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Modeling how to achieve localized areas of reduced white-tailed deer density

Amanda N. Van Buskirk [a,*], Christopher S. Rosenberry [b], Bret D. Wallingford [b], Emily Just Domoto [c], Marc E. McDill [d], Patrick J. Drohan [d], Duane R. Diefenbach [e]

[a] Pennsylvania Cooperative Fish and Wildlife Research Unit, Intercollege Graduate Degree Program in Ecology, The Pennsylvania State University, University Park, PA 16802, United States
[b] Pennsylvania Game Commission, Harrisburg, PA 17110, United States
[c] Pennsylvania Department of Conservation and Natural Resources, Bureau of Forestry, Harrisburg, PA 17105, United States
[d] Department of Ecosystem Science and Management, The Pennsylvania State University, University Park, PA 16802, United States
[e] U.S. Geological Survey, Pennsylvania Cooperative Fish and Wildlife Research Unit, The Pennsylvania State University, University Park, PA 16802, United States

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ABSTRACT

Localized management of white-tailed deer (*Odocoileus virginianus*) involves the removal of matriarchal family units with the intent to create areas of reduced deer density. However, application of this approach has not always been successful, possibly because of female dispersal and high deer densities. We developed a spatially explicit, agent-based model to investigate the intensity of deer removal required to locally reduce deer density depending on the surrounding deer density, dispersal behavior, and size and shape of the area of localized reduction. Application of this model is illustrated using the example of abundant deer populations in Pennsylvania, USA. Most scenarios required at least 5 years before substantial deer density reductions occurred. Our model indicated that a localized reduction was successful for scenarios in which the surrounding deer density was lowest (30 deer/mi^2), localized antlerless harvest rates were $\geq$ 30%, and the removal area was $\geq$ 5 mi^2 . When the size of the removal area was $<$ 5 mi^2, end population density was highly variable and, in some scenarios, exceeded the initial density. The shape of the area of localized reduction had less influence on the ability to reduce deer density than the size. There were no differences in mean deer density in the same size circle or square removal areas. Similarly, increasing the ratio of sides (length: width) in rectangular removal areas had little influence on the ability to locally reduce deer densities. Situations in which deer density was higher (40 or 50 deer/mi^2) required antlerless removal rates to exceed 30% and took more than 5 years to considerably reduce density in the localized area regardless of its size. These results indicate that the size of the removal area, surrounding deer density, and antlerless harvest rate are the most influential factors in locally reducing deer density. Therefore, localized management likely can be an effective strategy for lower density herds, especially in larger removal areas. For high density herds, the success of this strategy would depend most on the ability of resource managers to achieve consistently high antlerless harvest rates.

1. Introduction

In the eastern United States, white-tailed deer (*Odocoileus virginianus*) are considered a dominant species in forested landscapes (Diefenbach et al., 1997). Successful restoration of deer populations during the twentieth century resulted in an increase in abundance and the expansion of their distribution (Garrot et al., 1993). Today, abundant deer populations can have negative effects on plant communities via excessive browsing (Côté et al., 2004) and on human health through vehicle collisions, crop depletion, and disease spread (Côté et al., 2004; Nugent et al., 2011). Selective browsing by ungulates, particularly in forests, can lead to changes in the stand structure and compositional shifts of tree species (Miller et al., 2010; Simard et al., 2013). Consequently, some forest stands may experience reduced stocking rates, prolonged rotation lengths, and regeneration failure (Horsley et al., 2003; Marquis 1974). These forest changes also can induce changes in

* Corresponding author. University of Georgia, Warnell 3-511, Athens, GA 30602.
E-mail addresses: av94646@uga.edu (A.N. Van Buskirk), chrosenber@pa.gov (C.S. Rosenberry), bwallingfo@pa.gov (B.D. Wallingford), edomoto@pa.gov (E.J. Domoto), mem14@psu.edu (M.E. McDill), pjd7@psu.edu (P.J. Drohan), drd11@psu.edu (D.R. Diefenbach).

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associated animal communities (Nuttle et al., 2011). To help alleviate issues induced by abundant deer populations, management actions often involve reducing deer densities, and strategies to do so include culling (Kilpatrick et al., 1997; Nugent et al., 2011), fertility control (Merrill et al., 2006), predator reintroductions (Ripple and Beschta 2003), and most commonly, hunting (Heusmann 1999; Woolf and Roseberry 1998). In North America, regulated hunting has historically been used as a population management tool (Rutberg 1997), but management actions are typically applied at larger scales (hundreds of mi^2) because state agencies have difficulty collecting data at finer scales to assess deer abundance (Rosenberry and Diefenbach 2019). Consequently, management actions by wildlife agencies may not be effective for controlling locally abundant populations (Waller and Alverson 1997).

Research that has investigated the social structure of female (or antlerless) deer suggests that a targeted removal of female social groups has the potential to alleviate issues regarding locally abundant populations (McNulty et al., 1997; Porter et al., 1991). Female social groups are family units of primarily matriarchal females (older, presumably dominant females), female offspring, and siblings. The rose-petal hypothesis (Mathews 1989) suggests that deer populations expand as an array of family units composed of related females. Matriarchal females occupy a home range that is at the center of the family unit, with several generations of female offspring occupying home ranges that overlap. These overlapping home ranges expand in a form that is analogous to the petals of a rose. The rose-petal hypothesis depends on female deer in the target populations exhibiting low dispersal rates and high philopatry (Campbell et al., 2004). Localized management is a deer management strategy that aims to exploit the rose-petal hypothesis by targeting these social groups through the removal of female deer in specific geographical areas with the goal of creating areas of persistent reduced deer density (McNulty et al., 1997; Porter et al., 1991). For this approach to be applicable, particularly on small areas ($\leq$ 0.5 mi^2), the rose-petal hypothesis must be a suitable model of population social structure.

Porter et al. (1991) proposed that the minimum area needed for the application of localized management would be 1.5–8 mi^2. However, the minimum area estimate from their study is based solely on the home range size of female white-tailed deer and does not account for the surrounding deer density (i.e. deer density in a larger management unit consisting of the removal area and a buffer around it). In addition, the proposed minimum area size stems from the idea that the management action taking place is a targeted removal of female family units (through sharp-shooting or relocation) and does not consider hunting as a potential tool, despite being the most popular and common deer management method (Woolf and Roseberry 1998). Furthermore, evidence for successful localized management at the small-scale ($\leq$ 0.5 mi^2) and large-scale ($\geq$ 8 mi^2) is conflicting (Boyce and McDonald 1999; Kilpatrick et al., 2001; McDonald et al., 2007; McNulty et al., 1997; Miller et al., 2010; Oyer and Porter 2004; Simard et al., 2013). Documented successes often have low surrounding deer densities, high antlerless harvest rates, and population monitoring immediately following the deer removal for only a few years (Kilpatrick et al., 2001; McDonald et al., 2007; McNulty et al., 1997; Oyer and Porter 2004). However, evidence suggests that the success of localized management may depend on a variety of environmental, spatial, temporal, and biological factors that are often difficult to test empirically. There are currently no empirical tests of localized management that have evaluated what effect, if any, the shape of a removal area has on the ability to reduce deer density. This variable is important to consider because potential removal areas may be restricted in shape by landscape features (e.g. streams, roads) or other factors, such as boundaries for timber harvest sites or disease management areas.

Accordingly, in Pennsylvania, USA, deer populations are considered abundant statewide, and agencies such as the Pennsylvania Game Commission (PGC) have created numerous programs to manage deer across the state. One such program is the Deer Management Assistance Program (DMAP), which was developed to help landowners meet their land-use goals by providing hunters the opportunity to harvest additional antlerless deer on properties that participate in the program. The Pennsylvania Department of Conservation and Natural Resources, Bureau of Forestry (DCNR) implements DMAP in specific areas across approximately 3,500 mi^2 of state forest land according to numerous criteria (e.g. deer impact data) in order to meet deer management goals (Conserving Forests and Native Plants through Deer Management [INTERNET] 2019) . However, DMAP areas vary considerably in size ($<$ 4 to $>$ 39 mi^2), and logistical and financial constraints may limit the ability of managers to effectively monitor deer populations on these units. Therefore, it is difficult to determine if DMAP is achieving its intended goals and objectives. Due to the limitations that state wildlife agencies may face when evaluating deer management programs such as DMAP, model-based approaches are becoming increasingly popular for assessing new and existing management actions. Models serve as an important tool for wildlife management because they are generally low cost, pose less risk than field experiments, and allow managers to test different management strategies and assess each strategy's effectiveness as it pertains to objectives (McCarthy 2004). Several models have evaluated the effects of different harvest strategies on the ability to locally (Kilpatrick et al., 2004; McDonald et al., 2007; Weckel and Rockwell 2013) or regionally (Xie et al., 1999) reduce deer numbers. These models were able to simulate realistic deer populations for their respective study area(s), predict the factors that contribute to the success (or failure) of deer management actions, and were validated by comparing model output with empirical data. A similar model-based approach could be beneficial for deer populations in Pennsylvania, particularly those in DMAP areas, so that managers can evaluate the efficacy of their deer management programs.

