the cull. Labor cost was accrued at the OPS4 hourly labor rate in increments of 7.5 h day^{-1}, based on 37.5 h week^{-1}, equating to US \$182.51 (AU \$276.53) day^{-1}. Marksman accommodation and meals were charged separately to those of the helicopter crew, costing US \$82.5 (AU \$125) day^{-1}. A fuel-resupply charge of US \$822.36 (AU \$1246) was incurred every 30 days, equivalent to 111 h of flight effort based on average flight effort of 3.7 h day^{-1}.

TABLE 2 Comparison of models (log, logarithmic; exp., exponential; lin, linear) fitted to the relationship between effort per pig and proportion of pig population remaining for trapping, shooting, thermal-assisted aerial culling, and poisoning.

	w_i			Evidence ratio		
Control method	**Log**	**Exp**	**Lin**	**Log:exp**	**Exp:lin**	**Log:lin**
Trapping	**0.3361**	0.3345	0.3294	1.00	1.02	1.02
Shooting	0.3776	**0.4877**	0.1346	0.77	3.62	2.80
Thermal-assisted aerial culling	0.3232	0.3292	**0.3476**	0.98	0.95	0.93
Poisoning	0.3315	0.3214	**0.3471**	1.03	0.93	0.95

Note: AIC weights (w_i) in boldface indicate the top-ranked model for each control method.
Abbreviation: AIC, Akaike's information criterion.

2. Shooting—Costs largely comprised hourly labor and bullets per pig, as described in the generic costs above. Additionally, free-feeding cost was accrued at US \$5.43 (AU \$8.23) h^{-1} (US \$9.24 (AU \$14) h^{-1} multiplied by 0.588) based on the proportion of shooting effort estimated to have occurred with free feeding.
3. Trapping—We assumed effort per trapping event and the number of events per trap per projection interval to be constant, such that the number of pigs per trap and number of traps required could both be calculated for each projection interval based on the current population size, proportional harvest rate, and the density-dependent effort predicted by the functional response model. We rounded effort to 30 h $trap^{-1}$ based on mean observed effort of 9.875 h $event^{-1}$, plus an estimated additional 20 h $event^{-1}$ trap set-up time that was not included in reported effort (M. Korcz, Kingscote, South Australia, personal observation). We calculated grain cost at US \$91.25 (AU \$138.25) $event^{-1}$ based on mean observed effort multiplied by generic, free-feeding cost h^{-1}. Labor cost US \$928.03 (AU \$1406.10) $event^{-1}$ based on 30 h $trap^{-1}$ multiplied by the sum of generic labor and vehicle cost per hour. Jager Smart Traps cost US \$6270 (AU \$9500) each (M. Tarran, Adelaide, South Australia, personal observation). A single trap has capacity to complete an average of 10 trapping events $year^{-1}$ based on estimated deployment time of 4–6 weeks $event^{-1}$ (M. Korcz, Kingscote, South Australia, personal observation), equating to annual effort of 300 h $trap^{-1}$ $year^{-1}$ (30 h $trap^{-1} \times 10$ events $year^{-1}$). We assumed traps were reusable for the duration of the projection intervals such that additional traps were only purchased in subsequent years if the model projected an increase in trap numbers over time, such that the number purchased in any year equalled the number required minus the sum of traps purchased in all previous years.
4. Baiting—We assumed the mean observed baiting effort of 12.692 h $event^{-1}$ to be constant for cost estimation. Labor cost was US \$392.61 (AU \$594.89) $event^{-1}$ based on mean observed baiting effort multiplied by the sum of generic labor cost per hour and vehicle cost per hour. Cost of grain for free-feeding was US \$71.08 (AU \$107.69) $event^{-1}$ (mean observed baiting effort minus 5 h $event^{-1}$ multiplied by the generic free-feeding cost per hour). We deducted 5 h because grain is replaced by placebo baits (4 h $event^{-1}$) and toxic baits (1 h $event^{-1}$) in the final stages of baiting. Bait dispensers cost US \$320.1 (AU \$485) each and have capacity for 6 placebo bait or toxic baits. Multiple dispensers were used at baiting sites in some instances, with a mean rate of 1.45 dispensers $site^{-1}$ during the collection period. An individual dispenser or set of dispensers were capable of servicing 28.76 events $year^{-1}$, assuming constant deployment at 365 days $year^{-1}$, 1 h effort day^{-1}, and 12.692 h $event^{-1}$. As with trapping, we assumed that bait dispensers were reusable for the duration of the projection intervals and additional dispensers only purchased in subsequent years to make up shortfall if dispensers purchased in previous years did not satisfy the number of traps required. Placebo baits cost US \$147.84 (AU \$224) $dispenser^{-1}$ $event^{-1}$ (US \$9.24 (AU \$14) each at 6 day^{-1} $dispenser^{-1}$ for 4 days). Toxic baits cost US \$102.96 (AU \$156.00) $dispenser^{-1}$ $event^{-1}$ (US \$17.16 (AU \$26) each at 6 day^{-1} $dispenser^{-1}$ for 1 day).

Culling scenarios

We estimated effort and cost for six different culling scenarios, comprising four scenarios in which 100% of the harvest quota was achieved by each of the four control methods (i.e., shooting, thermal-assisted aerial culling, trapping, and poison baiting) individually. The remaining two scenarios applied the four control methods in combination, simulating generic integrated pest-management approaches. These included an equal proportion harvest scenario where each method removes 25% of the annual harvest quota, and a relative cost-proportional-allocation

TABLE 3 Summary of generic and method specific costs.

