



Forty-five years of removal campaigns for feral ungulates reveal strategies for success and future directions

Nathan P. Snow · Keely J. Kohen · Ingrid A. Messer · Abigail Pagels · Seth M. Cook · Scott Beckerman · Travis Guerrant · Kurt C. VerCauteren · Kim M. Pepin

Received: 7 April 2025 / Accepted: 12 August 2025 / Published online: 29 August 2025

This is a U.S. Government work and not under copyright protection in the US; foreign copyright protection may apply 2025

Abstract Feral or invasive ungulates (hereafter: feral ungulates) exist worldwide, and their ability to thrive threatens biodiversity, degrades ecosystems, and causes damage to agriculture and properties. Strategies for removing feral ungulates from their introduced insular and mainland ranges have varied greatly, successes have been difficult, and the need is increasing. We reviewed published scientific literature on feral ungulate eradication and maximum control campaigns during 1978–2023 to identify practices that led to greater success. Of 54 campaigns, 32 (59%) reported success. Most campaigns focused on feral swine (61%; *Sus scrofa*) or feral goats (24%; *Capra hircus*). The average duration of a campaign was 61 months and cost an average of \$1.9 m (\$USD

2024) or \$636/km²/month. The most important components for success included ensuring adequate funding was secured for the campaign (\$0.5–1 million/km² is recommended) and population recovery or reinvasion were minimized. The frequency of campaigns has increased during the last 45 years; however, the areas worked (km²), monthly durations, removal techniques used, funding, and ultimately the rates of success have not changed. A lack of increasing success for larger and more complex campaigns indicated that modernization of technologies for population control has been minimal, and larger breakthroughs are needed. Safe and effective toxicants and sterilants may provide those advances if developed. Lessons learned from campaigns indicate that pilot testing control methods prior to initiating full campaigns may help to alleviate uncertainties, produce more reliable plans, and help inform the biology of the animals being targeted for removal.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10530-025-03652-y>.

N. P. Snow (✉) · K. J. Kohen · I. A. Messer · A. Pagels · S. M. Cook · K. C. VerCauteren · K. M. Pepin
USDA/APHIS/Wildlife Services, National Wildlife Research Center, 4101 LaPorte Ave., Fort Collins, CO 80521, USA
e-mail: nathan.p.snow@usda.gov

S. Beckerman
USDA/APHIS/Wildlife Services, Eastern Region, Gravois Mills, MO 65037, USA

T. Guerrant
USDA/APHIS/Wildlife Services, 1714 Commerce Ct., Suite C, Columbia, MO 65202, USA

Keywords Control · Deer · Elimination · Eradication · Goat · Invasive · Swine · Wildlife damage management

Introduction

Invasive species pose major risks to many of the world's ecosystems (Daniel et al. 2025; Mack et al. 2000). Campaigns to remove invasive species have been ongoing for the last century, with

sundry successes, failures, and reinvasions (Simberloff 2009). Many attempted campaigns have been outpaced by the magnitude of an invasion and limited resources for control (Green and Grosholz 2021). As such, recommendations for prioritizing the control of the most urgent invasions using strategies that can achieve the greatest conservation benefit and best use of resources are increasingly important (e.g., functional eradication; Green and Grosholz 2021; Prior et al. 2018). Despite this, scientists have been apprehensive to attempt campaigns with difficult species (e.g., invertebrates, aquatic, plant, etc.) or complex environments (e.g., difficult terrain, landcover, scope, stakeholder groups, etc.) because risks of failures or unacceptable collateral damage were high (Simberloff 2009). Meanwhile, campaigns for some groups of species like invasive, non-native, and feral ungulates (hereafter: feral ungulates) are regularly attempted and successes have been common (Campbell and Donlan 2005). With these successes, campaigns against feral ungulates have been growing in complexity (e.g., multiple stakeholders, human presence, and intermixing with domestic animals; Campbell and Donlan 2005), scope (e.g., elimination throughout larger areas; Hartin and Hutton 2007), and need (e.g., increasing ecological consequences; VerCauteren et al. 2024) during the last few decades. Identifying strategies to ensure continued successes for these campaigns is becoming increasingly valuable.

Feral ungulates have been introduced around the world primarily for food provisioning and sport hunting opportunities (Jaksic et al. 2002; Lever 1985; Lever and Yalden 1995; Nelle 1992; VerCauteren et al. 2019), as well as escapees from captive facilities and gifts between governments (Hulme et al. 2008; Long 2003). Feral ungulates make up three of the 14 most destructive feral mammals in the world, including feral swine (*Sus scrofa*), goats (*Capra hircus*), and red deer (*Cervus elaphus*) (Lowe et al. 2000). However, other species of feral ungulates have become established and are detrimental to ecosystems throughout the world, including domestic ungulates such as sheep (*Ovis aries*), horses and burros (*Equus ferus*), donkeys (*E. asinus*), and cattle (*Bos taurus*); as well as wild ungulates such as camels (*Camelus dromedarius*), axis deer (*Axis axis*), fallow deer (*Dama dama*) and many others (Lever 1985; Long 2003). At least 86 species of ungulates have been introduced throughout the world (Long 2003).

Feral ungulates have been increasing and spreading globally during recent decades. For example, at least six species of feral deer (*Cervidae* spp.) have become established and are expanding in Australia (Burgin et al. 2015; Davis et al. 2016). During recent decades feral swine expanded in densities and range through the US and Australia (McClure et al. 2015; Snow et al. 2017b; West 2008), more recently in Canada (Aschim and Brook 2019), and in many other parts of the world (Barrios-Garcia and Ballari 2012). Feral goats have already been successfully removed from > 120 islands worldwide, although this is just a small proportion of places impacted with the species (Campbell and Donlan 2005). Feral cattle (*Bos taurus*); horses, donkeys, and burros (*Equus* spp.); sheep, camels and more can all be found in multiple regions of the world (Long 2003). The negative impacts from these species to their non-native ranges have been severe (Spear and Chown 2009; VerCauteren et al. 2024), thus continued efforts to remove these animals is expected to continue.

Introductions of ungulates can cause ecological and economical losses and threaten human and animal health (Long 2003; Lowney et al. 2005; Meng et al. 2009; Miller et al. 2017; Ruiz-Fons et al. 2008; Teer 2003; VerCauteren et al. 2024). These introductions have led to extirpation of plant species and losses of biodiversity (Spear and Chown 2009), depredation of threatened and endangered species (McClure et al. 2018), and promotion of invasive plant species (Blossey and Gorchov 2017; Vavra et al. 2007). Consequences of feral ungulates are largest where the ungulates perform novel functions in new environments (Spear and Chown 2009), such as islands that heretofore were not home to ungulates. Attempts to alleviate these consequences frequently involve removing introduced ungulates from non-native environments, however some ungulates are considered “tricky species” because of a lack of effective control tools, they learned quickly to avoid control efforts, and are neophobic (Parkes and Panetta 2009).

Rapid removal of feral ungulates is sometimes needed in response to a new invasion or an introduced disease into a new geographic area. Identifying factors that can enhance campaign success have been useful for planning such responses. A current example of this is African swine fever virus (ASFv), a highly contagious and deadly disease for domestic swine (*Sus scrofa domesticus*), wild boar (*S. scrofa*),

and feral swine (mixture of *S. scrofa domesticus* and *S. scrofa*), which has spread across Europe, Asia, sub-Saharan Africa, and the Caribbean (Cwynar et al. 2019; Gonzales et al. 2021; Penrith and Vosloo 2009; Sur 2019), but is currently absent in countries with widespread feral swine populations such as US, Canada, Mexico, Australia, New Zealand, and many more. Another example is foot-and-mouth disease (FMD), which feral swine and deer can be infected with and may serve as reservoirs for; and ultimately transmit to domestic cattle (Ward et al. 2007, 2009). Stopping the spread of diseases such as ASFv and FMD necessitates intensive removals of feral ungulates, given they represent a high-risk pathway to a new disease introduction in livestock (Brown et al. 2021; Chenais et al. 2018; Ward et al. 2007). In a scenario such as this, an evaluation of previous intense control campaigns is useful for identifying and planning effective responses to transboundary animal diseases in feral ungulates.

Initiating a new campaign to remove feral ungulates can be daunting, especially considering little may be known about the ecology or biology of the species in its newly invaded environment (Beasley et al. 2018). Additionally, new techniques and technology may enable larger-than-ever campaigns, which inherently necessitate broader, more complex, and more collaborative approaches (Campbell and Donlan 2005). Relatedly, it is difficult to determine the absence of feral ungulates across large regions to assess success (Davis et al. 2018), especially when the reinvasion potential is uncertain. These challenges, along with others, generate a need for a guide to assist with future campaigns.

In this paper, we consider elimination and eradication campaigns but use the less stringent terminology of elimination to encompass all. Elimination of feral ungulates means that all feral ungulates from a defined area are removed, but there may be a possibility of reinvasion (i.e., a local population in a large geographical area; Davis et al. 2018). Whereas eradication is elimination without the possibility of reinvasion (Bomford and O'Brien 1995). Attempts at elimination can be thwarted by missing elusive individuals, reinvasions of animals from surrounding areas, or reintroductions of the feral ungulates by humans (Bomford and O'Brien 1995; Davis et al. 2018). If there is reinvasion potential, a plan for long-term monitoring and removal of reintroductions will

be needed. We intended to focus on just the initial elimination campaigns in this review but found that there were relatively few published reports (details below). Therefore, we also considered campaigns that focused on maximum control for feral ungulates, such that maximum numbers of feral ungulates were removed using limited resources or time. A best-case-goal of maximum control is elimination, but elimination is not a predetermined end point. Lastly, we also considered campaigns that focused on removal of feral ungulates for the sake of eliminating or maximum control of the damages caused by those species. Finally, occasionally managers attempted eliminating ≥ 2 feral ungulate species from a region at once with a combined-campaign (e.g., Kessler 2002; Masters et al. 2018), thus increasing the complexity for success. We consider each species-campaign combination separately in this manuscript but recognize there may competing or complementary strategies for managers to consider.

Our aim was to evaluate reports of previous campaigns of removing feral ungulates to identify strategies that increased the probabilities of success and efficiency. Our goal was to provide a future guide for upcoming campaigns and identify any challenges or gaps in knowledge that should be addressed. We also summarized the reported suggestions from authors of previous campaigns to provide a synthesis of lessons learned as recommendations for developing successful removal campaigns.

Materials and methods

We compiled data from published campaigns aimed at eliminating or removing feral ungulates and/or eliminating or reducing the damage caused by feral ungulates. We performed a Web of Science search using all available years conducted on 02 January 2024. Our search was defined as follows: ((invasi* or feral or pest or wild) and (goat or pig or boar or hog or swine or ungulate or deer or cow or cattle or horse or camels or sheep or nilgai) and (control or manag* or eliminat* or eradicat* or mitigat* or remov* or cull*)) not (weed or insect or beetle or fly or fish or reptile or amphibian or bird or ape or non-invasive or domestic* or disease or plant or guinea or invertebrat* or infection or medical or medicine or bacteria or peccary or gene* or neuro* or parasit* or climat*

or respiratory or model* or entomology or chemistry or dairy or predator* or bear or wolf or coyote or fox or puma or lion or hyena or jaguar or leopard or tiger)). Terms to exclude were determined by doing a preliminary search that returned numerous articles that were not relevant to our study. We conducted a similar search in Google Scholar to identify additional literature that may not have been present in Web of Science.

