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Kim M. Pepin

*USDA National Wildlife Research Center, kim.m.pepin@aphis.usda.gov*

Amy J. Davis

*USDA National Wildlife Research Center, Amy.J.Davis@usda.gov*

Kurt C. Vercauteren

*USDA National Wildlife Research Center, kurt.c.vercauteren@aphis.usda.gov*

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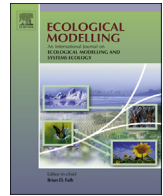
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## Original Article

# Efficiency of different spatial and temporal strategies for reducing vertebrate pest populations



Kim M. Pepin\*, Amy J. Davis, Kurt C. VerCauteren

National Wildlife Research Center, United States Department of Agriculture, 4101 Laporte Ave., Fort Collins, CO, 80526, USA

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## ABSTRACT

Understanding effectiveness of control strategies of pest species is fundamental for planning efficient and cost-effective management programs. In addition to culling rates, there are many potential factors that can determine efficiency of different management strategies, including demographic processes such as immigration rates, birth dynamics, and spatial ecology. We developed a stochastic, data-based simulation model of feral swine population dynamics which accounted for social dynamics in space. We tested the impacts of different spatio-temporal management strategies (i.e., culling rates, timing of culling during the year, spatial pattern of culling and strength of a barrier to immigration) on population response and efficiency. The spatial culling strategy dramatically impacted efficiency of control – using zonation required removal of fewer pigs (up to 46% less) to achieve similar reductions compared with other spatial strategies. Also, our spatially-explicit model predicted that lower culling intensities could be used to achieve population reductions when zonation was applied relative to predictions from harvesting theory based on simple logistic models. As culling intensity increased ( $\geq 50\%$  of target population annually) and the target population reached low density ( $< 5\%$  of original density), effects of spatial strategy became less pronounced relative to immigration barrier effects. Lastly, for the same level of moderate culling effort, prioritization of culling during the low-birthing period generally resulted in faster population reduction to near zero abundance relative to prioritization during the high-birthing period, or spreading the work over a year period, but the significance of this effect depended on the spatial culling strategy and culling intensity. Our results imply that continually updating knowledge of current abundance during management may not only be important for determining culling quotas, but also for updating and optimizing management strategies. When the management goal is maximum population control, consideration of birth and spatial dynamics can increase return on management effort and bring to light management inefficiencies.

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## 1. Introduction

Determining effective strategies for reducing invasive or pest species is challenging due to complex population ecology in space and time. However, efficacy is not the only important management metric – identifying control strategies that maximize efficiency can be equally essential for satisfying control objectives because fiscal and personnel resources for many vertebrate pest control programs are limited. By interpreting the interplay of realistic ecological complexities, population models develop our mechanistic understanding of ecological conditions that affect the efficacy and

efficiency of pest control, providing a science-based foundation for management planning. For example, population models have guided management by: identifying levels of culling pressure that limit population growth rate or abundance (Hone, 2012; Servanty et al., 2011; Gamelon et al., 2012), planning implementation of control techniques (Hone, 1990; Hone, 1992; Choquenot et al., 1993), evaluating combined control techniques (McCarthy et al., 2013; Yoak et al., 2016; Pepin et al., 2017), determining population densities that reduce damage (Hone, 2012; Krull et al., 2016), choosing spatial (McMahon et al., 2010) or temporal strategies (Grarock et al., 2014; Lieury et al., 2015), and planning strategies within the cost constraints of particular situations (Beeton et al., 2015; Anderson et al., 2016). In planning resource allocation for control of pests, primary questions include when, where and how much effort should be expended and how should it be distributed. There is a strong theoretical foundation for answers to some of

\* Corresponding author.

E-mail addresses:

[kim.m.pepin@aphis.usda.gov](mailto:kim.m.pepin@aphis.usda.gov) (K.M. Pepin), [amy.j.davis@aphis.usda.gov](mailto:amy.j.davis@aphis.usda.gov) (A.J. Davis), [kurt.c.vercauteren@aphis.usda.gov](mailto:kurt.c.vercauteren@aphis.usda.gov) (K.C. VerCauteren).

these questions individually but a much weaker understanding of their combined effects, and effects of different spatial strategies are poorly understood in particular (Epanchin-Neill and Hastings, 2010). Thus, guiding principles for how to implement pest control in space and time remain elusive (Hone et al., 2015), which makes it difficult to plan pest control programs at the outset before much data are available.

Many wildlife species exhibit distinct seasonality in births (Zerbe et al., 2012), and conducting harvest at the wrong time can drive the population below a target abundance (Boyce et al., 1999; Kokko, 2001). The theory is based on the idea that after the birthing season there is an excess of individuals who are doomed to be lost naturally by density-dependent causes ('doomed excess', Errington, 1945), and thus hunting mortality compensates other types of mortality leading to a similar abundance the following year (Burnham and Anderson, 1984; Bartmann et al., 1992). Thus, conversely, if the goal is to substantially reduce the population efficiently, it is best to time culling when the population is at its lowest abundance, after the doomed excess have died (Grarock et al., 2014), when culling might have additive effects on total mortality. However, these effects have primarily been studied in populations with distinct birth pulses and it is less clear if similar guidelines would apply in populations with continuous or variable birth patterns.

Recent advances in conservation planning have highlighted the importance of spatial prioritization (prioritizing a particular spatial arrangement of control) in the success of conservation initiatives (Margules and Pressey, 2000; Moilanen et al., 2005). Conservation planning theory is partly based on metapopulation theory (Hanski and Ovaskainen, 2000), which shows that the fate of a metapopulation is determined by the connectivity of its component subpopulations. Although applicable, these concepts have been under-used for controlling invasive species (Glen et al., 2013). In one example (Parkes et al., 2010) zoning was applied to eradicate wild pigs from an island, but the efficiency of zoning relative to other strategies was not investigated. Similarly, an analysis of spatial culling strategies suggested that prioritization of high-density areas is best (McMahon et al., 2010) but there appears to be no consensus on general guidelines for spatial prioritization (Epanchin-Neill and Hastings, 2010).

Wild pigs are an example of a vertebrate pest species with breeding seasonality that varies greatly depending on geographic location (Saunders, 1993; Gethoffer et al., 2007; Mayer and Brisbin, 2009; Macchi et al., 2010; Fonseca et al., 2011; Ježek et al., 2011; Orłowska et al., 2013; Lombardini et al., 2014), making them ideal for identifying general guidelines for when it is most efficient to cull (temporal prioritization). Wild pigs are also a social ungulate species exhibiting a wide range of family-group sizes, spatial dynamics (Podgórski et al., 2014a; Morelle et al., 2015; Kay et al., 2017) and territoriality (Sparklin et al., 2009), suggesting that their spatial population dynamics could provide a useful platform for developing guidelines for spatial prioritization of culling. Wild pigs are targeted for management in many countries due to their overabundance and damage to agriculture, humans and the environment (Campbell and Long, 2009; Barrios-Garcia and Ballari, 2012; Bevins et al., 2014). Several studies have documented different eradication strategies for wild pigs (Katahira et al., 1993; Lombardo and Faulkner, 2000; Cruz et al., 2005; McCann and Garcelon, 2008; Parkes et al., 2010), providing a strong foundation for planning efficient culling programs. However, these empirical studies were not able to evaluate whether alternative strategies would have been more efficient, or provide insight into planning maximum control in areas with strong immigration pressure (e.g., Delgado-Acevedo et al., 2013; Bodenchuk, 2014). Similarly, models of wild pig population control have been helpful at guiding the implementation of different lethal control tools (Hone, 1992;

Choquenot et al., 1993; Choquenot et al., 1999), but general guidance on when, where and how much remains limited, especially in landscapes with immigration (Delgado-Acevedo et al., 2013).

