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Amy J. Davis
USDA/APHIS/WS National Wildlife Research Center

Mevin B. Hooten
Colorado State University, Mevin.Hooten@colostate.edu

Ryan S. Miller
United States Department of Agriculture

Matthew L. Farnsworth
Conservation Science Partners

Jesse Lewis
Conservation Science Partners

See next page for additional authors

Authors

Amy J. Davis, Mevin B. Hooten, Ryan S. Miller, Matthew L. Farnsworth, Jesse Lewis, Michael Moxcey, and Kim M. Pepin

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Amy J. Davis,[1,8] Mevin B. Hooten,[2,3,4] Ryan S. Miller,[5] Matthew L. Farnsworth,[6] Jesse Lewis,[6] Michael Moxcey,[7] and Kim M. Pepin[1]

[1]*National Wildlife Research Center, United States Department of Agriculture, 4101 Laporte Avenue, Fort Collins, Colorado 80521 USA*
[2]*U.S. Geological Survey, Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, Colorado 80523 USA*
[3]*Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado 80523 USA*
[4]*Department of Statistics, Colorado State University, Fort Collins, Colorado 80523 USA*
[5]*Center for Epidemiology and Animal Health, United States Department of Agriculture, 2150 Centre Avenue, Fort Collins, Colorado 80526 USA*
[6]*Conservation Science Partners, 5 Old Town Square, Suite 205, Fort Collins, Colorado 80524 USA*
[7]*Wildlife Services, United States Department of Agriculture, 2150 Centre Avenue, Fort Collins, Colorado 80526 USA*

Abstract. Evaluation of the progress of management programs for invasive species is crucial for demonstrating impacts to stakeholders and strategic planning of resource allocation. Estimates of abundance before and after management activities can serve as a useful metric of population management programs. However, many methods of estimating population size are too labor intensive and costly to implement, posing restrictive levels of burden on operational programs. Removal models are a reliable method for estimating abundance before and after management using data from the removal activities exclusively, thus requiring no work in addition to management. We developed a Bayesian hierarchical model to estimate abundance from removal data accounting for varying levels of effort, and used simulations to assess the conditions under which reliable population estimates are obtained. We applied this model to estimate site-specific abundance of an invasive species, feral swine (*Sus scrofa*), using removal data from aerial gunning in 59 site/time-frame combinations (480–19,600 acres) throughout Oklahoma and Texas, USA. Simulations showed that abundance estimates were generally accurate when effective removal rates (removal rate accounting for total effort) were above 0.40. However, when abundances were small (<50) the effective removal rate needed to accurately estimates abundances was considerably higher (0.70). Based on our post-validation method, 78% of our site/time frame estimates were accurate. To use this modeling framework it is important to have multiple removals (more than three) within a time frame during which demographic changes are minimized (i.e., a closed population; ≤3 months for feral swine). Our results show that the probability of accurately estimating abundance from this model improves with increased sampling effort (8+ flight hours across the 3-month window is best) and increased removal rate. Based on the inverse relationship between inaccurate abundances and inaccurate removal rates, we suggest auxiliary information that could be collected and included in the model as covariates (e.g., habitat effects, differences between pilots) to improve accuracy of removal rates and hence abundance estimates.

Key words: Bayesian hierarchical model; catch-effort method; feral swine; invasive species; population monitoring; removal sampling; Sus scrofa.

Introduction

Monitoring wildlife populations is an important component of management plans because estimates of population size in response to management can be used to guide resource allocation and implementation strategies as well as to evaluate program performance (Soulé 1987, Lyons et al. 2008). However, many common methods for estimating abundance of wildlife populations are not optimal for invasive species (e.g., the release aspect of capture–mark–release). The desired focus of time and labor spent on the management of invasive species is on diminishing or eradicating the species as opposed to monitoring. Therefore, data on invasive species are often obtained via removal efforts.

