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Research Article

Using a spatially explicit population model to evaluate management scenarios for an invasive deer population

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Abstract

Effective management of invasive species requires robust projections of how alternative management strategies influence long-term invasion outcomes, required effort, and associated trade-offs. We used a spatially explicit population model, linked with empirical data on aerial culling efficiency, to project (from 2023 to 2060) alternative management scenarios for limiting the spread and establishment of an invasive fallow deer (*Dama dama*) population in a high-value conservation area, the Walls of Jerusalem National Park (WJNP), Tasmania, Australia.

We compared six feasible aerial culling scenarios that varied in the frequency (annual, biennial, or five-yearly) and spatial extent (broad versus concentrated management zones) of control, relative to a baseline scenario with no future management. Scenarios were evaluated in terms of their ability to limit deer occupancy and abundance within the WJNP, the cumulative presence of deer over time, the amount of management effort required, and population-level animal welfare outcomes.

All management scenarios reduced deer invasion into the WJNP relative to no management, but strategies that applied culling across a broad spatial extent were consistently more effective than those targeting only high-density source areas. More frequent culling further improved outcomes, although gains were modest relative to changes in spatial extent. Strategies that combined broad-scale culling with annual or biennial frequency achieved the best balance between reducing invasion pressure and limiting management effort, while also resulting in fewer deer being culled overall. Complete exclusion of deer from the WJNP was achievable only under a more intensive strategy involving annual culling across a substantially expanded area, but this required a nearly four-fold increase in effort compared to the scenarios aimed at minimising, rather than eliminating, invasion.

Our results highlight trade-offs between management effectiveness, effort, and welfare outcomes, and demonstrate how spatial population models coupled with operational data can support practical, evidence-based decisions for managing invasive species.

Key words: Aerial culling, aerial shooting, animal welfare, Australia, catch-per-unit-effort, *Dama dama*, invasive species, removal model

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Introduction

Invasive species are a major driver of biodiversity loss worldwide, acting through predation, competition, habitat modification, and disease transmission (Blackburn et al. 2019). In many invasions, populations undergo a prolonged lag phase following establishment before rapidly increasing in abundance and expanding their geographic range (Spear et al. 2021). Preventing the spread and establishment of invasive populations into high-value conservation areas is therefore a critical priority, requiring management strategies that are effective and efficient in their use of resources.

Simulation modelling has increasingly been recognised as a useful approach for evaluating potential invasive species management strategies before they are implemented in the field (Thompson et al. 2021; Pepin et al. 2022). Spatially explicit population models (SEPMs) are especially useful because they integrate demographic processes (survival, reproduction) with spatial processes (dispersal), allowing managers to explore how population abundance and occupancy change across landscapes over time (Gallien et al. 2010; Merow et al. 2011; Bertolino et al. 2020). When validated against empirical data, for example using pattern-oriented modelling approaches (Fordham et al. 2021; Gallagher et al. 2021), SEPMs can provide credible, robust projections of invasion dynamics and management outcomes under uncertainty.

Management effectiveness is often quantified using simple metrics such as the proportion of a population removed or the reduction in abundance achieved (Veltman and Pinder 2001; Bengsen et al. 2023). However, for managers aiming to limit the ecological impacts of invasive species in specific areas, additional considerations are often more relevant, including the spatial extent of invasion (occupancy), the abundance of animals over time, and the effort required to achieve particular outcomes. For many lethal control techniques, including aerial culling of large mammals, the relationship between effort and population density is non-linear: removal rates increase with density but saturate at higher densities, meaning that marginal gains in population reduction can require disproportionately greater effort (Bengsen et al. 2023). Understanding these trade-offs is essential for designing cost-effective and sustainable management strategies.

Concerns about animal welfare further complicate decisions about invasive species management (Nimmo and Miller 2007). At the individual level, welfare outcomes depend on how control is implemented, and quantitative methods exist to assess these outcomes (Hampton et al. 2015). At a broader scale, there is increasing recognition of "population-level welfare", defined by the total number of animals exposed to or killed by management actions (Warburton et al. 2012). Simulation studies suggest that long-term strategies that minimise the total number of animals killed may also minimise costs (Warburton et al. 2012). These considerations are increasingly important for public and policy acceptance of invasive species management programs, particularly where control must be maintained over long time scales.

In Tasmania, Australia, non-native fallow deer (*Dama dama*) have expanded rapidly in abundance and distribution over recent decades, threatening conservation values within the Tasmanian Wilderness World Heritage Area (TWWHA) (Cunningham et al. 2022; Game Services Tasmania 2022; Botterill-James et al. 2024). One such area is the Walls of Jerusalem National Park (WJNP), a high-value alpine landscape that is currently at the invasion front of an expanding deer population. The size and connectivity of surrounding populations mean that eradication is not considered feasible; instead, management policy focuses on minimising deer occupancy and abundance within and around the WJNP to limit ecological impacts. Thermally assisted aerial culling is currently the only practical method for controlling deer in this remote and rugged environment, but uncertainty remains about how best to allocate effort through time and space to achieve long-term containment.

Despite a growing body of research into the use of aerial culling for management in a range of invasive species (including a strong focus on feral pigs *Sus scrofa*, feral goats *Capra hircus*, and deer species; Davis et al. 2018; Bengsen et al. 2023, 2025; Cox et al. 2025), there remains a lack of evidence on how alternative combinations of culling frequency and spatial extent influence long-term invasion outcomes, management effort, and population-level welfare. In particular, managers often face a strategic choice between concentrating effort in high-density source areas or spreading effort more broadly across invasion fronts, and between frequent low-intensity control or less frequent high-intensity interventions. Evaluating these options over ecologically relevant, long-term timescales, is critical for management decisions.

Here, we use a spatially explicit population modelling framework, validated with empirical data, to project and compare alternative management strategies for limiting the invasion of fallow deer into the WJNP. Specifically, we compare the effectiveness of different frequencies and spatial extents of aerial culling in reducing deer occupancy and abundance within the park, and required management effort, along with assessing population-level animal welfare among scenarios. We also explore the feasibility and cost of completely excluding deer from the WJNP. By linking spatial population projections with operational data on control effort, our study aims to provide an analytical approach and decision-relevant insights that are applicable not only to invasive deer management, but more broadly to the management of other invasive vertebrate populations.

Methods

Study system and management context

Fallow deer (*Dama dama*) were introduced to Tasmania in the 1830s and remained at low abundance and restricted distribution for more than a century (Chapman and Chapman 1980; Potts et al. 2015). Fallow deer are the only free-ranging deer species present in the study area (accordingly, unless otherwise specified, the term "deer" is used throughout this manuscript to refer to fallow deer). Since 1985, the population has increased some 40-fold and expanded its core area of distribution by threefold (Cunningham et al. 2022). An aerial survey in October 2024 (at the end of the antlerless hunting season and just prior to the birth season) estimated that there were 71,655 fallow deer (± 19.6%) in their 'traditional' core range (~20,000 km^2) in the middle and east of the island (Lethbridge et al. 2024; Lethbridge et al. 2025). Modelling of camera trap and spotlight survey data suggest that deer currently occupy approximately 27% of Tasmania and could potentially expand to more than half of the island (Cunningham et al. 2022). Several areas of high conservation value within the Tasmanian Wilderness World Heritage Area (**TWWHA**) lie at or near the invasion front and are therefore at risk of future invasion.

Our focal conservation area was the Walls of Jerusalem National Park (**WJNP**, 41°52'08"S, 146°15'31"E [2]), an alpine and subalpine landscape that covers 518 km^2 within the TWWHA and that supports slow-growing endemic vegetation communities likely to be sensitive to deer impacts (Guy et al. 2024). At the start of our study period (2023), deer were absent or occurred at extremely low densities within the WJNP, based on rare observations of their presence. For example, two male deer (both antlered) were detected on camera traps in the WJNP in 2023, and one male deer (antlered) on a camera trap in 2024 (16 cameras deployed each year for 3–4 months, Department of Natural Resources and Environment Tasmania, unpublished data, 2024). However, the park is contiguous with suitable habitat to the east that supports an established and expanding deer population, creating ongoing invasion pressure (Locke 2007; Cunningham et al. 2022; Botterill-James et al. 2024; Fig. 1).