To facilitate the planning and resource allocation for controlling a social, vertebrate pest such as wild pigs, we examined the efficiency of different realistic management strategies in space and time. To address a new level of complexity with this problem, we considered multiple aspects of management implementation in a full-factorial design, by varying culling intensity, timing, spatial prioritization, and immigration control. We examined these scenarios in landscapes with different patch sizes (differing by carrying capacity) and in populations with different birth patterns (pulse versus continuous) to investigate whether general guidelines emerged. In line with previous work (Grarock et al., 2014), we hypothesized that focusing culling during months when abundance was low (pre-births) would be more efficient than focusing culling during months when births were high (post-births) because resources would not be wasted on the doomed excess (Boyce et al., 1999). We sought to determine if this hypothesis held true for populations with more continuous birth seasonality that includes multiple peaks (Gethoffer et al., 2007; Mayer and Brisbin, 2009; Macchi et al., 2010; Orłowska et al., 2013), relative to ones with a more focused birth pulse (Fonseca et al., 2011; Lombardini et al., 2014), upon which the hypothesis has been formulated. We also investigated whether zoning would be more effective than spatially random strategies or strategies that target high-density patches, because zoning is applied in practice (Parkes et al., 2010) but its benefits relative to other spatial methods are poorly understood (Epanchin-Neill and Hastings, 2010). As many population control scenarios are not conducted in areas closed to re-invasion, we also compared effects of different culling patterns with and without immigration from surrounding populations.

## 2. Methods

To identify efficient management outcomes that consider the complex ecological processes of social, vertebrate-pest species, we developed an individual-based model (IBM) which explicitly accounted for individual-level variation in movement behavior, reproduction, social dynamics, and shifts in space. All analyses were conducted using Matlab R2016b (Version 9.1.0, The MathWorks, Inc., Natick, MA). Below we describe our approach using the updated Overview, Design concepts, and Details (ODD) protocol for individual-based models (Grimm et al., 2010).

### 2.1. Purpose

Our goals were to 1) understand how different spatio-temporal strategies of vertebrate-pest management determine the effectiveness and efficiency of population reduction given birth seasonality, social and spatial dynamics, and 2) identify efficient strategies for greatly reducing vertebrate pests in landscapes with immigration. For our case study, we were interested in reducing the population substantially, which we evaluated by how much the population was reduced within 5 years and how much effort/time was required to reduce the population by 90%. Specifically, we set out to answer:

- Is it efficient to time culling activities relative to birth seasonality, and if so, what timing is most efficient?
- Considering social dynamics and landscape patchiness, is there a spatial culling pattern which is most efficient, and if so, what is it?
- What combination of culling intensity and immigration barrier allows a particular population management goal to be reached efficiently?

## 2.2. Entities, state variables, and scales

Individual pigs were the entities which were subject to the following states: age, sex, family group ID, natal dispersal status, longevity, minimum age at first conception, litter size, reproductive status, gestation time, postnatal time, home range centroid (x, y coordinates), and grid cell ID. Pig population dynamics were simulated on a 50 km by 50 km (2500 km<sup>2</sup>) heterogeneous landscape with 5 km by 5 km grid-cell resolution. Each grid cell had a carrying capacity of 25 or 125 pigs (1 or 5 pigs per km<sup>2</sup>; Saunders, 1993; Davis et al., 2017; Keiter et al., 2017). Individuals in the same family group had the same home range centroid and grid cell ID. Longevity, minimum age at first conception and sex were fixed for life at birth while the other states were updated based on time, age or population density.

## 2.3. Process overview and scheduling

### 2.3.1. Overview by comparison to a logistic model

The general behavior of our IBM was similar to the following logistic model (Figs. S1 and S2 in SI2 File, Pepin et al., 2017):

$$N_t = N_{t-1} + r_{t-1}N_{t-1} \left(1 - \frac{N_{t-1}}{K}\right) + m \left(\frac{1}{N_{t-1}} - \frac{1}{K}\right) - c_{t-1}, \quad (1)$$

Eq. (1) represents logistic population dynamics with density-dependent immigration and population control due to culling.  $N_t$  represents pig abundance in week  $t$ ,  $r_t$  is the intrinsic rate of increase in week  $t$ ,  $m$  is the density-dependent net immigration rate,  $K$  is the population carrying capacity, and  $c_t$  is a vector of the target number of pigs to be culled in week  $t$  (see Figs. S1 and S2 caption in SI2 File for parameter values that compare to our IBM). When initial abundance was 10% of carrying capacity, the weekly birth probability vectors of the IBM (derived from empirical data, Table 2) generated mean annual finite rates of increase ( $\lambda$ ; for the first 5 years) of 1.30 and 1.36 for the two birth patterns respectively (where mean net  $r = \log_e(\lambda) = 0.26$  and 0.31, respectively). Because the IBM incorporates age and sex structure as well as lag times between conception and births, the annual birth probabilities in the IBM (sum of weekly birth probability vectors: 0.6 and 0.65 for the Czech Rep. and USA data respectively) are not equivalent to the intrinsic rate of increase ( $r$ ) in the logistic model. Thus, in order to compare the dynamics of our IBM model to those of the logistic model, we applied a scaling factor to the birth probability vectors such that the logistic model generated net  $r$ 's similar to those of the IBM (i.e., 0.26 and 0.31). This yielded intrinsic rates of increase ( $r$  parameter in Eq. (1)) in the logistic model of 0.335 and 0.406. Once we calibrated the  $r$ 's for the logistic model, we applied a similar procedure to derive the  $m$ 's in the logistic model to compare the two models on equal grounds (Figs. S1 and S2 in SI2 File). With immigration, mean annual  $\lambda$ 's for the first 5 years were of 1.54 and 1.72 (where mean net  $r = \log_e(\lambda) = 0.43$  and 0.54, respectively). Applying the logic of Hone (1999) to our model structure, the theoretical annual proportion culled to maintain zero growth in the population ( $p = 1 - e^{-r}$ ) is 0.23 (for  $r = 0.26$ ) and 0.27 (for  $r = 0.31$ ) without immigration, or 0.35 (for  $r = 0.43$ ) and 0.42 (for  $r = 0.54$ ) with immigration. Note that the major difference between our IBM and Eq. (1) is that our IBM is spatial and density-dependent mortality is a separate process acting at the level of individual grid cells, whereas Eq. (1) implements density-dependent regulation at the full population level through the carrying capacity parameter.

### 2.3.2. IBM overview and scheduling

In the IBM, states were updated at a weekly time step. Each 10-year simulation was seeded with a population that had undergone demographic dynamics on the landscape for 10 years ("burn-in")

prior to starting the formal run (Fig. 1). In the post-burn-in simulation, the order of updating and processes per time step was:

- Update abundance, ages, gestation time, reproductive status, postnatal time
- Natural mortality: remove individuals that reach longevity age
- Culling: choose individuals to be culled and remove them, record the number culled
- Natal dispersal: change the home range centroid and grid cell ID (if applicable) for individuals that reach dispersal age, update natal dispersal status to complete (this is a one-time per life event)
- Other relocation: For family groups that become too large, relocate half to another home range centroid; for any females that end up alone, associate them to the nearest family group (Gabor et al., 1999)
- Habitat-dependent mortality: find overpopulated grid cells and remove a family group or male
- Conception: identify new conceptions, initialize gestation clocks, choose litter sizes, reset post-natal clock to zero
- Births: assign sex in 1:1 ratio, assign age of 1, assign location and group ID the same as mother's, assign natal dispersal age, assign longevity, assign minimum age at first reproduction (females only)

The order of processes that could change abundance was: natural mortality, relocation due to oversized family groups, habitat-dependent mortality and births. Note, individuals can die before the longevity age due to other causes such as culling or density-dependent mortality. To control density, we allowed relocation of family groups before density-dependent mortality because in the event of overcrowding we expected that most pigs would seek another location rather than die. The weekly number of pigs culled for a particular year was determined once per year using the abundance at the start of that year.