Today, agent-based models (ABMs, also referred to as individual-based models) are also being used to help researchers model wildlife management problems. ABMs describe population dynamics by explicitly simulating the behavior of individuals in a population on the landscape, capturing local interactions, and integrating individual life history information (Grimm and Railsback, 2005; Wiens et al., 1993). These features allow population properties to emerge from the behavior and interactions of individuals (Grimm and Railsback, 2005; Semeniuk et al., 2012). An advantage of ABMs is that they can capture fine-scale spatial resolutions (e.g. at the scale of a single population, Grimm et al., 2006) that allow managers to use existing empirical data to test wildlife management scenarios (Salinas et al., 2015). In addition, ABMs are useful for modeling species whose population structure is influenced by social cues (e.g. white-tailed deer; Federico et al., 2013; Mathews, 1989; Watkins et al., 2015). ABMs have been used to model a variety of wildlife management and conservation problems for many species, such as the endangered huemul deer (*Hippocamelus bisulcus*; López-Alfaro et al., 2012), jaguars (*Panthera once*; Watkins et al., 2015), endangered tigers (*Panthera tigris*; Carter et al., 2015), wolves (*Canis lupus*; Chapron et al., 2016), red howler monkeys (*Alouatta seniculus*; Wiederholt et al., 2010), and feral hogs (*Sus scrofa*; Salinas et al., 2015). For deer and other ungulates, many spatially-explicit ABMs have focused on modeling the impacts of landscape heterogeneity on species movement (Tierney 2015; Turner et al., 1993), dispersal behavior (Stanke et al., 2018), or disease spread (Belsare et al., 2020; Kjær 2010).

We developed a spatially explicit, agent-based model to evaluate the influence of different harvest management strategies on the ability to reduce white-tailed deer densities in localized, forested areas in Pennsylvania, USA. We considered the surrounding deer density, intensity of antlerless harvest, and size and shape of the removal area as the parameters to vary in our model because we predicted they would have the greatest effect on white-tailed deer population dynamics. The size and shape of the removal area is of particular interest because deer density reductions often occur in specific geographical areas bounded by landscape features and the significance of these factors on deer numbers is not well understood (McNulty et al., 1997; Simard et al., 2013). To date, no spatially explicit ABMs have investigated the role of the size and

shape of a localized area on the ability to reduce deer density or the influence of the surrounding deer density and level of harvest on deer population dynamics. These effects may be important for localized management of white-tailed deer because the species exhibits behaviors such as male dispersal (Long et al., 2008), density-dependent female dispersal (Lutz et al., 2015), and density-dependent reproduction that could influence recolonization and reproductive rates of areas where a localized deer density reduction is desired. While our model focuses on localized reductions for white-tailed deer populations in forested landscapes in Pennsylvania, the approach is applicable to other areas where local species and environmental data are available to parameterize models.

2. Model description

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm et al., 2006), as updated by Grimm et al. (2020). The model was implemented using Netlogo, an agent-based modeling program (Center for Connected Learning and Computer-Based Modeling, Northwestern University, version 6.0.4, 1999).

2.1. Purpose

The purpose of the model is to predict changes in localized white-tailed deer density in response to hunting pressure, landscape deer density, and size and shape of localized removal areas. The framework is adapted for white-tailed deer populations in forested landscapes in Pennsylvania, USA.

2.2. Entities, state variables, and scales

Model entities are male and female adult deer, male and female juvenile deer, fawns, and patches. All state variables characterizing these entities are listed in Table 1. Each deer has a combination of seven state variables that include age, sex, location, reproduction, and dispersal. Deer are categorized into 3 age-classes: fawn (0 years), juvenile (1 year), and adult (2 – 10 years). We considered male juveniles and male adults to be "antlered" deer, and fawns, female juveniles, and female adults to be "antlerless deer". Patches have one state variable: *habitat,* which can take on a value of 1 to identify cells that make up the "removal area" or a value of 2 to identify cells that make up the "surrounding area". We defined the "removal area" to be a set of cells where antlerless deer harvest rates were greater, potentially resulting in reduced deer densities, and these areas could be one of three different shapes: circle, square, or rectangle. Circle and square removal areas could take on one of seven different sizes: 0.5, 1, 5, 10, 15, 20, or 25 mi^2. Rectangular removal areas could be 5, 10, or 20 mi^2, and at each size, we varied the ratio of sides (length: width) to be 1.3:1, 1.5:1, 2:1, 3:1, 4:1, 5:1 (in the 5 and 20 mi^2 areas), 6:1 (in the 10 mi^2 area) and 10:1 (in the 5 and 10 mi^2 areas). We defined the "surrounding area" be a set of cells that were not included in the removal area, where antlerless harvest rates kept the population size constant.

Simulations were carried out on a 2-dimensional grid of 77 × 77 cells representing a 11 mi × 11 mi forested landscape (121 mi^2). Each cell represented an area of 0.14 mi^2, and a 7 × 7 group of cells represented an area of one square mile. We used miles rather than kilometers as the measurement unit because that is the scale for which wildlife management agencies typically implement their management actions, and the results of this model need to be applicable those agencies (Belsare et al., 2020). The model has an annual time step, and it runs for a 20-year period, with the model output being exported every year.

2.3. Process overview and scheduling

At each time step (1 year), the following processes for deer occur in the given order (Fig. 1). Model entities are processed in a randomized order, and changes in state variables are updated immediately. The submodels implementing these processes are described in detail in Section 2.7 below.

Table. 1
Summary of state variables in model for male and female adult deer, male and female juvenile deer, and fawns.

Entity	Variable	Description	Possible values
male adult	age	age in years	2 – 10
	location	cell that individual is positioned	0 – max X, 0 – max Y
female adult	age	age in years	2 – 10
	location	cell that individual is positioned	0 – max X, 0 – max Y
	reproductive-status	indicates whether an individual reproduced	true/false
	births	number of offspring at a given time	0, 1, 2, 3
male juvenile	age	age in years	1
	location	cell that individual is positioned	0 – max X, 0 – max Y
	mom	mother's id number	identity of mother
	dispersal-status	indicates whether an individual dispersed	true/false
	dispersal-distance	distance traveled by an individual (miles)	0 – 26
female juvenile	age	age in years	1
	location	cell that individual is positioned	0 – max X, 0 – max Y
	mom	mother's id number	identity of mother
	reproductive-status	indicates whether an individual reproduced	true/false
	births	number of offspring at a given time	0, 1, 2
	dispersal-status	indicates whether an individual dispersed	true/false
	dispersal-distance	distance traveled by an individual (miles)	0 – 33
fawn	age	age in years	0
	location	cell that individual is positioned	0 – max X, 0 – max Y
	mom	mother's id number	identity of mother
patch	habitat	Cell that is either part of the "removal area" or "surrounding area"	1 = removal area 2 = surrounding area

2.3.1. Age and growth

All individuals update their state variable *age* by one year. Juveniles and fawns simultaneously advance to the next age-class.

2.3.2. Dispersal

Male and female juveniles disperse. Female dispersal rates and distances are density-dependent while male dispersal rates and distances are density-independent.

2.3.3. Reproduction

Adult females reproduce according to density-dependent reproduction while juvenile females reproduce according to density-independent reproduction.