Item	Unit cost	Unit	Accrual interval (effort hours)	Detail
Generic costs				
labor	US \$24.33 (AU \$36.87)	$person^{-1}$ h^{-1}	1	South Australia Public Sector Award OPS4 classification (Commissioner for Public Sector Employment, 2017)
ammunition[a]	US \$2.64 (AU \$4.00)	pig^{-1}	NA	US \$1.32 (AU \$2.00) $bullet^{-1}$ at an average rate of 2 bullets pig^{-1} allowing for misses and sight zeroing
feed grain	US \$9.24 (AU \$14.00)	day^{-1} $site^{-1}$	1	10 kg grain at US \$0.92 (AU \$1.4) kg^{-1} and assuming grain-deployment effort of 1 h day^{-1}
vehicle[b]	US \$6.60 (AU \$10.00)	h^{-1}	1	arbitrary cost inclusive of fuel, milage, maintenance and administration
Method-specific costs				
thermal-assisted aerial cull				
Project initialisation	US \$8016.36 (AU \$12,146.00)	Once off cost	NA	
helicopter crew and flight time	US \$1876.16 (AU \$2482.66)	day^{-1}	3.7	3.7 h effort day^{-1} based on mean observed daily cull effort (flight time)
helicopter crew accommodation and meals	US \$277.20 (AU \$420.00)	day^{-1}	3.7	
government marksman labor	US \$182.51 (AU \$276.53)	day^{-1}	3.7	OPS4 hourly labor rate × 7.5 h day^{-1}; assumes marksman daily cost accrued for each 3.7 cull effort
government marksman accommodation and meals	US \$82.5 (AU \$125.00)	day^{-1}	3.7	estimated cost of meal and accommodation allowance
fuel resupply	US \$822.36 (AU \$1246.00)	30 $days^{-1}$	111	30 × mean observed daily flight time
shooting				
free feeding	US \$5,43 (AU \$8.23)	h^{-1}	1	0.588 × generic feed-grain cost, based on proportion of shooting estimated to have occurred with free feeding
trapping				
trap[c]	US \$6270.00 (AU \$9500.00)	$trap^{-1}$	300	estimated 10 events $year^{-1}$ based on estimated deployment rate of 4–6 weeks $trap^{-1}$
labor	US \$928.03 (AU \$1406.10)	$trap^{-1}$ $event^{-1}$	30	constant effort $trap^{-1}$ $event^{-1}$
free feeding	US \$91.25 (AU \$138.25)	$trap^{-1}$ $event^{-1}$	30	mean observed effort per trap × generic cost of feed-grain h^{-1}
baiting[d]				
bait dispenser[c]	US \$320.10 (AU \$485.00)	$dispenser^{-1}$	365	each dispenser services a maximum 28.76 events $year^{-1}$, assuming constant deployment at 365 days $year^{-1}$, 1 h effort day^{-1}, and 12.692 h $event^{-1}$
labor	US \$392.63 (AU \$594.89)	$dispenser^{-1}$ $event^{-1}$	12.692	Constant effort per dispenser, based on mean observed baiting effort × generic labor h^{-1}
free feeding	US \$71.02 (AU \$107.69)	$dispenser^{-1}$ $event^{-1}$	12.692	hourly cost of feed grain × (mean observed baiting effort − 5)

TABLE 3 (Continued)

Item	Unit cost	Unit	Accrual interval (effort hours)	Detail
				5 h deducted from mean observed baiting effort as grain is replaced by placebo and toxic baits for the final 5 h of baiting effort
placebo baits	US \$147.84 (AU \$224.00)	dispenser^{-1} event^{-1}	12.692	US \$9.24 (AU \$14) bait^{-1} at 6 baits day^{-1} dispenser^{-1} for 4 days
Ttoxic baits	US \$102.96 (AU \$156.00)	dispenser^{-1} event^{-1}	12.692	US \$17.16 (AU \$26) bait^{-1} at 6 day^{-1} dispenser^{-1} for 1 day

Note: Cost in US\$ calculated based on a conversion rate of AU \$1 = US \$0.66 (31 October 2024). Accrual interval is the time interval in effort h at which the cost is incurred.

[a]We applied ammunition cost per pig killed for thermal-assisted aerial cull, shooting and trapping.

[b]We applied vehicle cost to all control methods, except thermal-assisted aerial cull, at the rate of \$10 labor h^{-1}.

[c]Additional traps and bait dispensers were purchased in subsequent years if the model projected an increase in trap numbers over time, with the number purchased in any year equal to the number required minus the sum of traps or dispensers purchased in all previous years.

[d]We applied a multiplication factor of 1.45 to all baiting costs, except labor, based on the mean reported dispenser deployment rate of 1.45 dispensers site^{-1}.

scenario that used all four control methods in varying proportions weighted in favor of the most cost-effective control method, recalculated at each time interval according to the following equation:

$$P_t = \frac{(1/(C_t/\Sigma C_t))}{\Sigma(1/(C_t/\Sigma C_t))}, \tag{6}$$

where P_t is a 1×4 matrix with elements 1 to 4 being the proportion of annual offtake assigned to thermal-assisted aerial culling, shooting, trapping, and poisoning at time t, and C_t is a 1×4 matrix with elements 1 to 4 being the total cost of thermal-assisted aerial culling, shooting, trapping, and poisoning at time t, if each method were used to complete 100% of the required offtake.

Cost and effort estimates

We applied the six different culling scenarios at varying harvest proportions in increments of 0.05 from 0.35 to 0.95 over projection intervals of 3 and 10 years for 1000 simulations, as per the constant proportional cull simulations described above. At each time increment for all simulations, we projected stochastic population growth by randomly sampling survival and fertility for each age class from the ranges provided in Appendix S2: Table S1 and calculated the total number of pigs to be harvested by multiplying the projected population by the harvest proportion. We then subtracted the total number of pigs to be harvested from the total population at that time increment to give the population remaining after harvest, which we then multiplied by the stable stage distribution

TABLE 4 Method-specific maximum efficiency (in hours per pig) derived from operational observations.

Control technique	Minimum effort kill^{-1} (h pig^{-1})
thermal-assisted aerial culling	0.128
shooting	0.222
trapping	0.333
poisoning	0.308

to give the number of pigs per age class for population projection in the next time increment.

For all scenarios, we determined the efficiency of harvest at each time increment by applying efficiency rates (Equation 6) relative to the proportion of pigs remaining prior to harvest. Due to the asymptotic shape of the exponential functional response models, we limited minimum effort per kill (in hours per pig) for all control methods according to the maximum observed efficiency calculated from operational records (Table 4), such that we did not apply unrealistically high efficiencies derived from the functional response model.

Proportion of pigs remaining (P) was:

$$P = \frac{2n_t}{957}, \tag{7}$$

where n_t is the number of females remaining at the beginning of the time increment, multiplied by 2 (to represent total population of male and females), divided by the population size used to determine the efficiency rates ($n = 957$). We calculated effort (in hours) by multiplying the total number of pigs to be harvested by the relevant method's proportion-specific efficiency rate.

At each time increment, we calculated the cost to reduce the population by the required annual harvest proportion by applying method-specific costs as defined above. For each simulation, we recorded cost and effort per year, as well as total cost and effort for the projection interval. For each scenario, we used the outcomes after all simulations to calculate median and the 2.5th and 97.5th percentiles of cost and effort per year, and totals for both projection intervals. For each cull scenario, we compared cost estimates generated using the most cost-effective harvest rates to the Government of South Australia operational budget for feral pig eradication to test if they could be achieved with the existing funding allocation.