Our searches initially identified 1685 articles. We excluded all articles from disease or forestry-related journals because these contained articles that were not relevant to our purpose, which reduced the number of articles to 340. We reviewed all 340 of these papers to identify articles that met our inclusion criteria and screen their reference lists to identify additional articles that our search may not have identified (including gray literature). Our inclusion criteria were all articles that described a case study of feral ungulate population or damage elimination/maximum control and were experimental, records of management efforts, or observational analyses of population or damage elimination efforts. We excluded any articles with primary objectives of testing new management tools (e.g., new toxic baits or traps) if the study was not focused on elimination or maximum control of the animals. If an article contained information on ≥ 2 independent campaigns, we included each campaign as a separate record. Occasionally, a campaign was reported in ≥ 2 published articles which we combined to provide an overall assessment of the campaign. Overall, we identified 54 articles that met our inclusion criteria. Four campaigns had ≥ 2 articles written which we combined, respectively. Five articles had ≥ 2 campaigns which we separated into unique campaigns. Overall, our dataset consisted of 54 unique campaigns against feral ungulates, and a PRISMA flow diagram is available in Supplemental File 1 (Page et al. 2021).

We judged the success or failure of a campaign based on the reported goals and outcomes by the authors of the article. We considered the campaign a success if the authors considered the campaign to have met their original goal(s) (e.g., complete elimination of feral ungulates, maximum reduction of feral ungulates, or maximum reduction of damage caused by feral ungulates). We considered the campaign unsuccessful if the authors reported that their goal was not achieved (e.g., elimination of feral ungulates not fully completed, maximum control of

feral ungulates not accomplished, or damages from feral ungulates not reduced) or it did not appear that the objectives were met. We extracted variables we considered relevant to increasing the success of a campaign, including where the campaign occurred (island vs. mainland), initial population size, number of animals removed, area of campaign (converted to km^2), types of removal methods used (e.g., aerial hunting, trapping, dogs, etc.), duration of the campaign (months), monitoring methods used (e.g., cameras, observations, etc.), and costs of the campaign (converted to USD in 2024). We designated island campaigns only if the campaign attempted to encompass an entire island. Campaigns that took place on regions within an island, such as Hakalau Forest National Wildlife Refuge in Hawaii, USA (Hess et al. 2006), were considered mainland campaigns. For all campaigns we estimated removal intensity as:

$$\text{removal intensity} = \frac{\frac{\text{total feral ungulates removed}}{\text{km}^2}}{\text{total months of the campaign effort}}$$

We also tabulated data on the types and costs of damage attributed to feral ungulates prior to the campaigns, and the costs of any damages reduced after the campaigns were finished. Finally, we summarized what the goals of the campaigns were (i.e., elimination or maximum control of feral ungulates, or elimination or maximum control of damages), and what (if any) recommendations by the authors for increasing the success of the campaign.

We created a ranking system to quantify the complexity of the campaigns and evaluate how this impacted success. Specifically, we developed a rating system of 1–3, where 3 represented the most complex campaign. Three researchers independently ranked two metrics of complexity for each campaign, operational complexity (e.g., logistics, land access, diversity of stakeholders) and environmental complexity (e.g., land cover, topography, climate). For example, a highly complex campaign was an elimination attempt on a remote island, without ability for aerial hunting, dense land cover, and steep terrain. Another example of highly complex was a large site on a mainland with ample reinvasion potential, many private landowners with diverse interests, and dense canopy with poor road access. We averaged the rankings of each researcher and then averaged the two levels of

complexity to generate an overall level of complexity for each campaign.

Metanalysis

We conducted an exploratory analysis to evaluate the influence of extracted covariates (Table 1) on the probability of a successful campaign using binomial general linear models in Program R (v 4.1.1, The R foundation for statistical computing, Vienna, Austria). Our intent was to conduct a model selection from the global model: $\text{success} \sim \text{location} + \text{goal} + \text{duration} + \text{count of methods} + \text{monitoring} + \text{adaptive} + \text{complexity} + \text{area} + \text{intensity} + \text{cost}$ and all possible two-way interactions of those main effects; however, we had to conduct a tiered approach (described below) because of low sample sizes. We also evaluated the main effects for pairs of highly correlated variables ($r \geq 10.6$), and found that location and goal were collinear, therefore we removed Goal from analyses.

First, we conducted a model selection approach to reduce the number of possible predictors by examining all combinations of the model: $\text{success} \sim \text{location} + \text{duration} + \text{count of}$

methods + Monitoring + adaptive + complexity + area. From the 128 models, we calculated and ranked the relative importance of each covariate (Burnham and Anderson 2002) to exclude the least important predictors. We excluded any variables with weights of < 0.25 as having very weak support for influencing the probability of success compared to the other predictors. Next, we conducted another model selection approach for making inferences about the probability of success. For the relatively important variables, we generated a reduced model and examined all possible combinations of: $\text{success} \sim \text{location} + \text{count of methods} + \text{complexity} + \text{area}$ and all possible two-way interactions. We ranked the 113 models using Akaike's information criterion adjusted for small sample sizes (AICc) and considered any models $\leq \Delta 2$ AICc as competing top models (Anderson and Burnham 2002; Burnham and Anderson 2002). We model averaged the top models and made inferences from the conditional results. We evaluated the parameter estimates and 95% confidence intervals (CIs) of those estimates for non-overlap of zero to indicate statistical differences for the covariates and generated predictive plots to evaluate the biological relevance.

Table 1 Covariates of interest for predicting the probability of a successful campaign removing feral ungulates from 54 total campaigns during 1978–2023

Covariate	No. campaigns reporting	Description	Reason for inclusion
Location	54	Island or mainland	Remote locations (e.g., islands) may be more difficult
Goal	54	Elimination or maximum control	Elimination may be more difficult
Duration	54	Number of months	Shorter durations may reduce population rebound
Count of methods	54	Count of removal methods used	More methods may reduce avoidance by feral ungulates
Monitoring	54	Whether population monitoring was conducted at any time	Monitoring may inform how to achieve success
Adaptive	54	Whether an adaptive removal strategy was used at any time	Adaptive techniques may reduce ineffective measures
Complexity	54	Average of logistical and environmental complexity	More complex situations may be more difficult
Area	52	Area of campaign (km ²)	Larger areas may be more difficult
Intensity	46	Total number of animals removed per km ² per month	Lower intensity may result in more population rebound
Cost	27	Cost of the campaign per month (\$USD 2024)	Increased spending may afford more effective techniques

We wanted to evaluate how removal intensity and cost per month, respectively, influenced the probability of campaign success within the global model above, but both the cost data and removal data were incomplete across different studies (Table 1). This reduced the sample size in the global model when cost and removal intensity were included. Instead, we ran 3 models: (1) a global model with all covariates with complete data, (2) a single variable model with cost/km² as the predictor, and (3) a single variable model with removal intensity as the predictor. For each model, we examined how the covariates influenced the probability of success using binomial generalized linear models. We examined the parameter estimates and 95% CIs for each model as described above.

Finally, we conducted two additional analyses to examine which factors influenced the costs of the campaigns, and whether there were any trends in how the campaigns were conducted through time. For costs, we used a series of separate linear models in program R representing *a priori* hypotheses to examine if the costs were dependent on the intensity of removals, years, number of removal techniques, duration of the campaign, location (island or mainland), and goal (eradication or maximum control). For trends, we used similar models to examine if the sizes (km²) or the probabilities of success increased throughout the years.

Recommended strategies from campaigns

We evaluated the recommended strategies of the authors from each campaign for optimizing, ensuring, or obtaining success. Specifically, we categorized the recommendations into 26 strategies based on how many unique recommendations were offered by the authors (e.g., obtain more funding, obtain more public support, use a specific management technique, evaluate feral ungulate densities prior to implementation, etc.). We summed the total number of campaigns that recommended each specific strategy and ranked them to identify the most recommended strategies for success. Specifically, we summarized the top five recommendations from all successful and unsuccessful campaigns.

We also sub-divided and summarized the rankings based on island versus mainland, small versus large areas, minimal versus maximal costs, and

minimal versus maximal complexities to assist future campaigns with these specific circumstances. Not every campaign reported areas, costs, or complexities, therefore sample sizes of recommended strategies varied among sub-divisions. When there were ties with >6 recommended strategies, we excluded the tied recommendations because there was no clear priority beyond the top recommendations. For ties with ≤6 recommendations, we summarized all but did not rank the tied strategies.

Results

Summary of campaigns

Of the 54 campaigns we identified (Table 2), 33 were focused on removing feral swine (61%), 13 on feral goats (24%), 4 on feral deer (7%; including 1 each for axis deer, fallow deer, sambar deer [*C. unicolor*], and sika deer [*C. nippon*]), 3 on feral sheep (6%), and 1 on feral donkeys (2%). Overall, 25 (46%) of the campaigns took place on islands and 29 (54%) were on a mainland (Fig. 1). Thirty-two of the 54 campaigns reported success in removing feral ungulates to achieve desired levels, and two additional campaigns reported achieving satisfactory reductions in damages from feral ungulates, for an overall success rate of 63%. The primary objectives of the campaigns included 36 campaigns (67%) that were focused on removing feral ungulates, and 9 (17%) that were focused on removing the damages caused by feral ungulates, and 9 (17%) campaigns that focused on both. To reach those objectives, each study had 1–3 primary goals. Those goals included reducing density of established populations of feral ungulates (51 campaigns), protecting resources being damaged by feral ungulates (16 campaigns), and stopping the spread of feral ungulates (e.g., rapidly removing newly established populations; 5 campaigns).

The motivations for the removal campaigns were driven by protecting 7 primary classes of resources from negative effects from feral ungulates. We identified that 40 (74%) of the campaigns were initiated to protect natural resources or sensitive landscapes (e.g. islands, wetlands, or other), 38 (70%) to protect sensitive species (i.e., threatened or endangered plants, invertebrates, or vertebrates), 9 (17%) to protect crops, 5 (9%) to protect livestock, 5 (9%) to

Table 2 Summary of 54 total campaigns reviewed during 1978–2023

Lead author	Year	Country	Species	Success	Location	Goal	Duration (months)	Count of methods used	Monitoring used	Adaptive strategy used	Complexity score (1–3)	Area (km ²)	Removal intensity	Total costs (\$USD 2024)
Andrzejewski (1978)	1978	Poland	Feral swine	No	Mainland	Max control	60	1	No	No	1.33	25.00	NA	NA
Barrett (1988)	1988	United States	Feral swine	Yes	Island	Elimination	36	4	No	Yes	1.17	20.00	0.20	\$430,046
Baron(2011)	2011	United States	Feral swine	Yes	Mainland	Elimination	13	4	No	Yes	2.50	58.83	0.27	NA
Brennan (1993)	1993	New Zealand	Feral goat	No	Mainland	Max control	0.37	2	No	Yes	1.33	6.38	42.71	\$11,096
Campbell (2004)	2004	Ecuador	Feral goat	Yes	Island	Elimination	348	3	Yes	Yes	2.33	60.00	2.00	\$133,252
Carrion (2007)	2007	Ecuador	Feral donkey	Yes	Island	Elimination	360	2	No	No	2.50	5172.77	0.00	NA
Carrion (2011)	2011	Ecuador	Feral goat	No	Island	Elimination	21	4	No	Yes	1.83	5000.00	1.33	\$5,892,474
Comte (2023)	2023	Australia	Feral deer	No	Mainland	Max control	60	1	Yes	Yes	1.67	334.67	0.03	NA
Cowled (2006)	2006	Australia	Feral swine	No	Mainland	Max control	2	1	Yes	Yes	1.67	4430.00	0.03	NA
Cruz (2005)	2005	Ecuador	Feral swine	Yes	Island	Elimination	32	5	Yes	Yes	2.00	584.65	1.00	NA
Cruz (2009)	2009	Ecuador	Feral goat	Yes	Island	Elimination	52	5	No	Yes	2.17	584.65	2.62	\$8,859,398
Ditchkoff (2017)	2017	United States	Feral swine	No	Mainland	Max control	7	2	No	No	1.00	737.00	0.22	\$72,071
Engeman (2004)	2019	United States	Feral swine	Yes	Island	Elimination	96	4	Yes	Yes	2.67	18.00	0.19	\$230,043
Engeman (2004)	2004	United States	Feral swine	Yes	Mainland	Max control	12	1	No	Yes	1.50	5.70	3.35	\$12,242
Engeman (2006)	2006	United States	Feral swine	Yes	Mainland	Max control	36	2	No	Yes	1.67	1877.80	0.01	\$214,118
Engeman (2016)	2016	United States	Feral swine	Yes	Island	Elimination	1	2	Yes	Yes	1.00	5.26	7.41	\$20,169
Engeman (2018)	2018	United States	Feral swine	Yes	Island	Max control	24	3	No	Yes	1.83	10.00	0.69	NA

