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A METAPOPULATION MODEL FOR FERAL HOGS IN GREAT SMOKY MOUNTAINS NATIONAL PARK

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ABSTRACT. Feral Hogs (*Sus scrofa*) are an invasive species that have occupied the Great Smoky Mountains National Park since the early 1900s. Recent studies on vegetation, mast, and harvest history were important for our work. Using these data, a model with discrete time and space was formulated to represent the feral hog dynamics in the Park. Management strategies and key characteristics of the population were investigated. The model uses observed mast variation to help govern population dynamics and results indicate that Park control efforts have limited the growth of the population.

KEY WORDS: Discrete metapopulation model, Great Smoky Mountains National Park, feral hog, invasive species.

1. Introduction.

Invasive species are among the world's most significant and urgent environmental concerns as they inflict ecological and economic damages that are both costly as well as detrimental to the environment (Olson [2006]). These concerns are exacerbated as an invasive species becomes established in an area (Epanchin-Niell and Hastings [2010]). European Wild Boar (*Sus scrofa*) were brought to the United States in the early 1400s by settlers as a source of food. Since their introduction, feral hogs have been expanding their range, increasing in density, and disrupting natural ecosystems and posing a significant disease threat

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to livestock and native animals (Witmer et al. [2003]). See Engeman et al. [2003], Engeman et al. [2004], Engeman et al. [2007], and Olson [2006] for more details on economic and ecologic impacts of feral hogs in the United States.

In 1912, hunters near Hoopers Bald, North Carolina, imported European wild boar (*Sus scrofa*) to populate a hunting preserve and were left to breed and expand their population for a span of 8–10 years (Jones [1957]). During this time, a number escaped and dispersed throughout the surrounding area (Stegeman [1938]). They bred with hogs of domestic ancestry and have since spread throughout Great Smoky Mountains National Park (GSMNP). We refer to this hybrid population using the term feral hogs.

GSMNP is a 2080 km^2 plot of land that straddles the border between Tennessee and North Carolina, the vast majority of which is undeveloped forest. GSMNP is surrounded by three National Forests, the eastern border of a Cherokee Indian reservation, and Fontana reservoir (Stiver and DeLozier [2005]). Elevation throughout the Park ranges from as low as 270 m to as high as 2024 m. The Park is characterized by a high elevation ridgeline that runs diagonally through the center of the Park and by its unique and flourishing habitats. Due to its undeveloped nature, elevation gradient and rich environmental viability, GSMNP is home to over 6000 flora and 400 fauna (Stiver and DeLozier [2005]).

Feral hogs in the Park consume acorns, known as hard mast, which fall from oak trees at the end of the summer. They also scavenge for tubers, roots, and other food that can be found underground (Scott and Pelton [1976]). We refer to these additional food sources as the base food source. Since the feral hogs depend heavily on oak mast, it plays a significant role in their life cycle affecting reproduction and movement patterns (Johnson et al. [1982]; Singer et al. [1981]). We capture these dynamics by updating the corresponding mast-dependent parameters each month in our model.

One main concern about the presence of the invasive species *Sus scrofa* in GSMNP is that they compete with native species and are destructive to the surrounding environment. Rooting activities are extremely disruptive to vegetative communities, alter nutrient cycles, and may even alter forest succession patterns in the long term (Bratton [1974]; Howe and Bratton [1976]). Feral hogs are in direct competition for oak mast with black bears and are known to scavenge for and consume salamanders (Singer [1981]). There are several National Park policies that state that the control or eradication of non-native species is necessary when such species endanger the protection and interpretation of natural resources in the Park. Since the Park is considered the salamander capitol of the world and the black bear is perhaps the most beloved and publicized species in the Park, in addition to the damage done to the grounds, direct negative impacts on these species by feral hogs is of great concern.