RESULTS

Unmanaged population projection

The deterministic matrix (without stochastic variation) produced an instantaneous rate of exponential change (r) of 0.57 ($\lambda = e^r = 1.769$) and mean generation length of 2.48 years. Incorporating stochastic variation, the median projected population increased rapidly from N_0, overshot carrying capacity (i.e., >2500 females; Figure 2) after 4 years and reached a maximum size of $13.2N_0$ after 5 years ($N_5 = 3265$; 2.5th and 97.5th percentiles: 1936 and 4539). The population subsequently declined to $9.7N_0$ after 10 years ($N_{10} = 2419$; 2.5th and 97.5th percentiles: 1981 and 3281) and reached equilibrium after approximately 15–20 years following a series of minor perturbations (Figure 2).

Constant proportional cull

Constant annual harvest proportions of ≥0.8 and ≥0.6 were projected to achieve reduction to $0.1N_0$ (25 females) after 3 and 10 years, respectively (Figure 3). Annual harvest proportions = 0.45 produced the minimum population reductions relative to N_0 after either projection interval (<10.8% and <28.7% over 3 and 10 years, respectively), and annual harvest proportions ≤0.4 produced no reduction from N_0 after either projection interval.

Effort abundance relationships

The logarithmic model was top-ranked for trapping (Figure 4), but differences between other models were negligible (Table 2). The exponential model was top-ranked for shooting, being 1.29 times (1/0.77) more likely to describe the relationship than the logarithmic model and 3.62 times more likely than the linear model. The linear model was top-ranked for both thermal-assisted aerial culling and poisoning, although differences between ranking of other models were negligible.

We derived parameters for estimating the required effort per pig killed (in hours per pig) from an exponential model of the form:

$$E_t = \alpha e^{-\beta p N_t}, \tag{8}$$

where E_t is the efficiency (in hours per pig) at time t, pN_t = proportion of pigs remaining, e is the exponential constant, and α and β are constants unique to each control method (see Appendix S2: Table S1).

Thermal-assisted aerial culling was the most efficient control method for all proportions of the remaining pig population (Appendix S1: Figure S5), ranging from 0.45 h pig^{-1} (proportion pigs remaining = 1) to 2.58 h pig^{-1} (proportion pigs remaining = 0.01). For a proportion of the remaining pig population = 1, thermal-assisted aerial culling was between 2.73 and 8.13 times more efficient than other control methods, increasing to between 8.15 and 12.67 times more efficient for a remaining proportion = 0.01.

Shooting was the second-most efficient control method for proportions of pigs remaining ≥0.45, but the least-efficient method for proportions of pigs remaining <0.27. The efficiency of shooting ranged from 1.23 h pig^{-1} (proportion pigs remaining = 1) to 32.68 h pig^{-1} (proportion pigs remaining = 0.01). The efficiency of poisoning ranged from 2.08 h pig^{-1} (proportion pigs remaining = 1) to 30.60 h pig^{-1} (proportion pigs remaining = 0.01). The efficiency of trapping ranged from 3.66 h pig^{-1} (proportion pigs remaining = 1) to 21.03 h pig^{-1} (proportion pigs remaining = 0.01), making it the least efficient method when a large proportion of the pig population remained, but more efficient than poisoning and shooting for proportions of pigs remaining <0.52 and 0.45, respectively.

Costs

Estimated cost to achieve the reduction target varied widely among control scenarios, annual harvest rates, and durations. Shooting with a 0.95 annual harvest rate was most cost-effective scenario over both 3- and 10-year projection intervals and cost US \$158,484 (AU \$240,127) (US \$119,039 [AU \$180,362]–US \$238,550 [AU \$361,439])

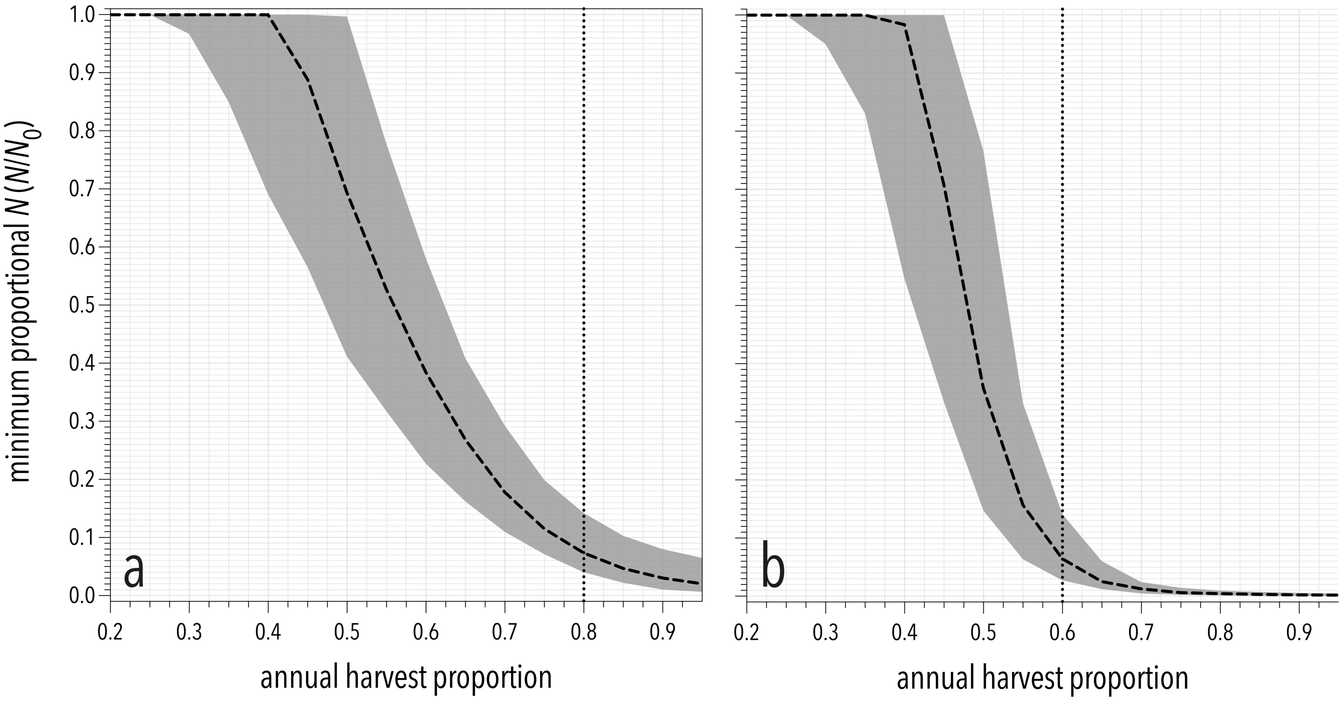

FIGURE 3 Proportion of initial population ($N = 250$) remaining after (a) 3 years and (b) 10 years of annual harvest at rates ranging from 0.2 to 0.95, increasing in increments of 0.05. Harvest targets all age classes equally. Black dashed line represents median proportion of population remaining along with 2.5th and 97.5th percentiles (gray shaded area); vertical dotted lines represent harvest threshold required to reduce N to $\leq 0.1N_0$.