Table 2 (continued)

Lead author	Year	Country	Species	Success	Location	Goal	Duration (months)	Count of methods used	Monitoring used	Adaptive strategy used	Complexity score (1–3)	Area (km ²)	Removal intensity	Total costs (\$USD 2024)
Gaskamp (2018)	2018	United States	Feral swine	Yes	Mainland	Max control	24	1	No	No	1.17	20.93	0.34	NA
Gaskamp (2018)	2018	United States	Feral swine	Yes	Mainland	Max control	24	1	No	No	1.17	10.24	0.68	NA
Gaskamp (2018)	2018	United States	Feral swine	Yes	Mainland	Max control	24	1	No	No	1.17	9.30	0.09	NA
Giacomelli (2018)	2018	Italy	Feral swine	No	Mainland	Max control	6	2	Yes	Yes	2.00	2255.00	NA	NA
	2016	Argentina	Feral swine	Yes	Mainland	Max control	108	2	Yes	Yes	1.67	85.00	0.22	NA
Gurtler (2017)	2017	Argentina	Feral deer	No	Mainland	Max control	120	2	Yes	Yes	1.50	85.00	0.23	NA
Hadjisterkottis (2006)	2006	Cyprus	Feral swine	Yes	Island	Elimination	84	1	No	No	1.17	9251.00	NA	NA
Heriot (2019)	2019	Australia	Feral goat	Yes	Island	Elimination	144	4	Yes	Yes	1.83	633.00	0.18	\$971,803
Heriot (2019)	2019	Australia	Feral sheep	Yes	Island	Elimination	144	4	Yes	Yes	1.83	633.00	0.18	\$971,803
Hess (2006)	2006	United States	Feral swine	No	Mainland	Max control	180	3	Yes	Yes	2.33	20.24	0.40	NA
Higginbotham (2014)	2014	United States	Feral swine	Yes	Mainland	Max control	84	5	No	Yes	2.33	NA	NA	\$3,770,566
Hone (1983)	1983	Australia	Feral swine	No	Mainland	Elimination	2	2	No	Yes	1.33	50.00	0.95	\$11,387
Hone (2002)	2002	Australia	Feral swine	Yes	Mainland	Max control	180	1	Yes	Yes	1.83	1060.00	NA	NA
Katahira (1993)	1993	United States	Feral swine	Yes	Mainland	Elimination	36	6	No	Yes	2.17	48.40	0.10	\$1,892,978
Keegan (1994)	1994	United States	Feral goat	Yes	Island	Elimination	27	3	Yes	Yes	1.83	148.00	0.07	NA
Kessler (2002)	2002	Mariana Islands	Feral goat	Yes	Island	Elimination	36	5	No	Yes	2.50	5.00	5.02	NA
Kessler (2002)	2002	Mariana Islands	Feral swine	Yes	Island	Elimination	36	5	No	Yes	2.50	5.00	0.38	NA

Table 2 (continued)

Lead author	Year	Country	Species	Success	Location	Goal	Duration (months)	Count of methods used	Monitoring used	Adaptive strategy used	Complexity score (1–3)	Area (km ²)	Removal intensity	Total costs (\$USD 2024)
Kilgo (2023)	2023	United States	Feral swine	No	Mainland	Max control	24	1	Yes	Yes	1.17	NA	NA	NA
Lombardo (2000)	2000	United States	Feral swine	Yes	Island	Elimination	33	4	No	Yes	2.17	214.50	0.17	NA
Masters (2018)	2018	Australia	Feral deer	Yes	Island	Elimination	114	2	Yes	Yes	2.17	4400.00	0.00	NA
Masters (2018)	2018	Australia	Feral goat	Yes	Island	Elimination	120	3	No	Yes	2.17	4400.00	0.00	NA
May (2014)	2014	United States	Feral swine	No	Mainland	Elimination	12	5	No	No	2.00	20,639.00	0.00	\$1,588,260
McCann (2008)	2008	United States	Feral swine	Yes	Mainland	Elimination	34	5	No	No	1.33	57.00	0.10	\$3,757,194
Mentaberre (2014)	2014	Spain	Feral swine	No	Mainland	Max control	96	2	No	Yes	2.33	280.00	0.03	NA
Multiple campaigns	1990	United States	Feral swine	Yes	Island	Elimination	162	5	Yes	Yes	2.00	194.00	0.46	\$5,458,783
Multiple campaigns	1993	Seychelles	Feral goat	Yes	Island	Elimination	300	2	Yes	Yes	2.83	155.00	0.05	\$227,176
Multiple campaigns	2005	United States	Feral swine	Yes	Island	Elimination	14	6	Yes	Yes	2.25	250.23	1.84	\$8,251,019
Multiple campaigns	2009	United States	Feral swine	Yes	Mainland	Elimination	96	3	No	Yes	1.67	73.00	0.05	\$22,372
Ortiz-Alcaraz (2016)	2016	Mexico	Feral sheep	Yes	Island	Elimination	36	5	No	No	2.17	132.00	0.37	\$654,174
Parkes (1990)	1990	New Zealand	Feral goat	No	Mainland	Elimination	780	2	Yes	Yes	2.17	330.00	NA	\$7,907,176
Parkes (1990)	1990	New Zealand	Feral goat	Yes	Island	Elimination	144	2	No	No	2.00	29.38	NA	\$5,447,043
Parkes (1990)	1990	New Zealand	Feral goat	No	Island	Elimination	36	2	No	No	2.33	40.30	0.66	\$101,282
Parkes (1990)	1997	United States	Feral swine	No	Mainland	Elimination	16	3	Yes	Yes	1.17	445.00	0.01	NA
Saunders (1988)	1988	Australia	Feral swine	No	Mainland	Max control	0.16	4	No	Yes	1.50	120.00	51.51	\$21,467

Table 2 (continued)

Lead author	Year	Country	Species	Success	Location	Goal	Duration (months)	Count of methods used	Monitoring used	Adaptive strategy used	Complexity score (1–3)	Area (km ²)	Removal intensity	Total costs (\$USD 2024)
Schuyler (1993)	1993	United States	Feral sheep	No	Island	Elimination	79	2	No	No	1.00	248.00	1.85	\$816,640
	1999	Australia	Feral goat	No	Mainland	Max control	201	3	Yes	Yes	1.67	755.88	0.28	NA
	2022	Japan	Feral deer	No	Mainland	Max control	204	2	Yes	Yes	2.33	1175.00	0.27	NA

protect pasture, 5 (9%) to protect public recreation or private property, and 5 (9%) to protect against other damages to resources (e.g., archaeological sites, impeding military training, or disease spread). Forty-one (76%) of the campaigns were initiated to protect ≥ 2 of those resources listed above. Very few of the campaigns measured the values of the damages being caused (pre-or post-campaign), or the value reduced by the campaign, which also has been reported in a recent review of feral swine damage (VerCauteren et al. 2024). From 5 campaigns that estimated values, the average costs of damage from feral ungulates (all five focused on feral swine) pre-campaign were estimated at \$3.63 m. Of those, the estimates of damages averted after removing the feral ungulates were reported in 4 campaigns and averaged \$3.95 m, indicating a large net benefit (i.e., 109%). However, only 3 campaigns empirically measured damage pre- and post-campaign and estimated an average of 83% reduction in damage (range = 72–100%).

We were able to determine the duration of all 54 campaigns (from start until end of removal efforts), averaging 91.1 months (range = 0.16–780). Thirty-three of the campaigns had continuous effort (i.e., removals occurred continuously in time in the target area without breaks until the campaign ended) which lasted for an average of 74.9 months. The 21 campaigns with periodic efforts (i.e., removals occurred discontinuously throughout the campaign with periods of no removals due to reasons such as personnel having multiple responsibilities) lasted for an average of 116.6 months, with an average of 0.28 periods of effort per month. Twenty-one (64%) of the continuous campaigns reported success in eliminating feral ungulates, and 16 (48%) reported success in eliminating the associated damages. For the periodic campaigns, 11 (52%) reported success in eliminating feral ungulates and 10 (48%) reported success in eliminating damages. The densities of feral ungulates removed/km² averaged 32.1 for continuous campaigns and 51.4 for periodic campaigns throughout their entire durations. These estimates include reproduction and possibly immigration that occurred during the campaign, thus were greater than typical population density estimates. In addition, the intensity of removals was 7.6 times greater during continuous campaigns (mean = 3.58 removed/km²/month) than periodic campaigns (mean = 0.47 removed/km²/month).