Thermally assisted helicopter-based culling is currently the only feasible method for controlling deer in remote and rugged environments (Pulsford et al. 2022; Cox et al. 2023). In May 2023, the Tasmanian Government undertook such a cull in 2023 in the northeastern area of the TWWHA, focused on the WJNP and adjacent Central Plateau Conservation Area (Tasmania Parks and Wildlife Service 2023, Fig. 1).

Modelling framework

We combined a spatially explicit population model (SEPM) with an empirical catch-per-unit-effort (CPUE) model to evaluate alternative long-term management strategies for limiting deer invasion into the WJNP. The SEPM was used to project deer population dynamics and spatial spread from 2023 to 2060, in discrete yearly timesteps, under a baseline scenario and multiple management scenarios differing in culling frequency and spatial extent. Outputs from the SEPM describing deer density within management zones were then linked to the CPUE model to estimate the helicopter flying time required to implement each scenario. This integrated framework allowed us to evaluate trade-offs among invasion outcomes, management effort, and population-level animal welfare.

Constructing the spatially explicit population model (SEPM)

The SEPM used in this study was derived from a previously published Tasmania-wide model that was validated using pattern-oriented modelling to reproduce observed changes in fallow deer occupancy and abundance from 1985 to 2019 (Botterill-James et al. 2024). Full details of model development, calibration, and validation are provided in Botterill-James et al. (2023, 2024), and relevant code and data are publicly available (Botterill-James et al. 2023).

Briefly, we used the R package *poems* (Fordham et al. 2021), v.1.0.5, to construct a stage-structured matrix model for female fallow deer. The model was divided into four stages: juvenile (first year), yearling (1–2 years), adult (3–11 years), and senescent adult (12–16 years). We obtained estimates of age at first reproduction and survival and fecundity for each stage from the literature (Suppl. material 1: table S1 and references therein). We included stochasticity for fecundity and survival of each stage (Suppl. material 1: table S1). This demographic model was implemented on a 5 × 5 km lattice grid (multi-layer, total grid size = 3,575 km^2)

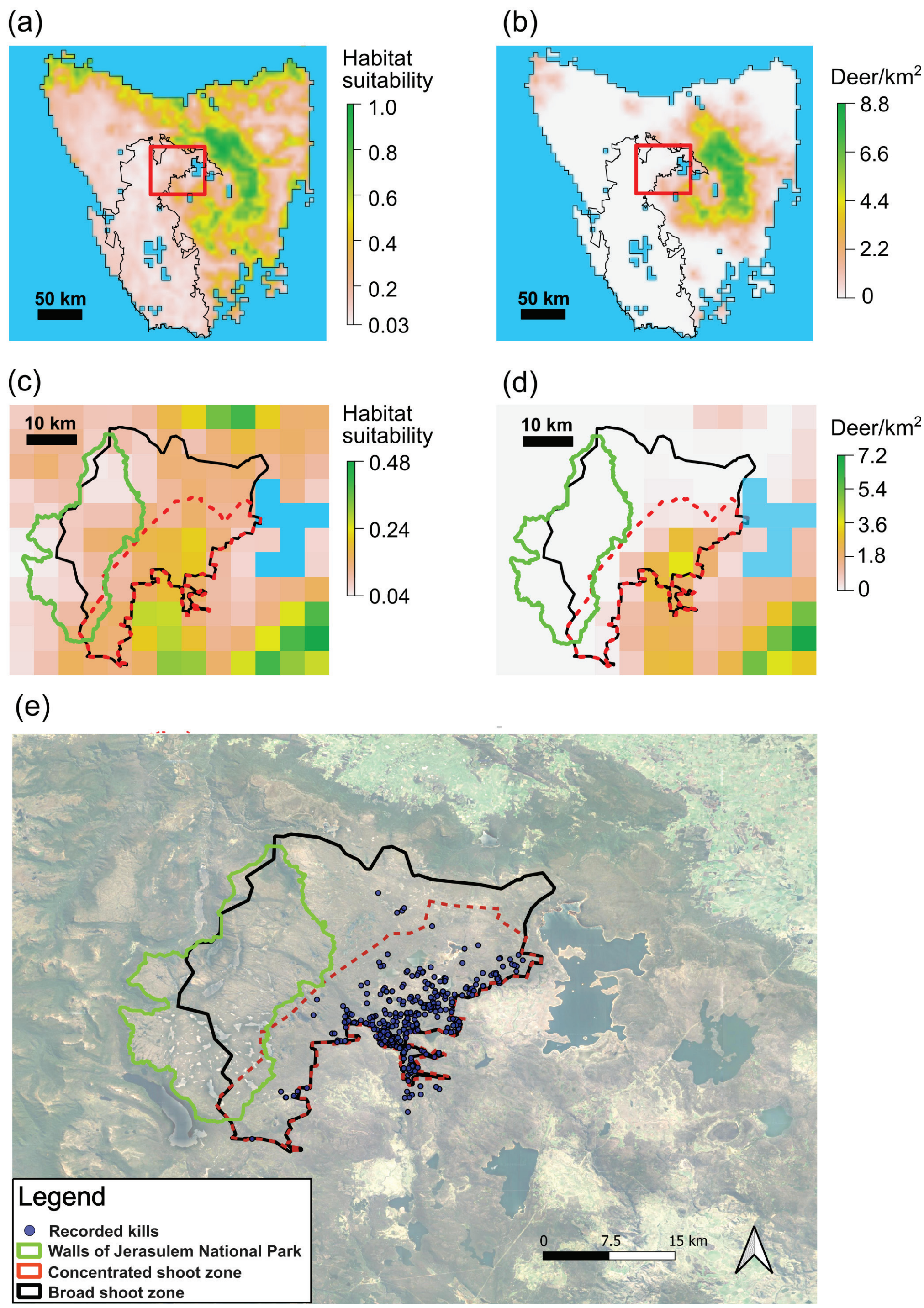

Figure 1. Fallow deer habitat suitability and distribution maps for Tasmania and the model study area. **a.** Habitat suitability map of Tasmania (excluding islands in the Bass Strait to the North) (source; Cunningham et al. 2022). The black border shows the boundary of the Tasmanian Wilderness World Heritage Area, and the red box shows the boundaries of our spatially explicit population model; **b.** Deer distribution and density map of Tasmania for 2023, with boundaries as for (**a**). The map was generated from a validated population model (Botterill-James et al. 2024); **c.** Habitat suitability map for our model area. The green border shows the boundary of the Walls of Jerusalem National Park, the black border shows the boundary for the broader shoot zone (1,056 km^2), and the red dashed border shows the boundary for the concentrated shoot zone (425 km^2). Note the shared south/eastern boundary for the broad and concentrated shoot zones; **d.** Deer distribution and density map for the model area at the start of 2023, used to initialise our model. Boundaries are the same as (**c**); **e.** Locations of fallow deer (male, female, and juvenile combined) kills (blue dots, n = 711) recorded in the May 2023 cull. Some deer were killed outside the broad shoot zone boundary because they were detected inside the shoot zone and then moved outside the shoot zone, where they were killed. Boundaries are the same as (**c, d**). For all plots, light blue represents water bodies.

of habitat suitability, which was constrained between 0 (totally unsuitable habitat) and 1 (totally suitable habitat). For a full description of the habitat suitability model, see Cunningham et al. (2022). Our study area is characterised by a harsh alpine/sub-alpine climate and rugged terrain, features that reduce fallow deer habitat suitability (Cunningham et al. 2022). Hence, the most suitable habitat in our study area had a value of 0.48 (Fig. 1). Outside our model area boundaries, the lower-lying midlands, consisting of fertile agricultural land interspersed with forest cover, had areas of habitat suitability near 1 (Fig. 1).