2.3.4. Mortality

Independent individuals of all age-classes (fawn, juvenile, adult) are subject to two types of mortality: natural and harvest. Natural mortality

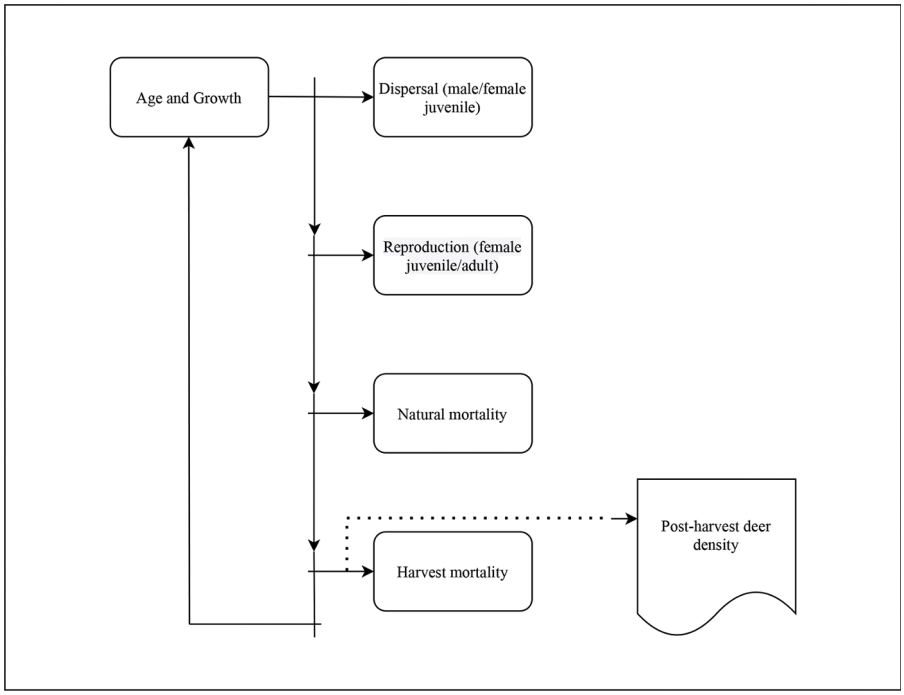

Fig. 1. Flow diagram of operational rules for each deer agent, iterated at each time-step.

occurs according to the annual survival rate of the model and the age of the individual. Harvest mortality occurs according to sex and age specific harvest rates as well as the location of the individual on the landscape.

2.4. Design concepts

2.4.1. Emergence

Population density in the removal area emerges from individual behavior (reproduction and dispersal) and mortality (natural and harvest). Behavior incorporates logical rules based on biological information from deer populations in Pennsylvania, USA and mortality is dictated by probabilities.

2.4.2. Adaptation

Male and female juveniles make the decision to disperse from their initial location to a new, unoccupied cell on the landscape. The model includes dynamic feedback on the reproduction and female juvenile dispersal parameters. These values are density-dependent and can change over time according to an individual's location on the landscape.

2.4.3. Sensing

A fawn that is born can sense the identity of its mother, and will inherit its mother's location. Although each cell on the landscape can have multiple agents, individual deer exist independent of one another, and individuals cannot distinguish between the surrounding area and removal area. However, individuals that experience density-dependent behavior can sense the number of individuals in either the surrounding area or removal area depending on their position on the grid.

2.4.4. Stochasticity

We incorporated stochastic processes into reproduction, dispersal, and mortality. Reproduction and female juvenile dispersal are density dependent. For all other stochastic processes, the model generates a random floating-point number between 0 and 1, and the action occurs if the number is less than the probability of occurrence for each process. See Section 2.7 for details. We did not include environmental stochasticity in the model; therefore, the landscape remains constant for the simulation period (20 years).

2.4.5. Observation

At the end of each time step, we observe population-level processes. These include the total number of deer harvested in the removal area, the number of antlered and antlerless deer harvested in the removal area, the total number of deer and post-harvest population density in the removal area, and the number of antlered and antlerless deer in the removal area. The model also has two graphical displays: one plots the abundance of deer in each patch type versus time, and the other plots a frequency distribution of deer in all sex-age classes.

2.5. Initialization

The model is initialized with a landscape that contains a certain size and shape of the removal area. Model deer population for the landscape is initialized using a specific population density (30, 40, or 50 deer/mi^2), sex-age composition (fawns: male juveniles: female juveniles: male adults: female adults), antlerless harvest rate in the surrounding area, and antlerless harvest rate in the removal area. Each agent (deer) is placed in a randomly selected cell (without replacement) within the surrounding area or removal area. We evaluated 30 deer/mi^2 because it emulates current deer density estimates in Pennsylvania that were obtained using a sex-age-kill model (Norton et al., 2013). We evaluated 40 and 50 deer/mi^2 to explore the effects of implementing different localized management strategies on high density populations. We created the model's initial deer population from a baseline model that was developed in Netlogo (version 6.0.4) without any removal areas (see Appendix A for details). The 30, 40, and 50 deer/mi^2 densities in the baseline model were run to determine the antlerless harvest rates that would stabilize the population at each density (Table S1) and the resulting sex-age composition of the stable population (Fig. 2, Table S2), which was then used to initialize all simulations.

2.6. Input data

The model does not use input data to represent time-varying processes.

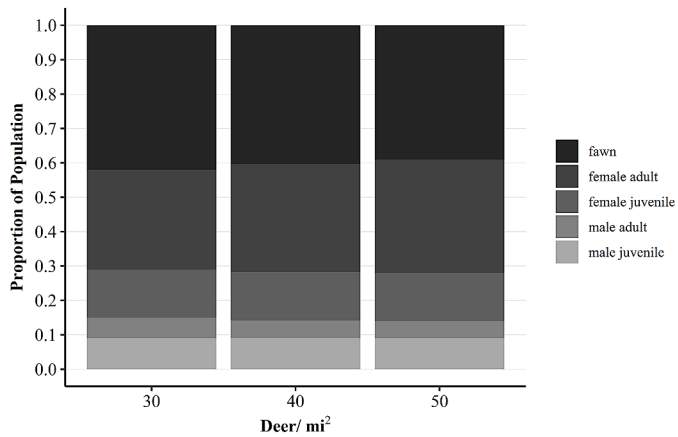

Fig. 2. Sex-age composition of simulated deer population.

2.7. Submodels

All model parameters are listed in Table 2. Details on the initial deer population sex-age composition and the antlerless harvest rates in the surrounding area at each deer density (30, 40, and 50 deer/mi^2) can be found in Appendix A. All other population parameters were derived from peer-reviewed literature, harvest data collected by the Pennsylvania Game Commission, or are based on expert opinion.

2.7.1. Age and growth

At the beginning of each time step, individuals update their state variable *age* (age in years) by one year. Juvenile deer grow to become adults, and fawns grow to become juveniles. Fawns have a 0.50 chance of being male and a 0.50 chance of being female, which reflects the 1:1 sex ratio of fawns at birth (Ditchkoff 2011).

2.7.2. Dispersal

Male and female juveniles have the potential to disperse from their initial location to a new location on the landscape. We modeled dispersal rates and distances for these individuals. Dispersal rate refers to the proportion of dispersing juveniles and is set using the parameters *male-juv-disp-rate* and *fem-juv-disp-rate*. Individuals who disperse travel a calculated distance in a random direction using the parameters *male-juv-disp-dist* and *fem-juv-disp-dist*. If a dispersing individual reaches a cell that contains one or more agents, it moves to the nearest unoccupied cell on the landscape. Dispersing juveniles can move from the surrounding area to the removal area and vice versa, or disperse to a cell within the patch type they originated in. Our model assumes that the number of individuals dispersing out of the model landscape is equal to the number of individuals dispersing into the model landscape (immigration = emigration). The model space is toroidal, so if a dispersing individual moves past the edge of the landscape, it will reappear on the opposite edge.

The dispersal rate for male juveniles is modeled as 0.75 (Long et al. 2015) and dispersal distance is modeled by randomly drawing from a log-normal distribution with $\mu = 8.2$ km and $\sigma = 7.6$ km (Diefenbach et al., 2008). The dispersal distance is then converted into miles, and the individual disperses the calculated distance in a random direction. Female juvenile dispersal rates and distances are modeled as density-dependent (Lutz et al., 2015). Deer density in both the surrounding area and removal area are first converted from deer per square mile to deer per square kilometer, then dispersal rate is modeled (Using a subset of the data presented in Lutz et al. (2015), which excludes data from two populations in Illinois due to the small proportion of forest and high dispersal rates) according to the equation

$$Dispersal\ \ rate = \frac{1}{1 + e^{2.345385 - 0.007345 \times D_{forest}}}$$

where D_{forest} is deer/km^2 of forest. Female juvenile dispersal distance is modeled according to the equation

Table. 2
Parameter information used in agent-based model of white-tailed deer populations in forested landscapes in Pennsylvania, USA.