Feral swine (*Sus scrofa*) are an invasive species in North America and Australia and are a pest species in several European, Asian, and African countries (Barrios-Garcia and Ballari 2012). In the United States, they cause significant damage to agriculture, natural resources, and endangered species (Roemer et al. 2002, Seward et al. 2004). Additionally, they threaten human and livestock health

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[8]E-mail: amy.j.davis@aphis.usda.gov

(Meng et al. 2009) due to their rapid geographic expansion and increasing population size, the propensity for humans to hunt and translocate them, and their frequent occurrence near livestock (Bevins et al. 2014). In response to these threats, the United States Department of Agriculture (USDA) has recently established a multi-agency program to control damage from feral swine (APHIS National Damage Management Program), although control (removals) of feral swine has been ongoing in the United States for decades. Currently, only coarse-scale estimates are available for the distribution (Mayer and Brisbin 2008, Barrios-Garcia and Ballari 2012, McClure et al. 2015) of feral swine across the United States and population size estimates are limited to local areas (e.g., Waithman et al. 1999, Sweitzer et al. 2000). The benefits of obtaining reliable population estimates from ongoing control practices are the ability to monitor spatial and temporal changes in populations, evaluate the effectiveness of management strategies, and determine the cost/benefits of different management actions.

Removal (or depletion) sampling is a commonly used method to estimate abundance of animal populations (Zippin 1958, Seber 1982, Williams et al. 2002, Royle and Dorazio 2006). Removal models have been used to estimate population size for many species including birds (Farnsworth et al. 2002), mammals (Chee and Wintle 2010, Rout et al. 2014), and fish (Dorazio et al. 2005). Removal models are ideally suited for estimating invasive species populations as they coincide with desirable management actions (i.e., the reduction or eradication of populations). Models that use data from management actions need to account for variations in removal effort as these data are unlikely to be standardized across events. St. Clair et al. (2012) showed that removal models that account for removal effort are effective at estimating abundance, particularly when removal rates are high.

Removal models have been used to estimate population size of feral swine on island populations using hunter harvest data (Ramsey et al. 2009, Barron et al. 2011). Barron et al. (2011) used a Weibull catch-effort model to estimate swine populations sizes in a Bayesian framework in Hawaii, USA to evaluate effectiveness of management actions. Additionally, Ramsey et al. (2009) used a similar Bayesian method to model the probability of eradication using a removal model on Santa Cruz Island, California, USA. These applications demonstrate the utility of catch-effort based removal models for designed feral swine population monitoring. The goal of our study was to extend the removal modeling framework including catch-effort to nonstandardized management data, including opportunistic sampling.

We used a Bayesian hierarchical approach to develop a removal model accounting for effort using data augmentation to estimate feral swine population sizes from removal data. This is a method that can be used by any management program that conducts removals of invasive species. The Wildlife Services (WS) program of the USDA Animal and Plant Health Inspection Service (APHIS) conducts removal efforts across the United States for feral swine. WS personnel collect detailed information for each removal effort including: location, timing, number of animals removed, and amount of effort employed. Our objectives were to: (1) evaluate whether reasonable estimates of population size with practical uncertainties can be obtained from these data using a removal model, (2) determine under which conditions estimates of population size are reliable, and (3) identify actions that are in accordance with current management plans that would enable improved population estimation going forward.

Methods

Data

In the United States, USDA-APHIS-WS manages conflict at the human–wildlife interface by providing wildlife control assistance to land owners based on the authority of the Animal Damage Control Program of 1985 in compliance with the National Environmental Policy Act. All management activities are recorded in a national database, the Management Information System (MIS). The types of land that management actions are conducted on include federal, state, tribal, and private land. Management is conducted based on agreements with property owners; here we will refer to properties as sites. The information on management actions in the database include: site location, size of the site, and type of land (e.g., private land, military land, state land, city property) date and time of management, type of management, amount of effort (e.g., hours of flying time), and, for example, the number of swine removed. For our analysis we modeled removal by aerial gunning, which is implemented using either helicopters or fixed wing aircraft. In all cases, there is one pilot and one gunner. The pilot searches the site based on personal judgement and positions the gunner as close as possible to visible feral swine.