Each 5×5 km cell had its own population growth model determining local increase in deer to the cell's carrying capacity, which was calculated by multiplying each cell's habitat suitability by 670 (based on carrying capacity in similar habitats of 26.8 female deer/km^2 – Suppl. material 1: table S2 – equivalent to 670 females/25 km^2 cell). The model used a post-breeding census (i.e., population statistics were extracted at the beginning of each yearly timestep, immediately after births, which occur in December).

Cells were linked by a distance-based dispersal function defined by four parameters (density dependence of dispersal, average proportion of dispersers per cell, average dispersal distance, and maximum dispersal distance). Dispersal parameters were derived from, and validated against, observed patterns of fallow deer range expansion in Tasmania using a pattern-oriented modelling approach (Cunningham et al. 2022; Botterill-James et al. 2024). Full details of dispersal parameterisation and model validation are provided in Botterill-James et al. (2024).

The model had seven fixed and seven variable parameters (Suppl. material 1: table S2), including the four dispersal parameters. The other variable parameters were carrying capacity, survival, and fecundity. Ranges for variable parameters were initially set from the literature and then calibrated through the pattern-oriented modelling approach (Botterill-James et al. 2024). This used 100,000 simulations, each with a unique set of parameter values. Parameter posteriors were then estimated from the 100 simulations that best recreated known changes in the occupancy and abundance of the fallow deer population from 1985–2019 (Botterill-James et al. 2024).

Model extent and spatial configuration

The model domain encompassed the WJNP and surrounding landscapes to capture population growth and dispersal pressure from established deer populations east of the park (Locke 2007; Botterill-James et al. 2024). Model boundaries were defined to include areas of known or likely deer occupancy while excluding regions considered deer-free or separated by major natural barriers (Cunningham et al. 2022).

Two management zones were defined within the model domain (Fig. 1):

1. a broad shoot zone (1,056 km^2) encompassing the majority of the WJNP (65%) and adjacent areas across a gradient from high-density source populations to the invasion front, and
2. a concentrated shoot zone (425 km^2) within the broad zone where deer densities were highest at the start of the study, covering only a small extent (6%) of the WJNP

These zones were aligned closely with those used during the May 2023 aerial cull (Tasmania Parks and Wildlife Service 2023).

Initial population distribution and abundance

Initial deer abundance within the broad shoot zone (pre-May 2023 cull) was estimated using two independent methods. First, index-removal calculations (Eberhardt 1982) applied to camera trap data from 15 monitoring sites (Suppl. material 1: supplementary information S1: pre-cull population estimate) yielded an estimated population size of 758 deer (95% CI: 711–954), corresponding to 505 female deer. We therefore set the baseline initial abundance at 530 female deer (we used a slightly higher initial abundance the mean estimate of *Ni* = 505 female deer, given the high upper 95% CL relative to the mean)

Second, a Bayesian removal model applied to operational culling data from the 2023 cull in the area, estimated a higher initial abundance of 1,025 female deer (95% CI: 661–1,669) (Suppl. material 1: supplementary information S2: Ramsey et al. 2023). To account for this uncertainty, we conducted sensitivity analyses using alternative initial abundances of 760 and 1,050 female deer (details in Sensitivity analysis subsection in Methods, below).

Deer were spatially distributed within the shoot zone based on observed kill locations from the 2023 cull (Suppl. material 1: fig. S1a). Based on the pre-cull estimate, we added additional female deer to match the initial abundance target. These additional deer were added randomly to cells where deer had been shot, or adjacent to cells where deer had been shot, with each cell receiving a maximum of one additional deer. Outside the shoot zone, deer abundance and distribution were initialised using projections from the validated Tasmania-wide model (Botterill-James et al. 2024). Age structure across the model domain followed the stable age distribution derived from the Leslie matrix (Suppl. material 1: table S1).

Management scenarios

We evaluated seven scenarios over the period 2023–2060: one baseline scenario (that included the 2023 cull but no further management) and six active management scenarios. For clarity, we refer to active management scenarios throughout using concise labels that reflect the combination of culling frequency and spatial extent (Table 1).

The active management scenarios varied in two aspects:

1. culling frequency (every year, every two years, or every five years), and
2. spatial extent (culling restricted to the concentrated shoot zone or applied across the broad shoot zone).

Culling was assumed to occur once per year in May, reflecting operational constraints related to weather, recreational use, and ecological considerations (Tasmania Parks and Wildlife Service 2023). More frequent culling within a year was therefore not considered feasible.

With each cull event, the model assumed that deer could be completely removed from cells within the active shoot zone. This is a reasonable assumption given that a previous study of helicopter culling operations for fallow deer populations on mainland Australia found no support for the existence of a prey refuge (i.e., a threshold density below which no deer could be shot; Bengsen et al. 2023). Allowing complete eradication within cells represents a 'best case' management scenario, but overall results would likely be similar if we only allowed reduction of

Table 1. Summary statistics describing projected female fallow deer abundance, maximum deer densities (deer/km^2), and occupancy (percentage of cells occupied) for 2060, for all the study area and for the Walls of Jerusalem National Park (WJNP), Tasmania, Australia, 2023–2060. The first row shows values for 2023, taken from the deer distribution and abundance raster used to initialise all models. Mean values are shown, with 95% confidence intervals for each scenario's set of 1,000 simulations in parentheses. Each scenario is described in detail in Methods.

Scenario	Abundance		Maximum density		% occupancy		Total deer-years in WJNP
	Study area	WJNP	Study area	WJNP	Study area	WJNP	
Initial (start of 2023) values	*2,390*	*0*	*7.2*	*0*	*50.74*	*0*	*NA*
Baseline	9,548 (9,502–9,594)	314 (307–322)	16.98 (16.91–17.06)	3.64 (3.57–3.73)	77.69 (77.37–77.99)	52.01 (50.91–53.11)	5,005 (4,922–5,088)
Broad shoot zone, every year	6,934 (6,908–6,960)	90 (89–91)	16.97 (16.89–17.05)	3.60 (3.57–3.62)	48.78 (48.61–48.95)	5.24 (5.18–5.31)	3,237 (3,223–3,251)
Broad shoot zone, every 2 years	6,944 (6,918–6,970)	92 (91–93)	17.06 (16.98–17.14)	3.62 (3.59–3.64)	49.13 (48.94–49.32)	5.82 (5.66–5.99)	3,247 (3,231–3,262)
Broad shoot zone, every 5 years	6,988 (6,962–7,015)	99 (97–100)	17.03 (16.96–17.12)	3.63 (3.61–3.66)	53.48 (53.23–53.48)	7.78 (7.47–8.10)	3,306 (3,287–3,325)
Concentrated shoot zone, every year	8,276 (8,243–8,310)	182 (178–187)	16.99 (16.91–17.06)	3.62 (3.60–3.65)	67.98 (67.63–68.32)	31.98 (30.92–33.03)	3,951 (3,904–3,998)
Concentrated shoot zone, every 2 years	8,287 (8,253–8,320)	188 (184–193)	17.03 (16.95–17.11)	3.61 (3.58–3.63)	68.35 (68.10–68.68)	32.91 (31.83–33.99)	4,019 (3,969–4,068)
Concentrated shoot zone, every 5 years	8,317 (8,283–8,351)	201 (196–207)	16.98 (16.90–17.06)	3.63 (3.61–3.66)	71.18 (70.84–71.53)	35.64 (34.50–36.77)	4,125 (4,070–4,179)

cell populations to low densities, given that deer invasion and population growth in the WJNP will be driven largely by dispersal of individuals from established, relatively high-density populations outside the WJNP and shoot zones (Locke 2007; Botterill-James et al. 2024).

The above management scenarios used culling frequencies currently considered feasible by the Tasmanian Government to *minimise* fallow deer occupancy and abundance in the WJNP. Because none of these scenarios eradicated deer from the WJNP (see Results), we also used our model to explore the feasibility and effort required to keep fallow deer out (i.e. zero occupancy and abundance) of the WJNP in 2060 ('eradication scenario'). We did this by running our model as outlined above, but with culling occurring every year across a further expanded cull zone of 2,013 km^2 (Suppl. material 1: fig. S1b).