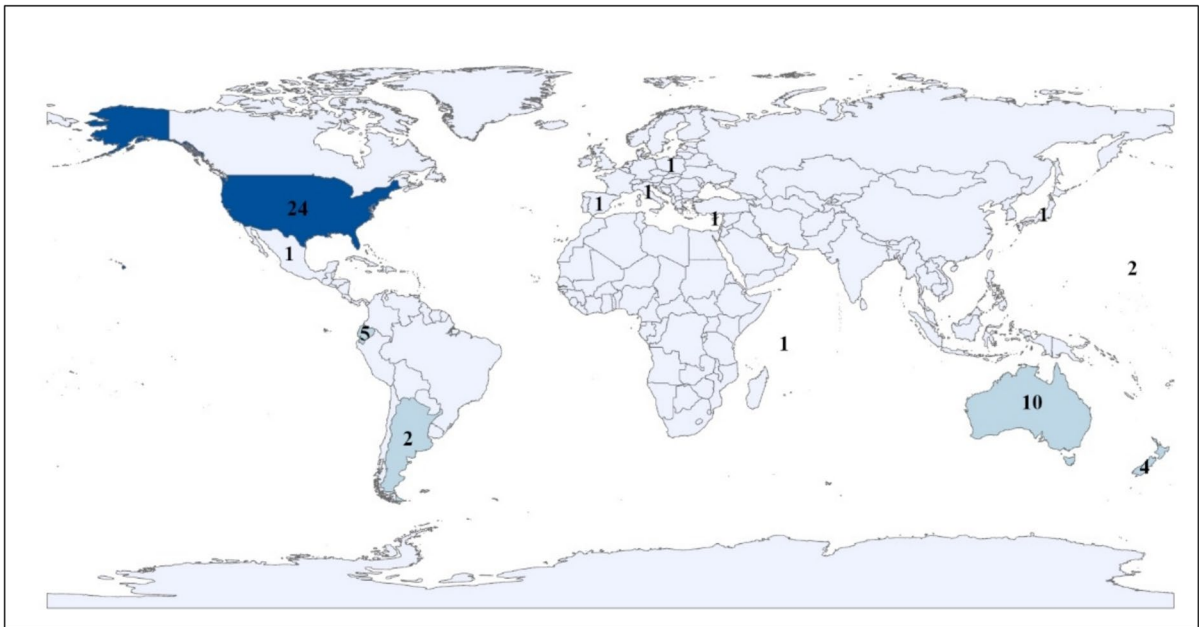


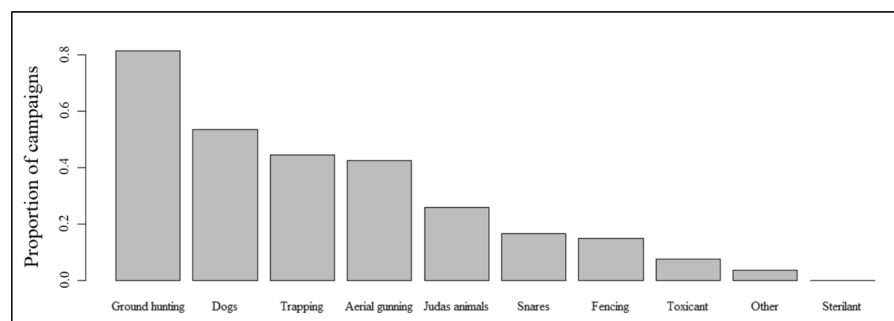
Fig. 1 Count of feral ungulate removal campaigns per country ($n=54$ total) focused on eliminating populations of feral ungulates or the damages they cause from scientific literature or gray literature during 1978–2023. Darker shades repre-

sent more campaigns. Campaigns for countries like Australia, Ecuador, and United States had campaigns that took place on their islands but are attributed to the mainland countries for simplicity in this map

We identified 9 common techniques that were used to remove feral ungulates, as well as 2 other techniques that we grouped together as “other” (e.g., live mustering and supplemental feeding; Fig. 2). Forty-four (81%) of the campaigns used ≥ 2 methods for removing feral ungulates. We found that 43 (80%) of the campaigns used an adaptive strategy for their campaign (i.e., monitored their success and adapted their techniques using real-time results), and 11 (20%) used a non-adaptive approach (i.e., planned at the onset and implemented without change). Of campaigns with adaptive strategies, 20 (37%)

campaigns used raw monitoring data (e.g., observations of animals) to guide their efforts, 23 (43%) generated estimates of population density to guide their efforts, and 13 (24%) used dynamic modeling (e.g., cost–benefit analyses) to guide efforts. On average, campaigns without an adaptive strategy took 79.6 months, removed a total of 5369 feral ungulates, and had a removal intensity of 0.48 feral ungulates/km²/month. Campaigns with an adaptive strategy took 94.1 months, removed a total of 14,682 feral ungulates, and had a removal intensity of 3.28 feral ungulates/km²/month.

Fig. 2 Proportion of techniques used to remove feral ungulates reported from 54 campaigns during 1978–2023



Only 2 campaigns were planned and conducted with an estimate of density of feral ungulates before the campaign started. Both of those were mainland campaigns with feral swine. Nineteen of the campaigns (35%) reported an estimate of initial density of feral ungulates using a removal-model or population-rebuilding-method of the removal data collected during the campaign. Of these 21 campaigns (2 + 19), 16 (76%) were considered successful in either removing feral ungulates or the damage they caused. Most of the campaigns (17 of 21) used an adaptive strategy in attempt to meet removal goals, which is not surprising considering monitoring the population was an important part of an adaptive strategy.

Unsuccessful campaigns

Of the 22 campaigns that reported not being successful, they spent an average of 95.6 months (range=0.16–780) attempting to meet their goals. Ten of the unsuccessful campaigns reported costs, which averaged \$2.0 m (range=\$11,095–\$7.9 m). Twelve unsuccessful campaigns were with feral swine, 5 with feral goats, 1 with feral sheep, and 4 with feral deer. These equated to non-success rates of 36% with feral swine, 38% with feral goats, 33% with feral sheep, and 100% with feral deer (although feral sheep and feral deer had sparse data). Seventeen of the unsuccessful campaigns were on a mainland, equating to a 59% failure rate on mainland and 16% on islands. Combined, it appeared that campaigns against feral deer and campaigns on mainlands had the most notable chances of failure.

Factors influencing campaign success

We found that location, area, number of removal techniques, duration, and complexity of the campaigns were the most important main effect variables for determining the probability of success (Table 3). Ultimately, the model-averaged top model for determining the probability of success was reduced to ~location + area + location × area + number of removal techniques + complexity. None of these covariates were statistically significant. However, because our sample size and power for detecting statistical significances were low, we opted to still describe the trends informing the success of campaigns (Fig. 2). Island campaigns tended to have more success than

Table 3 Relative importance of covariates for predicting the probability of a successful campaign removing feral ungulates from 54 total campaigns during 1978–2023

Covariate	Relative importance
Location	0.98
Area	0.70
Count of methods	0.30
Duration	0.28
Complexity	0.26
Monitoring	0.23
Adaptive	0.23

mainland campaigns, and smaller campaigns tended to be more successful than larger campaigns for both locations. However, the probability of success trended greater on islands covering larger areas until the areas got very large (e.g., ~1000 km²), compared to mainland campaigns which quickly became less successful as area increased. Success did not seem to be influenced by the number of removal techniques or the complexity of the campaigns (Fig. 3).

When we examined how cost/km² influenced the probability of success, we found that the likelihood of success increased substantially with how much was spent ($\beta = 1.76$, 95% CI = 0.51–3.58). The probability of success increased exponentially until ~\$10,000/km², then increased more slowly as additional funds were used (Fig. 4). We did not find statistical evidence that the removal intensity influenced the probability of success.

Costs of removal campaigns

Total costs were reported for 27 campaigns and averaged \$1.90 m (range=\$11,095–\$8.86 m), although the majority were <\$0.5 m (Fig. 5). The costs averaged \$636/km²/month (SE = 243.1). The average cost/km² to remove feral ungulates was \$17,398 (SE = 7418). The total cost was not dependent on the intensity of removals ($\beta = -31,590$; 95% CI = -109,505–46,325). The costs/km² did not vary throughout years ($\beta = -807.3$, 95% CI = -2106.3–491.7), was not influenced by the number of removal techniques used ($\beta = 1524$; 95% CI = -9284–12,331) and was not dependent on the duration of the campaign ($\beta = 19.7$; 95% CI = -76.6–116.1). The

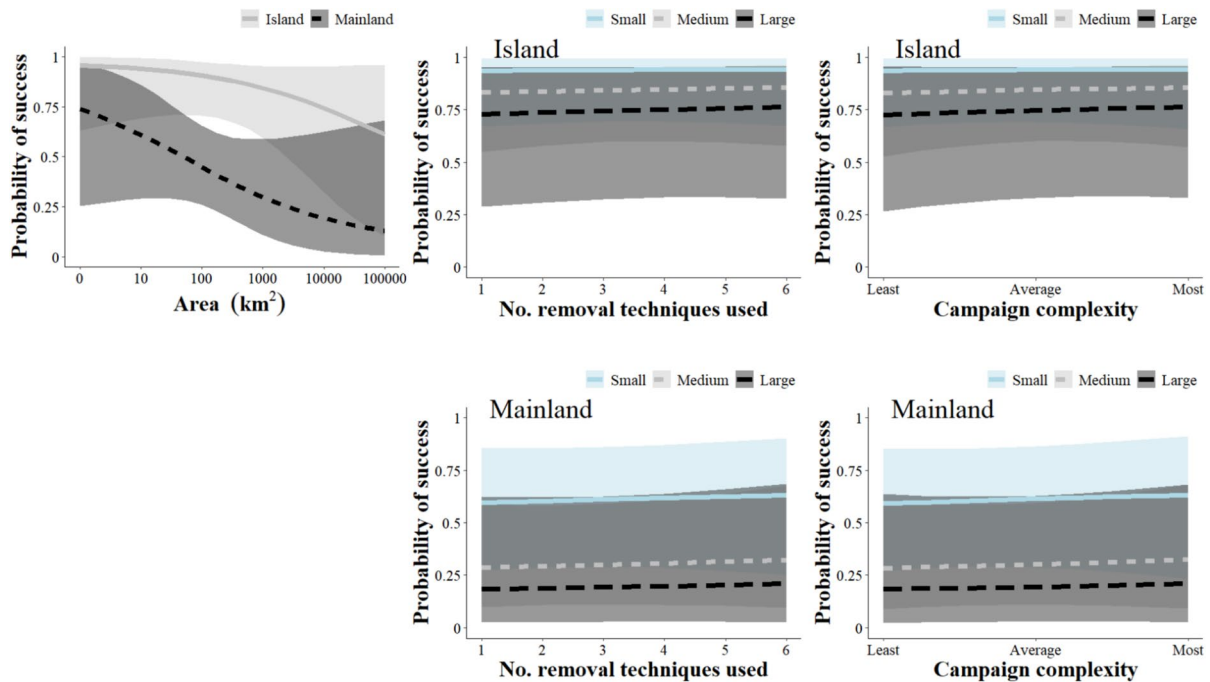


Fig. 3 Model predicted probabilities of success for removal campaigns of feral ungulates during 1978–2023. For display purposes, small campaigns were considered $\sim 10 \text{ km}^2$, medium $\sim 1000 \text{ km}^2$, and large $\geq 10,000 \text{ km}^2$. Complexities of

campaigns included an index of operational (e.g., logistics, access, stakeholders) and environmental (e.g., land cover, topography, climate) complexity. Shaded areas represent 95% CIs

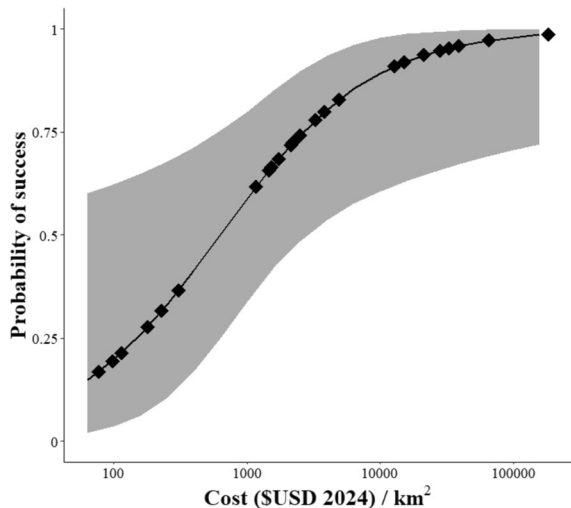


Fig. 4 Model predicted probabilities of success for removal campaigns of feral ungulates during 1978–2023. Black diamonds represent actual data. Shaded areas represent 95% CIs. Cost/ km^2 represents the reported total cost of the campaign, converted to \$USD 2024

reported costs/ km^2 were also similar between mainland and island campaigns ($\beta = 9061$, 95% CI = $-22,333$ – $40,456$), and were similar between campaigns that were focused on eradication or maximum control ($\beta = 20,481$; 95% CI = $-18,214$ – $59,177$).