Parameter	Description	Value	Reference
chance-survive	Annual survival	0.90	Wallingford et al., 2017
adult-repro-2	Mean number of fawns per 2-year-old adult female	1.32[d]	Pennsylvania Game Commission
		1.21[e]	
		1.10[f]	
adult-repro-3	Mean number of fawns per ≥ 3-year-old adult female	1.52[d]	Pennsylvania Game Commission
		1.39[e]	
		1.26[f]	
juv-repro	Mean number of fawns per juvenile female	0.18	Diefenbach et al., 2019
male-juv-disp-rate	Proportion of dispersing juvenile males	0.75	Diefenbach et al., 2008; Long et al., 2005
fem-juv-disp-rate	Proportion of dispersing juvenile females	0.09[d]	Lutz et al., 2015
		0.09[e]	
		0.10[f]	
male-juv-disp-dist	Dispersal distance for juvenile males (miles)	0 - 26	Diefenbach et al., 2008; Long et al., 2005
fem-juv-disp-dist	Dispersal distance for juvenile females (miles)	0 - 33	Lutz et al., 2015
s-ma-hunt	Harvest mortality for adult males in the surrounding area	0.59	Wallingford et al., 2017
s-mj-hunt	Harvest mortality for juvenile males in the surrounding area	0.50	Wallingford et al., 2017
s-ant-hunt	Harvest mortality for antlerless deer in the surrounding area	0.245[d]	Determined from baseline model (Table S1)
		0.225[e]	
		0.205[f]	
r-ma-hunt	Harvest mortality for adult males in the removal area	0.59	Wallingford et al., 2017
r-mj-hunt	Harvest mortality for juvenile males in the removal area	0.50	Wallingford et al., 2017
r-ant-hunt	Harvest mortality for antlerless deer in the removal area	0.26, 0.28, 0.30, 0.35, 0.40, 0.45, 0.50	Parameter varied in model

[d] Value for scenarios with 30 deer/mi^2 population density
[e] Value for scenarios with 40 deer/mi^2 population density
[f] Value for scenarios with 50 deer/mi^2 population density

$$Dispersal\ distance = a + (bc)$$

where $a = 18.703$ (SE = 3.710), $b = 0.02533$ (SE=0.857), and c = deer/km^2. The dispersal distance is then converted into miles, and the individual disperses the calculated distance in a random direction. After dispersal, an individual's state variable *dispersal-status* is updated to true, *dispersal-distance* is updated to the distance traveled (in miles), and *location* is updated to the cell where it lands.

2.7.3. Reproduction

All juvenile and adult females have the potential to get pregnant and produce offspring (fawns). The mean number of fawns per female for 2-year-old female adults is determined by the parameter *adult-repro-2*. The mean number of fawns per female for ≥ 3-year-old female adults is determined by the parameter *adult-repro-3*, and the mean number of fawns per female for female juveniles is determined by the parameter *juv-repro*. Reproduction is modeled as density-dependent among 2 and ≥ 3-year-old females according to the equation

$$R = \frac{R_{max}}{\left(1 + e^{(0.024\times(D_t - 58))}\right)}$$

where R_{max} is the maximum reproductive rate (2.0 fawns per female for 2-year-old females; 2.3 fawns per female for ≥ 3-year-old females) and D_t is deer/mi^2. The number of fawns per female is determined by randomly drawing from a Poisson distribution with $\lambda = R$. We modeled $R = 0.18$ fawns per female for juvenile females regardless of population density (Diefenbach et al., 2019). If the number of fawns per female drawn from the Poisson distribution for a given individual is zero, that individual does not produce any fawns that year. Female adults that reproduce can give birth to 1, 2, or 3 offspring and female juveniles that reproduce can give birth to 1 or 2 offspring. After giving birth, an individual's state variable *reproductive-status* is updated to true and its state variable *births* is updated to the number of fawns it produces. All new fawns have their state variable *mom* set to the id number of their mother.

2.7.4. Mortality

Mortality is divided into two groups: natural and harvest. Natural mortality is any non-hunting mortality for a deer (e.g. deer-vehicle collision, disease) and we chose to model annual survival, which is the complement of natural mortality, using the parameter *chance-survive*. The annual survival rate for all deer from the conclusion of one hunting season to the next is 0.90 (Wallingford et al., 2017). Male and female adults can also experience age-specific mortality, and adults will die if they reach the maximum age of 10 years old.

Harvest mortality differs according to the population density, the sex and age class of an individual, and the individual's position on the landscape. All individuals that survive non-hunting mortality are susceptible to harvest mortality. Harvest rates represent the probability of mortality for white-tailed deer from a hunting program. In all cases, harvest rates are 0.59 for male adults (determined by the parameters *s-ma-hunt* and *r-ma-hunt*) and 0.50 for male juveniles (determined by the parameters *s-mj-hunt* and *r-mj-hunt*, Wallingford et al., 2017). See Section 2.8.1 for further information. Female adults, female juveniles, and fawns are all considered "antlerless deer" and experience the same harvest rates. Antlerless deer in the surrounding area experience harvest rates of 0.245, 0.225, and 0.205 according to the parameter *s-ant-hunt*, which results in stable population densities of 30, 40, and 50 deer/mi^2, respectively (see Appendix A, Table S1) and these harvest rates remain constant over time. Antlerless deer in the removal area experience harvest rates of either 0.30, 0.35, 0.40, 0.45, or 0.50 for 30 deer/mi^2, 0.28, 0.30, 0.35, 0.40, 0.45, or 0.50 for 40 deer/mi^2, and 0.26, 0.30, 0.35, 0.40, 0.45, or 0.50 for 50 deer/mi^2 according to the parameter *r-ant-hunt* (Table 2). The addition of 0.28 for 40 deer/mi^2 and 0.26 for 50 deer/mi^2 allows the percent increase from each population density's stabilizing harvest rate (0.245, 0.225, 0.205) in the surrounding area to its lowest increased harvest rate (0.30, 0.28, 0.26) in the removal area to be proportional.

2.8. Parameterization and simulation experiments

2.8.1. Parameterization and calibration

Population parameters used to initialize the model deer population at each desired density (30, 40, 50 deer/mi^2) are available in Appendix A. All parameters used in our model simulations are derived from peer-review literature, based on expert opinions (Table 2) or are estimated using a baseline model (Appendix A) and are meant to simulate realistic deer behavior and dynamics of white-tailed deer populations in Pennsylvania, USA. See Appendix A for model calibration and validation of the initial model deer population.

The model's annual survival rate for all sex-age classes, male adult harvest rate, and male juvenile harvest rate were derived from data collected from radio-collared deer in two Pennsylvania counties after antler-point restrictions (APRs) were enforced in the state (Wallingford et al., 2017). Although Wallingford et al. (2017) estimated a male juvenile harvest rate of 0.31 (95% CI = 0.23–0.38) for two Pennsylvania counties, statewide harvest rates for male juveniles are highly variable across units where selective harvest criteria, such as APRs, are implemented. The intention of APRs in Pennsylvania is to protect ≥ 50% of male juveniles from harvest to increase the male age structure (Wallingford et al., 2017). We used a value of 0.50 for the male juvenile harvest rate in our model to reflect this regulation, and because this value allowed the model population to exhibit male: female ratios that were comparable to statewide male: female ratios (Norton et al., 2013, Appendix A).

Dispersal rates for male juveniles range between 0.46 and 0.80, but proximate causes of dispersal are still not well understood (Long et al., 2005). Based on expert opinion, we used a male juvenile dispersal rate of 0.75 for our model deer population. Female juvenile dispersal rates and dispersal distances were modeled as density-dependent, but on average, mean dispersal rate was 9% and mean dispersal distance was 12 miles (Lutz et al., 2015).

We modeled reproductive rates for female adults and female juveniles as the mean number of fawns per female according to harvest data collected by the Pennsylvania Game Commission from female deer in Pennsylvania from 1999 to 2006 (Diefenbach et al., 2019). There is evidence to suggest that reproductive rates for female adult deer are density-dependent, and we modeled this relationship for 2 and ≥ 3-year-old females (see reproduction submodel, Section 2.7.3). The average reproductive rates for these age-classes are comparable to the rates that were estimated for females after APRs were implemented in Pennsylvania (Diefenbach et al., 2019).