Response metrics

For each scenario, the SEPM was run 1,000 times, using a unique combination of values for the variable parameters in each simulation. Latin Hypercube Sampling was used to sample from uniform prior distributions, with upper and lower limits taken from parameter posteriors estimated by Botterill-James et al. (2024). We did this to estimate uncertainty in scenario projections due to uncertainty around the exact values of the variable parameters in the SEPM (Fordham et al. 2021).

Each simulation was run at an annual time step from 2023 to 2060. At the end of each simulation, we calculated summary metrics describing invasion outcomes for both the full model area and the WJNP, calculating mean values and 95% confidence intervals. Primary response metrics included: deer abundance; spatial occupancy (proportion of cells containing ≥1 deer), and maximum deer density. To quantify cumulative invasion pressure within the WJNP, we calculated total deer-years, defined as the cumulative sum of deer abundance in the park across all annual time steps from 2023 to 2060. This metric integrates both the magnitude and duration of deer presence and is used here as an index of cumulative invasion pressure and potential deer damage (rather than as a direct measure of ecological damage). Population-level animal welfare outcomes were quantified as the total number of deer culled under each scenario (Warburton et al. 2012).

Catch-per-unit-effort model and estimation of management effort

To estimate management effort, we developed an empirical CPUE model describing the relationship between deer density and the number of deer removed per hour of helicopter flying. The model was parameterised using spatially explicit operational data from the May 2023 cull, including helicopter flight paths and kill locations (Suppl. material 1: supplementary information S3: catch-per-unit effort model).

For each simulated cull event, we extracted the predicted deer density within the active shoot zone immediately prior to culling and used the CPUE model to estimate the helicopter flying time required to remove the simulated number of deer. Cumulative helicopter hours from 2023 to 2060 was used as our measure of management effort.

Cost-benefit analysis

We calculated a cost-benefit ratio for each scenario as the total helicopter flying time required (the cost) divided by the number of deer-years avoided, relative to the baseline scenario (the benefit). Deer-years avoided were calculated as the difference in total deer-years between each management scenario and the baseline. Lower values for the cost-benefit ratio indicate more efficient management strategies. Uncertainty in cost-benefit ratios reflects uncertainty in estimated effort across simulations.

Sensitivity analysis

To assess robustness to uncertainty in initial population size, all scenarios were re-run with initial abundances of 760 and 1,050 female deer within the shoot zone. Patterns in invasion outcomes, effort, and cost-benefit ratios were compared across initial conditions to evaluate the sensitivity of management rankings. We focus our study on model simulation results with N_i = 530, but also report and discuss the results of our sensitivity analysis with N_i = 760 and 1050 (general results were the same across all sets of simulations). We set the baseline initial abundance within the shoot zone at Ni = 530 female deer, which is close to the camera-based mean estimate (505 females) but slightly higher to reflect uncertainty and to adopt a conservative starting condition (i.e. higher invasion pressure). To assess sensitivity to initial abundance, we repeated analyses using Ni = 760 and Ni = 1,050 females, selected to span plausible lower and upper initial conditions across independent estimation approaches. Specifically, 760 corresponds closely to the camera-based estimate of total deer abundance (~758 deer) expressed under the female-only modelling framework, while 1,050 provides a rounded upper value consistent with the Bayesian removal model estimate (~1,025 females).

Results

In our baseline scenario, in which no management was implemented (other than replicating the cull conducted in May 2023) the female deer population in the whole model study area increased 4-fold from 2,390 at the start of 2023 to > 9,500 by 2060, largely driven by increases of deer in suitable habitat outside of the shoot zone and the WJNP (Fig. 2a–c). It took 15 years for deer to return to their pre-cull abundance within the shoot zone. Our initial population had no deer in the WJNP at the start of 2023. By 2060, more than 300 deer occupied 52% of the WJNP (Fig. 2b, d). Under this baseline 'no future management' scenario, there were 5,005 total deer-years in the WJNP (95% CI: 4,922–5,088) (Table 1).

Relative to the baseline scenario, all management scenarios reduced deer abundance and occupancy in the WJNP. The broad shoot zone scenarios were all more effective than the concentrated shoot zone scenarios (Fig. 3a–c). When culling was restricted to the concentrated shoot zone, there were more deer in the WJNP at the end of the simulation period (2060) and more cumulative impacts in terms of more total deer-years in the WJNP compared to the broad shoot zone scenario, as well as a trend for increasing deer numbers by 2060 (Fig. 3). In contrast, deer numbers stabilised by 2040 when culling occurred in the broad shoot zone (Fig. 3).

The most effective scenario was culling every year across the broad shoot zone. In this scenario, 90 deer were projected to occupy 5% of the WJNP by 2060, with a total of 3,237 (3,223–3,251) deer-years in the WJNP (Table 1, Figs 3, 4). The least effective management scenario was culling every five years only within the concentrated shoot zone; 201 deer were projected to occupy 36% of the 20 cells in the WJNP by 2060, with a total of 4,125 (4,070–4,179) deer-years in the WJNP (Table 1, Figs 3, 4). The larger effect size observed in endpoint metrics (deer abundance and occupation of the WJNP in 2060) compared to cumulative deer-years was due to deer populations remaining relatively low until a marked increase after 2050 (Fig. 3).

All scenarios involving culling across the broad shoot zone required more effort, measured in helicopter flying hours, than those restricted to the concentrated shoot zone (Table 2). The five-year broad shoot zone required the most effort (298.56 helicopter flying hours cumulative to 2060, 95% CI: 189.47–884.96 hours), while the concentrated shoot zone/culling every five years required the least effort (177 helicopter flying hours, 110.44–745.58).

The higher-frequency culls resulted in fewer deer shot in total from 2023 to 2060. For example, when considering culls across the broad shoot zone, a total of 954 (943–965) deer were shot under the yearly cull scenario, whereas 1,152 (1,137–1,167) deer were shot when culls occurred every five years. Fewer deer were shot when culls were focused in the concentrated zone compared to when culls were across the broad shoot zone. At a yearly frequency, 776 (767–784) deer were shot in the concentrated shoot zone compared to 954 (943–965) deer shot in the broad shoot zone (Table 2, Fig. 4).

In our eradication scenario, complete eradication (i.e., zero deer in the WJNP by 2060) was achieved in 65.5% of 1000 simulations (Fig. 5). The mean number of deer in the WJNP in 2060, across all eradication simulations, was 0.62 (0.55–0.68), and the maximum number of deer remaining in the WJNP in 2060 for any given simulation was 8 (Fig. 5). The estimated amount of effort was 1151.36 helicopter flying hours (697.70–4998.16 hours).