We observed that most campaigns reported total costs for an entire campaign, and only 1 campaign reported variation in real-time costs throughout the campaign. This campaign revealed that removing the last few feral swine became exponentially more expensive, such that the last 1% of animals took an 84-fold increase in costs to remove (Fischer et al. 2020). We also observed that only 1 campaign compared the expenses of removing feral ungulates to reductions in the costs associated with damages caused by the species. This study revealed the expense of removing the ungulates was minor (9.7%) compared to the costs of damages from feral swine (Engeman et al. 2019a, b).

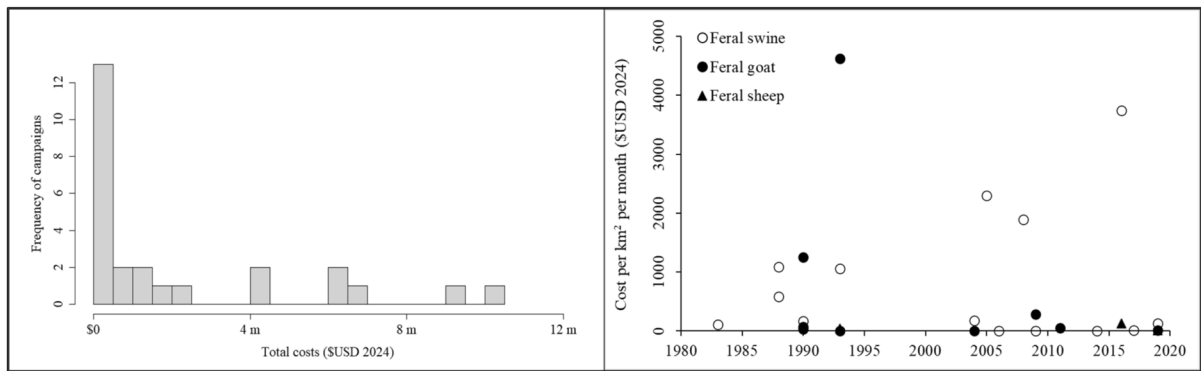


Fig. 5 Histogram of total costs (in millions) and costs per km² per month reported from 27 campaigns removing feral ungulates during 1978–2023

Temporal trends in removal campaigns

During the 45 years of removal campaigns, we identified a proportionally equivalent increase in both mainland and island campaigns (Fig. 6). Ground shooting, trapping, aerial gunning, and dogs made

up $\geq 75\%$ of the methods used for removing feral ungulates throughout all decades. Fencing, judas animals, and snares were used only occasionally throughout. Toxicants have rarely been used but were more popular in earlier years. Sterilants were

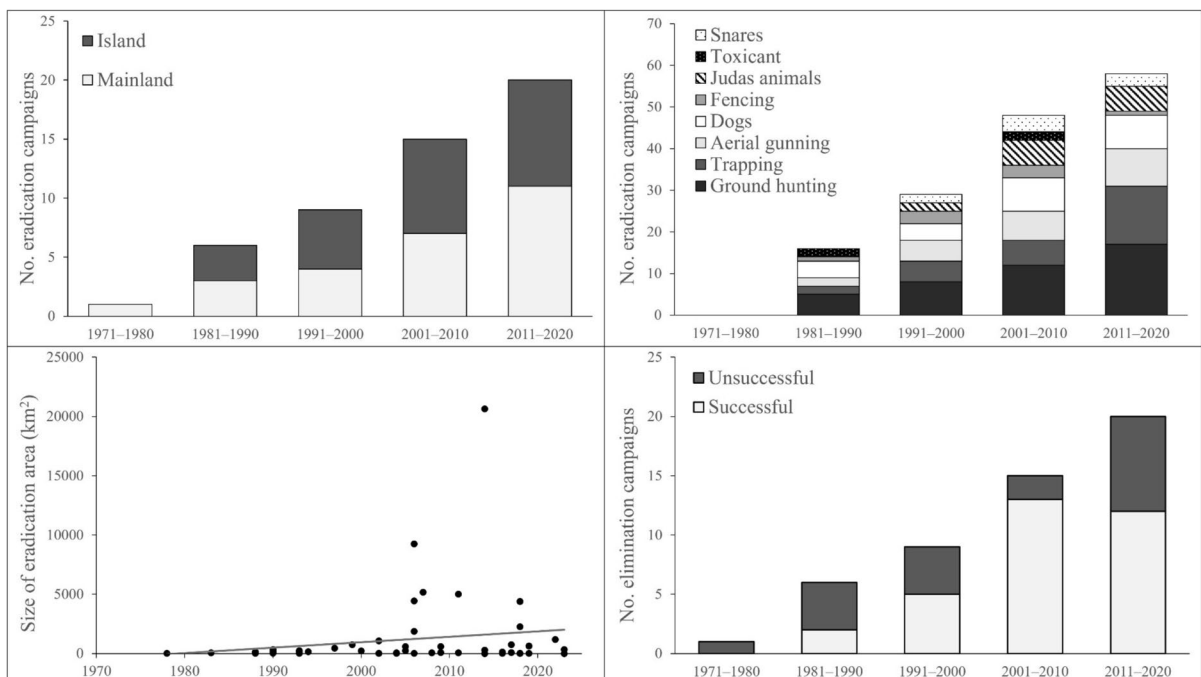


Fig. 6 Trends in removal campaigns for feral ungulates reported during 1978–2023 (top right). Number of methods used in removal campaigns for feral ungulates 1978–2020 (top left). Sizes (km²) of removal campaigns for feral ungulates

1978–2023 (bottom right). Number of successful versus unsuccessful removal campaigns for feral ungulates 1978–2020 (bottom left)

not used as part of a removal campaign in any of the studies that fit our criteria.

We found no statistical evidence that the areas of removal campaigns increased throughout the years ($\beta=52.3$; 95% CI = -25.9 – 132.4). Areas averaged 1292.1 km^2 (SE = 455.1), with the largest area covered by a campaign = $20,639 \text{ km}^2$ for feral swine in New Mexico, USA, albeit this campaign was not considered successful. In addition, the count of successful campaigns has increased since the 1970s, with a total of 13 successful during 2000–2010, and 12 during 2011–2020. However, we found no evidence that the probability of successes for a campaign increased through years ($\beta=0.01$; 95% CI = -0.03 – 0.06), indicating the greater number of successes in latter decades were proportional to the increased numbers of campaigns attempted, and not an increase in success rate.

Recommended strategies from campaigns

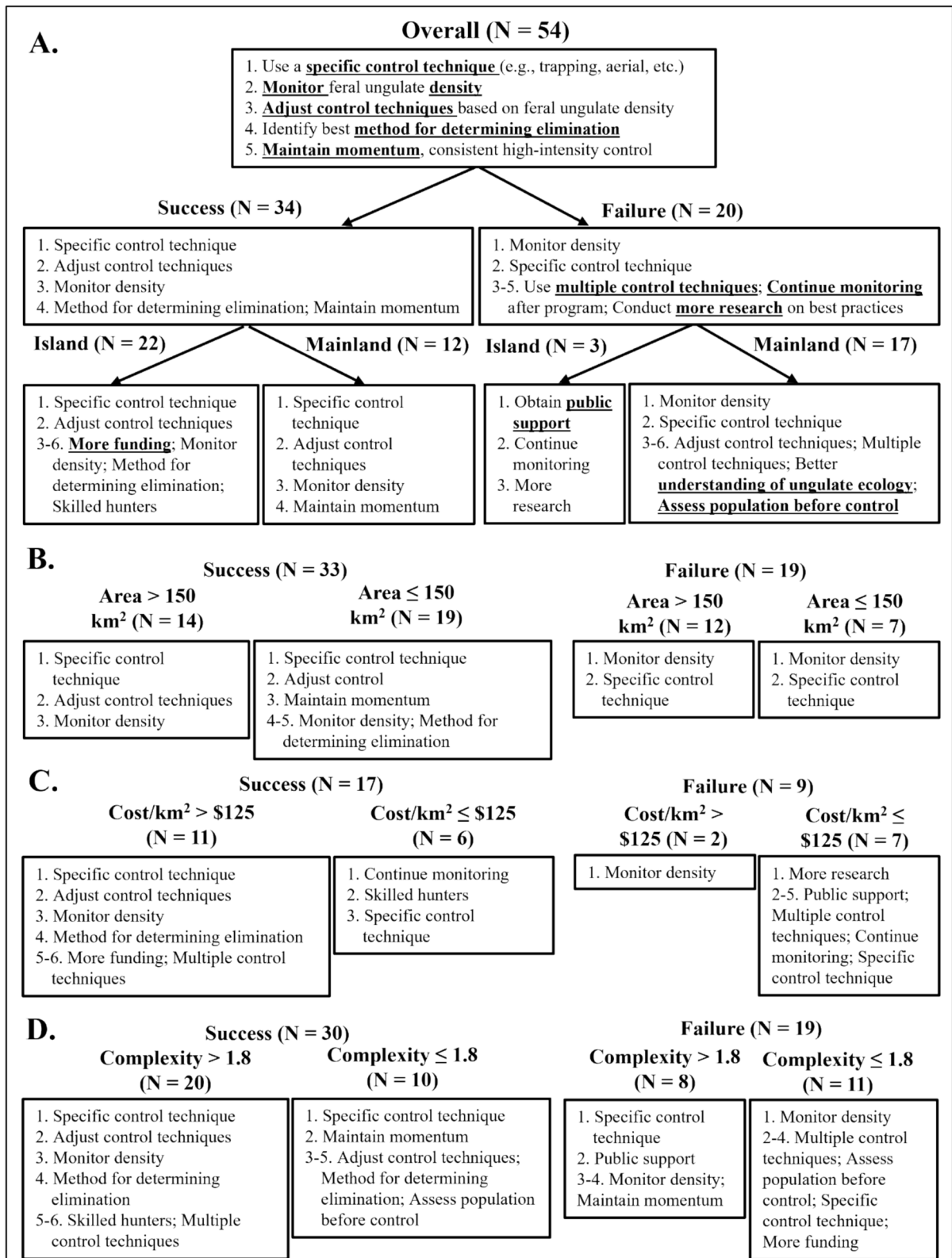
The most frequently recommended advice provided by authors of campaigns was to use a particular type of removal technique (Fig. 7). Of those, the recommended techniques included: aerial hunting, ground hunting, monitoring post-removal, Judas animals, stopping immigration (i.e., fencing), dogs, and trapping. Of the successful campaigns, further recommended strategies were to adjust the control technique, evaluate densities or presence of the feral ungulates, and have a plan for determining when elimination is complete. Unsuccessful campaigns recommended using multiple control techniques, more monitoring, and more research on best practices. Notable differences between island and mainland campaigns were that successful campaigns on islands recommended obtaining more funding, whereas failures on islands recommended obtaining more public support. Unsuccessful campaigns on mainlands also recommended a better understanding of feral ungulate ecology and better assessments of the population before initiating the campaign.

Discussion

During the last 45 years, feral swine have been the most targeted feral ungulate for elimination and maximum control campaigns, likely because of the

intensive damages they cause to natural ecosystems and agriculture (Barrios-Garcia and Ballari 2012; Mayer and Brisbin 2009), and their rapid expansion across the globe (Corn and Jordan 2017; Hone 1990; Snow et al. 2017b; Tisdell 1982). Feral swine are the only omnivorous and generalist forager from other targeted feral ungulates, as well as the only rooting (i.e., digging) species. Both these qualities exacerbate the damages caused by feral swine and explain why they are frequently targeted for removal. Feral goats were the second most targeted because of their overgrazing and extirpation of endemic plant species (Coblentz 1978). Multiple species of feral deer have been targeted although there were no reports of successful campaigns in our dataset. We expect that feral deer may be more challenging because their evasiveness and physical abilities (e.g., to jump fencing) may outpace other feral ungulates with domestic ancestry.