## 2.4. Design concepts

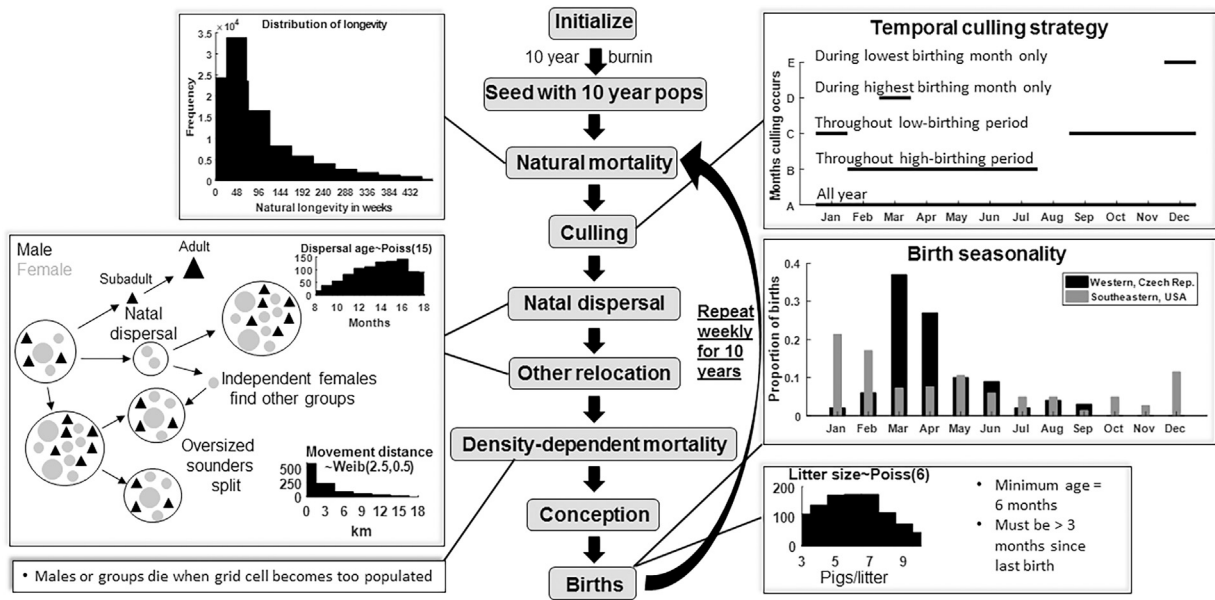
### 2.4.1. Basic principles

We explicitly represented social associations and spatial structure of pigs on the landscape. Group membership was dynamic over time, due to processes such as overcrowding, territoriality (Sparklin et al., 2009), and natal dispersal. We examined two types of management actions (culling and barriers against immigration) and three aspects involved in planning culling (intensity, temporal strategy, and spatial strategy; described in Table 1). Because seasonal birth dynamics of vertebrate pests can be quite different even within the same species, we examined the effects of temporal culling strategy using two different data-based birth patterns as a means of investigating the generality of our results. Also, because habitats are rarely homogeneous and habitat heterogeneity can affect management outcomes (Glen et al., 2013), we examined the effects of spatial management strategies on two different landscapes which differed in density-based patch sizes (Fig. S3 in SI2 File, Table 1). Analyzing results in a stochastic framework allowed us to account for potential differences in the sensitivity of different management strategies to stochastic events as the target population neared elimination.

### 2.4.2. Emergence

Although strength of the immigration barrier constrained maximum rates of immigration to the managed area, realized immigration rates (actual number of pigs per week) emerged from the amount of available space which changed due to births and deaths in the target zone. Similarly, although the dispersal distance was defined by a random distribution with fixed parameters, the real-





**Fig. 1.** Model overview. Main processes in the IBM are shown in the center. Details of each process are linked with black lines. In addition to culling intensity (proportion culled annually) and timing (plotted on the upper right of the culling label), we also examined spatial strategies (not shown here) as described in the Methods and Table 1.

**Table 1**  
Design of simulations. Description of how wild-pig birth patterns, landscape structure, and implementation of management differed in simulations. A full factorial design was used (all possible combinations of the specified levels of each factor).

Factor	Levels	Description
Birth pattern	1 or 2	Seasonal birth patterns in Fig. 1 top – either Western Czech Republic or Southeastern USA.
Landscape	1 or 2	Overall maximum density of landscapes were the same; patch size for high-density patches varied (Fig. S1). Two types were: large (450 km <sup>2</sup> patch size) or small (100 km <sup>2</sup> patch size).
Temporal culling strategy	0–5	Timing of culling relative to birth dynamics; 0 = no culling (control), values 1–5 are for patterns A–E described in Fig. 1 middle and bottom plots.
Immigration barrier	0–1 in 0.1 increments	Strength of the fence barrier (Fig. S1) at blocking immigration (where 0 = not at all and 1 = 100% effective) from outside the target area to the inside.
Culling intensity	0.1–1 in 0.1 increments	Proportion of the population in the target area (Fig. S1) culled annually. Although this is unlikely to reflect how management would occur once populations reach low densities, it is useful for understanding the relationship between culling pressure and population reduction.
Spatial culling strategy	1, 2 or 3	Spatial strategy for implementing culling. The three methods were: 1) Random with respect to space and family group (random), 2) Prioritizing the highest-density grid cells and individuals in closest proximity (group-based), 3) Zoning from east to west, where the culling front moves in a wave-like manner and immigrants enter at the back of the wave front (i.e., where culling has been completed) are prioritized for culling along with the moving front (zoning).

ized average dispersal distance at a particular time point emerged from the spatial distribution of population density. That is, our dispersal algorithm forced individuals to search for space farther away when space nearby was at capacity. Lastly, annual population growth rate was limited by cell-based population densities, such that intrinsic rates of increase (*r*) were close to zero when the landscape was near carrying capacity, and creating a non-linear population response to culling.

**2.4.3. Adaptation**

We implemented culling by removing a fixed proportion of pigs each year. Thus, the number of pigs culled per year by managers changed based on current pig abundance at the start of each year (January 1st), such that fewer pigs were culled per year as abundance decreased. We assumed all pigs in the target zone could be found and culled regardless of geographic location or movement behavior.

**2.4.4. Objectives**

The overarching goal was to study how the population could be reduced as rapidly and efficiently (i.e., requiring less effort) as

possible while considering realistic, non-linear ecological processes such as social structure, birth seasonality and immigration.

**2.4.5. Learning**

We did not consider learning by the pests or the managers. Management conditions (i.e., culling intensity, strength of the immigration barrier or spatio-temporal culling patterns) were fixed for the entirety of the simulation. Capture rates of pigs did not change due to capture of group members.

**2.4.6. Prediction**

We assumed that pigs did not have any mechanisms for predicting future conditions (i.e., no density-dependent reproduction).

**2.4.7. Sensing**

Individual pigs were able to sense and respond to social group dynamics and density on the landscape.

**2.4.8. Interaction**

Explicit interactions between pigs or between pigs and managers did not occur in our model. We assumed managers could find and capture all pigs they set out to remove in a given week, which

is a simplification because capture success can vary with density in reality (Choquenot et al., 1999). We also assumed that conception of females occurred regardless of the location or presence of males.

#### 2.4.9. Stochasticity

Longevity, dispersal age, dispersal distance and litter size were random variables. Individuals chosen to conceive and the order at which conception was implemented was also modelled randomly. In terms of management, the number of individuals to be culled weekly during the year was a random sequence which depended on the culling period and total individuals to be culled during the year.

#### 2.4.10. Collectives

Pigs were born into family groups and remained within them until natal dispersal (Gabor et al., 1999).

#### 2.4.11. Observation

Weekly abundance in the target zone and the number of pigs culled per week were stored for analyses.

### 2.5. Initialization

We initialized the landscape with pigs equal to the carrying capacity of each cell. We chose ages and longevity at random from the distribution of longevity. We assigned sex at random in a 1:1 ratio. Based on current age, we set natal dispersal status to complete or not complete. We initialized group structure by grouping all individuals that were younger than the dispersal age at random with females that were older than the dispersal age. The algorithm ensured that no groups were beyond the maximum group size (Table 2) and that each group had at least one reproductive age female. Unique group and grid cell IDs were assigned at random to each family group and male older than dispersal age. Home range centroids for each group or male were chosen at random within their respective unique grid cells. Reproductive status was set based on current age. After initialization, the population was allowed to undergo demographic dynamics (as in the main model) for 10 years. This process was repeated 50 times on each of the two landscapes. The endpoint population for each of the 50 runs was stored and used as the initial conditions for each replicate (1–50) in the formal analysis. We chose 50 replicates because it was sufficient to produce unbiased estimates of the mean with relatively low uncertainty (e.g., for  $N_0 = 500$  and no culling, the abundance after 4 years was  $1947.8 \pm 20.7$  with 50 replicates,  $1949.0 \pm 14.0$  with 100 replicates, and  $1948.0 \pm 4.6$  with 1000 replicates).

### 2.6. Input data

Inputs were longevity distribution, weekly conception probability, litter size distribution, sex ratio of litters, age at reproductive maturity for females, minimum time between farrowing and conception, gestation time, distribution of age of natal dispersal, distribution of dispersal distances, and maximum group size for family groups (Table 2).

### 2.7. Submodels

#### 2.7.1. Natural mortality

Natural mortality was chosen from a random distribution (Table 2) at birth. Once the age of longevity was reached, the individual was permanently removed from the population. It was possible for the individual to be removed earlier due to culling or density-dependent mortality.