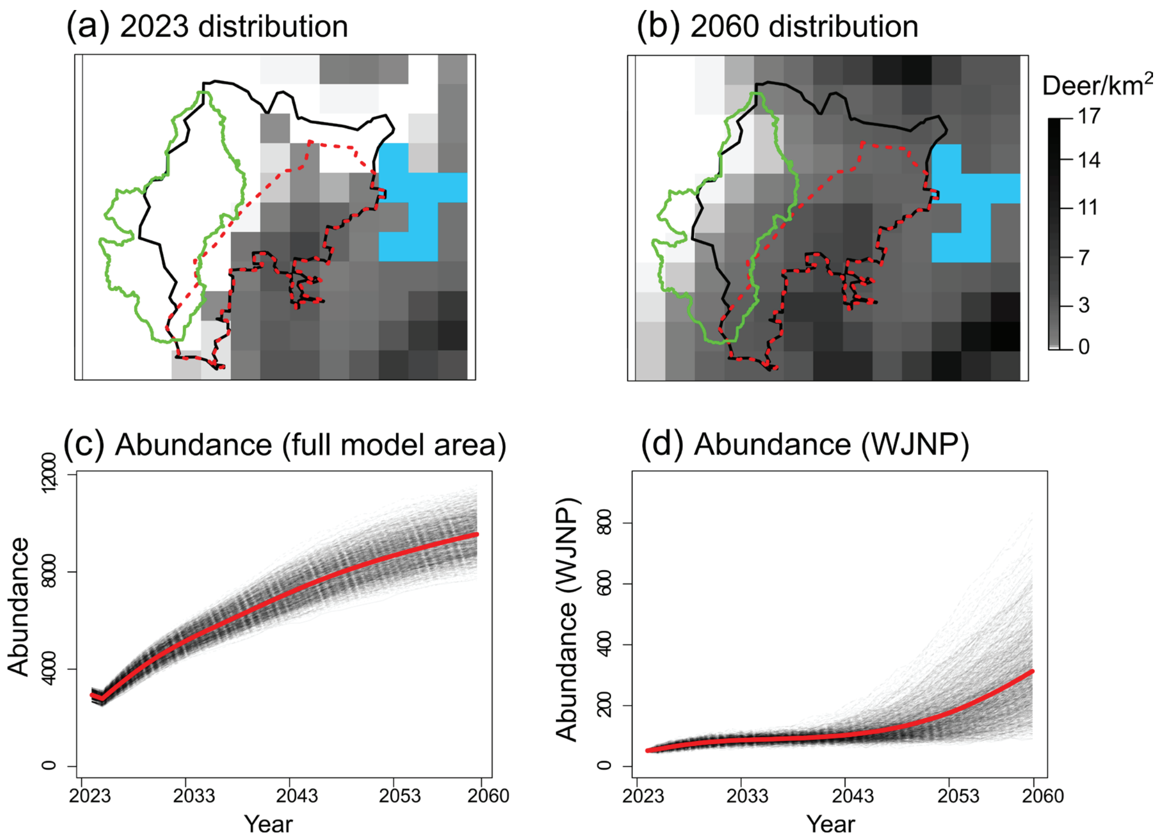

Figure 2. Predicted distribution and density of female fallow deer in and around the Walls of Jerusalem National Park (WJNP), Tasmania, Australia under the baseline no management scenario following the May 2023 aerial cull (see Methods for full scenario details). **a.** Initial (2023) and **b.** Predicted (2060) deer distribution and density. Green, black and red dashed lines denote the boundaries of WJNP, the broad shoot zone, and concentrated shoot zone, respectively; light blue indicates water bodies. **c, d.** Show simulated deer abundance (2023–2060) in the full model area and WJNP, with 1,000 simulations (black lines) and the mean (red line).

Table 2. Summary statistics describing projected numbers of female fallow deer culled under a baseline scenario of no management and six culling scenarios in and around the Walls of Jerusalem National Park (WJNP), Tasmania, Australia, 2023–2060. Estimated management effort, measured as helicopter flying time required to remove deer, are presented for each scenario. Values are means, with 95% confidence intervals for each scenario's set of 1,000 simulations in parentheses (No confidence intervals are provided for the Baseline scenario, as it reports empirical values from the cull performed in 2023 by Paks Tasmania). Details for all scenarios flight time estimation are provided in Methods.

Scenario	Total number of female deer culled	Helicopter hours required
Baseline	450	72.4
Broad shoot zone, every year	954 (943–965)	265.13 (161.43–1200.83)
Broad shoot zone, every 2 years	985 (973–998)	270.35 (166.03–1083.26)
Broad shoot zone, every 5 years	1,152 (1,137–1,167)	298.56 (189.47–884.96)
Concentrated shoot zone, every year	776 (767–784)	177.25 (110.44–745.58)
Concentrated shoot zone, every 2 years	800 (791–809)	178.54 (113.06–625.22)
Concentrated shoot zone, every 5 years	920 (908–931)	187.38 (125.86–446.98)

The cost-benefit analysis for each scenario – calculated as amount of helicopter flying time in hours divided by total deer-years avoided (i.e., total deer-years in the baseline scenario minus total deer-years for a given scenario) – revealed that the scenario with the lowest cost-benefit ("best" scenario) was culling across the broad shoot zone every two years or every year (Fig. 6, Table 3). The scenario with the highest cost per benefit ("worst" scenario) was the eradication scenario (Table 3).

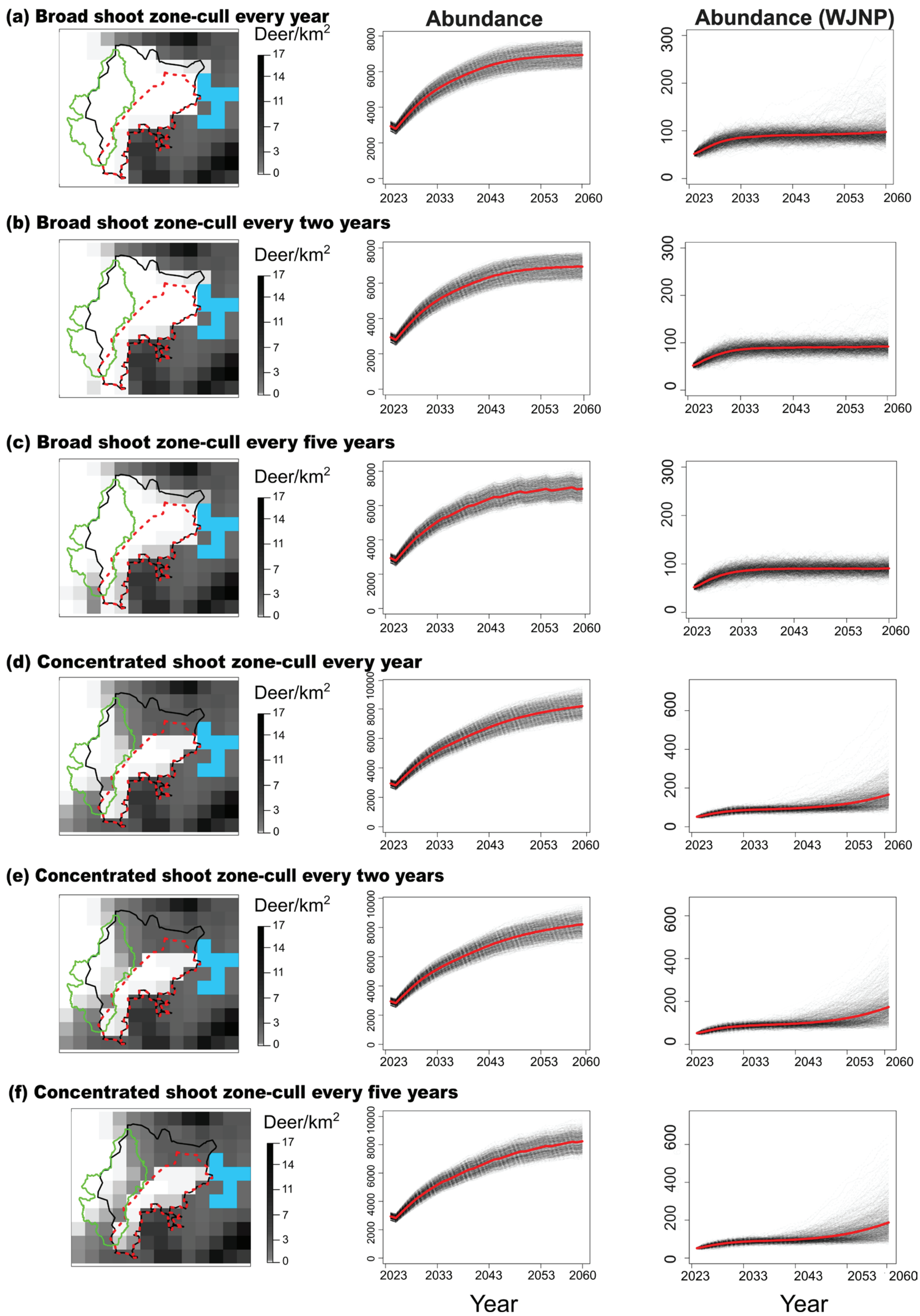

Figure 3. Changes in the predicted distribution and abundance of female fallow deer in and around the Walls of Jerusalem National Park, Tasmania, Australia, 2023–2060, under six management scenarios. For 2060 distribution plots (left column), the green line is the boundary of the Walls of Jerusalem National Park, the black line is the boundary of the broad shoot zone, and the red line is the boundary of the concentrated shoot zone. Light blue cells indicate water bodies. For abundance time series plots (middle column showing the abundance for the whole model area, right column showing abundance just for the Walls of Jerusalem National Park), the thin black lines show the result from each of 1000 simulations, and the red line is the mean estimate from all simulations. Plots **(a–c)** show results from culls of different frequencies, across the broad shoot zone. **a.** Cull every year; **b.** Cull every two years; **c.** Cull every five years. Plots **(d–f)** show results from culls of different frequencies, when removing deer from the concentrated shoot zone with high deer density. **d.** Cull every year; **e.** Cull every two years; **f.** Cull every five years.