Although very few campaigns reported the costs of damages caused by feral ungulates, we found evidence that even if a campaign is not fully successful and damage is not fully eliminated, a monetary benefit may still be realized (Engeman et al. 2019a, b). We predicted that the more financial resources that can be contributed to a campaign, the greater the probability of success. The greatest probabilities were predicted with costs of $> \$10,000/\text{km}^2$ and even greater chances of success at $\$0.5$ – $1.0 \text{ m}/\text{km}^2$. For example, the largest campaign ($20,639 \text{ km}^2$) was in New Mexico, USA against feral swine, and operated on $\sim \$77/\text{km}^2$ for 12 months and was unsuccessful (May 2014). Whereas, the largest campaign from any with $> \$10,000/\text{km}^2$ took place on Santiago Island, Ecuador (584 km^2), and was successful at eliminating feral goats operating on $\$15,153/\text{km}^2$ for 52 months (Cruz et al. 2009). We also suggest that attempting to reduce the duration of a campaign should reduce the cost by reducing the need to remove newly born or immigrated animals. Continuous campaigns tended to have the shortest durations and removed fewer ungulates perhaps because less reproduction or immigration occurred. These campaigns also accomplished greater intensities of removals. For example, a small campaign (5.26 km^2) on Keewaydin Island, Florida, USA operated intensely for ~ 1 month to successfully eradicate 36 feral swine (Engeman et al. 2016). Furthermore, campaigns with adaptive strategies had higher intensities of removals. For example, all campaigns that used multiple adaptive strategies (i.e.,



◀**Fig. 7** Summary of ranked recommendations based on different campaign conditions including island versus mainland (A), area of the campaign (B), cost (C), and complexity (D). The top 5 recommendations were determined by summing the number of papers that listed each recommendation (not mutually exclusive) and sorting the counts in order of frequency from highest to lowest. When there were ties beyond 6 recommendations, we dropped the recommendations that were tied because there was no clear priority beyond the top recommendations listed in the box (leading to less than 5 recommendations for some conditions). For ties up to 6 recommendations, we listed them with multiple numbers. Each time a new recommendation was listed (starting from the top of the schematic and working downward) we bolded and underlined those keywords and used the abbreviated text in the rest of the schematic for simplicity

used raw data, estimated population sizes, and used dynamic modeling to guide strategies) were all successful (e.g., Engeman et al. 2019a, b; Heriot et al. 2019; Parkes et al. 2010; Ramsey et al. 2009). Combined, these results lend toward rapid, intensive, and adaptive strategies to reduce costs and optimize success. The last animals were exponentially more costly and time-intensive to remove (Fischer et al. 2020).

Regardless of cost, location and area of a campaign were the most important factors for increasing the probabilities of success. Similar to costs, we also expected that location and area were indicators of campaigns being able to counteract population recovery or reinvasion by feral ungulates during the campaign. Success on islands may be greater because the chances of immigration or re-invasion from surrounding populations of feral ungulates are reduced. For example, only 3 of the 25 reported island campaigns were not successful (Carrion et al. 2011; Parkes 1990; Schuyler 1993). Similarly, smaller areas likely contain fewer feral ungulates and/or they can be removed more rapidly before new births negate removal efforts. We predicted the probabilities of success for mainland campaigns to be <0.50 for any campaigns larger than 100 km^2 , which does not bode well for continental situations in which feral ungulates have become well-established. In these situations, it may be necessary to subdivide large tracts of land using ungulate-proof fencing, of which we predicted ≥ 0.90 probabilities of success for areas up to 100 km^2 (on islands).

We found little evidence of changes in methodologies used during campaigns, sizes (km^2) of campaigns, or the frequency of successes from campaigns

during the last 45 years. Despite the $\sim 60\%$ success reported in the campaigns reviewed, our results do not support calls that future campaigns tackle larger and more complex removals because successes should be increasingly achievable (Campbell and Donlan 2005; Cruz et al. 2009). Instead, success rates for campaigns against feral ungulates have been mostly stagnant and have lacked breakthroughs in technologies or strategies that enhance success. The most frequently used methods for removing feral ungulates were ground hunting, hunting with dogs, trapping, and aerial hunting, all of which have undergone only marginal modernization in recent decades (e.g., Bengsen et al. 2020). Some technologies that were rarely used or available were toxicants and sterilants. New toxicants are being developed for feral swine (Poché et al. 2019; Snow et al. 2017a) but have yet to be deemed safe or effective for widespread use. For sterilants, Warren and Warnell (2000) published 25 years ago that sterilants were ineffective at reducing populations of problematic ungulates, which does not appear to have advanced much since then (Pepin et al. 2017). Safely delivering pharmaceuticals to feral ungulates has been especially challenging because of their large body sizes and keeping smaller non-targets from having access (e.g., Snow et al. 2021, 2017c). Major advances in this arena may provide the breakthrough necessary to achieve greater success for larger campaigns.

Despite the lack of major advances in technologies, authors of campaigns frequently recommended using traditional strategies (e.g., ground hunting, hunting with dogs, trapping, and aerial hunting) likely because they have proven effective. Less common methodologies recommended were monitoring for success post-removal, Judas animals, and stopping immigration (i.e., fencing). Unsuccessful campaigns recommended that multiple methodologies might have helped to achieve success, therefore having multiple tools and applying each of those when appropriate may increase success. Unsuccessful campaigns also recommended that more research is needed on best practices for conducting the campaigns, suggesting that it may not be obvious which technique would be best applied as the densities of feral ungulates are reduced throughout the campaign. Unsuccessful campaigns similarly recommended more research on the ecology of feral ungulates and assessing their populations would help inform which methodologies might

be best applied. These recommendations can be condensed to a general theme of reducing uncertainty about the most effective methods and biology of the population prior to the campaign.

Challenges with comparing campaigns

We observed that case studies described the campaigns in different ways making it difficult to compare in a standardized fashion. An important consideration for comparison was defining the scope of the campaign. Specifically, how challenging the campaign was from the beginning. We also noticed that case studies applied different approaches when reporting feral ungulate densities, spatial area targeted, and time frames over which work was conducted. Density was rarely known or measured before the program started. Most campaigns only reported numbers removed over time. This makes it difficult to understand the scope and budget needed to be successful from the outset. Also, using the total number of feral ungulates removed can include biases from reproduction and immigrations, especially if the campaign spans a long timeframe. Monitoring density was reported as a common recommendation for success, yet very few studies did this.

Campaigns also reported a lot of variation in approaches to estimating costs and effort relative to the spatial area worked. Without this information, it is challenging to identify funding needed for success at different scales which can be important for maximizing return on investment (Pepin et al. 2022, 2020). Lessons from comparison of past campaigns could be extracted more readily if campaigns reported the following information: estimate of initial density, density throughout the campaign, removal numbers per km², spatial area worked in km² (measure of area worked), and costs over time. If campaigns develop efficient data collection and reporting mechanisms for this type of information *a priori*, comparisons of case studies could provide more rigorous information about resources and spatial strategies needed for success.

We pooled species because of limited sample sizes for each type of feral ungulate; therefore, our interpretations may not capture the nuances and challenges for each species. For example, feral goats and feral deer may utilize rougher terrain than feral swine, which may limit the types of removal methods

that could be employed for goat and deer. However Koriakin et al. (2024) found that extreme cliff lines were traversed by feral deer and feral swine, therefore the differences between these species may be more minimal than expected. Also, considering some campaigns removed multiple species within the same campaign, we expect that our results can be useful across multiple feral ungulates. We encourage the publishing of campaigns for lesser-reported species (e.g., feral deer, feral donkeys, feral cattle, etc.) to help better inform future successes with those species.

Finally, we recognize that publication bias (i.e., successful campaigns were more likely to be published) may have skewed our results and interpretations. Approximately 60% of the campaigns we reviewed reported success, therefore we expect that publication bias could exist at a low–moderate level. Considering our binomial response, publication bias could increase the uncertainty around significance of the predictors, making it more difficult to determine which variables influenced success. As such, we encourage the publishing of failed campaigns to help better inform future successes.

Conclusions

Reviewing 45 years of campaigns against feral ungulates revealed that the frequency of these campaigns has been increasing steadily, feral swine are the most targeted for removal, and success is uncertain. The most important components that predicted success in these studies included ensuring adequate funding was secured for the campaign (\$0.5–1 million/km² is recommended) and population recovery or reinvasion were minimized (e.g., island environments). Keeping campaigns restricted to smaller areas (≤ 100 km²) either as islands or by using fencing may aid in keeping the population rebound minimized and increase success. Most commonly, authors of the studies reported the following five elements as being the most critical components of successful implementation: (1) using a specific control technique that was best for their situation, (2) monitoring feral ungulate density as part of the effort, (3) adjusting control techniques based on feral ungulate density, (4) identifying the best method for determining elimination *a priori*, and (5) maintaining momentum (i.e., consistent high-intensity removal). In situations where the campaign

failed, authors additionally reported that success in these cases requires: (1) use of multiple control techniques, (2) continued monitoring after the program finishes, and (3) more research to understand best practices for elimination. A lack of increasing success for larger and more complex campaigns indicated that modernization of technologies for population control has been minimal, and larger breakthroughs are needed. Safe and effective toxicants and sterilants may offer these breakthroughs if they can be developed. Based on recommendations from campaigns, pilot testing control methods prior to initiating full campaigns may help to alleviate uncertainties, produce more reliable plans, and help inform the biology of the animals being targeted for removal.

Acknowledgements The research was supported by the United States Department of Agriculture (USDA). The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USA Government determination or policy. Mention of commercial products or companies does not represent an endorsement by the USA government. We thank anonymous reviewers for their comments on this manuscript.

Author contributions NPS and KMP conceived the idea and analyzed the results. KJK, IAM, AP, and SMC assisted with reviewing articles. All authors contributed to the writing of the manuscript.

Funding The research was supported by the United States Department of Agriculture (USDA).

Data availability Data are available in Table 2.

Declarations

Conflict of interest The authors have no relevant competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

References marked with an asterisk * were used in the review.