Another impact of *Sus scrofa* is the potential for transmission of Porcine parvovirus, leptospirosis, toxoplasmosis, and pseudorabies, as each were found during various serological surveys of feral hogs in GSMNP (Cavendish et al. [2008]; Sandfoss et al. [2012]). More alarming, the prevalence of pseudorabies has increased dramatically in recent years (Cavendish et al. [2008]; Sandfoss et al. [2012]). The spread of these diseases have serious implications for a large number of domestic and wild animals throughout the region. For example, although studies have shown the impact of pseudorabies on feral hogs is minor, clinical signs in commercial swine is well documented (Stallknecht and Howerth [2001]). Further, park officials believe the transportation of feral hogs due to illegal hunting interests may be increasing the presence and spread of these various diseases.

Due to the aforementioned concerns, GSMNP implemented a feral hog control program beginning in 1959. Although the program's procedures have varied since its implementation, recent efforts to control the feral hog population have been both opportunistic as well as active. Opportunistic activities include dispatching feral hogs when encountered by park rangers as well as setting traps in suspected high activity areas that are convenient for park employees to access and maintain. The Park also hires seasonal employees to actively search for and harvest feral hogs. Most of the active hunting takes place between January and May, as this is a time during which bears are hibernating, foliage is at a minimum and the feral hog population is concentrated in the lower elevation regions. Throughout the remainder of the year harvesting is much more limited, taking place only in the absence of more pressing park needs. Hunting laws in both Tennessee and North Carolina have changed a number of times over the last 30 years and we have no data to measure its impact outside the Park.

The negative impacts that feral hogs have on natural resources, in addition to the fact that feral hogs are hosts for infectious diseases, have resulted in government and park officials having a vested interest in knowing the whereabouts, threat levels, and optimal management strategies for controlling the feral hog population (Stiver [2012a]). These factors and others propelled the creation of a working group at the National Institute for Mathematical and Biological Synthesis (NIMBioS) entitled "Feral swine/pseudo-rabies in Great Smoky Mountains National Park." This group provided data, background information, and input relevant to the formulation of our model.

Its pristine conditions and biodiversity have prompted a great deal of scientific research and documentation related to the Park. Important to this project are detailed vegetation data and corresponding records of yearly acorn crop levels over the last 30 years. We also make use of harvest records that have resulted from the control efforts conducted by GSMNP. As a result, the main goals of this work were to use modeling in coordination with available harvest and mast data to estimate the population and to assess the effect of harvesting on the population.

There has been previous work modeling feral hogs in different parts of the world, each of which differs depending on the specific goal of the research. Spatially explicit models using partial differential equations have been formulated to model feral hog populations in different geographic areas (Clayton et al. [1997]; Keeling et al. [1999]; Gaines et al. [2013]). Though insightful, these initial models are centered around basic ecological concepts such as logistic growth and contain limited feral hog features. An age structured model (without spatial features) has also been considered in an attempt to determine the structure and characteristics of specific population dynamics (Focardi et al. [1996]). Most recently, an individual-based model (IBM) was constructed for feral hogs in GSMNP that resulted from the same NIMBioS working group and is based on the similar harvest data (Salinas et al. [2015]). In the IBM, the annual total of the harvest data was only used to estimate constant harvest and mortality rates. Models constructed with differential equations, agent-based models, and discrete formulations each have benefits and drawbacks that depend upon the available information and specific goals of a project. With the harvest and mast data (Harvest Data [1980]; Hard Mast Index [1981]) given in monthly intervals, we were able to carefully estimate a range for monthly mast-dependent parameters to best match the observations of feral hog behavior in the Park. We fit yearly harvest rates in each region over two seasons per year. With our goals of analyzing general population dynamics and measuring the importance of the control program, we formulate a discrete, data-driven metapopulation model to describe the feral hog population in the Park.

The remainder of the paper will take the following form: First, the formulation of the model will be discussed. This section will include a description of the data used, an overview of the study area, a summary of the population dynamics, the assumptions made, and how all of components combine in a mathematical formulation. Discussion of parameters being used will follow and will include how we estimated their values using the harvest data. The subsequent section will include a discussion of the results of the model and state any conclusions that can be made. The final section will outline specific uses of the model and future work related to feral hogs in the Park.

2. Model formulation.

2.1. Data and regions.

Increased interest and technological advances have made research relating to feral hogs in GSMNP more tractable in recent years. One key contribution from the working group was data expressing vegetation types and distributions obtained through remote sensing (Madden et al. [2004]). The data were used to create a digital vegetation map and database of overstory and understory flora found throughout GSMNP. This information is used to divide the Park and its immediate surrounding area into eight regions as determined by vegetation type and also to establish where oak trees and other food sources are located.