2.9. Sensitivity analysis

Density-dependent relationships in a deer population can greatly influence the population density in an area where a deer density reduction is desired. Particularly strong or weak density-dependent relationships can significantly bolster or hinder population growth, and may alter certain aspects of deer behavior, such as dispersal, which can be difficult to monitor. Predicting density-dependence relationships with certainty is notoriously challenging, therefore, we wanted to assess how sensitive our model outputs were to changes in the way these relationships are modeled. In particular, we measured the sensitivity of model derived end population density in the removal area to variation in four density-dependent relationships: a) 2-year-old adult female reproduction, b) ≥ 3-year-old adult female reproduction, c) female juvenile dispersal rate, d) and female juvenile dispersal distance. Sensitivity was calculated as the relative change of the output quantity. We initialized the model with one of the three desired densities (30, 40, or 50 deer/mi^2) and all parameter values listed in Table 2. The landscape included a

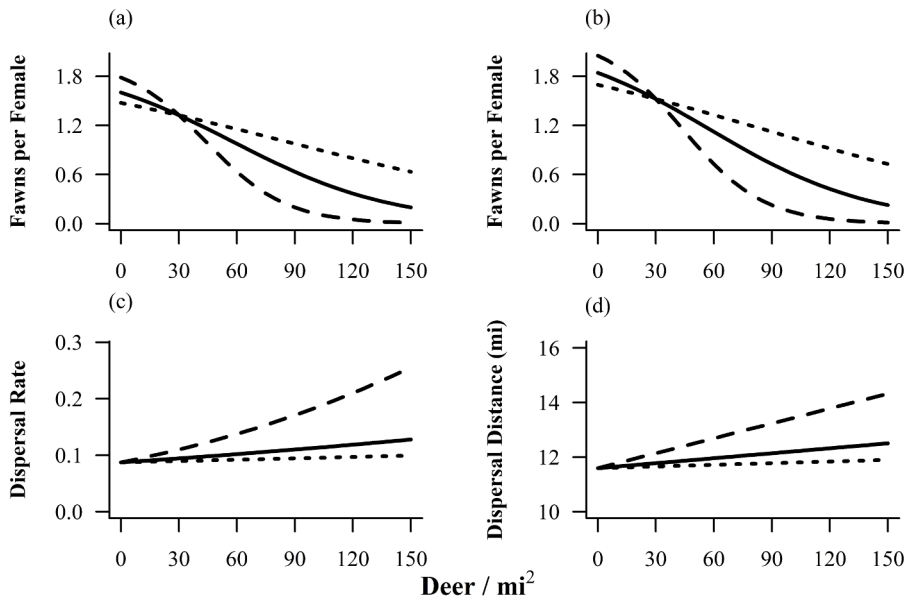

Fig. 3. Sensitivity analysis parameters for the four density-dependent relationships in the model: (a) 2-year-old adult female reproduction, (b) ≥ 3-year-old adult female reproduction, (c) female juvenile dispersal rate, (d) and female juvenile dispersal distance. Model sensitivity was assessed using the baseline relationship (solid line), a strong relationship (dashed line), and a weak relationship (dotted line).

20 mi^2 circular removal area.

The way in which we modeled the four density-dependent relationships in Sections 2.7.2 and 2.73 served as the baseline relationships for the sensitivity analysis. These relationships were either taken directly from peer-reviewed literature (female juvenile dispersal rate and distance, Lutz et al., 2015) or resulted in values that were comparable to estimates derived from peer-reviewed literature (female adult reproductive rates, Diefenbach et al., 2019). For each of the four density-dependent relationships, we tested a stronger and weaker relationship from the baseline (Fig. 3). We ran the baseline, strong, and weak relationships for a 20-year period over 100 repeated simulations and calculated the mean end population density in the 20th year.

2.10. Statistical analysis

The model was run using BehaviorSpace, a Netlogo tool that can run multiple model simulations by systematically varying parameters and recording the results of each model run. We ran each scenario, which included a specific size and shape of the removal area, landscape deer density, and antlerless harvest rate in the removal area for a 20-year period and 100 iterations. We compared mean end population density in the removal area among different scenarios using Unpaired Two-Samples Wilcoxon Tests ($\alpha = 0.05$) In Program R (R Core Team, 2020). Unless otherwise stated, mean end population density in the removal area was computed after the 20th year using the 100 model iterations. Because of the large number of scenarios evaluated, we assessed hundreds of comparisons of removal area shapes, removal area sizes, landscape deer densities, and antlerless harvest rates; therefore, we present only the largest difference in mean end population density for a given scenario.

3. Results

3.1. Sensitivity analysis

Deer population density in the removal area was most sensitive to fluctuations in ≥ 3-year-old density-dependent reproduction (Table S3), which is expected because female deer in these age classes make up a majority of the breeding population. In particular, a strong density-dependent relationship in ≥ 3-year-old reproduction increased end population density in the removal area by as much as 16%, while a weak density-dependent relationship decreased it by as much as 12%. For all other density-dependent relationships, sensitivity of end population density in the removal area was low, with strong and weak relationships resulting in changes of < 10% in the model output in most cases (Table S3).

3.2. Circle and square removal areas

3.2.1. Population changes

There were no differences between end population density among the same size circle and square removal areas (largest difference in mean end population density = 6.8 deer/mi^2). In addition, there were no differences between mean end population density among different size removal areas within the same shape (largest difference in mean end population density = 6.2 deer/mi^2). For each surrounding deer density (30, 40, and 50 deer/mi^2), populations in the removal area took, on average, 5 steps (years) to be reduced by 20% at their lowest antlerless harvest rate (Fig. 4). For all other antlerless harvest rates, populations in the removal area were reduced by 26% - 76% after 5 years (Fig. 5). For instance, a harvest rate of 0.35 with a surrounding density of 30 deer/mi^2 reduced the end population density after 5 years by 40% and a harvest rate of 0.50 reduced it by 74% (Fig. 5a). For 40 and 50 deer/mi^2, a harvest rate of 0.30 reduced the end population density after 5 years between 26% and 32% and a harvest rate of 0.50 reduced it between 70% and 76% (Fig. 5b and c).

The magnitude of change in end population densities in removal areas over time was largest for the 30 deer/mi^2 scenarios (Fig. 4). At the lowest antlerless harvest rate for each population density (0.30, 0.28, 0.26 for 30, 40, and 50 deer/mi^2, respectively), the largest decline in end population density in the removal area over the 20 year period occurred in the 30 deer/mi^2 scenarios and the smallest decline occurred in the 50 deer/mi^2 scenarios. Particularly, in the 30 deer/mi^2 scenarios, a 34% decrease in end population density occurred after 10 years and a 43% decrease occurred after 20 years (Table 3). The percent decrease in end population density was smaller for the 40 and 50 deer/mi^2 scenarios, with 29% and 25% decreases after 10 years and 38% and 32% decreases after 20 years, respectively (Table 3). The 40 and 50 deer/mi^2 scenarios

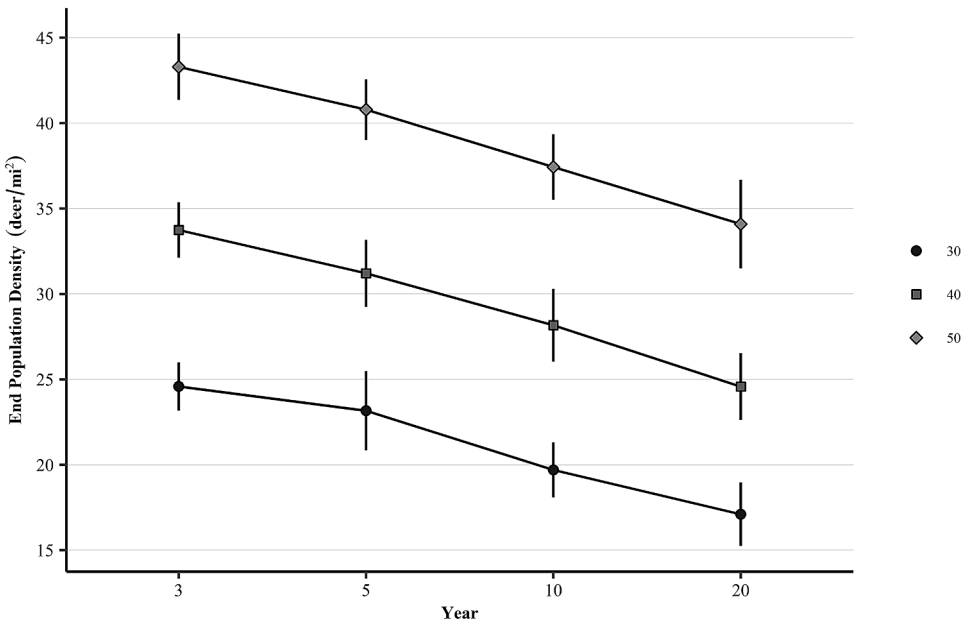

Fig. 4. End population density over multiple years starting with 30 deer/mi^2 and applying a harvest rate of 0.30 (circles), starting with 40 deer/mi^2 and applying a harvest rate of 0.28 (squares), and starting with 50 deer/mi^2 and applying a harvest rate of 0.26 (diamonds) in a 20 mi^2 circular removal area. Error bars are ± 1 s.d.

required harvest rates of ≥ 30% to obtain a similar percent decrease as the 30 deer/mi^2 scenarios at its lowest harvest rate (30%; Table 3).