and US $246,121 (AU $372,910) (US $186,025 [AU $281,856]–US $379,868 [AU $575,558]), respectively. The least cost-effective scenarios to achieve successful reduction over 3 years (thermal-assisted aerial culling; 0.8 annual harvest rate) and 10 years (poison baiting; 0.6 annual harvest rate) cost US $327,990 (AU $496,954) (US $253,422 [AU $383,973]–US $431,330 [AU $653,530]) and US $722,161 (AU $1,094,183) (US $497,344 [AU $753,551]–US $1,039,133 [AU $1,574,444]), or 207% and 293% of the most cost-effective combination of control scenario and annual harvest rate over the 3- and 10-year projection intervals.

The annual harvest rate of 0.95 produced the lowest total median costs for all individual control scenarios over both 3- and 10-year projection intervals (Figure 5a,b). Additionally, both culling scenarios that simulated generic integrated pest management were most cost-effective when applied at the highest annual harvest of 0.95. After 3- and 10-year projection intervals, the 25% harvest per method scenario produced total median costs of US $254,555 (AU $385,689) (US $193,862 [AU $293,731]–US $335,087 [AU $507,708]) and US $407,788 (AU $617,861) (US $321,089 [AU $486,498]–US $536,620 [AU $813,061]), respectively, or 161% and 166% of the most cost-effective scenario, whereas the relative cost-proportional-allocation scenario produced total median costs of US $212,220 (AU $321,546) (US $179,993 [AU $272,716]–US $312,106 [AU $472,888]) and US $367,172 (AU $556,321) (US $282,497 [AU $428,026]–US $501,554 [AU $759,930]), respectively, or 134% and 149% of the most cost-effective scenario.

At the maximum annual harvest (0.95), the reduction target ($\leq 0.1N_0$) was achieved after just 1 year (~$0.08N_0$; 20 females remaining) and reduction to $<0.02N_0$ (<5 females remaining) was achieved after 2 years. Comparison of costs estimated after 1 and 2 years with total median cost estimates after the full 3- and 10-year projection intervals therefore identified cost savings that could be achieved if control activities ceased after 1 or 2 years rather than continuing for the duration of the 3- or 10-year projection interval. Shooting remained the cheapest control method, with a median minimum cost of US $87,013 (AU $131,838) (US $71,713 [AU $108,656]–US $103,635 [AU $157,022]) after 1 year and US $134,575 (AU $203,903) (US $105,335 [AU $159,599]–US $183,190 [AU$277,561]) after 2 years. Cessation of shooting at 0.95 harvest after 1 year saved US $71,471 (AU $108,289) (46% reduction) and US $1,793,141 (AU $2,716,881) (95% reduction) compared to total median costs accrued over the 3- and 10-year projection intervals. If shooting ceased after 2 years, the project saved US $24,603 (AU $37,277) (16% reduction) and US $1,746,144 (AU $2,645,673) (93% reduction) relative to the 3- and 10-year cost estimates. Similar cost savings occurred in all other culling scenarios.