Other significant data for our model were provided by GSMNP officials. The Park provided harvest and oak mast data in GSMNP from 1980 to 2010 (Harvest Data

[1980]; Hard Mast Index [1981]). The harvest data contain over 11,000 entries and include quantity, age, month, and geographical location of feral hogs harvested. Mast index data consist of visual estimations of white and red oak acorns that existed throughout the Park in each given year. Values range from 0.45 to 5.1 with a higher value indicating a more bountiful year. We use the harvest data to set an initial distribution of feral hogs throughout the Park, to estimate parameter values, and to check the accuracy of the model. The driving force behind feral hog behavior is their primary diet of oak acorns (Scott and Pelton [1976]; Singer [1981]). Therefore, knowing the quantity and location of the key food supply is ideal for this model. The aforementioned data were paramount in the formulation of our data-driven metapopulation model that is discrete in both time and space.

The discrete time step is 1 month as we wish to model several discrete events that occur on a scale that is not less than a month including births, mast deployment, and seasonal movement.

The current month is denoted by t. We take $t = 1$ to be January. To denote any periodic or other type of time-based events, we use m for the month (1–12) and y for the year.

The model spatial domain is divided into eight regions based on overstory vegetation types as they produce the food that drives population dynamics (see Figure 1) (Scott and Pelton [1976]). The overstory data are from Madden et al. [2004] and are detailed in Table 2. There are six regions inside the Park (regions 1–6) with region 6 constituting an upper-elevation ridge line that runs diagonally through the center of the Park. Two of the regions are outside the Park, one on the north side (region 8) and one on the south side (region 7).

For each region r, we record the area in acres (A_r) and the length of boundary between connected regions r and s (given in $BL_{r,s}$). These are used in determining yearly food supplies and governing movement between regions, each of which will be explained in detail in later sections.

There is a feral hog population in each region that varies over time and is not differentiated by sex or by age. The initial conditions for the model are based on harvest data from 1988 (Harvest Data [1980]). The initial population in each region is reconstructed by dividing the number of feral hogs harvested from each region in 1988 by rough estimates from the Park of yearly on- and off-season monthly harvest rate of 0.03 and 0.01.

The population in region r at time t is denoted by $P_{r,t}$. The specific population in a given region r at time t depends on all the parameters and variables that comprise the model. For a complete list of all parameters in the model see Table 3.

2.2. Order of events. The order of events in a discrete model is very important as it impacts the dynamics of the system (Bodine et al. [2012]). Given the