#### 2.7.2. Culling

The culling process was governed by three features: intensity (how many pigs were culled per year), temporal strategy (the timing of culling during the year), and spatial strategy (the plan for how pigs were removed in space). Intensity was implemented as a constant proportion per year. Although this is not the most common strategy for implementing culling (due to its reliance on monitoring abundance and hence requirement for additional resources) we used this strategy because it allowed us to examine the effects of culling intensity similarly across other aspects of management (i.e., spatial strategy, temporal strategy, immigration barrier). We examined the full range of culling intensity (10%–90%) to understand if optimal culling strategies could change based on culling intensity. At the start of each year, the total number to be culled during the year was determined based on the current abundance and the annual culling intensity ( $N$  on Jan.1st  $\times$  proportion). Instead of removing all of the annual target number of individuals during a single week, we allowed culling to occur throughout the year by generating random sequences of the weekly number culled (where each week was a number between zero and an arbitrary upper weekly limit). This randomization weekly culling added stochasticity to the culling process and realism in how management, which is often persistent, consistent trapping, would be conducted. Time frames of temporal culling strategy were designed to overlap different patterns of population density as determined by birth seasonality (Fig. 1). Our goal was to examine the effects of limiting culling to specific times relative to birth seasonality. Lastly, we examined three spatial strategies of culling (Table 1): random with respect to group ID and space (random), targeting individuals in proximity to each other in high density patches (group-based), and wave-like where culling began on the east side and continued west while prioritizing reinvasions on the east side of the wave (zonation). The random strategy is unlikely to be used in practice (except if recreational hunting is the main control strategy) and served mainly as a null model – although in some instances aerial gunning could have a random-like characteristic (random points but also culling related individuals at those points). The group-based method is similar to how trapping is typically conducted: traps are placed in areas where pigs are believed to be most abundant and it is common to use corral traps to target all individuals in a family group. We examined zoning because we hypothesized that removal of all individuals in sections of the target zone would be most efficient (Parkes et al., 2010) due to reproductive feedbacks on overall population growth.

#### 2.7.3. Density-dependent mortality

To limit populations from reaching unrealistic densities, we implemented an additional source of population regulation. Both density-dependent mortality (Okarma et al., 1995; Keuling et al., 2013) and reproduction (Baber and Coblenz, 1988; Gethoffer et al., 2007; Orłowska et al., 2012) may occur in wild pigs. We included only density-dependent mortality as follows: when grid cells reached carrying capacity (determined by the landscape structure,  $SI_2$  – Fig. S1), groups or individual males were chosen at random to die due to density-related causes (because pigs exist and forage in groups). This mechanism simplifies reality because typically density-dependent mortality would occur over time (Okarma et al., 1995).

#### 2.7.4. Dispersal

Our model included three mechanisms for movement: natal dispersal, relocation due to overcrowded family groups, and relocation of solitary females to join a family group (Fig. 1). Natal dispersal occurred at dispersal age (a random variable; Table 2, Fig. 1). Relocation due to overcrowded family groups occurred when groups were larger than the maximum group size (Table 2) by removing

**Table 2**  
Description of demographic parameters for wild pig populations.

Parameter	Values	Refs.
Longevity (time before natural death occurs)	A random variable from an exponential distribution with a mean of 1.8 years.	Diong (1982), Henry (1978), Hanson (2006), Mayer and Brisbin (2009) (Table 6; pg 173)
Weekly conception probability (seasonally varying; two different patterns)	Fig. 1 (bottom, right); these values for birth seasonality were shifted by ~4 months (the gestation period); weekly probability of conceiving = monthly proportion that conceive (values in Figs. 1)/4 weeks per month. These values were then multiplied by a scaling factor (0.6–Czech Rep. or 0.65 – USA) to generate population dynamics (Fig. S1 in SI2 File) similar to observed data ( $\lambda = 1.30$ (pulse) and 1.36 (continuous)).	Mayer and Brisbin (2009) (Fig. 1 pg 67), Ježek et al. (2011), Timmons et al. (2012), Mellish et al. (2014)
Litter size (number of viable offspring per litter)	A random variable from a truncated Poisson distribution with a mean of 6 pigs per litter; truncated at 3 and 10 pigs.	Baber and Coblentz (1986), Belden and Frankenberger (1990), Saunders (1993), Gethoffer et al. (2007), Ditchkoff et al. (2012)
Sex ratio (in litters)	1:1	Wood and Brenneman (1977), Lombardini et al. (2014)
Age at reproductive maturity (minimum age of conception)	24 weeks	Wood and Brenneman (1977), Johnson et al. (1982)
Minimum time between birthing and conception	12 weeks	Barrett (1978)
Gestation time	16 weeks	Henry (1968)
Age at natal dispersal	A random variable from a truncated Poisson distribution with a mean of 15 months; truncated at 8 and 18 months.	Podgórski et al. (2014b)
Dispersal distance	A random variable from a Weibull distribution with scale and shape parameters of 2.5 and 0.5.	Keuling et al. (2010), Podgórski et al. (2014b)
Maximum group size (carrying capacity for groups; at carrying capacity some females will disperse and form new groups)	20 wild pigs	expert opinion (note this is an upper maximum, not a mean)

half of the group to form a new unique group with a new location (while ensuring that at least one reproductive-age female was in each group). Relocation of solitary females occurred by joining the female to the nearest family group that was below maximum group capacity. The algorithm for all types of movement was the same. Movement to grid cells at carrying capacity was not allowed. When all grid cells within the movement radius were at carrying capacity, movement to a farther location occurred, which sometimes resulted in movement off the grid (emigration from the target zone). The movement algorithm proceeded as follows: 1) for each 45° angle from the home range centroid, a new possible set of [x,y] coordinates was obtained by choosing a movement distance at random (Table 2) and calculating the potential new coordinates (i.e.  $x = \text{distance} \times \cos(\text{angle}) + \text{current } x \text{ coordinate}$ ,  $y = \text{distance} \times \sin(\text{angle}) + \text{current } y \text{ coordinate}$ ). If at least one of the potential locations were valid (i.e., in a grid cell with fewer pigs than the carrying capacity or a location off the grid), then a valid potential location was chosen at random and pig(s) were moved there. Pigs that traveled off the grid were deleted from the population matrix. If there were no valid locations, the distance value was doubled and the process repeated until a valid location was obtained (thus the realized movement distance distribution did not always match the input distribution).

### 2.7.5. Immigration barrier

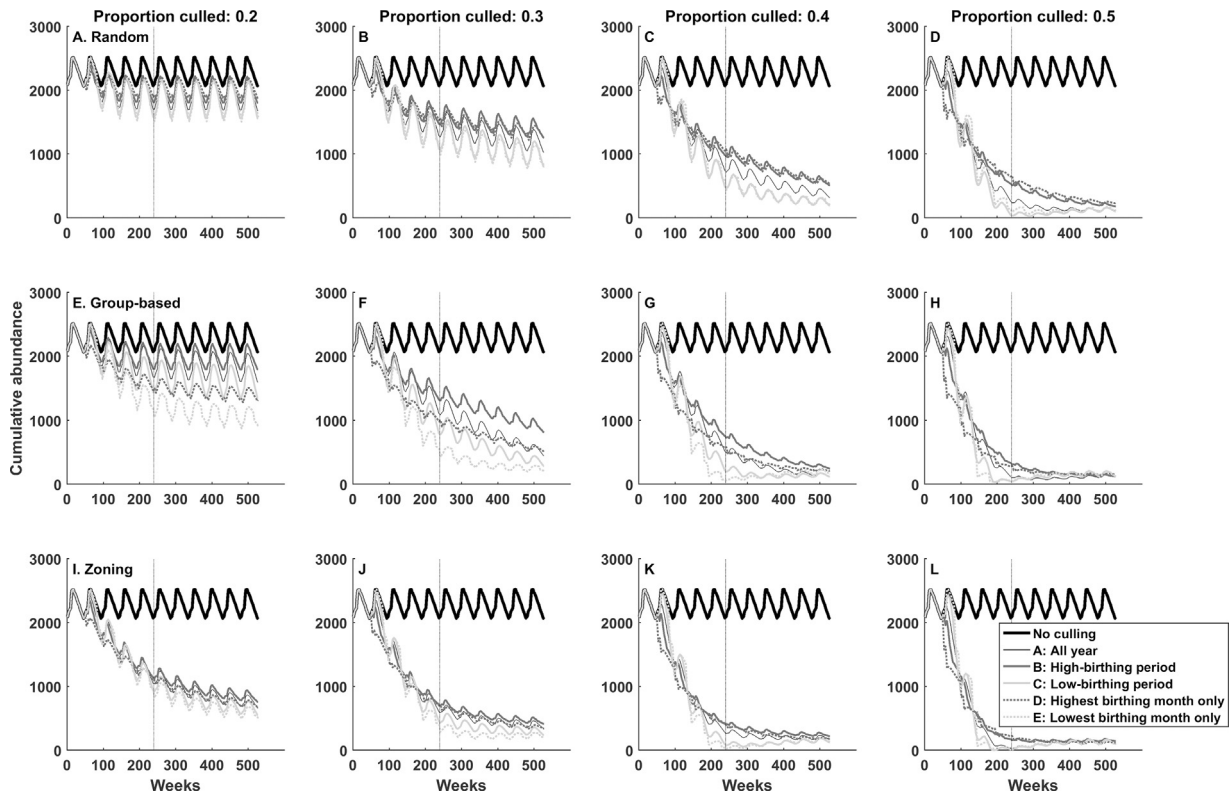
Immigration from the surrounding population to the target (managed) area occurred through natal dispersal or other relocation events as described above. Thus, immigration rates into the target zone decreased when the population was near capacity because space was limited. To implement an immigration barrier, we assigned candidate immigrants a uniform random number and only allowed immigration if their number was greater than the barrier strength. For unsuccessful attempts, we assumed that these individuals relocated off the landscape and were permanently removed from population.