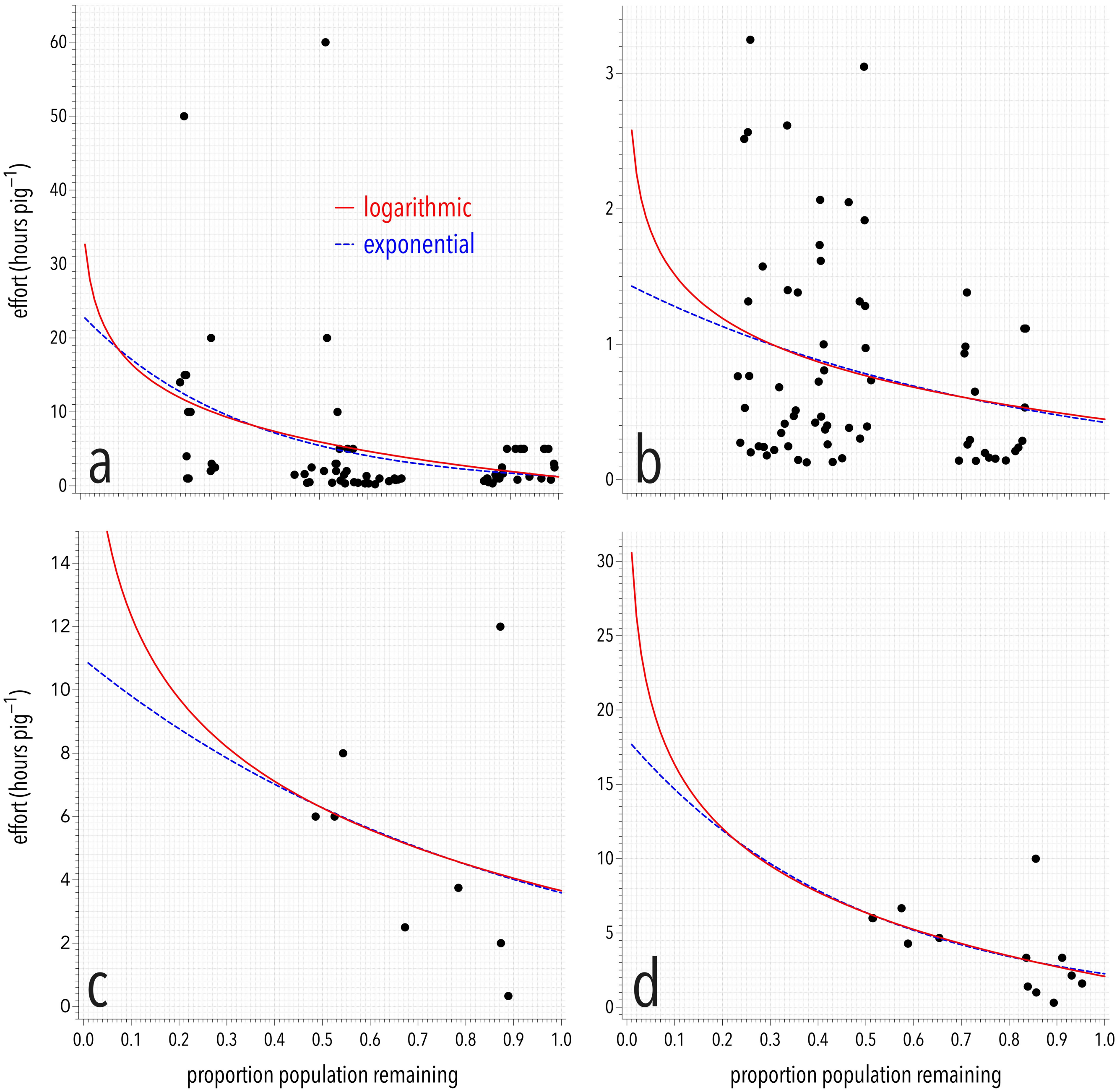

FIGURE 4 Effort per kill (in hours per pig) relative to proportion of pigs remaining for (a) shooting ($n = 74$), (b) thermal-assisted aerial culling ($n = 112$), (c) trapping ($n = 8$), and (d) poisoning ($n = 13$). Black dots represent individual events. Solid red and dashed blue lines represent the line of best fit for logarithmic and exponential models, respectively.

Of the original ~US \$1.76 million (AU \$2.66 million) budget for the feral pig eradication on Kangaroo Island over 3 years from July 2020 to June 2023, ~US \$1.188 million (AU \$1.8 million) was allocated to operational costs (Primary Industries and Regions South Australia, 2020), with remaining funds directed to program management and administration. Annual operational budget for each year of the program was US \$370,411 (AU \$561,229) (2020–2021), US \$363,660 (AU \$551,000) (2021–2022), and US \$452,760 (AU \$686,000) (2022–2023). Comparing the operational budget to annual and cumulative cost estimates over the 3-year projection interval gave estimated total costs to achieve the reduction target ($\leq 0.1N_0$) that were less than the actual amount allocated to operational costs in the first year of the program for all cull scenarios when applied at harvest rates >0.8, the threshold for achieving the population target within 3 years (Figure 5a). Additionally, for all control scenarios applied at 0.95 annual harvest, the estimated cost for continuing population reduction in the second and third year decreased

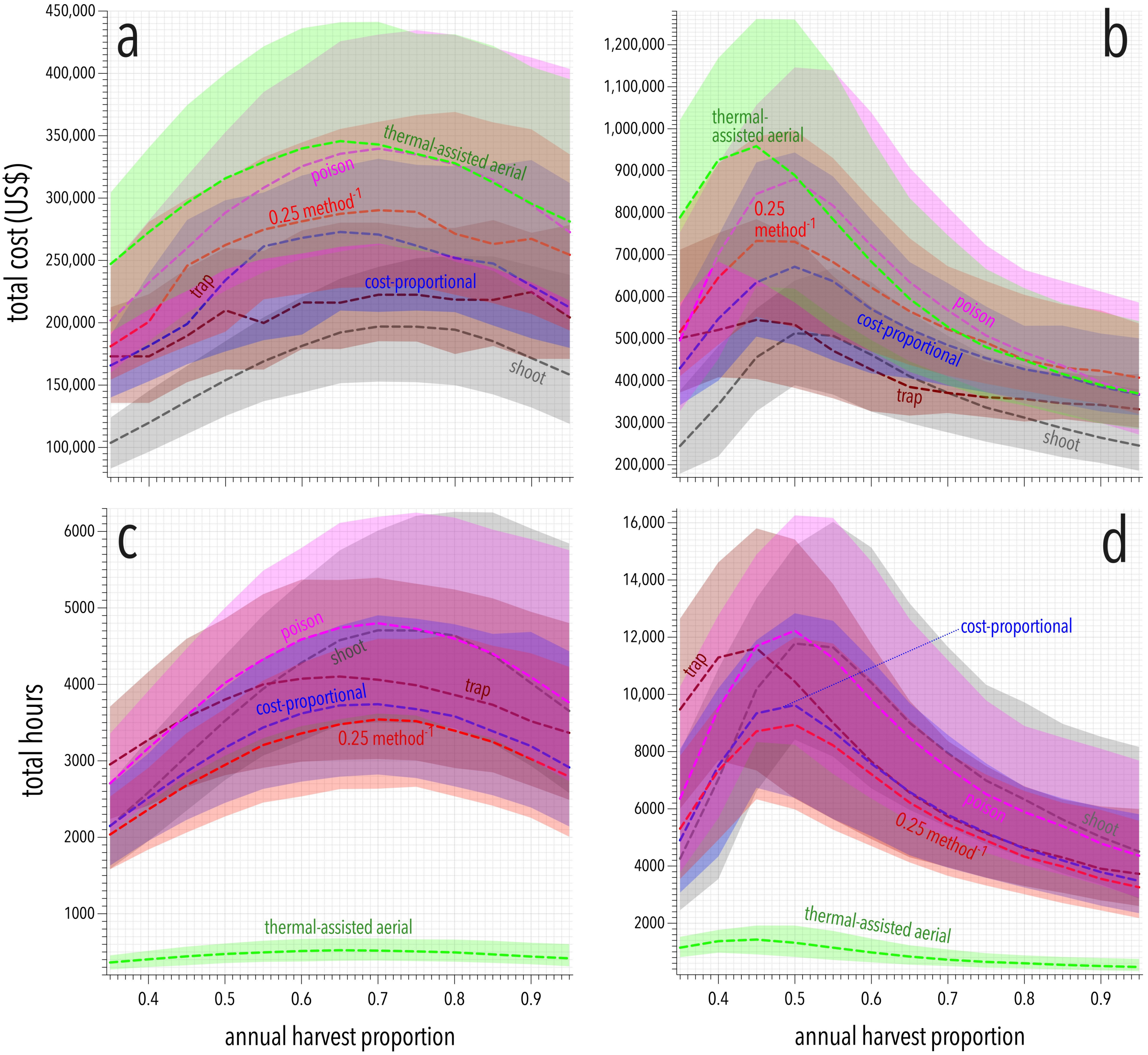

FIGURE 5 (a, b) Projected total cost (shaded areas indicate 2.5th and 97.5th percentiles) per cull scenario over (a) 3 and (b) 10 years, and (c, d) projected total effort (in hours) per cull scenario over (c) 3 and (d) 10 years under increasing harvest proportions. Minimum harvest required to achieve reduction to $N \leq 0.1N_0$ is 0.8 (a, c) and 0.6 (b, d). Thermal-assisted aerial, thermal-assisted aerial culling; 0.25 method^{-1}, 25% harvest per method; cost-proportional, cost-proportional allocation. Cost in US$ calculated based on a conversion rate of AU $1 = US $0.66 (31 October 2024).