- Anderson DR, Burnham KP (2002) Avoiding pitfalls when using information-theoretic methods. *J Wildlife Manage* 66:912–918
- *Andrzejewski R, Jezierski W (1978) Management of a wild boar population and its effects on commercial land. *Acta Theriol* 23:309–339
- Aschim RA, Brook RK (2019) Evaluating cost-effective methods for rapid and repeatable national scale detection and mapping of invasive species spread. *Sci Rep* 9:7254
- Barrios-Garcia MN, Ballari SA (2012) Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. *Biol Invasions* 14:2283–2300
- *Barrett RH, Goatcher BL, Gogan PJ, Fitzhugh EL (1988) Removing feral pigs from Annadel state park. *Transact West Sect Wildlife Soc* 24:47–52
- *Barron MC, Anderson DP, Parkes JP, Gon SMO III (2011) Evaluation of feral pig control in Hawaiian protected areas using Bayesian catch-effort models. *N Z J Ecol* 35:182–188
- Beasley JC, Ditchkoff SS, Mayer JJ, Smith MD, Vercauteren KC (2018) Research priorities for managing invasive wild pigs in North America. *J Wildlife Manage* 82:674–681
- Bengsen AJ, Forsyth DM, Harris S, Latham ADM, McLeod SR, Pople A (2020) A systematic review of ground-based shooting to control overabundant mammal populations. *Wildlife Res* 47:197–207
- Blossey B, Gorchov DL (2017) Introduction to the special issue: ungulates and invasive species: quantifying impacts and understanding interactions. *AoB Plants* 9:plx063
- Bomford M, O'Brien P (1995) Eradication or control for vertebrate pests? *Wildlife Soc Bull* 23:249–255
- *Brennan M, Moller H, Parkes JP (1993) Indices of density of feral goats in a grassland/forest habitat, marlborough, New Zealand. *N Z J Ecol* 17:103–106
- Brown VR, Miller RS, McKee SC, Ernst KH, Didero NM, Maison RM, Grady MJ, Shwiff SA (2021) Risks of introduction and economic consequences associated with African swine fever, classical swine fever and foot-and-mouth disease: a review of the literature. *Transbound Emerg Dis* 68:1910–1965
- *Bunbury N, von Brandis R, Currie JC, van de Crommenacker J, Accouche W, Birch D, Chong-Seng L, Doak N, Haupt P, Jean-Baptiste M, Fleischer-Dogley F (2018) Late stage dynamics of a successful feral goat eradication from the UNESCO World Heritage site of Aldabra Atoll, Seychelles. *Biol Invasions* 20:1735–1747
- Burgin S, Mattila M, McPhee D, Hundloe T (2015) Feral deer in the suburbs: an emerging issue for Australia? *Hum Dimens Wildl* 20:65–80

- Burnham KP, Anderson DR (2002) Model selection and multimodel inference. A practical information-theoretic approach second edition. Springer Science & Business Media, New York
- *Campbell K, Donlan CJ (2005) Feral goat eradication on islands. *Conserv Biol* 19:1362–1374
- *Carrion V, Donlan CJ, Campbell KJ, Lavoie C, Cruz F (2011) Archipelago-wide island restoration in the Galápagos Islands: reducing costs of invasive mammal eradication programs and reinvasion risk. *PLoS One* 6:e18835
- *Carrion V, Donlan CJ, Campbell K, Lavoie C, Cruz F (2007) Feral donkey (*Equus asinus*) eradications in the Galápagos. *Biodivers Conserv* 16:437–445
- Chenais E, Ståhl K, Guberti V, Depner K (2018) Identification of wild boar–habitat epidemiologic cycle in African swine fever epizootic. *Emerg Infect Dis* 24:810
- Coblentz BE (1978) The effects of feral goats (*Capra hircus*) on island ecosystems. *Biol Conserv* 13:279–286
- *Coblentz BE, Van Vuren D, Main MB (1990) Control of feral goats on Aldabra Atoll. *Atoll Res Bull* 337:1–13
- *Comte S, Bengsen AJ, Thomas E, Bennett A, Davis NE, Brown D, Forsyth DM (2023) A before–after control–impact experiment reveals that culling reduces the impacts of invasive deer on endangered peatlands. *J Appl Ecol* 60:2340–2350
- Corn JL, Jordan TR (2017) Development of the national feral swine map, 1982–2016. *Wildlife Soc Bull* 41:758–763
- *Cowled BD, Lapidge SJ, Hampton JO, Spencer PB (2006) Measuring the demographic and genetic effects of pest control in a highly persecuted feral pig population. *J Wildlife Manage* 70:1690–1697
- *Cruz F, Carrion V, Campbell KJ, Lavoie C, Donlan CJ (2009) Bio-economics of large-scale eradication of feral goats from Santiago Island, Galápagos. *J Wildlife Manage* 73:191–200
- *Cruz F, Donlan CJ, Campbell K, Carrion V (2005) Conservation action in the Galapagos: feral pig (*Sus scrofa*) eradication from Santiago Island. *Biol Conserv* 121:473–478
- Cwynar P, Stojkov J, Wlazlak K (2019) African swine fever status in Europe. *Viruses* 11:310
- Daniel WM, Sofaer HR, Jarnevich CS, Erickson RA, DeGregorio BA, Engelstad PS, Freedman J, Canavan S, Dean EM, Adams MJ (2025) Vertebrates in trade that pose high invasion risk to the United States. *Biol Conserv* 302:110887
- Davis AJ, McCreary R, Psiropoulos J, Brennan G, Cox T, Martin A, Pepin KM (2018) Quantifying site-level usage and certainty of absence for an invasive species through occupancy analysis of camera-trap data. *Biol Invasions* 20:877–890
- Davis NE, Bennett A, Forsyth DM, Bowman DM, Lefroy EC, Wood SW, Woolnough AP, West P, Hampton JO, Johnson CN (2016) A systematic review of the impacts and management of introduced deer (family *Cervidae*) in Australia. *Wildlife Res* 43:515–532
- *Ditchkoff SS, Holtfreter RW, Williams BL (2017) Effectiveness of a bounty program for reducing wild pig densities. *Wildlife Soc Bull* 41:548–555
- *Engeman RM, Addison D, Griffin J (2016) Defending against disparate marine turtle nest predators: nesting success benefits from eradicating invasive feral swine and caging nests from raccoons. *Oryx* 50:289–295
- *Engeman RM, Stevens A, Allen J, Dunlap J, Daniel M, Teague D, Constantin B (2007) Feral swine management for conservation of an imperiled wetland habitat: Florida's vanishing seepage slopes. *Biol Conserv* 134:440–446
- *Engeman RM, Wilson BE, Beckerman SF, Fischer JW, Dufford D, Cobban JB (2019a) Locating and eliminating feral swine from a large area of fragmented mixed forest and agriculture habitats in north-central USA. *Environ Sci Pollut Res* 26:1654–1660
- *Engeman RM, Avery ML, Shiels AB, Berentsen AR, VerCauteren KC, Sugihara RT, Duffiney AG, Clark CS, Eisemann JD (2018) Diverse examples from managing invasive vertebrate species on inhabited islands of the United States. *Australas J Environ Manage* 25:43–61
- *Engeman RM, Byrd RW, Dozier J, McAlister MA, Edens JO, Kierepka EM, Smyser TJ, Myers N (2019b) Feral swine harming insular sea turtle reproduction: the origin, impacts, behavior and elimination of an invasive species. *Acta Oecol* 99:103442
- *Engeman RM, Smith HT, Severson R, Severson MA, Woolard J, Shwiff SA, Constantin B, Griffin D (2004) Damage reduction estimates and benefit–cost ratios for feral swine control from the last remnant of a basin marsh system in Florida. *Environ Conserv* 31:207–211
- *Fischer JW, Snow NP, Wilson BE, Beckerman SF, Jacques CN, VanNatta EH, Kay SL, VerCauteren KC (2020) Factors and costs associated with removal of a newly established population of invasive wild pigs in Northern US. *Sci Rep* 10:11528
- *Garcelon DK, Ryan KP, Schuyler PT (2005) Application of techniques for feral pig eradication on Santa Catalina Island, California. In: Proceedings of the sixth California Islands symposium, National Park Service Technical Publication, CHIS-05-01, 331–340
- *Gaskamp JA, Gee KL, Campbell TA, Silvy NJ, Webb SL (2018) Damage caused to rangelands by wild pig rooting activity is mitigated with intensive trapping. *Cogent Environ Sci* 4:1540080
- *Giacomelli S, Gibbert M, Viganò R (2018) Community empowerment for managing wild boar: a longitudinal case study of northern Italy 2001–2018. *Ecol Soc* 23:12
- Gonzales W, Moreno C, Duran U, Henao N, Bencosme M, Lora P, Reyes R, Núñez R, De Gracia A, Perez AM (2021) African swine fever in the Dominican Republic. *Transbound Emerg Dis* 68:3018–3019
- Green SJ, Grosholz ED (2021) Functional eradication as a framework for invasive species control. *Front Ecol Environ* 19:98–107
- *Gürtler RE, Martín Izquierdo V, Gil G, Cavicchia M, Maranta A (2017) Coping with wild boar in a conservation area: impacts of a 10-year management control program in north-eastern Argentina. *Biol Invasions* 19:11–24
- *Gürtler RE, Rodríguez-Planes LI, Gil G, Izquierdo VM, Cavicchia M, Maranta A (2018) Differential long-term impacts of a management control program of axis deer and wild boar in a protected area of north-eastern Argentina. *Biol Invasions* 20:1431–1447

- *Hadjisterkotis E, Heise-Pavlov PM (2006) The failure of the introduction of wild boar *Sus scrofa* in the island of Cyprus: a case study. *Eur J Wildl Res* 52:213–215
- Hartin RE, Hutton TA. eds (2007) Missouri's feral hog task force: addressing increasing feral swine populations. In: (eds) Nolte D., Arjo WM, Stalman D Proceedings of the 12th Wildlife damage management conference, Utah State University, Logan UT, USA, pp 188–195
- *Heriot S, Asher J, Williams MR, Moro D (2019) The eradication of ungulates (sheep and goats) from Dirk Hartog Island, Shark Bay world heritage area, Australia. *Biol Invasions* 21:1789–1805
- *Hess SC, Jeffrey JJ, Ball DL, Babich L (2006) Efficacy of feral pig removals at Hakalau forest national wildlife refuge. *Trans West Sect Wildl Soc* 42:53–67
- *Higginbotham B, Bodenchuk MJ (2014) Wild pig damage abatement in Texas: an integrated strategy of landowner education and direct control. *Proc Vertebr Pest Conf* 26:243–257
- *Hone J (1983) A short-term evaluation of feral pig eradication at Willandra in western New South Wales. *Wildlife Res* 10:269–275
- Hone J (1990) How many feral pigs in Australia. *Wildlife Res* 17:571–572
- *Hone J (2002) Feral pigs in Namadgi national park, Australia: dynamics, impacts and management. *Biol Conserv* 105:231–242
- Hulme PE, Bacher S, Kenis M, Klotz S, Kühn I, Minchin D, Nentwig W, Olenin S, Panov V, Pergl J (2008) Grasping at the routes of biological invasions: a framework for integrating pathways into policy. *J Appl Ecol* 45:403–414
- Jaksic FM, Iriarte JA, Jiménez JE, Martínez DR (2002) Invaders without frontiers: cross-border invasions of exotic mammals. *Biol Invasions* 4:157–173
- *Katahira LK, Finnegan P, Stone CP (1993) Eradicating feral pigs in montane mesic habitat at Hawaii Volcanoes national park. *Wildlife Soc Bull* 21:269–274
- *Keegan DR, Coblenz BE, Winchell CS (1994) Feral goat eradication on San Clemente Island, California. *Wildlife Soc Bull* 22:56–61
- *Kessler C (2002) Eradication of feral goats and pigs and consequences for other biota on Sarigan Island, commonwealth of the Northern Mariana Islands. In: (eds) Veitch CR, Clout MN Turning the tide: the eradication of invasive species: proceedings of the international conferences on eradication of island invasives. International Union for Conservation of Nature and Natural Resources, Gland Switzerland and Cambridge UK, pp. 132–140
- *Kilgo JC, Vukovich M, Cox KJ, Larsen M, Mims TT, Garabedian JE (2023) Assessing whole-sounder removal versus traditional control for reducing invasive wild pig (*Sus scrofa*) populations. *Pest Manag Sci* 79:3033–3042
- Koriakin K, Jolley DB, Smith B, VerCauteren KC, Snow NP (2024) Effects of ungulate-proof fencing on space use by wild pigs. *J Wildlife Manage* 88:e22592
- Lever C (1985) Naturalized mammals of the world. Longman, London, England
- Lever C, Yalden D (1995) Naturalized animals: the ecology of successfully introduced species. *Biol J Linn Soc* 55:91
- *Lombardo CA, Faulkner KR (2000) Eradication of feral pigs (*Sus scrofa*) from Santa Rosa Island, Channel Islands national park, California. In: (eds) Browne DH, Chaney H, Mitchell K Proceedings of the fifth California islands symposium., Santa Barbara Museum of Natural History, Santa Barbara, California pp 300–306
- Long JL (2003) Introduced mammals of the world: their history, distribution, and influence. CSIRO publishing, Collingwood, Victoria, Australia
- Lowe S, Browne M, Boudjelas S, De Poorter M (2000) 100 of the world's worst invasive alien species: a selection from the global invasive species database the invasive species specialist group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN), p 12 www.issg.org/booklet.pdf.
- Lowney M, Schoenfeld P, Haglan W, Witmer G (2005) Overview of impacts of feral and introduced ungulates on the environment in the eastern United States and Caribbean. In: (eds) Nolte DL, Fagerstone KA Proceedings of the 11th wildlife damage management conference, Traverse City, Michigan, USA, pp 64–81
- Mack RN, Simberloff D, Mark Lonsdale W, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* 10:689–710
- Masters P, Markopoulos N, Florance B, Southgate R (2018) The eradication of fallow deer (*Dama dama*) and feral goats (*Capra hircus*) from Kangaroo Island, South Australia. *Australas J Environ Manage* 25:86–98
- *May A (2014) A cooperative approach to feral swine eradication in New Mexico. In: (eds) Timm RM, Brien JMO Proceedings of the 26th vertebrate pest conference, University of California, Davis, USA, pp 272–276
- Mayer JJ, Brisbin IL, eds. (2009) Wild pigs: biology, damage, control techniques and management. Savannah River National Laboratory, SRNL-RP-2009-00869, Aiken, South Carolina, USA
- *McCann BE, Garcelon DK (2008) Eradication of feral pigs from Pinnacles National Monument. *J Wildlife Manage* 72:1287–1295
- McClure ML, Burdett CL, Farnsworth ML, Lutman MW, Theobald DM, Riggs PD, Gear DA, Miller RS (2015) Modeling and mapping the probability of occurrence of invasive wild pigs across the contiguous United States. *PLoS One* 10:e0133771
- McClure ML, Burdett CL, Farnsworth ML, Sweeney SJ, Miller RS (2018) A globally-distributed alien invasive species poses risks to United States imperiled species. *Sci Rep* 8:5331
- Meng XJ, Lindsay DS, Sriranganathan N (2009) Wild boars as sources for infectious diseases in livestock and humans. *Philos Trans R Soc Lond B Biol Sci* 364:2697–2707
- *Mentaberre G, Romero B, De Juan L, Navarro-González N, Velarde R, Mateos A, Marco I, Olivé-Boix X, Domínguez L, Lavín S, Serrano E (2014) Long-term assessment of wild boar harvesting and cattle removal for bovine tuberculosis control in free ranging populations. *PLoS One* 9:e88824
- Miller RS, Sweeney SJ, Sloomaker C, Gear DA, Di Salvo PA, Kiser D, Shwiff SA (2017) Cross-species transmission potential between wild pigs, livestock, poultry, wildlife,