### 2.7.6. Conception and births

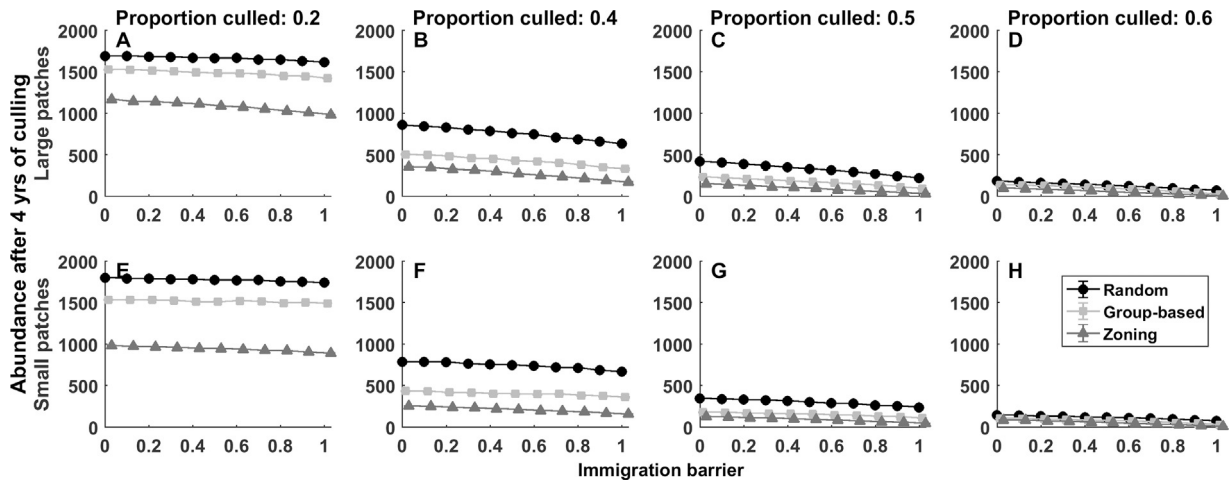
The conception probability varied monthly according to data-based birth seasonality in the USA (continuous) and Czech Republic (pulse) (Fig. 1, Table 2, Mayer and Brisbin, 2009; Ježek et al., 2011). We shifted the monthly birth patterns (Fig. 1, Table 2) back in time by 4 months to allow for the gestation period prior to birth, and then divided monthly conception probabilities by 4 to approximate weekly conception probabilities which were each repeated 4 times to generate the annual vector of weekly conception probabilities. The annual vector was then multiplied by a scaling factor (0.6–pulse or 0.65 – continuous) to generate population dynamics similar to observed data for populations below carrying capacity ( $\lambda = 1.30$ ; Timmons et al., 2012, Mellish et al., 2014; Fig. S1 in SI2 File). At each time step, conception occurred randomly in females that were reproductively active (older than the minimum age at first conception, not gestating, and beyond the minimum time since last birth). Conception success was determined by choosing females with random numbers greater than the conception probability for the current week. For individuals that conceived successfully, a litter size was chosen at random (Table 2, Fig. 1), and clocks for gestation and post-natal time, and reproductive status, were updated accordingly. Once the gestation period (Table 2) was reached, the litter was added to the population. For the new individuals, the following assignments were made at birth: sex in 1:1 ratio, current age of 1, location and group ID the same as mother's, natal dispersal age chosen at random (Table 2), and longevity chosen at random (Table 2).

### 2.7.7. Simulations and analyses

For the simulations, we used a full factorial design of the factors being evaluated (Table 1), except we only ran one control (no culling treatment) per set of immigration barrier, landscape and birth pattern conditions which results in a total of 6644 parameter sets. For each parameter set, we ran 50 replicate simulations which each started with a different base population (as described above in 2.5 Initialization). Because the experimental design was very high dimensional, we subset the data to address specific questions of interest using generalized linear models (GLM; SI1 File). Briefly,



**Fig. 2.** Effects of temporal culling strategy on weekly abundance. Results for four different annual culling intensities are shown (range: 0.2–0.5–labeled across the top) for each spatial culling strategy (Random: top row, Group-based: middle row, Zoning: bottom row). Labels for the patterns of temporal culling strategy indicated in the legend correspond to those in Fig. 1 (upper right). Each line is the mean of simulations (50 replicates × 44 parameter sets differing in birth pattern, immigration barrier, and landscape structure conditions; N = 2200). We evaluated the statistical difference between management treatments by comparing the endpoint abundance on the landscape after 4 years of management (the earliest time populations decreased to near 0 under moderate culling intensity – 0.4) using a generalized linear model (effects described in Table S1 in S11 File).