substantially relative to estimated first-year costs. Second-year costs decreased between 46% (shooting) and 82% (trapping), and third-year costs decreased between 72% (shooting) and 88% (trapping) relative to first-year costs. By comparison, actual allocated funding decreased slightly (2%) in the second year but increased to 120% of the first-year funding allocation in the third year (Figure 6). The least cost-effective harvest rates for all control scenarios in both 3- and 10-year projection intervals occurred at harvest rates slightly below the minimum required to achieve the density reduction target (3-year: 0.65–0.70; 10-year: 0.45–0.50), except for trapping in the 3-year projection interval, which achieved the least cost-effective harvest at a harvest rate of 0.9 (Figure 5a,b).

Effort

For all harvest scenarios, minimum effort to reduce the population to $\leq 0.1N_0$ was achieved using an annual

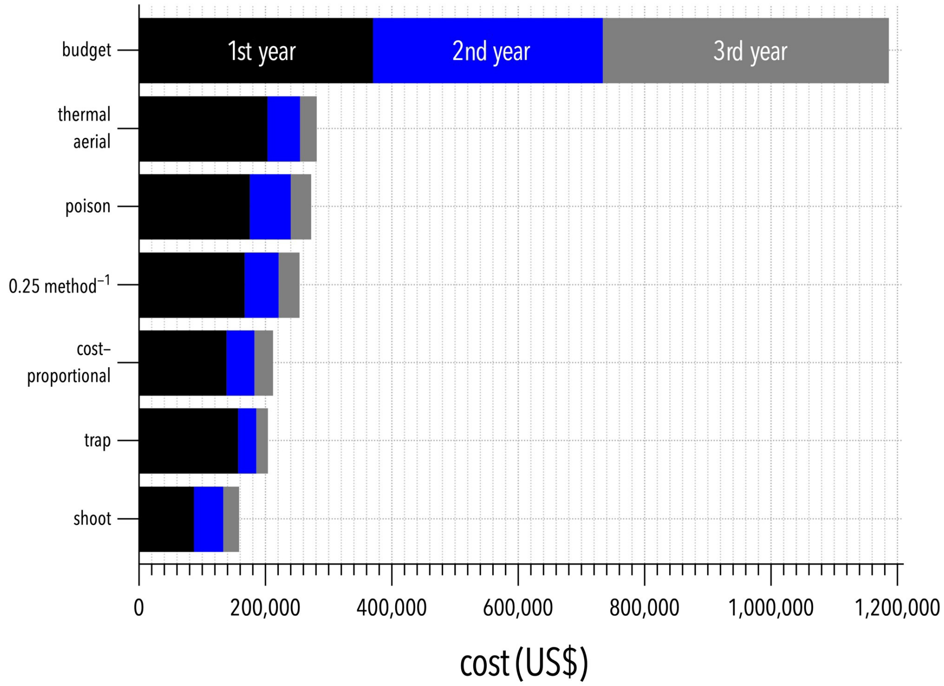

FIGURE 6 Median minimum cost per control scenario after 1, 2, and 3 years when applied at the most cost-effective annual harvest rate (0.95) to achieve reductions to $\leq 0.1N_0$. For comparison, "budget" shows the cumulative operational budget allocated by the Government of South Australia over 1, 2, and 3 years to achieve feral pig eradication. Cost in US$ calculated based on a conversion rate of AU $1 = US $0.66 (31 October 2024).

harvest of 0.95 (Figure 5c,d). Thermal-assisted aerial culling required the lowest effort over 3- and 10-year projection intervals, with a minimum effort of 419 h (315–605 h) over 3 years (Figure 5c) and 471 h (332–753 h) over 10 years (Figure 5d).

Compared to thermal-assisted aerial culling, all other scenarios were relatively time-intensive. At the annual harvest rate with the lowest median total effort to achieve the reduction target over 3 years (0.95), estimated median effort for all other scenarios required between 667% (25% per harvest per method) and 898% (poisoning) more effort than thermal-assisted aerial culling (Figure 5c,d). Over the 3-year projection interval, the 25% harvest per method and relative-cost-proportional-allocation scenarios required the second- and third-lowest effort at all harvest rates above the minimum (0.8) required to achieve the reduction target. Over the 10-year projection interval, the 25% harvest per method scenario was again the second-lowest effort scenario at all harvest rates above the minimum (0.6) required to achieve the reduction target. The third-lowest effort scenario fluctuated between relative-cost-proportional-allocation and trapping, with trapping being third-lowest effort for harvest rates 0.7, 0.75, and 0.8, and relative-cost-proportional-allocation being third-lowest for all other harvest rates above the minimum (0.6) required to achieve the reduction target.

As with cumulative cost estimates above (Figure 6), we derived estimates of median minimum effort over 1 and 2 years at the annual harvest of 0.95 to compare to median total effort after the 3-year projection interval (Figure 7). After 1 year, median effort for thermal-assisted aerial culling was 319 h (24% reduction) and 389 h (9% reduction) after 2 years compared to total median effort over the 3-year projection interval. We observed similar reductions for other cull scenarios, with reduction in effort ranging from 39% (shooting) to 16% (trapping) if culling stopped after 1 year, and 11% (shooting) to 4% (trapping) if culling stopped after 2 years compared to 3 years.