For this study we examined helicopter removal data in Texas and Oklahoma, USA from 2005 to 2013. In the full data set, some sites' sizes were as large as 320,000 acres (1 acre = ~4,047 m^2). However, because greater accuracy of abundance estimates is achieved when the proportion of the population that is sampled increases (Williams et al. 2002), we focused on sites that were 20,000 acres or smaller to minimize inadequate coverage of the sampling area (20,000-acre cut-off represents the amount of land that we assumed can reasonably be searched during one sampling event). Furthermore, multiple removals are a requirement to estimate population size using removal modeling and a fundamental assumption in removal modeling is that populations are closed to births, deaths, emigration, and immigration (Zippin 1958), therefore, we took a subset of the data to ensure that three or more removals (Zippin 1958) were conducted within a time frame less than the average gestation period (three months) to minimize the number of new births occurring in the population.

Although removal of feral swine includes multiple techniques in addition to aerial gunning (e.g., different types of traps, snaring, and ground shooting), take from helicopters comprises ~85% of removals in MIS data from Texas and Oklahoma. Additionally, the amount of effort for helicopter removal data is standardized by the number of hours in the air; therefore, we focused on removal from helicopters only for this study.

Model

We used a Bayesian hierarchical removal model to estimate abundance at each of n spatially distinct sites. We let y_{ijk} represent the fate (1 if the animal was removed and 0 if not) of individual k from site i during pass j. Let z_{ik} represent an indicator of the individual k being in the population i (1 if it is in the population and 0 if not). The data (y_{ijk}) are Bernoulli distributed (when the individual is in the population and has not been removed on a previous pass) with removal rate p_{ij} given the z_{ik} indicate the individual is in the population of interest:

$$y_{ijk} = \begin{cases} 0 & ,z_{ik}=0 \\ \begin{cases} \mathrm{Bern}(p_{ij}), & \sum_{l<j} y_{ilk}=0 \\ 0, & \sum_{l<j} y_{ilk}>0 \end{cases} & ,z_{ik}=1 \end{cases} \tag{1}$$

We used data augmentation (Tanner and Wong 1987) which supplements the data with individuals with all-zero encounter histories. This reparameterizes the model so that it is individual based and allows for individual effects. We determined that the number of augmented individuals (w_i) would vary by site depending on the number of animals removed at each site. Based on preliminary analyses we determined that w_i equal to four times the number of animals removed was large enough for the results to not be limited by the augmentation size. The parameter z_{ik} determines which of the augmented individuals are actually in the population; z_{ik} is modeled with a Bernoulli distribution with probability (ψ_i), where ψ_i has a uniform prior. Abundance estimates by site (N_i) are a derived parameter, which is the sum of the z values.

We define θ_i as the site-level probability that an individual will be removed from the population with one unit of effort. Similar to St. Clair et al. (2012), we assumed that effort is additive and θ_i is constant across all periods. Therefore, the probability of being removed will vary by pass as the amount of effort (g_{ij}, here the amount of hours in the helicopter) changes. Thus the probability of being removed on pass j for site i (p_{ij}) is modeled separately to reflect the probability of not being removed in the time period given θ_i and g_{ij}:

$$p_{ij} = 1-(1-\theta_i)^{g_{ij}} \tag{2}$$

We used a vague prior from the beta distribution to model the site-level removal rate (θ_i). The full model structure used is shown in the supporting information (Appendix S1).