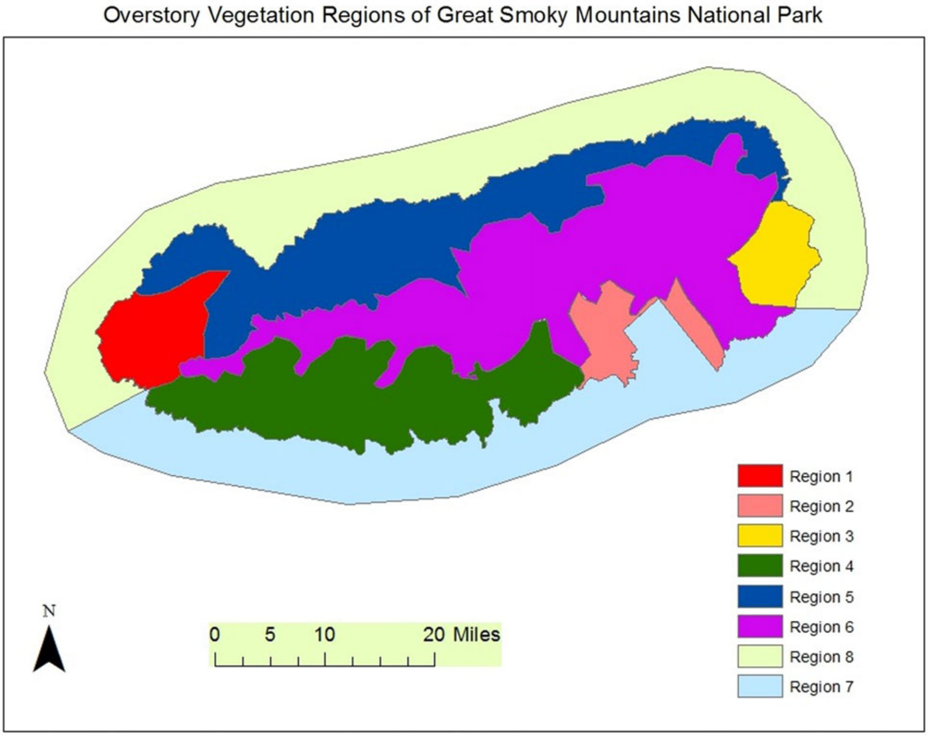

FIGURE 1. The Great Smoky Mountains National Park is broken into eight regions based on overstory vegetation types.

mast supply ($M_{r,t}$) and the populations ($P_{r,t}$) from the previous month, the events proceed in the following order:

i. Update the mast for the month since many of the parameters that govern feral hog dynamics in GSMNP are driven by hard mast availability (Scott and Pelton [1976]; Singer [1981]).
ii. Harvest at a rate determined by the month.
iii. Compute the portion of the postharvest population that survives. We do this before adding births because only surviving adults can reproduce.
iv. If the month is January, we then compute the number of births based on the surviving population and mast supplies. We keep track of the births and apply a different survival rate before adding them into the general population.
v. Perform movement, using either general movement or seasonal movement, dependent upon the time of year.

2.2.1. *Mast dynamics.* Each region has two food sources—the base food source and hard mast. The hard mast source is from white and red oak trees, which is believed to be preferred by feral hogs in GSMNP (Scott and Pelton [1976]). Hard mast becomes available in August, but varies in amount from year to year. The amount of hard mast in each region in each year is measured in kilocalories and based on a hard mast index for years 1981–2010 produced by Hard Mast Index [1981]. The mast index ranges from 0.45 to 5.1 with lower values indicating poor mast years and higher values for ample mast years. See Table 1 for a list of the 25 overstory types found in GSMNP, their total acreage and corresponding kilocalorie per acre (Inman [1997]). Of course, the location of hard mast is an important driver of the population and the top four overstory types in each region by total area covered can be seen in Table 2. Hard mast levels in a given year and region are derived by pairing the distribution of the 25 overstory types in each region with the assumed kilocalorie per acre of each to create a baseline level of hard mast. This value is scaled further according to the recorded hard mast data from 1981 to 2010 to properly model the impact changes in food levels has on the population (Hard Mast Index [1981]). With the aforementioned data in hand, the available kilocalories of hard mast that becomes available each year in August in each region is calculated.

The other food source is tubers, roots, small animals, and other items feral hogs can scavenge off the ground, which we refer to as the base food source (Scott and Pelton [1976]). The amount of available kilocalories of the base food source is assumed to be available in each region at the constant rate of 1000 kilocalories per acre. We consider this food source as a constant amount proportional to region size because at any given time, there are an unknown level of renewable food sources found on the forest floor in each region and because the base food source plays a minor role in a hogs diet. The reduced role it plays compared to hard mast is because it is less nutritious as well as less abundant and is thus less desirable. The role of the base food source in the life cycle of feral hogs is to ensure minimal sustenance in times and regions where there is not sufficient hard mast. This is modeled by including a smaller amount of soft mast in the model, which allows hard mast to more significantly influence parameter values that govern population dynamics.

Feral hog behavior and movement are believed to be driven by hard mast availability (Singer [1981]). Denote the time varying hard mast in region r at time t by $HM_{r,t}$. Hard mast is dropped from trees at the end of August and decreases over time due to feeding by feral hogs and competitors as well as natural decay. We will initialize the model in August using available mast, vegetation, and harvest data for this month from (Harvest Data [1980]; Hard Mast Index [1981]; Madden et al. [2004]). The hard mast index is a single number that indicates the level of oak mast in a given year. This single number is paired with the known acreage of oak trees in each region to produce $MI_{r,y}$, the amount of oak mast produced in region r in year

TABLE 1. Overstory vegetation types. Listed are the 25 overstory types that exist in Great Smoky Mountains National Park, their corresponding total acreage, and kilocalorie per acre.