DISCUSSION

Successful reduction of the pig population to $\leq 0.1N_0$ was achieved in all cull scenarios with annual harvest ≥ 0.8 over 3 years, or ≥ 0.6 over 10 years (Figure 3). All simulations achieved the reduction target within the allocated budget (US $1.76 million [AU $2.66 million]) at annual harvest ≥ 0.8 over 3 years (Figure 5), which indicates that eradication is achievable within the project time frame and budget if minimum harvest rates can be achieved. We recommend a combination of all four control

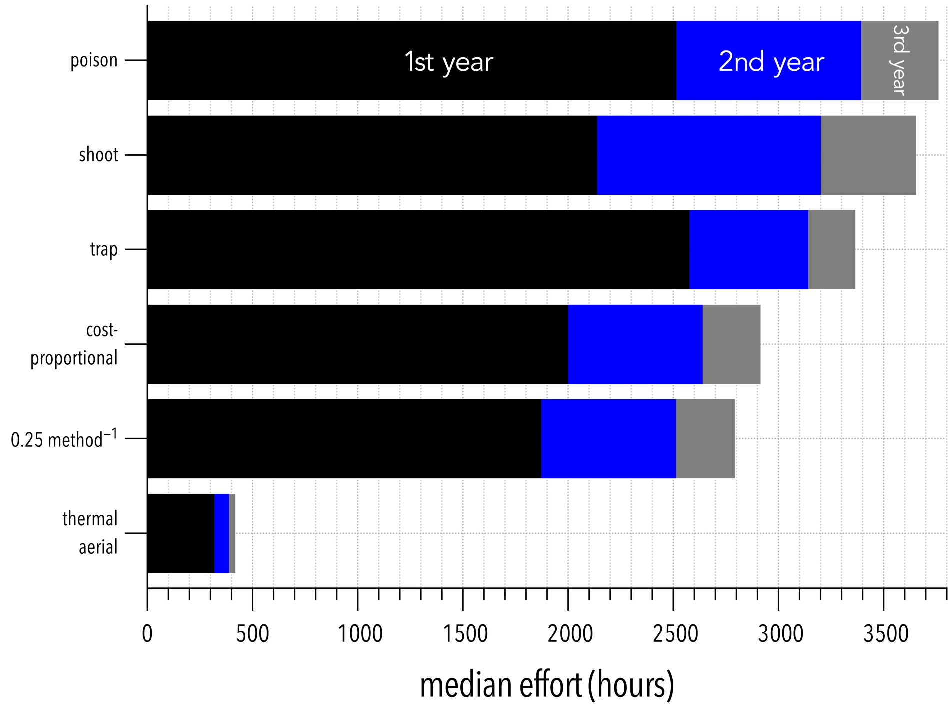

FIGURE 7 Median effort per year for each control scenario using the maximum annual harvest (0.95) over the 3-year projection interval.

methods in accordance with current best practice (Massei et al., 2011), applied at the highest practical annual harvest in the first year. Effective distribution of methods will be dictated by landscape, pig density, and behavior, as well as project-specific cost and time-constraints. While neither generic integrated pest-management scenarios achieved the lowest total median cost over either projection intervals (Figure 5), both reduced population size to target sizes within the project budget and time frame and simulated realistic approaches compared to relying on a single culling method.

For all control scenarios, the maximum annual harvest was the most cost-effective strategy to achieve reduction targets (Figures 5 and 6). This outcome is logical because our models recalculated efficiency annually, so maximizing offtake also maximizes the number of pigs controlled at the highest efficiency (i.e., lowest effort per pig). But population density is not static throughout the year, changing with every birth or death. Despite this simplification, our results agree with other studies reporting the benefits of rapid pig removal to achieve eradication based on the notion that rapid population reduction reduces potential for repopulation and development of avoidance behaviors (Cruz et al., 2005; McCann & Garcelon, 2008; Parkes et al., 2010). Rapid control can also reduce the probability that other pressures might undermine success, such as waning public support, reduced staff motivation, and funding insecurity (Massei et al., 2011), and is likely to curtail ongoing costs associated with pig damages and management. The relationship between pig density and damages is influenced by many environmental factors (e.g., elevation, gradient, climatic variation, vegetation type) (Hone, 2012), and the exact damage function relating pig density to damages has not been quantified for Kangaroo Island. However, it is reasonable to assume that a rapid reduction in pig density would lead to a greater immediate reduction in feral pig impacts, along with associated economic and environmental damage, compared to a more gradual reduction in density that allows more pigs to persist for a longer period.

By comparison, for all control scenarios except trapping, the highest total costs from all scenarios over both 3- and 10-year projection intervals occurred when harvest rates were slightly below the minimum required rate (3-year: 0.65–0.70; 10-year: 0.45–0.50) (Figure 5). In these simulations, the rate of pig harvest was sufficient to reduce pig density and elevate per capita effort and cost of pig removal, but insufficient to achieve population reduction targets, resulting in median minimum female population sizes of 45–68 after 3 years and 90–178 after 10 years. These scenarios illustrate that high expenditure does not guarantee project objectives will be met if harvest rates do not meet minimum thresholds exceeding the maximum rate of population growth.

Comparing median effort among control types revealed that thermal-assisted aerial culling required much lower effort to achieve reduction targets compared to other control scenarios (Figure 7), but it was the least cost-effective method (Figure 5). Despite the high cost, our model estimated that thermal-assisted aerial culling applied at an annual harvest rate of 95% would achieve the target population reduction with a median effort of 319 h within the budget allocated to just the first year of the Kangaroo Island Feral Pig Eradication program. In practice, only ~33 h was allocated to thermal-assisted aerial culling in the first 12 months of data collection, out of a total 1269 h of effort across all control methods. However, thermal-assisted aerial culling only began in the 11th month of data collection. This lag in implementation reflects the administrative and logistical complexity of organizing an aerial shoot using this novel approach, compared to conventional control methods that were mobilized rapidly following the 2019–2020 bushfires. Given its high efficiency and high cost, the utility of thermal-assisted aerial culling appears greatest where rapid control is required and cost is less important than achieving the aim of eradication, for example, in the event of a serious livestock disease, or difficult-to-access areas where cost-effective control methods are impractical (see below). However, managers must anticipate administrative and logistical delays to avoid implementation lag and capitalize on this high efficiency. Thermal-assisted aerial culling is also useful in the final stages of pig eradication when the population is at low densities (Katahira et al., 1993).

Shooting was the least-expensive method due to its low operational costs considered by the model (i.e., hourly labor and vehicle costs, and ammunition per pig). In practice, shooting attracts additional costs including the purchase of firearms and monitoring equipment. However, these additional costs are probably negligible compared to labor costs, and their inclusion is unlikely to affect the overall ranking of shooting as the least-expensive option among these simulations. However, our model does not consider the impact of vegetation cover on efficiency (i.e., reduced efficiency of shooting in areas of dense vegetation), so it likely underestimates the true cost of control by shooting. As such, we recommend that shooting is prioritized in the early stages of pig control and in open landscapes where high detectability supports efficient shooting.