To calculate the posterior distribution for the parameters of interest, we fit the removal model described previously using a Markov chain Monte Carlo (MCMC) algorithm with a Gibbs sampler and a Metropolis-Hastings step (Gelman et al. 2013) custom written in R (R Core Team 2014). Convergence was assessed graphically by visually assessing the convergence and mixing of the trace plot for each parameter. The posterior estimates for population size by site (N_i) were calculated for each MCMC iteration by summing the z values by site. Posterior estimates for the data are based on 50,000 iterations of the MCMC algorithm with the first 5,000 iterations discarded as burn-in.

Simulations

There are no independent estimates of population size available for the sites and time frames we examined in this study; and thus, there is no ground-truthing available to validate our results. In lieu of this information, we simulated data from a range of population sizes and removal probabilities and fit these data to our model to evaluate potential issues of accuracy and imprecision in our model. We defined accuracy as the estimate being within 10% of the true value.

The range of population sizes we used for simulations were based on estimates from MIS data: 20, 50, 100, 200, 500, and 1,000. The removal probabilities (θ_i) we used were 0.05, 0.15, and 0.25. The amount of effort in the observed data (g_{ij}, hours in the helicopter) ranged from 0.1 to 7.4 flight hours, with 80% between 1 and 6 h; therefore we restricted our simulated effort per pass to be between 1 and 6 h. We examined all permutations of effort (whole hours) for the different number of removal passes (e.g., 1,1,1; 1,1,2; to 6,6,6). We simulated all combinations of each condition of population size (six levels), removal rate (three levels), and variation in effort (216 permutations) for a total of 3,888 data-generating processes. We generated five samples from each data-generating process to evaluate consistency of estimates under a given set of conditions.

For each simulated condition we generated removal data and fit our removal model to the data to estimate the removal rates and population sizes. Based on the large number of simulated conditions we ran 10,000 iterations of the MCMC algorithm for each simulation discarding 1,000 iterations as burn-in for each simulation. We assessed convergence graphically using the same methodology as with the observed data. Convergence took longer to achieve for low removal rates and effort thus the burn in is greater than the 10% we used for the actual data. We then compared the results to the conditions that simulated the data ("truth") and examined how accuracy and precision were influenced by population size, removal rate, number of removal passes, and removal effort.