Overstory type	Abbreviation	Total acreage	Kilocalorie per acre
Bare Ground	Bare	1223	0
Cove Hardwood Forest	CHx	78,655	19,154
Dead	Dd	335	0
Human Influence	Hi	4828	0
Rhododendrom	Rhd	8054	0
Mixed Hardwood Forest	Hx	34,781	15,465
Montane Alluvial Forest	MAL	6605	4,000
Montane Oak Forest- White Oak	MOa	2414	8,000
Montane Oak Forets- Red Oak	MOr	18,554	8,000
Northern Hardwood (Birch)	NHx	77,184	4,066
Meisic Chestnut Oak Forest	OcH	9163	8,000
Meisic Oak Forest (Red Oak)	OmH	103,221	8,337
Xeric Oak Forest (Red &White Oak)	OzH	79,886	8,127
Xeric Oak Forest (Pine Mix)	OzH-P	1447	6,000
Yellow Pine Forest	P	27,283	7,117
Meisic Oak Forest Mix (Oak & Pine)	P-OmH	548	5,915
Xeric Oak Forest Mix (Oak & Pine)	P-OzH	22,678	5,915
Pasture	Pa	449	0
Rock	Rk	528	0
Spruce-Fir Mix	S-F	37,278	4,578
Shrub	Sb	2363	0
Hemlock	T	15,762	6,000
Vines	V	1116	0
Water	W	7498	0
Wetland	Wtl	108	0
Total		219,440	542,015

y. After mast is dropped in August, we assume each feral hog consumes at rate C_P, which takes the value of 5000 kilocalories per day (Inman [1997]). Hard mast also depletes as a result of natural decay and consumption by other animals at rate δ, which is assumed to be 8% per month to ensure most food is consumed each year. To be ecologically consistent, we ensure the hard mast value in each region does not become negative. All the previous years hard mast is entirely depleted before the following August when the next hard mast drop occurs. Thus, the specific amount of hard mast available in region r at time t is dependent on time, the specific region,

TABLE 2. Dominant Overstory type by region. This table displays the top four overstory types by total acreage in each region, with percentage of total area covered in parenthesis (Madden et al. [2004]).

Region	Total acreage	Type 1 (% area)	Type 2 (% area)	Type 3 (% area)	Type 4 (% area)
1	13,091	OzH (32.2)	P-OzH (21.5)	OmH (16.3)	CHx (15)
2	18,546	OmH (21.9)	CHx (21.7)	OzH (11.9)	Sb (10.4)
3	18,546	OmH (21.9)	CHx (21.7)	OzH (11.9)	Sb (10.4)
4	44,441	OcH (38)	OzH (19.7)	CHx (13.9)	Hx (7.1)
5	55,412	OzH (24.4)	OmH (21.5)	CHx (20.1)	Hx (9.8)
6	74,988	NHx (39)	S-F (20.1)	CHx (10.2)	MOr (6.6)
7	22,220	OcH (38)	OzH (19.7)	CHx (13.9)	Hx (7.1)
8	27,706	OzH (24.4)	OmH (21.5)	CHx (20.1)	Hx (9.8)

TABLE 3. A list and description of variables found in the model.

Name	Description
t	Time (in months), start with $t = 1$ in January and run for 20 years
m	Month in the given year
y	Number of years
N	Number of regions
r	Region number
$BL_{i,j}$	Proportional boundary length between regions i and j
$MI_{r,y}$	Hard mast produced in region r in August in year y (in kilocalories)
$SM_{r,t}$	Base food source in region r at time t in kilocalories
$M_{r,t}$	Total mast in region r at time t in kilocalories
$BR_{r,m=1}$	Births in regions r. Occur in January
$P_{r,t}$	Feral hog population in region r at time t
$H_{r,t}$	Feral hog population harvested in region r at time t
$SH_{r,t}$	Number of surviving feral hogs in region r at time t
$MH_{r,t}$	The number of feral hogs moving out of region r at time t
F	Scale function that determines mast-dependent parameters

the hard mast index value for the given year, and the number of feral hogs in the region and is given by

$$HM_{r,t+1} = \begin{cases} MI_{r,y} & m = 8, \\ ((1-\delta)HM_{r,t} - C_P P_{r,t})^+ & m \neq 8. \end{cases}$$

Denote the constant amount of the base food source in region r by SM_r. Since the base food source is assumed to exist at the constant rate of 1000 kilocalories per acre, $SM_r = 1000A_r$.