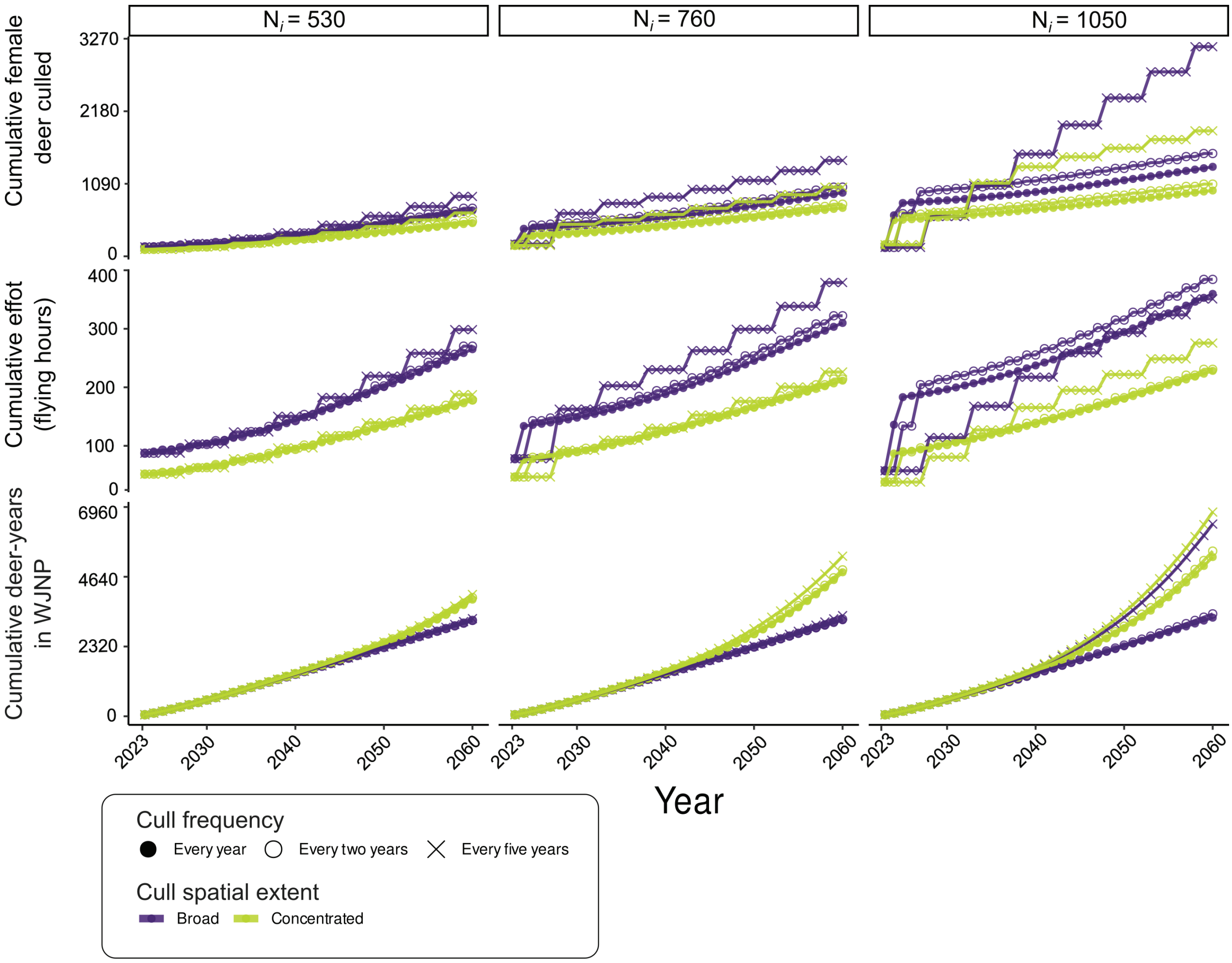

Figure 4. Changes in the cumulative number of female fallow deer culled (upper row), effort, in terms of required helicopter flying time in hours (middle row), and female fallow deer-years in the Walls of Jerusalem National Park (WJNP), Tasmania, Australia, 2023–2060, for the three initial shoot zone abundances (N_i) used in the sensitivity analysis.

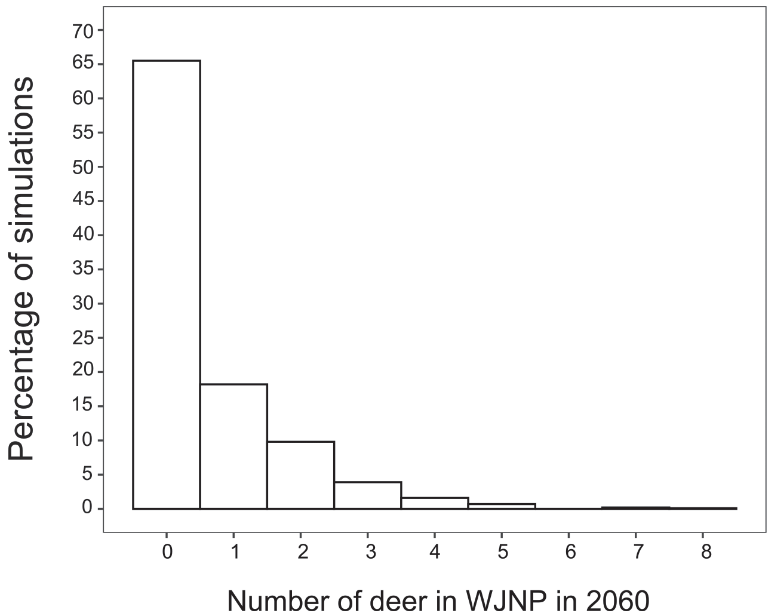

Figure 5. Histogram of female fallow deer abundance in the Walls of Jerusalem National Park (WJNP), Tasmania, Australia, in 2060, for 1000 simulations of our eradication scenario.

Sensitivity analysis

Our sensitivity analysis revealed that, across all scenarios, the overall amount of management effort, number of deer culled, and cumulative deer-years in the WJNP increased with increasing initial abundance in the shoot zone, but the patterns across scenarios remained qualitatively similar (Fig. 4). The biggest change was observed when N_i was set at 1050; the effectiveness of the five-year frequency cull decreased for both spatial scenarios, with a large increase in the number of