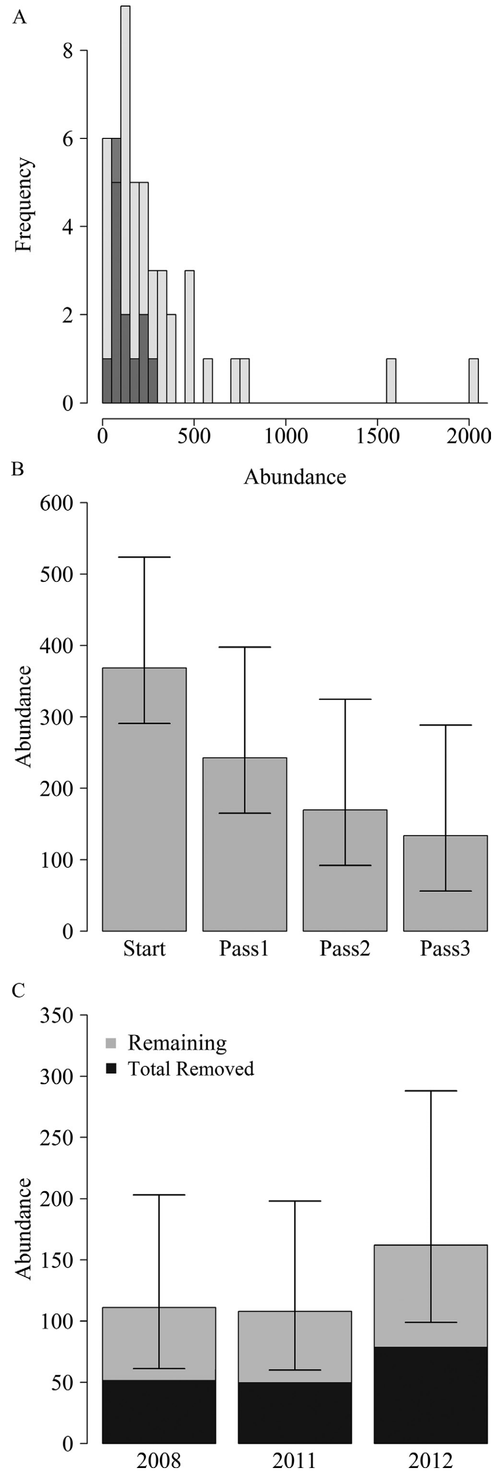

Fig. 1. (A) A histogram of the abundance estimates from the 59 site/time frame combinations that were examined in our study. The histogram is split by post-validated accurate (gray bars) and inaccurate (black bars) estimates. (B) An example from one site of the change in abundance from the start of the study and after each subsequent removal pass. Error bars represent 95% credible intervals. (C) Proportion of the population removed by aerial gunning from the total abundance at the beginning of the study over time for one example property that was visited on three separate occasions. Error bars represent 95% credible intervals.

Results

Forty-nine sites, 18 in Oklahoma and 31 in Texas, met our criteria for inclusion in the analysis (≤20,000 acres in size and ≥3 removals within 3-month period). Since we examined data spanning many years (2005–2013), some of the sites (eight total) we examined had more than one 3-month time period that fit our criteria. For the sites with multiple periods, we estimated population sizes for each time period separately, treating the multiple time periods independently in the analysis. Six of these sites had two different time periods that fit the criteria, and two sites had three different time periods that fit the criteria, thus we had a total of 59 site/time frame periods that fit our criteria. There was a total of 5,758 swine removed across all sites and time frames included. The fewest number of swine killed by site/time frame was 11 and the most killed was 585.

The mean population estimate from the removal model was 252.7 (standard error [SE] = 336.1), with a low of 23.2 (95% credible interval of 15–53) and a high of 2007.8 (95% credible interval of 1,410–2,580; Fig. 1A, site-specific estimates are shown in Appendix S2). The population size estimates are from the start (pre-removal) of the study, however, it is possible to see how the population size changes after each pass by subtracting the removed individuals at each pass (example shown in Fig. 1B). Extending this idea, we can also obtain the proportion of the population of removed due to management actions. The mean proportion of individuals removed in our study was 46.5% (with a range of 25.4–97.1%; we show an example in Fig. 1C). As site sizes increased, the estimated population size generally

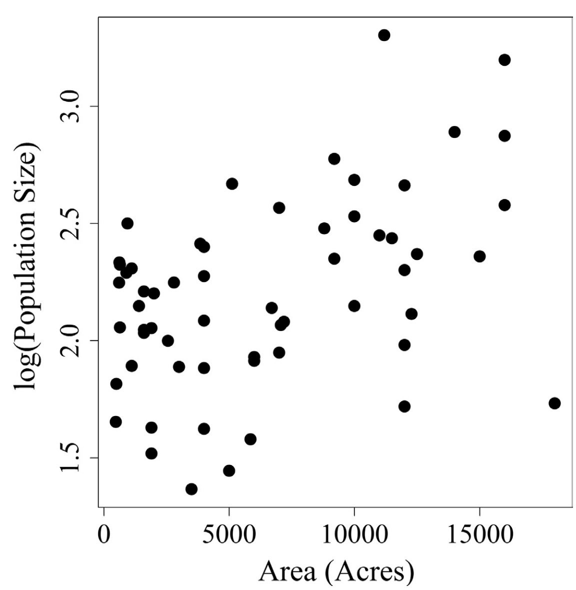

Fig. 2. Log_{10} transformed estimates of abundance plotted against the area (1 acre = ~4047 m^2) of the site where feral swine were removed.