3.2.2. Success rates

While there were individual simulations where ending deer densities in the removal area exceeded the starting density, in all scenarios, averaging across individual simulations within the scenario, average ending deer densities were lower than the starting density (Table 4). The range of end population densities among simulations was large in small (0.5 and 1 mi^2) removal areas, particularly at the lowest harvest rate for each surrounding density. There was less variability in end population densities among simulations in the medium (5 mi^2) and large (10, 15, 20, 25 mi^2) removal areas. For instance, for a scenario with 30 deer/mi^2 starting density, an antlerless harvest rate of 0.30, and a 0.5 mi^2 removal area, 29% of simulations resulted in higher end population densities than the starting density, while only 48% of simulations reduced the end population density by 20% after 5 years (Fig. 6). In contrast, ≤ 1% of simulations exceeded the starting density and ≥ 70% of simulations reduced the end population density by 20% after 5 years in scenarios with the same starting density and harvest parameters but where removal areas were medium (5 mi^2) or large (10, 15, 20, 25 mi^2; Fig. 6).

The variability in end population densities in each scenario remained relatively constant over time. For instance, in the 30 deer/mi^2 scenarios at antlerless harvest rates of < 0.35, and in the 40 and 50 deer/mi^2 scenarios at antlerless harvest rates of < 0.30, small removal areas (0.5 and 1 mi^2) had high variability in end population densities and these scenarios required higher antlerless harvest rates in order to reduce variability over the 20 year period. Medium and large removal areas (≥ 5 mi^2) had lower variability in end population densities after 5 years and maintained that small variability over the 20 year period, even at the lowest harvest rate for each surrounding density (0.30, 0.28, 0.26 for 30, 40, and 50 deer/mi^2, respectively). Regardless of the surrounding deer density or size of removal areas, antlerless harvest rates of ≥ 0.40 had the least variability in end population densities and the lowest harvest rate for each surrounding deer density had the greatest variability.

3.2.3. Rectangle removal areas

There were no differences in end population density among different size removal areas with the same ratio of sides (largest difference in mean end population density = 2.1 deer/mi^2), nor were there differences among different ratios of sides within removal areas of the same size (largest difference in mean end population density = 2.9 deer/mi^2). For all sizes of rectangular removal areas (5, 10, and 20 mi^2), and surrounding deer densities (30, 40, and 50 deer/mi^2), increasing the ratio of sides from 1.3:1 to 5:1 (in the 20 mi^2 area) and 1.3:1 to 10:1 (in the 5 and 10 mi^2 areas) did not change the average end population density in the removal area (Fig. 7). Similarly, the variability in end population density changed little as the ratio of sides of the removal area increased. However, variability decreased as the size of the removal area increased. In addition, there were no differences in end population density among rectangular removal areas with different ratios of sides compared to square removal areas of the same size (i.e. ratio of sides 1:1; Fig. 7). While there was a slight increase in the variability in end population densities for rectangular compared to square removal areas, this variation was minimal given the variation in length: width ratios.

4. Discussion

Hunting has historically been utilized as a population management tool, and managers often use hunters to reduce deer densities in specific geographical areas in order to meet land-use and human health objectives (e.g. promote forest regeneration, reduce deer-vehicle collisions). However, the decline of hunting license sales across the United States poses a challenge to deer management programs that rely on hunter harvest to manipulate deer populations. In addition, state wildlife agencies nationwide that have observed a decline in hunting license sales have simultaneously observed an increase in the number of antlered males harvested (U.S. Fish and Wildlife Service and U.S. Census Bureau, 2016). Research that has investigated the social structure of female deer suggests that localized management, a deer management strategy that focuses on the removal of related female family units, has the potential to reduce locally abundant populations (McNulty et al., 1997; Porter et al., 1991). Still, hunter preference for antlered males has led to considerably higher harvest rates for these individuals than for antlerless female deer (Wallingford et al., 2017). State agencies across the eastern United States have created programs to incentivize hunters to harvest antlerless deer (e.g. DMAP in Pennsylvania), but the effectiveness of such programs, and their impact on localized deer populations, remains poorly understood.

Our results indicate that the landscape deer density, localized ant-

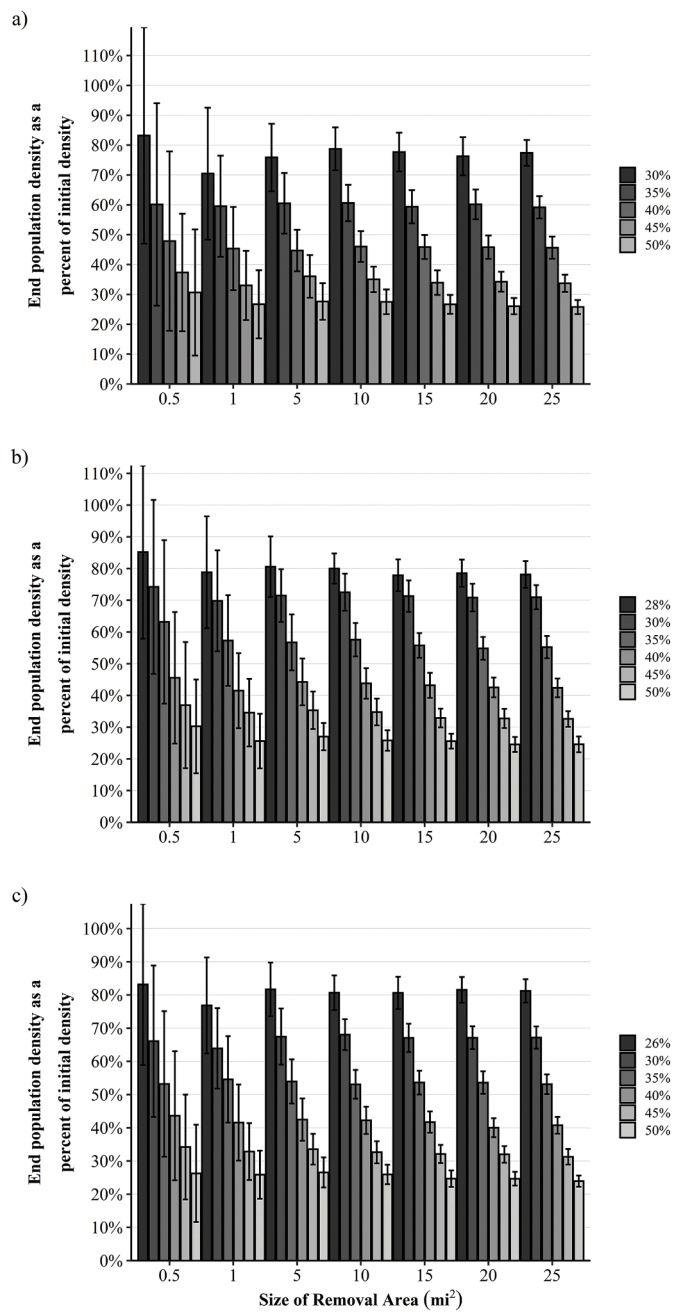

Fig. 5. End population density as a percent of initial population density in a circular removal area for (a) 30 deer/mi^2, (b) 40 deer/mi^2, (c) and 50 deer/mi^2 at various harvest rates after 5 years. Error bars show ± 1 s.d.

lerless harvest rate, and size of the removal area have the greatest influence on the ability to locally reduce deer density while the shape of the removal area (circle, square, or rectangle with different ratios of sides) has little influence. The application of a localized antlerless removal may therefore be an effective strategy for lower density herds (≤ 30 deer/mi^2) in larger areas (≥ 5 mi^2). For higher density herds, consistently high antlerless harvest rates may be needed to see substantial localized deer density reductions. In our model, all scenarios had, on average, a reduction in deer density in the removal area over the 20-year time period and a 20% reduction was obtained in 5 years. However, the magnitude of change over time was smaller for the higher density scenarios (40 and 50 deer/mi^2) than for the lower density scenario (30 deer/mi^2), particularly at the lowest harvest rate for each deer density (Table 3). Furthermore, the success of a localized deer density

Table. 3
End population density at various years, surrounding deer densities, and antlerless harvest rates in a 20 mi^2 circular removal area.