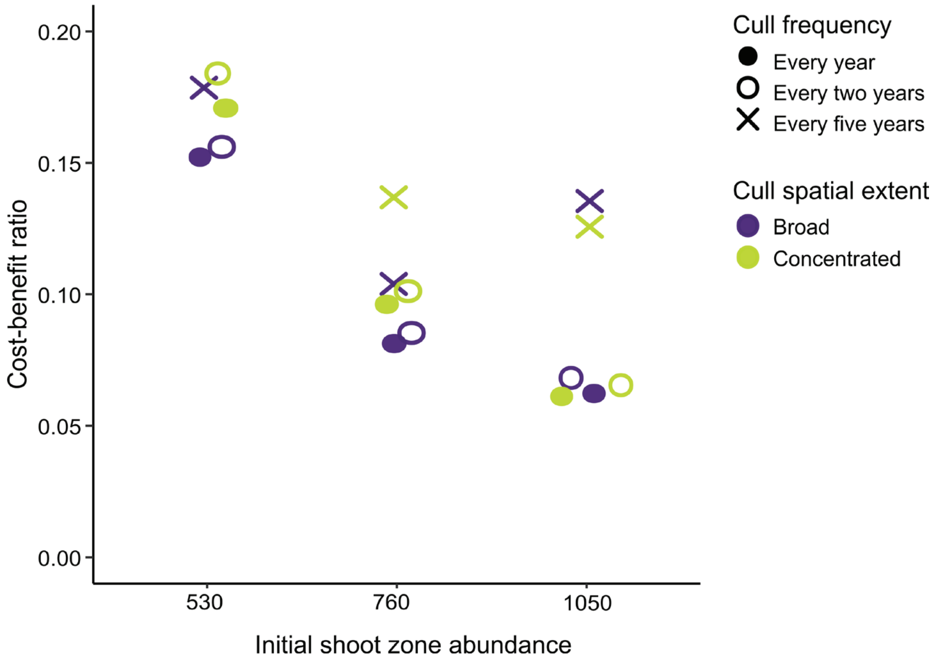

Figure 6. Cost-benefit ratio (ratio of total cost to benefit, measured in terms of number of deer-years avoided in each scenario relative to baseline) for the three initial shoot zone abundances (*Ni*) used in our model of the management effectiveness of culling deer in and around the Walls of Jerusalem National Park, Tasmania, Australia, 2023–2060. Lower cost-benefit ratios indicate more beneficial management scenarios, and points are slightly 'jittered' to reduce overlap.

Table 3. Cost-benefit ratio for seven scenarios for actively managing fallow deer to minimise their occupancy and abundance in the Walls of Jerusalem National Park, Tasmania, Australia, 2023–2060. Scenarios are ranked from best (least cost per benefit, Rank =1) to worst (greatest cost per benefit (Rank = 5. Note that some scenarios are tied, so the number of rankings is less than the total number of scenarios). The ratio was calculated as the required flight time for each given scenario divided by number of deer-years avoided (number of deer-years in the baseline scenario minus number of deer-years for the given scenario). The mean flight time for each scenario was used in the calculation, with upper and lower estimates for the ratios reflecting the 95% CIs for the flight time of each scenario (see Table 2).

Rank	Scenario	Cost-benefit ratio
1	Broad shoot zone, every 2 years	0.15 (0.09–0.62)
1	Broad shoot zone, every year	0.15 (0.09–0.68)
2	Concentrated shoot zone, every year	0.17 (0.10–0.71)
3	Broad shoot zone, every 5 years	0.18 (0.11–0.52)
3	Concentrated shoot zone, every 2 years	0.18 (0.11–0.63)
4	Concentrated shoot zone, every 5 years	0.21 (0.14–0.51)
5	Eradication	0.23 (0.14–1.02)

deer-years in the WJNP (Fig. 4). For the broad shoot zone there were 3,340 deer-years when culling every year, 3,469 deer-years when culling every two years, and a large increase to 6,511 deer-years when culling every five years.

All scenarios had a lower ('better') cost-benefit ratio in the sensitivity analysis, with minor changes in the relative ranking of the scenarios according to their cost-benefit ratio (Fig. 6). Culling either every year or every two years in the broad shoot zone had the lowest cost-benefit when N_i = 760 or 1050. For the sensitivity analysis with the largest N_i (N_i = 1050), the cost-benefit ratio was similar for both spatial extent scenarios (i.e., similar cost-benefit ratios for both the broad and concentrated shoot zones), but there was a greater effect of cull frequency on the cost-benefit ratio: the large decrease in the effectiveness of the five year frequency culls meant they had a much higher (worse) cost-benefit ratio than all other scenarios when N_i = 1050 (Fig. 6), and culls in the concentrated shoot zone every year or every two years had lower ('better') cost-benefit ratios.

Discussion

Effective management of invasive ungulates in rugged landscapes depends on aligning the spatial extent and frequency of control with invasion dynamics and reinvasion pathways. Aerial culling is the only feasible method for removing ungulates such as deer from remote and rugged terrain such as the WJNP and surrounding areas (Tustin and Challies 1978; Pulsford et al. 2022). We used data from an aerial shooting operation in 2023 and applied it in a SEPM to evaluate potential culling strategies for minimising the invasion of a high-value conservation area by non-native fallow deer. There were four key findings. First, restricting culling to a concentrated area containing the source population greatly reduced the effectiveness of management compared to culling across a broader area incorporating the invasion front. Second, culling at a lower frequency slightly reduced effectiveness (for both occupancy and total deer-years in the WJNP), with slightly reduced effort (in terms of amount of helicopter flying time). The effects of changing the cull frequency were much less pronounced than the effect of changing the spatial extent of culls, except in our sensitivity analysis, where the effectiveness of culling every five years was greatly reduced when the assumed initial population size was almost doubled in the shoot zone. We found no interactive effects between the two scenario types (cull frequency and spatial extent) on management effectiveness or amount of effort. Third, population-level animal welfare outcomes were improved (i.e. the total number of deer culled was lower) when culls occurred more frequently, and when culling was restricted to the concentrated shoot zone. Again, there were no interactive effects between the two scenario types (cull frequency and spatial extent) on this outcome. Fourth, keeping fallow deer out of the WJNP is feasible, but would require yearly culling across an expanded area. This full eradication scenario would require almost four times the effort as any of the scenarios aimed at minimising deer occupancy and abundance in the WJNP, and had the worst cost-benefit ratio of any of the scenarios we examined.

Effective management of invasive species often requires broad and adaptive control strategies that account for species movement and pathways of reinvasion (Chadès et al. 2011; Baker 2017). In our scenario projections, the smaller shoot area did not include areas of suitable habitat linking deer in the northeast through into the WJNP via its northeastern border. This is the most likely pathway by which deer dispersed into the WJNP when culling was restricted to a smaller zone. The deer population in the WJNP then grew faster under this scenario because relatively few deer were being removed inside the WJNP. Studies that have modelled the control of other medium-sized invasive mammals have highlighted large differences in the effectiveness of different spatial control strategies and shown that invasive populations can be almost entirely maintained by immigration following control (Griffiths and Barron 2016; Parkes et al. 2017; Pepin et al. 2017). For example, a spatially explicit population model of invasive common brushtail possums (*Trichosurus vulpecula*) in New Zealand found that immigration, rather than *in situ* reproduction, was likely to initiate population growth and recovery post-control (Lustig et al. 2019). There, as in our study, a broad control area that reduced reinvasion pressure from all sources was most effective, particularly in the absence of natural landscape barriers to reinvasion (Patterson et al. 2024). This reinforces that containment strategies for mobile invasive species must address both source populations and dispersal corridors, rather than focusing solely on local abundance reduction.

Our catch-per-unit-effort model, using data from the 2023 cull, enabled us to estimate the functional response describing how the effort (number of helicopter hours) required to remove deer changed as culling reduced the density of deer within the shoot zones. This relationship was then used to estimate effort for each scenario, with the number of hours required for each cull event calculated from the simulated density within the shoot zones. The functional response will likely differ for fallow deer in other environments because the probability of detecting and killing deer will vary with topography and vegetation height and cover (Latham et al. 2018). For example, our functional response differed from that estimated for fallow deer removed during aerial culling operations on mainland Australia (Bengsen et al. 2023): there was a similar linear relationship for densities of 0–5 deer/km^2, but the slope differed. The different relationship could be because thermal imagery equipment was used in the 2023 WJNP cull but not in the operations analysed by Bengsen et al. (2023). Using this more general form of the CPUE-density relationship would have biased our effort estimates and given inappropriate uncertainty estimates. Our estimates could, however, have inaccuracies from other sources; for example, repeated operations in the same area using the same shooters may increase efficiency over time, thereby reducing helicopter charter time. We also note that there were large levels of uncertainty around the exact amount of effort required for each scenario, with upper confidence limits being ~3-fold greater than the mean estimate for each scenario (Table 2). Our estimates are most valuable, however, for evaluating the relative rather than absolute amount of effort for each scenario to identify the most time-effective options (Vaissière et al. 2022).