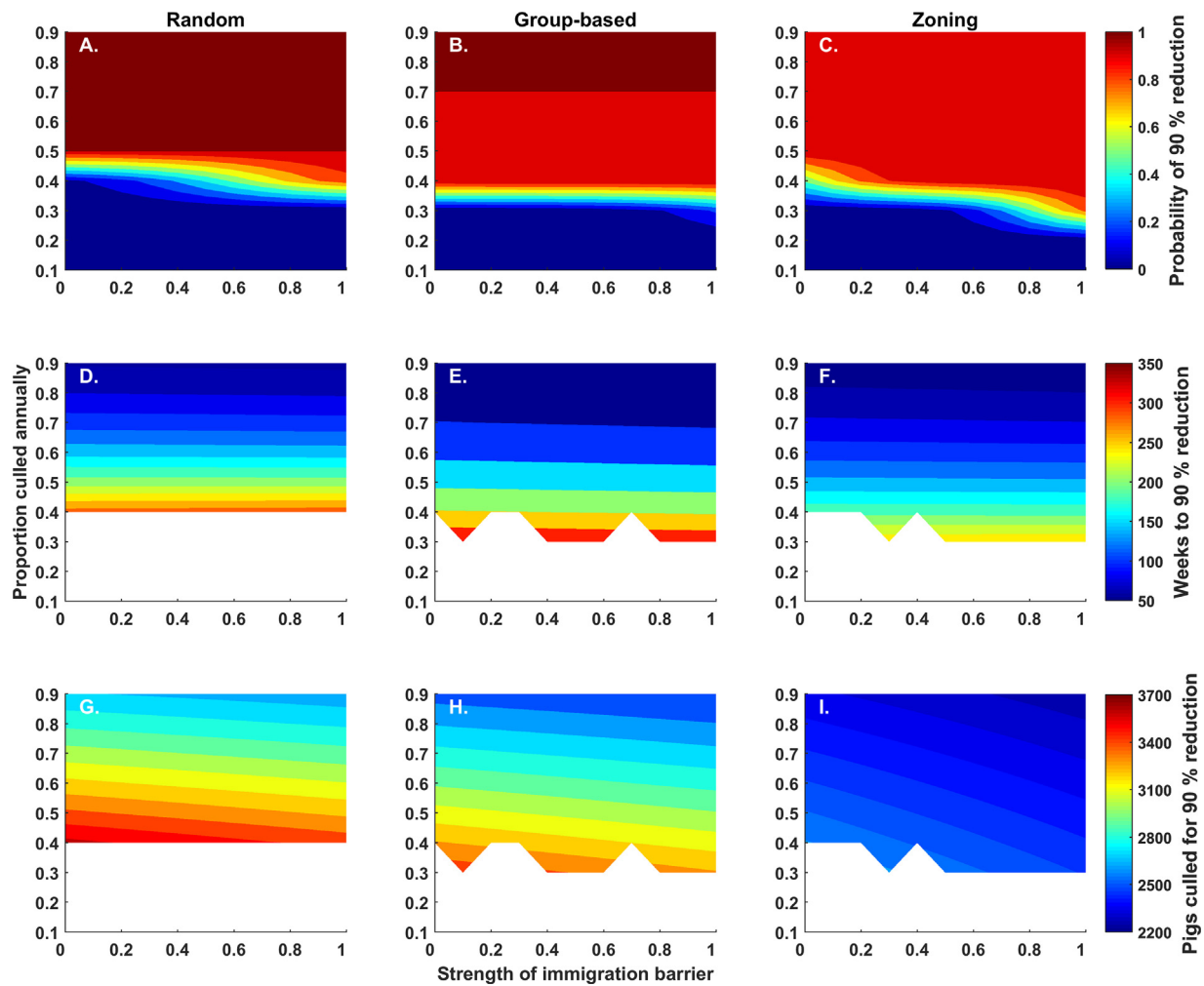


**Fig. 3.** Effects of patch size, immigration control and spatial culling strategy on population reduction. Results for four different annual culling intensities are shown (range: 0.2, 0.4, 0.5, and 0.6–labeled across the top) for two different landscapes: large patches (top), small patches (bottom) and each spatial culling strategy (lines within plots; Random: black circles, Group-based: light grey squares, Zoning: dark grey triangles). Each point is the mean endpoint abundance after 4 years of culling for simulation conditions shown on the X- and Y- axes as well as in the legend, while averaging over birth patterns and temporal strategies (50 replicates × 110 parameter sets differing in birth seasonality and temporal strategies; N = 5500). We evaluated the statistical difference between management treatments by comparing the endpoint abundance on the landscape after 4 years of management (the earliest time populations decreased to near 0 under moderate culling intensity – 0.4) using a generalized linear model (effects described in Table S2 in S11 File). Error bars are 95% confidence intervals of the mean (all smaller than the plot symbols and thus not visible).

we examined effects of parameters on four responses: 1) current abundance after 4 years of culling (Poisson GLM with log link, data in Figs. 2 and 3; we chose 4 years because this was the earliest time that treatments with moderate culling intensities reached near 0 abundance), 2) the proportion of simulations where the population

was reduced by at least 90% within 10 years (Binomial GLM with logit link, model predictions in Fig. 4A–C), 3) for populations that were reduced by at least 90%, the minimum number of weeks it took to reach 90%–reduction status (Negative binomial GLM with log link, model predictions in Fig. 4D–F), and 4) ‘Efficiency’: for pop-





**Fig. 4.** Combined effects of culling intensity (Y-axis) and immigration control (X-axis) on population reduction and efficiency. We fit generalized linear models to the simulation output (statistical design methods described in Tables S3–S5 in S11 File) and predicted corresponding responses (colors in the plots): predicted probability that the population ever reaches a 90% reduction relative to the initial abundance during 10 years of culling (A–C), for populations that reach a 90% reduction at some point, the earliest time it takes to reach 90% reduction status (D–F) and for populations that reach a 90% reduction at some point, the total number of pigs that were killed in order to first reach 90% reduction status (G–H). The first metric assesses efficacy while the second two assess effort and efficiency. Each column of plots shows results for a different spatial culling strategy (labeled across the top). Fixed factors were: temporal culling strategy pattern A, USA birth pattern and small-patch landscape.

ulations that were reduced by at least 90%, the total number of pigs culled to reach 90%-reduction status for the first time (Negative binomial GLM with log link, model predictions in Fig. 4G–I). To examine effects of temporal culling strategy, birth seasonality, and spatial culling strategy concurrently (data in Fig. 2), we ran separate models of abundance after 4 years of control for a range of culling intensities: 0.2–0.5. Each culling intensity model included the same three predictors and all their pairwise interactions, and left potential variation from landscape and immigration barrier unaccounted for. Similarly, to examine effects of landscape (factor), immigration barrier (continuous), and spatial culling strategy (factor) concurrently (data in Fig. 3), we ran separate models of abundance after 4 years of control for a range of culling intensities: 0.2 and 0.4–0.6. Each culling intensity model included the same three predictors and all their pairwise interactions, and left potential variation from temporal culling strategy and birth seasonality unaccounted for. For the last set of models (2–4 above), we were interested in the effects of spatial culling strategy (factor), culling intensity (continuous), immigration barrier (continuous), and all their pairwise interactions, while holding other factors constant at: landscape = small patches, birth pattern = USA, and temporal culling strategy = all year (i.e., a commonly used strategy).

### 3. Results

#### 3.1. Effects of temporal culling strategy

In general, temporal culling strategies that included the low-birthing period reduced populations significantly faster (Fig. 2, Table S1 in S11 File: coefficients are significantly more negative in effects where the temporal strategy included the low-birthing period – TempoC and TempoE), although the magnitude of the difference depended significantly on spatial strategy, culling intensity, and birth pattern (Fig. 2; Table S1 in S11 File: interactions of these factors are all highly significant at  $p < 0.0001$ ). When the culling intensity was high ( $\geq 0.5$ ), gains from temporal prioritization were weak (Fig. 2D,H,L, Table S1 in S11 File: size of coefficients for the interactions for spatial and temporal strategies are significant with  $p < 0.004$ , but the magnitude of difference between them is not as large in models where culling intensity = 0.5 compared with the models of lower culling intensity). Another interesting interaction is that when zoning was applied, the effects of temporal prioritization were generally weaker relative to a group-based strategy when culling intensity was  $< 0.4$ , stronger at 0.4, and then weaker again at 0.5 (Fig. 2I–L; Table S1 in S11 File: compare size of coefficients for the interactions of spatial and temporal strategies – all

are  $P < 0.0001$ ), indicating a complex interplay of culling intensity and spatial strategy on the magnitude of gain from temporal prioritization. For both birth patterns, when culling was limited to the low-birthing period (patterns C and E), abundances were generally lower relative to when culling occurred exclusively during the high-birthing periods (patterns B and D) across a range of culling intensities (Figs. S4–S8 in SI2 File, Table S1 in SI1 File). Also, prioritizing culling during the low-birthing period (patterns C and E) was generally more efficient in terms of requiring fewer pigs to be culled in order to reach a 90% population reduction (Fig. S9 in SI2 File).

### 3.2. Effects of spatial pattern, landscape and immigration control

Effects of immigration control on abundance after 4 years of culling increased significantly with higher culling intensity whereas immigration control contributed significantly less to population reduction at low culling intensity when abundances remained quite high (Fig. 3, Table S2 in SI1 File: for Barrier  $p < 0.0001$  and slope became more negative as culling intensity increases – compare barrier coefficients across the models of culling intensity). This was because populations with high culling intensities were reduced to very low abundances within 4 years, such that inputs from immigration began to make more substantial contributions to abundance (Fig. 3).