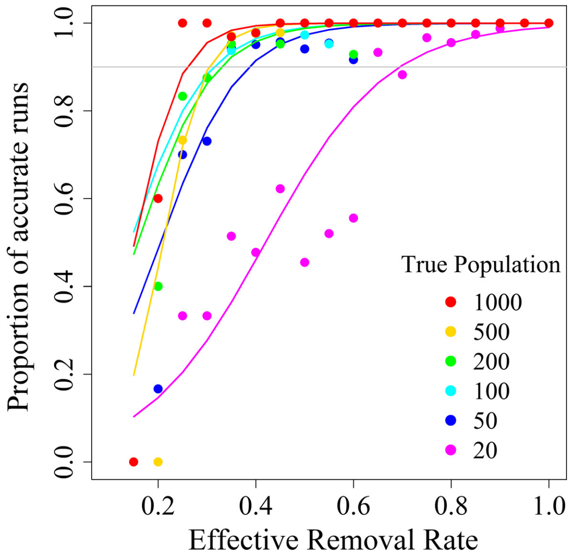

FIG. 3. Proportion of simulations that are accurate based on their effective removal rate and simulated true abundance. Effective removal rates greater than 0.70 resulted in 90% accurate runs regardless of abundance.

increased and had greater variability (Fig. 2). Estimates of site-level removal rates (θ_i) ranged from 0.02 to 0.54, and averaged 0.13 (SE = 0.12).

The majority (95%) of simulations had an estimated population size within 10% of the true population size. Of the 5% of estimates that were inaccurate, 92% were underestimated. With a true removal rate of 0.05, 14.0% of the model fits were inaccurate, whereas when the true removal rate was 0.15 or 0.25, only 0.1% and <0.001%, were inaccurate.

When the population estimates are plotted against the removal rate adjusted for the total sampling effort ($\hat{p}_{total}$ calculated using Eq. 2 with the effort summed across all passes by site, termed "effective removal rate") a strong pattern emerges: larger effective removal rates (>0.70) generally resulted in accurate estimates. We binned the effective removal rate values by 0.05 from 0 to 1 and investigated the proportion of simulations in each bin that were accurate, as a function of population size (Fig. 3). Larger true populations were able to be estimated more accurately with lower levels of effective removal rates than smaller true population sizes. For population sizes of 50 or more, estimates were accurate with effective removal rates >0.40, which is substantially lower than the 0.70 required for population sizes of 20.

We used the relationship between effective removal rates with at least 90% accuracy and the true population size to create a method to post-validate estimates. We fit an exponential curve to the relationship of population size and effective removal rates, which indicated 90% accuracy from Fig. 3 (Fig. 4); values below the curve are likely to be inaccurate and values above the curve are likely accurate based on the observed relationship. We added the estimates from the MIS data to this plot (Fig. 4) and found 46 of the estimates are likely accurate (shading in Fig. 1A shows estimates that were likely inaccurate based on this post-validation).

DISCUSSION

A primary challenge of this study was to determine if it was possible to use preexisting data on feral swine removal efforts to estimate population sizes. These data are reports of management activities by a federal agency in the United States (USDA-APHIS-WS) and were not collected according to any statistical sampling method. That is, the data are not from a random sampling design and the timing between the removal passes is based on management scheduling, not with the objective to estimate population size. Previous work that used removal models to estimate feral swine populations were implemented with the objective of estimating population sizes and were designed as such (Ramsey et al. 2009, Barron et al. 2011).