Year	Surrounding Deer Density (deer/mi^2)	Antlerless Harvest Rate	Mean End Population Density (deer/mi^2)	Standard Deviation	Percent Decrease (%)
3	30	0.30	24.6	1.40	18.0
5	30	0.30	23.2	2.32	22.7
10	30	0.30	19.7	1.61	34.3
20	30	0.30	17.1	1.85	43.0
3	40	0.28	34.1	1.61	14.8
5	40	0.28	31.5	1.95	21.3
10	40	0.28	28.2	2.13	29.5
20	40	0.28	24.6	1.95	38.5
3	40	0.30	32.0	1.56	20.0
5	40	0.30	28.4	1.93	29.0
10	40	0.30	23.6	2.06	41.0
20	40	0.30	19.9	1.72	50.3
3	50	0.26	43.3	1.95	13.4
5	50	0.26	40.8	1.77	18.4
10	50	0.26	37.4	1.93	25.2
20	50	0.26	34.1	2.58	31.8
3	50	0.30	37.3	1.66	25.4
5	50	0.30	33.2	1.59	33.6
10	50	0.30	27.4	1.98	45.2
20	50	0.30	22.5	1.85	55.0

reduction program may depend on the management objective, for example, if the objective is to reduce deer density below a certain threshold, the antlerless harvest rate and time required to reach that objective can vary greatly depending on the threshold value. For instance, Horsley et al. (2003) determined that the deer density threshold for negative impacts on forest vegetation under four experimental plots in northwestern Pennsylvania, USA was ~ 21 deer/mi^2. Using this value as a reference, our model shows that in order to reduce deer densities in 5 years at or below that threshold, antlerless harvest rates of ≥ 0.35 are needed in landscapes with deer densities of 30 deer/mi^2 (Fig. 5a), ≥ 0.40 in landscapes with deer densities of 40 deer/mi^2 (Fig. 5b), and ≥ 0.45 in landscapes with deer densities of 50 deer/mi^2 (Fig. 5c). It is important to note when interpreting these results that our model simulated a continuous removal effort, maintaining increased antlerless harvest rates in the removal area throughout the simulations while deer density in the surrounding area remained constant. If managers are unable to achieve consistent antlerless harvest rates, or if deer density surrounding a removal area changes substantially, the success of a localized deer density program may be impacted, and localized reductions may take longer to achieve than what our model predicted. Ultimately, to reduce deer densities in landscapes of higher deer densities (> 30 deer/mi^2) through hunting, our model suggests that managers will need to maintain antlerless harvest rates of ≥ 30% for > 5 years, which may be difficult as hunting license sales continue to decline.

To confirm our modeling exercise, we compare our results to a study conducted by McDonald et al. (2007), where controlled hunts occurred from 1991 to 2004 in 5 zones at Quabbin Reservation in central Massachusetts, USA. The hunted zones ranged in size from 7 to 19 mi^2, and initial estimated deer densities in each zone ranged from 29.7 to 71.8 deer/mi^2. The management goal, to achieve post-hunt deer densities of 10 deer/mi^2, was achieved after 2 - 4 years in each hunted zone, and hunters harvested 55–83% of antlerless deer annually. While it is likely that the high antlerless harvest rates in this study allowed the management goal to be achieved in such a short time frame, these harvest rates were able to be maintained for the entirety of the study, and as a result, the post- hunt deer densities were sustained at or below the management goal. In contrast, Simard et al. (2012) reduced deer densities within five 8 mi^2 areas on Anticosti Island (Québec, Canada) with initial deer densities ranging from 34 to 55 deer/mi^2 by removing 50% of antlerless deer in year 1 and 25% in years 2 - 5, but did not find

Table. 4
Range of end population densities after 5 years in scenarios with different removal area sizes, surrounding deer densities, and antlerless harvest rates.

			End Population Density (deer/mi^2)				
Size of Removal Area (mi^2)	Deer/mi^2	Antlerless Harvest Rate	Lowest	Highest	Range	Mean	Standard Deviation
0.5	30	0.30	2.34	53.67	51.33	25.0	10.87
1	30	0.30	9.24	38.35	29.11	21.1	6.61
5	30	0.30	14.59	33.09	18.50	22.8	3.38
10	30	0.30	17.85	27.86	10.02	23.6	2.16
15	30	0.30	17.79	27.08	9.29	23.3	1.95
20	30	0.30	17.07	27.34	10.28	22.9	1.90
25	30	0.30	19.33	25.86	6.53	23.2	1.93
0.5	40	0.28	9.34	58.32	48.99	34.1	10.93
1	40	0.28	16.34	52.55	36.21	31.5	7.05
5	40	0.28	23.75	41.39	17.64	32.2	3.82
10	40	0.28	26.64	36.37	9.73	32.0	1.90
15	40	0.28	26.35	35.64	9.29	31.1	2.00
20	40	0.28	26.98	35.25	8.27	31.4	1.72
25	40	0.28	27.06	35.95	8.90	31.2	1.69
0.5	50	0.26	16.34	74.66	58.32	41.6	12.15
1	50	0.26	22.01	57.52	35.51	38.4	7.23
5	50	0.26	29.40	50.73	21.33	40.8	4.03
10	50	0.26	33.66	46.59	12.93	40.3	2.60
15	50	0.26	33.51	47.37	13.87	40.3	2.42
20	50	0.26	35.20	45.03	9.83	40.8	1.93
25	50	0.26	35.82	43.91	8.09	40.6	1.74

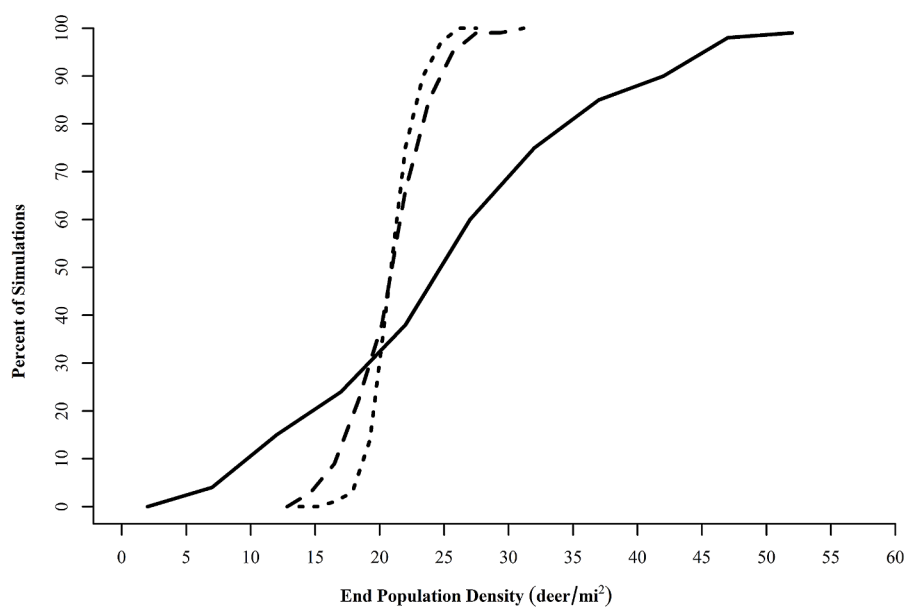

Fig. 6. Cumulative distribution of end population densities after 5 years for circular removal areas of 0.5 mi^2 (solid line), 5 mi^2 (dashed line), and 20 mi^2 (dotted line) at 30 deer/mi^2 surrounding density and an antlerless harvest rate of 0.30.

evidence of successful vegetative growth in experimental sites. Antlerless harvest rates in this study were reduced by half after one year, and our model would suggest that this decrease, coupled with the high initial deer densities, is likely what hindered the success of the localized deer density reduction.