Accurate estimates of initial population abundance are critical for invasive species management because they strongly influence the effectiveness and required intensity of control. The Bayesian removal model (Ramsey et al. 2023) estimated the female fallow deer population to be twice as large as did the index-removal method (1,025 and 505 deer, respectively). This difference in estimated N_i is likely due at least partly to the index-removal method's failure to account for imperfect detection probabilities (MacKenzie and Kendall 2002; Sollmann et al. 2013), generating a negatively-biased estimate (Forsyth et al. 2022). As well as accounting for imperfect detection and potentially providing a less biased estimate, an additional advantage of using the removal model approach is that pre- and post-cull population abundances and control efficacy can be estimated directly from data collected during control operations, without the need for additional monitoring data, thereby reducing overall program cost (Ramsey et al. 2023). Extensions to the removal model used here (Dail and Madsen 2011; Link et al. 2018; Ramsey et al. 2023) also allow estimates to be derived when demographic closure cannot be assumed (i.e., for fallow deer, immigration, deaths, and natural recruitment will occur when control operations occur across multiple years). Therefore, ongoing collection of operational data (locations of killed deer and helicopter flight paths) during any future management of this population will enable concurrent, and cheap, monitoring of the population and assessment of control efficacy using removal modelling.

Achieving effective control of an invasive population requires adequate culling effort (Bengsen et al. 2023). When we ran our sensitivity analysis using the larger estimate of the initial population size in the broad shoot zone, the effectiveness of culling at five-year intervals was substantially decreased relative to the other scenarios. This suggests that when there is uncertainty around the initial size of a large population of fallow deer, or where extra recruitment into the control area might be expected, a conservative approach of culling more frequently (at least every two years) should be adopted. Inadequate culling may result in a failure to achieve desired reductions in deer populations and their undesirable impacts (Husheer and Robertson 2005; Ramsey et al. 2018). For example, multiple sambar deer populations across Victoria were subject to repeated periods of aerial culling, but deer abundances increased at sites where helicopter search effort was low (Ramsey et al. 2023).

Lethal control operations trade-off management outcomes, effort, and animal welfare considerations. When culling less frequently, deer were removed when they occurred at higher densities in the shoot zones, and so efficiency was increased with more deer removed per hour compared to when they were maintained at lower densities when culling was conducted yearly or every second year. However, for the lower frequency cull scenario, there was a trade-off in terms of having to shoot more deer. This increase in numbers of deer shot with less frequent culling occurs because deer numbers increase more between cull events and deer are then removed from a population growing more quickly (Getz and Haight 1989). From a biodiversity perspective, this strategy also allows higher deer densities to persist for longer periods, increasing the likelihood of cumulative vegetation browsing and other ecological impacts, even if efficiency in terms of efforts and costs appears higher. This trade-off between effort/cost, impacts, and population-level animal welfare considerations, raises the question of willingness to incur extra costs to improve population-level animal welfare and ecological outcomes and will be an important consideration for managers controlling this and other invasive mammalian species (Warburton et al. 2012).

We used the metric 'total deer-years' (i.e. the sum of individual deer in the WJNP across all simulated timesteps) to compare the potential impacts of deer in the WJNP among scenarios. To our knowledge, this has not been previously used as a metric of impact of biological invasions. When compared to point estimates such as occupancy and abundance in 2060, this metric should better reflect the cumulative damage that deer may cause in the WJNP across the timeframe we examined. For example, when comparing management scenarios relative to the baseline, there were large effect sizes when using endpoint measures (occupancy and abundance of deer in the WJNP in 2060). Effects were still large but less pronounced when using the cumulative deer-years metric, given there was a lag before deer started to grow and spread in the WJNP (typically after 2050 in our scenarios). Our metric could be further improved as data are collected on the impacts of fallow deer in and around our study area, or in similar environments, including whether thresholds or non-linearities exist in the density-impact relationship (Yokomizo et al. 2009). With this information, we would be able to more directly estimate the impacts of deer under each scenario. Importantly, our deer-years metric is not intended to represent a direct or universally transferable measure of ecological damage. Rather, it provides a relative index for comparing scenarios in terms of cumulative deer presence and potential impact, and can be used in management alongside conventional metrics.

A limitation of our simulation model, which is necessarily a simplification of the real world, is that there are no data describing the dispersal of fallow deer in Tasmania. Dispersal is a key component of invasion dynamics and a key determinant of invasion outcomes (Pepin et al. 2022), and hence dispersal parameters can have a substantial influence on SEPM outputs. However, all dispersal parameters in our SEPM were previously validated in a state-wide version of the model that accurately reproduced changes in the occupancy and abundance of the Tasmanian fallow deer population during 1985–2019 (Botterill-James et al. 2024). Further, we accounted for the effects of uncertainty of dispersal parameters on our projections by running our model 1,000 times for each scenario, with each run using a unique combination of parameter values sampled from the validated parameter posterior distributions (Botterill-James et al. 2024). Dispersal rates of fallow deer in Australia have not been directly estimated; however, a study of male and female fallow deer fitted with GPS collars at three sites in New South Wales found that individuals surviving aerial culling did not disperse in the subsequent three months (Bengsen et al. 2024). In addition, an experimental study of the behavioural effects of aerial shooting detected only minor and temporary shifts in diel activity, with increased activity toward dusk but no sustained changes in space use or movement patterns (McCarthy et al. 2026). Taken together, available empirical evidence suggests that aerial culling of fallow deer is unlikely to induce dispersal into the WJNP or to generate persistent behavioural changes that would substantially reduce susceptibility to subsequent control efforts. While short-term behavioural plasticity may influence detectability immediately following culling operations, there is currently no evidence that such effects persist over longer time scales or meaningfully compromise the effectiveness of repeated aerial control.

Conclusions

Our study illustrates how the invasion of a high-value conservation area by invasive fallow deer can be minimised with the best available management technique – thermally-assisted aerial culling. Compared to a baseline scenario that had a single cull in 2023, all management scenarios greatly reduced the distribution and abundance of deer in the WJNP. Hence, culling will need to be repeated regularly to minimise the abundance and occupancy of deer in the WJNP. Culling across a broad zone incorporating both the invasion front and the established source population will be much more effective than targeting only the source population. Culling every year or every second year provided the greatest benefit relative to amount of management effort. These scenarios also resulted in lower population-level animal welfare impacts (i.e., total number of deer culled) compared to the scenario in which culling occurred every five years. Our conclusions were generally insensitive to initial population size in the shoot zone, with the broad shoot zone every two years or every scenario always having the best cost-benefit ratio; however, when N_i was nearly doubled, to 1050, which may be the more rigorous estimate, both spatial extent scenarios were similar, and the effectiveness of culling every five years was greatly reduced compared to the other scenarios. This suggests that more frequent culls could be a more conservative option to ensure effective control. Keeping fallow deer out of the WJNP is possible if the size of the broad shoot zone is doubled and culling is conducted every year, but this scenario required almost four times as much effort compared to any other scenario we examined. More broadly, our modelling framework provides a transferable approach for evaluating trade-offs between effectiveness, effort, and animal welfare in the management of invasive species, particularly where eradication is infeasible and long-term containment is the primary goal.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

All authors contributed to the study conception and design. Collection and analysis of camera trap data was performed by Michael M Driessen, all other data analysis was performed by Thomas Botterill-James. The writing of the manuscript was led by Thomas Botterill-James and David M. Forsyth, with contributions from all authors. All authors read and approved the final manuscript.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Supplementary information

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Explanation note: **fig. S1.** Map of study area showing all zones used in the scenarios, including the zone used in the eradication scenario. **supplementary information S1.** 2023 pre-removal population estimate. **fig. S2.** Location of fallow deer monitoring sites. **supplementary information S2.** 2023 pre-removal population estimate, using a second estimation method (removal model). **supplementary information S3.** catch-per-unit-effort model. **fig. S3.** Predictions from the catch-per-unit-effort model. **table S1.** Values used in the female fallow deer Leslie matrix. **table S2.** Parameters used in the spatially explicit female fallow deer population model.

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