The effects of different spatial strategies on abundance after 4 years of culling were qualitatively similar across the two landscapes (Fig. 3). However, the slope of the relationship for strength of the immigration barrier was significantly steeper on the landscape with large patches relative to the one with small patches (Fig. 3, Table S2 in SI1 File: for SmallPatch  $\times$  Barrier  $p < 0.0001$ ). Thus, immigration control had slightly stronger effects in the landscape with large patches. Although, there was a significant interaction of spatial culling strategy and landscape (i.e., the group-based strategy did proportionately better relative to the random strategy on small relative to large landscapes; Table S2 in SI1 File: for SmallPatch  $\times$  group & SmallPatch  $\times$  zoning  $p < 0.0001$  at all culling intensities evaluated; Fig. 3), these differences were subtle compared with the overall consistent differences in spatial strategy across landscapes, which differed in magnitude of advantage based on culling intensity (Fig. 3). Under low culling intensity, zoning was significantly more effective than other strategies (Table S2 in SI1 File: coefficients for Barrier  $\times$  zoning are smaller than for other spatial strategies  $p < 0.0001$ ; Fig. 3). Under moderate culling intensity, both zoning and group-targeted culling were significantly more effective than random culling (Table S2 in SI1 File: for SmallPatch  $\times$  zoning & Barrier  $\times$  zoning  $p < 0.0001$ ; Fig. 3). At strong culling intensity, all three strategies produced more similar effects (Fig. 3; also reduction in  $R^2$  in models with high culling intensity suggests that spatial strategy is explaining much less variation in models with high relative to low culling intensity), although random culling was slightly significantly less effective across immigration control conditions than the other two strategies (Table S2 in SI1 File: coefficients for Barrier  $\times$  zoning and Barrier  $\times$  group are significantly negative at  $p < 0.0001$ ; Fig. 3). Considering all conditions, zoning was the most effective management strategy across all temporal culling strategies in that fewer pigs were on the landscape after the same number of years of culling (Fig. 3, Figs. S7, S8 & S10 in SI2 File), indicating that it could maintain lower levels of pest damage. Zoning also was the most efficient across all temporal culling strategies (Fig. S9 in SI2 File) in that fewer pigs needed to be removed to reduce the population by 90% (Fig. 4G–I).

### 3.3. Combined effects of culling intensity and immigration barrier

Culling intensity was the strongest driver of management effectiveness (Fig. 4A–C) as expected, although some significant interaction effects of immigration control and spatial strategy occurred (Table S3 in SI1 File: for all effects with Barrier, group or zoning,  $p \leq 0.0001$ ). Probability of reaching a target of 90% reduction was significantly more influenced by immigration control when zoning was used relative to other strategies (Fig. 4A–C: predictions from model in Table S3 in SI1 File; for all effects with zoning,  $p \leq 0.0001$ ), although this effect only occurred over a small range of culling intensities (0.2–0.5; compare slopes of the different bands in Fig. 4A–C). Zoning was significantly less effective at high culling intensities relative to low culling intensities (Fig. 4F, Table S4 in SI1 File: culling intensity  $\times$  zoning,  $p \leq 0.0001$ ). All considered, annual culling intensities of 40–50% were needed to have a high probability of reducing the population by 90% at some point over 10 years (Fig. 4A–C: predictions from model in Table S3 in SI1 File). With zoning and a 50% culling intensity, the minimum time to reach a 90% reduction was  $\sim 3$  years while it took 3–4 years with the other methods, indicating that zoning required less time investment relative to the other strategies (Fig. 4D–F, predictions from model in Table S4 in SI1 File) when culling intensities were moderate. As culling intensity increased, the time to reach a 90% reduction became more similar among the spatial strategies (Fig. 4D–F, predictions from model in Table S4 in SI1 File). Similarly, under a 50% culling intensity, zoning was substantially more efficient, requiring removal of  $< 2500$  pigs to reach target abundance while the other strategies required removal of 3000–3400 (i.e., 20–36% more pigs by other strategies relative to zoning; Fig. 4G–I; predictions from model in Table S5 in SI1 File), but this effect became weaker as culling intensity increased (Fig. 4G–I). Zoning was significantly more sensitive to immigration control due to its relatively higher efficiency (Fig. 4I, compare barrier  $\times$  zoning [ $p = 0.004$ ] to barrier  $\times$  group [ $p = 0.029$ ] in Table S5 in SI1 File) as compared with other strategies (Fig. 4G–H).

## 4. Discussion

Our simulations highlighted three important findings for improving the efficiency of control: 1) a spatial zoning strategy can immensely increase control efficiency relative to other spatial strategies, 2) our spatially-explicit population model predicted that lower culling rates are needed to control populations relative to a non-spatial logistic model, and 3) concentrating resources during the low-birthing period can significantly increase efficiency, although potential gains from temporal prioritization are much weaker than effects of spatial prioritization, and they depend on the spatial strategy as well as culling intensity. Below we discuss these findings in the order of significance of results.

### 4.1. Where to cull

The most striking difference in effectiveness emerged from comparing different spatial patterns. Zoning, where culling occurred in a wave-like pattern across the landscape while concurrently removing invaders at the back end of the wave, was dramatically more efficient than other strategies – especially at low to moderate culling intensities. At very high culling intensities ( $> 70\%$  annually) the population is likely reduced below the exponential growth phase such that population growth rate was decreased intrinsically, becoming less sensitive to population structure. At moderate to high culling intensities (40%), both zoning and prioritization of high-density patches and groups were better than random culling which is consistent with McMahon et al. (2010). For lower culling

intensities (<40% annually), zoning was the much more effective strategy compared with other methods. Under lower culling intensities, removal of individuals in multiple patches throughout the target area frees space for nearby individuals to move into (Sparklin et al., 2009) and populate – similar to source-sink dynamics (Pulliam 1988). At these lower culling intensities, the culling pressure is not strong enough to curb population growth for individuals or groups that move into free space. In contrast, with the zoning method, the space is protected and thus no longer available for the population to occupy. Thus, at lower culling intensities, it can be much less efficient to spread resources over a large spatial area (unless patches can be eliminated – which we didn't examine) rather than focusing on elimination and protection of available space. In relation to previous work on conservation planning (Margules and Pressey, 2000), our zoning approach essentially decreased landscape linkages, leaving fewer suitable patches for dispersal and population growth.

#### 4.2. How much to cull

A classic question for managing overabundant species is: “how much do I need to cull in order to reach my population target?” Harvesting theory predicts that in order to cause a population decline the harvesting rate should be equal to or higher than the maximum intrinsic rate of population growth (Fryxell et al., 2014). Based on the intrinsic rates of population increase generated by the two birth patterns at low abundance, we expected that culling intensities above  $r=0.23$  (pulse) or  $r=0.27$  (continuous) would lead to population declines in the absence of immigration (see 2.3.1 Overview by comparison to a logistic model for reasoning). Correspondingly, when culling intensity was 0.3 in our model and the spatial culling strategy was random, the population generally showed a declining trend, whereas the population was slightly reduced but remained stable at culling intensities of 0.2. However, this result did not hold true when zoning was used as the spatial culling strategy. With zoning, even when annual culling intensity was as low as 0.2, the population was dramatically reduced and continued to show a declining trend after 10 years of culling. Thus, our results highlight that the annual culling intensity needed to cause a substantial population decline can depend strongly on spatial strategy, and could be below that predicted by sustainable harvest theory when spatial structure of the population is accounted for. Additionally, it has been shown that environmental variation generally leads to lower intrinsic population growth than in conditions with more stable environmental conditions (Beddington and May, 1977). Thus variable environmental conditions is another factor that could lead to population decline at lower culling intensities. Because culling intensity is a strong determinant of management efficiency, using recent management data to frequently update abundance information (e.g., Davis et al., 2016), followed by actions based on the updated abundance values, will increase the likelihood of reaching a particular management goal over the long-term.

#### 4.3. When to cull

We investigated the effects of timing culling relative to species-specific reproduction dynamics and found the same result for two different trends in breeding seasonality. Culling was most efficient when it was focused during the low-birthing period, which supports sustainable harvest theory (e.g., Boyce et al., 1999; Kokko, 2001) and its application to reduction of invasive species populations (as in Grarock et al., 2014; Lieury et al., 2015), and broadens its relevance to birth patterns other than a single annual birth pulse. That is, culling mortality may have additive effects on total mortality (Lobdell et al., 1972) in species which reproduce throughout the year, by focusing culling during times when birth rates

are lower. In addition to not wasting resources on killing the doomed excess, focusing culling during the low-birthing period has the added advantage of culling a higher proportion of gestating females, before they contribute to population growth. However, our spatially-explicit model also highlighted important qualifications of the importance of temporal prioritization. Effects of temporal prioritization reduced dramatically at high culling intensities (>0.4) and when the spatial culling strategy was zoning, indicating that there may not be much gain in efficiency from temporal prioritization under these conditions because the population is so quickly reduced well below carrying capacity that there is no doomed excess.