Porter et al. (1991) proposed that the minimum area needed to apply a localized deer removal would be 1.5–8 mi^2. Our results show that the minimum size necessary to successfully reduce deer density is 5 mi^2 and that localized reductions are also successful in areas as large as 25 mi^2. In our model, smaller removal areas (0.5 and 1 mi^2) had, on average, low success ($\leq$ 50%) in reducing deer density over time and noticeably high variability in end population density among simulations, whereas larger removal areas ($\geq$ 5 mi^2) had higher success ($\geq$ 70%) and more consistent results across simulations (Fig. 6). These results demonstrate that hunting alone is unlikely to successfully reduce locally abundant populations on small areas but may be an effective strategy for populations on larger areas. The difficulty with using hunters to manage small, local deer populations is further exacerbated in landscapes with high deer densities. Although higher antlerless harvest rates in our model resulted in larger deer density reductions in small areas on average, they did little to reduce the variability among simulations compared to larger areas (Fig. 5). Localized management, through actions such as culling, has been suggested as an alternative to hunting for small, locally abundant deer populations based on the rose-petal hypothesis (Mathews 1989; Porter et al., 1991). Using this technique, McNulty et al. (1997) was able to successfully reduce deer densities in a small (0.5 mi^2) area in New York, USA, but the landscape was characterized by low initial deer densities (5–15 deer/mi^2), which may have contributed to the success. Similarly, Miller et al. (2010) performed high intensity culling by removing approximately 60% of females from a 0.5 mi^2 area in West Virginia, USA where deer herds averaged 30–50 deer/mi^2, but found that deer adjacent to the removal area shifted their home ranges and recolonized the removal area within 3 years. These results and the results from our model suggest that localized management may be an

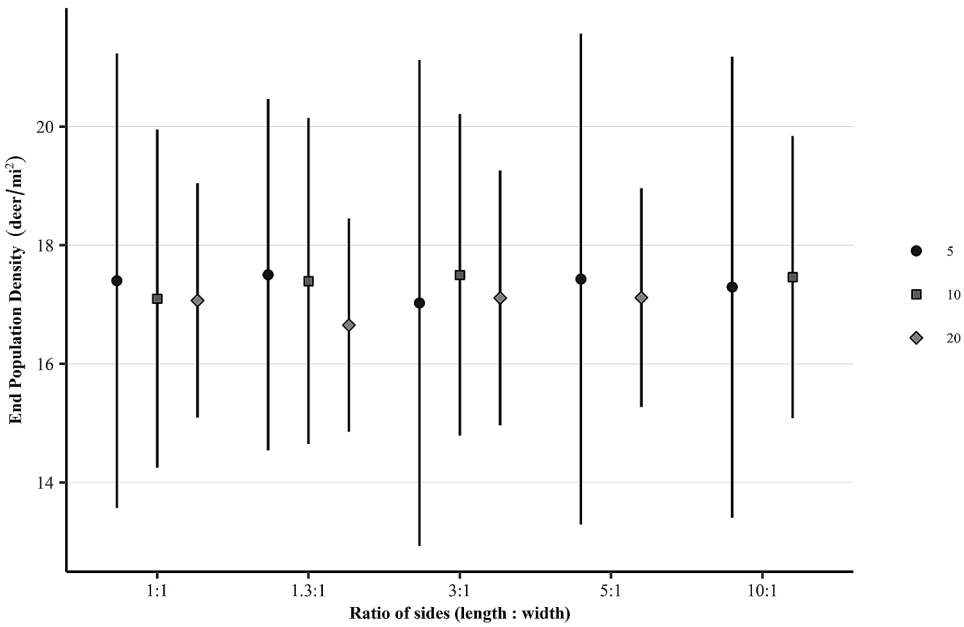

Fig. 7. End population density after 20 years in rectangular removal areas of different sizes (5 mi^2 (circle), 10 mi^2 (square), 20 mi^2 (diamond)), and various ratios of sides at 30 deer/mi^2 surrounding density and an antlerless harvest rate of 0.30. Error bars represent ± 1 s.d.

effective technique for reducing deer densities in small areas on landscapes with low deer density, but where deer density is high, neither culling nor hunting alone may be sufficient for reducing small, locally abundant populations. This is likely because in areas of high deer density, even if the populations are an ideal candidate for localized management (i.e. have high site-fidelity and low female dispersal, Campbell et al., 2004), larger deer numbers can still provide several opportunities for dispersal, even if the likelihood of any one female dispersing is low (Weckel and Rockwell 2013). Therefore, a combination of culling and antlerless deer hunting may be needed if managers want to reduce deer densities in small (< 5 mi^2) areas on landscapes of high deer densities. Further exploration via a model-based approach is necessary to determine if this combination of deer removal techniques is sufficient to reduce deer densities in small areas.

Areas to apply a deer density reduction often are chosen based on a variety of factors, such as areas where deer-vehicle collisions are common, or on recent timber harvest sites where adequate forest regeneration is desired. These areas may be surrounded by certain landscape features, (e.g. rivers, roads) that can constrain the size and shape of a unit. In our model, we tested three different removal area shapes: circle, square, and rectangle with different ratios of sides (length: width) to emulate removal areas that may be limited by spatial configurations. We found that the shape of the removal area, in particular increasing the ratio of sides in a rectangular area, had little effect on the ability to locally reduce deer density. This unexpected result is likely a product of long dispersal distances, particularly for females. Average male and female dispersal distance in forested landscapes is 4 –12 mi, with some males dispersing > 24 mi and some females dispersing > 30 mi (Long et al., 2005; Lutz et al., 2015). We would expect that, given the dispersal behavior of a deer population, that there is a threshold for how large the ratio of sides of a removal area can be, and once that threshold is reached, the longevity of spatial reductions would decrease. In our model, the largest ratio of sides was 10:1 for 5 and 10 mi^2 areas and 5:1 for 20 mi^2 areas, which corresponds approximately to 10 mi × 0.5 mi, 10 mi × 1.0 mi, and 10 mi × 2 mi, respectively. It is possible that these ratios were not extreme enough to counteract the long dispersal distances of simulated individuals and influence end population density in the removal area. Simulating scenarios with a greater ratio of sides (e.g., 15:1, 20:1, 25:1, etc.) may help elucidate what effect, if any, this variable has on the ability locally reduce deer density. In addition, dispersal is the primary mechanism that is driving the minimum size needed to affect a localized reduction in deer density. Based on our model results, we would expect the minimum size of a removal area to increase as juvenile dispersal rate and distance increases. That is, the larger the average dispersal rate and the longer the average dispersal distance for males and females in a deer population, the larger the removal area needed for long-term, sustained deer density reductions.

Moving forward, managers can use the results of our model to evaluate the effectiveness of their antlerless deer removal programs and possibly adjust their programs to help better achieve deer management goals. While our model simulated hunting patterns and behavior for white-tailed deer in forested landscapes in Pennsylvania, USA, our approach could be widely adopted for deer populations where local data are available to parameterize models. The design of our model landscape was meant to simulate a densely forested habitat, but it did not include any additional landscape features (e.g. streams, roads) or habitat fragmentation that could impact deer movement across the landscape. Incorporating these spatial configurations into the model could help determine if these factors have any effect on dispersal behavior and subsequent hunter success rates. In addition, other hunting regulations such as antler point restrictions and season length could be considered to elucidate the impacts of multiple hunting regimes on the ability to locally reduce deer density. Modeling deer density reductions in areas of mixed forested and agricultural land, areas with a specific spatial distribution of young and old forest, or in non-forested areas such as agricultural landscapes, parks, and urban/suburban regions may be useful in helping to design or modify deer management programs based on landscape and residential classifications.

5. Conclusions

Our study and other empirical studies have shown that localized antlerless deer harvest has the potential to create areas of persistent reduced deer density (Kilpatrick et al., 2001; McNulty et al., 1997; Oyer and Porter 2004; Porter et al., 1991, 2004). Hunter preference for large, mature, male white-tailed deer has led to considerably higher harvest rates for these individuals than for female deer (Wallingford et al., 2017). However, targeting female deer can reduce a population's

reproductive potential (Brown et al., 2000) and can help create areas of reduced deer density if females exhibit low dispersal and high site fidelity (Campbell et al., 2004). In forested landscapes, promoting forest regeneration in areas such as recent timber harvest sites is often a goal of land managers. Increasing antlerless harvest in these specific geographical areas can reduce deer density, which in turn can decrease deer browsing and stimulate regeneration, as well as provide hunters additional opportunities to hunt. Our results show that increasing antlerless harvest rates through hunting for lower density herds ($\leq$ 30 deer/mi^2) in areas $\geq$ 5 mi^2 can successfully reduce deer densities in 5 years and that these reductions can be maintained long-term with continuous removal efforts. However, it may take several seasons after an antlerless deer harvest program has been implemented before it can achieve the harvest rates required to see a localized reduction. In addition, the ability of managers to maintain constant antlerless harvest rates annually may be unlikely due to issues such as partial controllability and environmental variation (Williams 1997). Furthermore, for substantial deer density reductions to occur in small ($<$ 5 mi^2) areas or in areas of high ($\geq$ 40 deer/mi^2) deer density, managers need to consistently achieve considerably high antlerless harvest rates ($\geq$ 30%), which may not be feasible using hunting (Holsman et al., 2010). Our model did not consider factors such as changing hunting regulations or disease (e.g. chronic wasting disease) that could influence white-tailed deer population dynamics (DeVivo et al., 2017), nor did it consider the effects of spatial configurations (e.g. habitat fragmentation, landscape classification) on deer populations. Thus, the size of a removal area and hunting pressure needed to enact a localized deer density reduction may differ from those suggested by our model according to the specific environmental and biological influences of a given region.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.5061/dryad.m37pvmd18.

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