- and humans: implications for disease risk management in North America. *Sci Rep* 7:7821
- *Morrison SA, Macdonald N, Walker K, Lozier L, Shaw MR (2007) Facing the dilemma at eradication's end: uncertainty of absence and the Lazarus effect. *Front Ecol Environ* 5:271–276
- Nelle S (1992) Exotics—at home on the range in Texas. *Rangelands Arch* 14:77–80
- *Ortiz-Alcaraz A, Aguirre-Muñoz A, Méndez-Sánchez F, Ortega-Rubio A (2016) Feral sheep eradication at Socorro Island, Mexico: a mandatory step to ensure ecological restoration. *Interciencia* 41:184–189
- Page MJ, McKenzie JE, Bossuyt PM, Boutron I, Hoffmann TC, Mulrow CD, Shamseer L, Tetzlaff JM, Akl EA, Brennan SE (2021) The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. *BMJ* 372:n71
- *Parkes JP (1990) Eradication of feral goats on islands and habitat islands. *J R Soc N Z* 20:297–304
- Parkes JP, Panetta FD (2009) Eradication of invasive species: progress and emerging issues in the 21st century. In: (eds) Clout MN, Williams PA *Invasive species management, A handbook of principles and techniques*, Oxford University Press, Oxford, England, pp 47–60
- *Parkes JP, Ramsey DS, Macdonald N, Walker K, McKnight S, Cohen BS, Morrison SA (2010) Rapid eradication of feral pigs (*Sus scrofa*) from Santa Cruz Island, California. *Biol Conserv* 143:634–641
- Penrith M-L, Vosloo W (2009) Review of African swine fever: transmission, spread and control. *J S Afr Vet Assoc* 80:58–62
- Pepin KM, Davis AJ, Cunningham FL, VerCauteren KC, Eckery DC (2017) Potential effects of incorporating fertility control into typical culling regimes in wild pig populations. *PLoS One* 12:e0183441
- Pepin KM, Davis AJ, Epanchin-Niell RS, Gormley AM, Moore JL, Smyser TJ, Shaffer HB, Kendall WL, Shea K, Runge MC (2022) Optimizing management of invasions in an uncertain world using dynamic spatial models. *Ecol Appl* 32:e2628
- Pepin KM, Smyser TJ, Davis AJ, Miller RS, McKee S, VerCauteren KC, Kendall W, Sloomaker C (2020) Optimal spatial prioritization of control resources for elimination of invasive species under demographic uncertainty. *Ecol Appl* 30:e02126
- Poché RM, Davis N, Poché DM, Franckowiak GA, Tseveenjav B, Hartman DA, Polyakova L (2019) Development of a low-dose warfarin bait for controlling feral hogs. *Crop Prot* 120:134–140
- Prior KM, Adams DC, Klepzig KD, Hulcr J (2018) When does invasive species removal lead to ecological recovery? Implications for management success. *Biol Invasions* 20:267–283
- *Rainbolt RE, Coblenz BE (1999) Restoration of insular ecosystems: control of feral goats on Aldabra Atoll, Republic of Seychelles. *Biol Invasions* 1:363–375
- *Ramsey DS, Parkes J, Morrison SA (2009) Quantifying eradication success: the removal of feral pigs from Santa Cruz Island, California. *Conserv Biol* 23:449–459
- *Richardson CD, Gipson PS, Jones DP, Luchsinger JC (1997) Extirpation of a recently established feral pig population in Kansas. In: (ed) Armstrong JB *Proceeding of the seventh eastern wildlife DAMAGE control conference*, Mississippi State University, Jackson, Mississippi, USA, pp 100–103
- Ruiz-Fons F, Segalés J, Gortázar C (2008) A review of viral diseases of the European wild boar: effects of population dynamics and reservoir role. *Vet J* 176:158–169
- *Saunders G, Bryant H (1988) The evaluation of a feral pig eradication program during a simulated exotic disease outbreak. *Wildlife Res* 15:73–81
- *Schuyler P (1993) Control of feral sheep (*Ovis aries*) on Santa Cruz island, California. In: *Third California Islands symposium: recent advances in research on the California Islands*, Santa Barbara museum of natural history, Santa Barbara, California, USA pp 443–452
- *Schuyler PT, Garcelon DK, Escover S (2002) Eradication of feral pigs (*Sus scrofa*) on Santa Catalina island, California, USA, Turning the tide: the eradication of invasive species. IUCN SSC invasive species specialist group, IUCN, Gland, Switzerland and Cambridge, United Kingdom, 274–286.
- *Sharp A, Holmes K, Norton M (1999) An evaluation of a long-term feral goat control program in Mootwingee national park and Coturaundee nature reserve, far western new south Wales. *Rangel J* 21:13–23
- Simberloff D (2009) We can eliminate invasions or live with them. In: Langor DW, Sweeney J (eds) *Successful management projects*, In *Ecological impacts of non-native invertebrates and fungi on terrestrial ecosystems*. Springer, Dordrecht, Berlin Germany, pp 149–157
- Snow NP, Foster JA, Kinsey JC, Humphrys ST, Staples LD, Hewitt DG, VerCauteren KC (2017a) Development of toxic bait to control invasive wild pigs and reduce damage. *Wildlife Soc Bull* 41:256–263
- Snow NP, Halseth JM, Foster JA, Lavelle MJ, Fischer JW, Glow MP, Messer IA, Cook SM, VerCauteren KC (2021) Detering non-target birds from toxic bait sites for wild pigs. *Sci Rep* 11:19967
- Snow NP, Jarzyna MA, VerCauteren KC (2017b) Interpreting and predicting the spread of invasive wild pigs. *J Appl Ecol* 54:2022–2032
- Snow NP, Lavelle MJ, Halseth JM, Blass CR, Foster JA, VerCauteren KC (2017c) Strength testing of raccoons and invasive wild pigs for a species-specific bait station. *Wildlife Soc Bull* 41:264–270
- Spear D, Chown SL (2009) Non-indigenous ungulates as a threat to biodiversity. *J Zool* 279:1–17
- *Sternner JD, Barrett RH (1991) Removing feral pigs from Santa Cruz Island, California. *Trans West Sect Wildl Soc* 27:47–53
- Sur J-H (2019) How far can African swine fever spread? *J Vet Sci*. <https://doi.org/10.4142/jvs.2019.20.e41>
- *Suzuki KK, Kuwano Y, Yasuda M (2022) A 17-year study of the response of populations to different patterns in antlerless proportion of imposed culls: antlerless culling reduces overabundant deer population. *Biology* 11:1607
- Teer J (2003) Nonnative large mammals in North America. In: Feldhamer G, Thompson B, Chapman J (eds) *Wild mammals of North America*, Second Editon. Johns Hopkins University Press, Baltimore, MD, USA, pp 1180–1187

- Tisdell CA (1982) Wild pigs: environmental pest or economic resource? Pergamon Press Pty Ltd Rushcutters Bay, NSW, Australia
- Vavra M, Parks CG, Wisdom MJ (2007) Biodiversity, exotic plant species, and herbivory: the good, the bad, and the ungulate. *Ecol Manage* 246:66–72
- VerCauteren KC, Beasley JC, Ditchkoff SS, Mayer JJ, Roloff GJ, Strickland BK (eds) (2019) Invasive wild pigs in North America: ecology, impacts, and management. CRC Press, Boca Raton, FL, USA
- VerCauteren KC, Pepin K, Cook S, McKee S, Pagels A, Kohen K, Messer I, Glow MP, Snow N (2024) What is known, unknown, and needed to be known about damage caused by wild pigs. *Biol Invasions* 26:1313–1325
- Ward MP, Laffan SW, Highfield LD (2007) The potential role of wild and feral animals as reservoirs of foot-and-mouth disease. *Prev Vet Med* 80:9–23
- Ward MP, Laffan SW, Highfield LD (2009) Modelling spread of foot-and-mouth disease in wild white-tailed deer and feral pig populations using a geographic-automata model and animal distributions. *Prev Vet Med* 91:55–63
- Warren RJ, Warnell D (2000) Overview of fertility control in urban deer management. In: *Proceedings of the 2000 annual conference of the society for theriogenology* pp 237–246
- West P (2008) Assessing invasive animals in Australia 2008, National Land & Water Resources Audit, Canberra, AU. www.nlwra.gov.au. Accessed 23 May 2016

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.