For species with continuous birth patterns occurring in environments with constant seasonality (i.e., wet tropical areas), it is less obvious when low-birthing periods may exist. Previous work on best practice guidelines for rat eradication has suggested that environmental correlates of rat density could be used to predict low-density periods (Keitt et al., 2015). Although this method requires substantial historical data of the system, it could be a useful approach for other species with continuous births as long as appropriate lags due to gestation period are incorporated (i.e., environmental correlates of density are lagged), and supports the idea that basing management plans on accurate knowledge of low-density periods could improve efficiency of eradication programs. However, using seasonal changes in weather to predict low-density periods may only be applicable in climates where there are pronounced changes (e.g., temperate zones), as it has been found that rat eradications tend to be less successful in tropical areas where it is more difficult to target low-density periods (Holmes et al., 2015).

The fact that culling during the low-birthing period in Southeastern USA (Jun–Nov) is advantageous, does not compliment current wild pig management patterns, because trapping tends to be more successful during months where resources are more limited (Nov–Mar) and aerial gunning tends to be most successful when vegetation does not obscure sighting (also Nov–Mar). However, our model simplified density-dependent mortality and emigration by applying them instantaneously when abundance crept above carrying capacity. In reality, density-dependent mortality or emigration occurs over time suggesting that the actual months when culling is optimal could be later than the particular months we used. Nevertheless, the general guidance that control during lower abundance periods is optimal holds true even for populations which have less volatile dynamics (i.e., year-round births). This emphasizes the importance of monitoring abundance during population reduction programs (i.e., Chee and Wintle, 2010; Anderson et al., 2016) in order to plan optimal resource allocation, and that before abundance trajectories are available, allotting most resources to the perceived low-abundance time periods would be best.

Considering the effectiveness of pulse (short bursts) versus press (over a longer time period) strategies, pulsed culling appeared slightly more effective in the single, distinct birth pulse case whereas the opposite was true in the case with more continuous births. This makes sense because in the single birth-pulse situation, inputs only occurred once per year and thus culling at the low abundance time removes all the individuals that could contribute to standing abundance in the current year. In contrast, when births occur continuously throughout the year, there may be additional births after a culling pulse which could increase abundance and contribute to next birth pulse. Our finding supports a related idea from rat eradications on tropical islands (where low density periods are difficult to discern based on weather alone) that suggests timing between application of rodenticide baits should match the weaning period such that weaning rats are immediately exposed to poison baits upon nest emergence (Keitt et al., 2015).

In considering longer-term (across years) effects of culling patterns, we assumed that per-individual reproductive outputs

were constant. This is a simplification of reality as studies have shown annual variation in reproductive output (Santos et al., 2006; Holland et al., 2009) and seasonality (Santos et al., 2006; Canu et al., 2015) due to resource availability. Resource-based changes in per-individual reproductive output would introduce additional variation in reproductive output across years, which would increase the uncertainty in our quantitative predictions (Boyle and Hone, 2014) but should not affect the relative effects of different treatments. Similarly, we did not account for potential effects of density-dependent reproduction, which could decrease our predicted rates of population decline (i.e., efficiency; Melero et al., 2015).

#### 4.4. Caveats and considerations

As with all models, ours made several simplifying assumptions. For one, we assumed that the ability to capture a target number of individuals was unaffected by population density. In reality individuals become more difficult to locate and capture at low densities (Choquenot et al., 1999; Garcelon et al., 2005; McCann and Garcelon 2008), making it challenging to continually harvest fixed, high proportions of the population. We made this assumption in order to understand the behavior of our model from a theoretical standpoint. Also, because substantial changes in capture success only occur at low densities, the assumption of constant capture success should not affect the general behavior of our model, rather it would introduce uncertainty in culling effects only at low densities. Thus, while qualitative conclusions (i.e., comparison between culling strategies) are valid, our model should not be used to accurately predict expected time to elimination in the target zone in absolute terms (although model fitting with future data on abundance and removals could help bridge this gap).

Secondly, we assumed that each spatial strategy had the same capture success – i.e., the target number of individuals were captured at each event, regardless of the spatial strategy. The zoning strategy assumed that individuals reinvading the zone in the target area that had already been eliminated were prioritized along with individuals at the wavefront. In reality, it is possible that more effort must be expended in order to implement the zoning strategy relative to other spatial strategies because the reinvading individuals (which would be at low densities) could be more difficult to locate. Thus, although our zoning strategy was theoretically much more efficient than the other spatial strategies considering the population dynamics, it is unclear if the result holds true when financial and human logistics of a culling program are implemented. Nevertheless, because the ecological outcome is substantial, our results suggest that experimental examination of the cost-effectiveness of our proposed zoning strategy relative to other spatial strategies is warranted. This will require empirical studies that quantify capture probabilities and the associated levels of effort and costs, as a function of population density and spatial structure. Relationships of population density, damage and capture costs could then be incorporated into a decision-making framework that predicts the cost-effectiveness of situation-specific strategies. In addition, if the objective is minimizing damage, data on the relationship between population density and damage is critical for considering in cost-effectiveness estimation because the relationship of density and damage can be non-linear (Hone, 2012).

Thirdly, we simplified the process of density-dependent regulation by removing excess individuals (i.e., density-dependent mortality) from overpopulated grid cells immediately (i.e., once per week). Thus, density-dependent mortality was similar to density-dependent reproduction because it approximated the situation of individuals not being born, instead of allowing individuals to die of predation, starvation or disease over time once densities were too high (Okarma et al., 1995). However, there were two differ-

ences between our method and density-dependent reproduction. First, we implemented our method by choosing groups or individual males at random to die due to density-related causes (because pigs exist and forage in groups). In contrast, density-dependent reproduction would involve preventing younger individuals from being born while allowing older individuals to prosper despite high densities, such that at carrying capacity our density-regulation method could lead to more diverse age-structure relative to density-dependent reproduction. Also, in the presence of culling, our method would predict that higher culling intensities are needed relative to a model with density-dependent reproduction, in order to reach the same level of population control. Thus, our method is a conservative approach to our questions.

Although models are a simplification of reality, we considered several complexities that are not considered in a typical framework used for estimating sustainable harvest quotas, or, in our case, fixed-proportion quotas that would reduce abundance. Specifically, we modeled the spatial locations of individuals, individual-based variation in demographic processes, and non-random associations between individuals. Considering these complexities, we predicted culling intensities (i.e., fixed-proportion quotas) that were well below those predicted by a deterministic logistic model of population growth with the same intrinsic rate of increase as used in our model (data not shown). Because there is significant individual variation with regards to how pigs move and associate on landscapes in space and time (Podgórski et al., 2014a; Pepin et al., 2016; Kay et al., 2017), our results emphasize that these spatio-temporal complexities cannot be neglected in predicting culling the intensities needed to reach a particular management goal. More broadly, our results highlight that research aimed at improving our understanding of spatial ecology of overabundant pest species will be important for reducing uncertainty in management planning. Although our model included detailed spatial ecology, we did not link population dynamics to environmental changes which can be a significant determinant of fluctuations in abundance (Levy et al., 2016; Bieber and Ruf, 2005). In reality, carrying capacity of the environment would change, introducing additional uncertainty in the effects of different culling strategies. Again, these processes are unlikely to affect our results qualitatively (i.e., relative efficiency of different strategies), but would impact quantitative results (i.e., culling intensity needed to reach a particular management goal). Thus, in order to use our model for predicting culling intensities needed for a particular management goal, linking our dynamic spatial model to fluctuations in resource abundance will be important to consider.

## 5. Conclusion

As most wildlife management programs are underfunded and understaffed, allocation of limited resources is a consistent challenge and efficient strategies are needed to meet management goals. Our results suggest that under most culling intensities, using a wave-like spatial culling pattern requires removal of fewer pigs to reach a particular target abundance than targeting the entire target zone concurrently. In areas where the low-birthing period occurs in winter, culling during the low-birthing period may be additionally efficient (when culling intensity or spatial prioritization does not cause rapid population declines) because it overlaps the time when individuals tend to seek supplemental resources and thus capture rates are higher. However, if the low-birthing period occurs when food is abundant, it is possible that the efficiency gained from targeting populations during the low-birthing period could be reduced by lower capture rates. Thus, decisions on the most efficient time to cull should incorporate information on both resource abundance and birth dynamics. Similarly, from an ecological standpoint, using



zoning as a spatial strategy will be much more efficient, but this does not consider logistical costs associated with simultaneously targeting the high-density wavefront and reinvasers in low-density areas. Going forward, research to quantify effects of population density and environment on capture costs, in a framework that accounts for spatial ecology and spatial resource allocation, will be important for determining the most efficient spatial and temporal culling strategies in practice.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.ecolmodel.2017.10.005>.

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