There are considerable benefits to estimating population sizes by using data that are already collected by managers, i.e., evaluating efficiency of management actions with no additional field expense or materials to collect, and informing trends of abundance across space and time for management planning or assessing density-related impacts. A key advantage of removal models is the ability to obtain the abundance estimate prior to the start of removal events and the abundance after removals have taken place (the starting abundance minus the

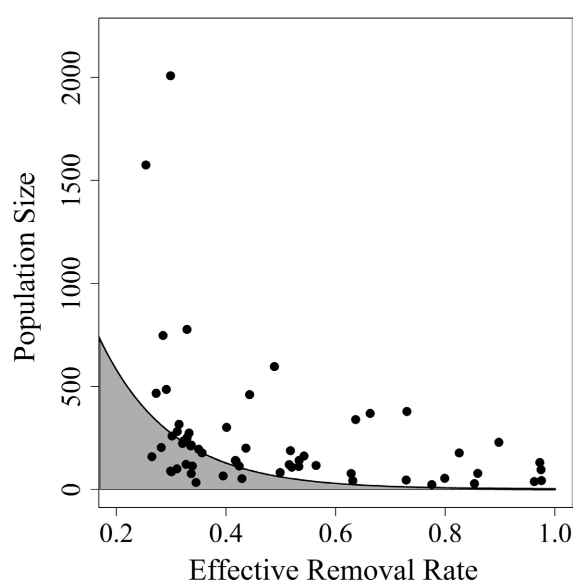

FIG. 4. Abundance estimates plotted against the effective removal rates for feral swine in sites in Texas and Oklahoma, USA. The shaded area represents the values that are likely inaccurate based on post-validation from simulation, and the white area represents likely accurate values.

number removed). When an area is visited in multiple years, the changes in the population can be tracked and the removal rates per year can be compared, giving additional assessment to managers.

We estimated population sizes for 59 site/time frame combinations from Texas and Oklahoma between 2005 and 2013. Our simulated results allowed us to post-validate these estimates, as no independent population size estimates were available to accomplish validation. Forty-six site/time frame combinations (78%) were found to be accurate based on this method. We demonstrate how it is possible to estimate population size from management removal data and to validate it without requiring additional effort from managers using this model. We were limited in the number of site/time frame combinations in which we could estimate population size in large part due to the lack of repeated removals conducted within the desired time frame. Modifications to current management actions that increase repeated removals in an area would increase the number of sites for which population size estimates can be obtained.

Our simulation work also demonstrated that inaccurate estimates of population size are more likely to be underestimated than overestimated based on this model. This is important to keep in mind when considering potentially inaccurate estimates based on post-validation. Although these estimates are not likely reliable based on our post-validation technique, there is a strong chance that these estimates are underestimated. The tendency for underestimation in our removal model may be a result of the ranges of values observed and/or an intrinsic element of this removal model. It should also be noted that when population sizes are underestimated the corresponding removal rates are overestimated and vice versa. Therefore, efforts that increase the accuracy in removal rates will increase the accuracy of the population sizes as well.

Because the removal data were not collected according to a design-based sample, we used a subset of the management data to adhere to the assumptions of a removal model. The criteria we used (i.e., only sites <20,000 acres, at least three removals within three months, helicopter take only) were restrictive, severely limiting the number of sites and time frames that we examined. Increasing the number of removal events conducted within a small time frame would allow population sizes to be estimated from more sites. We limited the areas of sites in our analysis because we wanted to ensure that the area of the site reflected the area being searched; it is unlikely that larger sites are searched completely. The restriction on site size could be relaxed if greater spatial detail on where removals occurred could be collected because this would enable us to ensure that the area we are making inference to is the area covered by the removal efforts.

Through simulation we were able to determine which factors were most influential in providing accurate population estimates. Removal models need to account for variation in removal effort, especially for post-hoc analyses (St. Clair et al. 2012). The effective removal rate accounts for the estimated site-level removal probability (θ) and the total amount of effort employed in all of the removal passes. This measure was strongly positively correlated with accurate population size estimates. Therefore, improvements in population size estimation reliability can be achieved by increasing the site-level removal rate or the total amount of effort involved. Generally, the accurate estimates from our simulations had more than seven total hours of effort (helicopter time) summed across all passes, whereas a total effort of less than five hours generally resulted in inaccurate estimates. True removal rates (θ) less than 0.10 resulted in inaccurate population estimates considerably more than those 0.10 or greater. Methods that can improve removal rates would also improve estimated population sizes. This method may not be optimal for estimating population sizes when populations are near eradication as removal rates are likely low in those cases and the effective removal rates necessary to estimate populations accurately at such low population sizes would be considerably high. These values are specific to helicopter removals of feral swine (in Texas and Oklahoma), however, the results would be applicable to other systems with similar ranges of population sizes and removal rates (and effort). In addition, these values will change as this method is applied to different removal methods and to different species.