Estimated costs for trapping over the 3-year projection interval showed a positive relationship between cost and pig density, with the highest costs for trapping occurring at a harvest rate of 0.9. This is attributed to the high effort per pig, costs per trap, and low efficiency of traps at low pig densities. We did not observe such a relationship in any other scenario, although it is reflected in the estimated cost for the 25% harvest per method where there was an increase in cost between harvest rates of 0.85 and 0.9 (Figure 5). Despite the increasing cost of trapping with increasing harvest rate, trapping was predicted to be the second-most cost-effective control method at all harvest rates above the required minimum, and we therefore consider it to be a cost-effective method for pig control, particularly at higher pig densities.

Programs that rely exclusively on ground-shooting, or any other individual control method, are often unsuccessful (Bengsen et al., 2020; Keiter & Beasley, 2017). An integrated pest-management approach using a combination of methods is considered the most effective because different strategies can be applied in response to changing densities, behaviors, and environmental conditions (Campbell & Long, 2009; Massei et al., 2011). For Kangaroo Island, large areas occupied by feral pigs cannot be accessed for shooting, trapping, or baiting, providing refuges from which reinvasion can occur (Choquenot, 1996; Hone et al., 1980). Using thermal-assisted aerial culling in areas untreatable by other means appears justified, despite being the least cost-effective method for control. Incorporating assessment of habitat suitability and probability of pig occurrence (e.g., McMahon et al., 2010) might provide justification for these costs, but requires data describing patterns of food abundance and habitat use/movement. Without relevant local data, our aspatial projection is still useful for applying locally derived functional responses to compare cost and effort outcomes under different culling scenarios. The shape of the functional response differed among control methods. Despite high efficiency of thermal-assisted aerial culling at all population sizes relative to other control methods, this efficiency was outweighed by high hourly costs. Shooting was relatively efficient when a large proportion of the population remained, but became increasingly inefficient with decreasing population density relative to other control methods, particularly to thermal-assisted aerial culling and trapping. However, shooting had the lowest operating costs of all control methods, resulting in this method being among the least-expensive control scenarios for all harvest rates in both 3- and 10-year projection intervals.

The realism of functional-response models could be improved with more accurate population estimates and reporting of operational effort. Systematic population estimates were unavailable, as were inferred changes in abundance. Efficiency data were not recorded for pig kills <0.21 of the assumed total population (<200 out of total 957) because the data-collection period ended when the estimated population fell below ~200 pigs and the functional response was estimated based on the expected form in lieu of operational data. It is reasonable to assume that per capita effort required to remove pigs will continue to increase with decreasing pig density according to a Type II response, but the site-specific accuracy of the functional responses could be improved if data were available for lower population densities. Furthermore, only thermal-assisted aerial culling records included events with no pigs killed (i.e., $f_i > 0$, $n_i = 0$). Trapping and baiting effort was maintained until control outcomes were achieved and no unsuccessful trapping or baiting events occurred. However, it is possible that unsuccessful shooting events were unreported, increasing its apparent cost-effectiveness relative to other culling scenarios. Indeed, insufficient reporting on effort-outcome relationships (Hone et al., 2018) and imprecise accounting of program costs (Holmes et al., 2015) limit opportunity for analysis or improvement of efficiency. To improve the predictive performance of this modeling approach, we recommended that invasive animal programs standardize methods for implementation of control methods, effort reporting and data management.

Model realism might also be affected by differences between the simulated and true sex ratio, and sex- and age-specific survival probabilities in each control method. Sex biases in control methods have been reported variously to suggest both higher vulnerability of males to trapping, ground-based hunting and aerial hunting (Parkes et al., 2010), as well as elevated female vulnerability to trapping (Choquenot et al., 1993) and baiting (Gifford, 2006). We observed a population sex ratio of 1.3:1 (female: male), with a female bias for poison baiting (2:1), ground-based hunting (1.5:1), and trapping (1.25:1); thermal-aerial assisted culling had a negligible bias toward males (0.98:1). The difference in sex ratios between the simulated (1:1) and observed (1.3:1) populations means that our modeled population estimates, when doubled to include both males and females, are likely to overestimate the true number of pigs and thus inflate control costs. Similarly, observed female bias for poison baiting, ground-based hunting, and trapping could result in underestimating the cost-effectiveness of these control methods when applied to both sexes. However, given the variability in reporting sex biases among pig control methods and the lack of local data regarding the sex ratio and sex-specific vulnerability of non-adult pigs to different control methods, our assumed 1:1 sex ratio with equal susceptibility to control methods is reasonable.

Despite these limitations of data quality, using locally estimated functional responses is a valuable approach for advancing the accuracy of cost estimates compared to ad hoc estimation. For example, our modeled estimates predict that operational costs decrease substantially if high harvest is achieved in the first year (Figure 6), contrasting most funding schemes that allocate higher budgets in the final year of the program. The difference between actual allocated operational funding and estimated costs for the most cost-effective approach are in the order of >US $660,000 (AU $1 million), representing a large savings that could be directed toward other environmental objectives.

CONCLUSIONS

Applying locally estimated functional responses to estimate management costs at different population sizes and harvest rates is a novel approach that provides defensible insights into the relative cost-effectiveness of control methods. The real value of this approach is not in predicting the true costs, but rather in evaluating the relative costs of each scenario to identify the most cost-effective approach from a suite of available methods under different conditions stochastically within the bounds of the estimated model parameters. We were able to project realistic population change under varying harvest rates and produce realistic cost estimates to rank different control methods and scenarios currently used for pig eradication on Kangaroo Island and to demonstrate the broader utility of this approach for informing decision-making in general invasive animal management. Eradication of feral pigs on Kangaroo Island appears achievable within the project budget using sustained, high annual harvest, echoing approaches achieving successful pig eradication on islands elsewhere (e.g., Cruz et al., 2005; McCann & Garcelon, 2008). Despite the potential for eradication on islands such as Kangaroo Island, the global feral pig distribution is predicted to expand (Lewis et al., 2017), and costs of biological invasions are projected to increase (Diagne et al., 2021). The use of operational control data to simulate management scenarios and maximize cost-effectiveness of control strategies will become increasingly necessary as pig distributions expand.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Hamnett & Bradshaw, 2024) are available from Zenodo: https://doi.org/10.5281/zenodo.7700781.

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SUPPORTING INFORMATION

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

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