Another option to improve population estimates would be to collect auxiliary data that could be influencing removal probabilities. As our simulations showed, population size estimates were underestimated when removal rates were overestimated. Therefore, if we can improve the estimates of removal rate through additional information we should be able to increase the accuracy of our population size estimates. Communication with managers suggests that success rates of removing feral swine from helicopters are strongly influenced by the habitat (e.g., forested habitats or thick brush diminish removal probabilities). Additionally, detection probabilities for ungulates, including feral swine, have been shown to be lower in denser habitats than in open areas (Focardi et al. 2002), which may also contribute to lower removal rates. The detection probability can be modeled as a function of covariates, which has the potential to improve estimates of removal rate and thus of population sizes.

Currently, our analysis is tailored to the most common method of removal for the states in our study; in this case we used helicopter data. Helicopter removal is the most efficient method for removing feral swine per hour of effort (Saunders and Bryant 1988) and represented 85% of all harvest. Additionally, sampling from a helicopter is more likely to result in coverage of the entire area of interest than other take methods, and there is a standardized measure of effort for helicopter removals (hours in flight). However, it is important to note that if other removal efforts were conducted during the time frame examined this would be a violation of the closure assumption. Auxiliary removals would result in an underestimated population size and an overestimated removal rate. Many other removal events are recorded by managers and inclusion of those methods provides another avenue for extension of this model. However, there still may be additional unrecorded removals if landowners conduct independent trapping or hunting during the time frame.

Here we have estimated removal rate per 1 h of time spent in a helicopter (θ) for each site. Removal rates or detection probabilities are often considered nuisance variables that can cause bias in abundance estimates if they are not accounted for. Therefore, the parameter of interest is typically abundance and removal rate (or detection) is of secondary interest. However, managers or researchers may be interested in removal rate values to help evaluate efficiency in different habitats or under different strategies. Currently it would be difficult to compare removal rates across sites in our study as the areas searched vary considerably from one site to the next (Fig. 2). Thus, removal rate per hour by area would be a better parameter to compare than removal rate per hour on its own. The area of a site does not vary from one pass to the next, therefore the removal rate can be converted to account for area post-analysis by simply multiplying by the area. It is important to keep in mind that the area for correction needs to be large enough such that the probability of capture in that area is not 1 or this will mean little in interpretation (e.g., use 10,000 acres not 1 acre for feral swine).

Our model is readily adaptable for other single methods of removal. For each different removal method, parameterizations of the different model components need to be tailored to the specific method. The area impacted by different sampling methods (i.e., the spatial extent from which pigs are removed) may not be the same as the site size, which was an assumption here. The measure of effort is less obvious for methods such as trapping or snaring. It is possible that pre-baiting could influence detection and thus should be included in effort, or simply the number of trap nights could be the strongest influences on removal rates. These are important questions that should be examined when extending this model to other scenarios.

The current framework does not allow for multiple removal methods simultaneously, as these would require separate effort data, and separate removal rates to be estimated. A future direction of this work is to incorporate different removal methods in a single model. The evaluation of multiple removal techniques and their removal rates simultaneously would also allow for economic comparisons of removal success rates. If ancillary sources of removal are being conducted during the time frames of used in a removal model, then initial population sizes are likely underestimates.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1383/suppinfo

Data Availability

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.67nb3.