The total mast in each region r and time t is denoted by $M_{r,t}$ and is given by

$$M_{r,t} = HM_{r,t} + SM_r. \tag{1}$$

The specific amount of total mast available in each region influences parameter values at each time step as determined by the scale function.

2.2.2. *The scale function.* Many of the parameters that comprise the model vary in time and space and are based on mast availability. Such parameters include percentage of adults that survive ($Surv$), how likely it is that feral hogs will move to an adjacent region during general movement ($Move$) as well as the yearly birth rate (BR). Due to this fact, each of these parameters are determined at each time step via a scaling function that produces appropriate values for each parameter based on the mast availability.

Let $Param_{r,t}$ denote one of the above-mentioned mast-dependent parameters in region r at time t. We will obtain the value of a given parameter in the current time step dependent upon the mast availability according to the following scale function (called F):

$$F(M, Param0, ParamMax, M_h) = \frac{Param0 \cdot M_h + ParamMax \cdot M}{M + M_h}, \tag{2}$$

where $M = M_{r,t}$ is the mast value in region r at time t, $Param0$ is the value of $Param_{r,t}$ when $M = 0$, $ParamMax$ is the value of $Param_{r,t}$ as $M \to \infty$, and M_h is the half-saturation mast constant. At the beginning of each month, the specific value of mast-dependent parameters values is determined by the scale function. See Figure 2 for a depiction of the form and asymptotic nature of the scale function.

2.3. Population dynamics. The population dynamics are driven in each region by three factors, which occur in the order listed: survival, birth, and movement. The remainder of the section is presented in the order in which the events take place

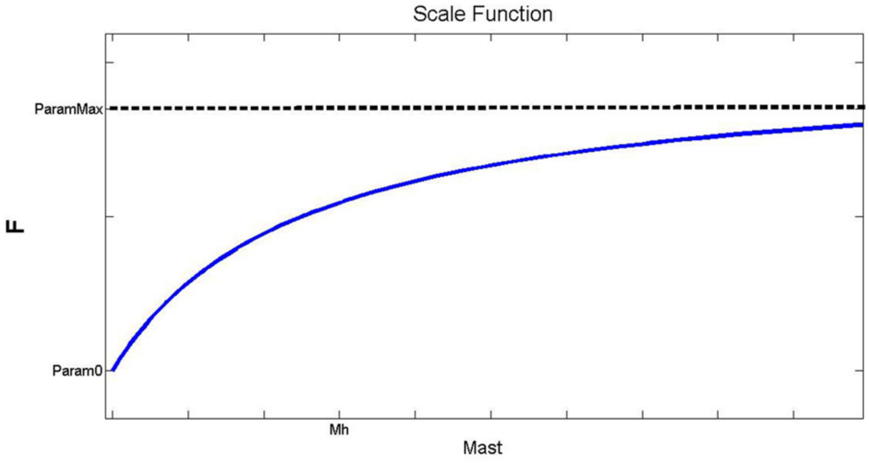

FIGURE 2. A number of the parameters that comprise the model are mast-dependent. The rational scale function ranges between a maximum and minimum parameter value as determined by the current mast level in each region.

in each region r at time t. Throughout the process, we calculate how many feral hogs survive each step and update the population accordingly. After movement takes place, $P_{r,t+1}$, the population that will start out in each region in the next month, is calculated.

2.3.1. *Survival.* Although park rangers are constantly making some effort to harvest feral hogs, the most opportune time to hunt is when the bears are hibernating, the foliage is at a minimum and the feral hogs are at lower elevations. Due to this fact, the Park hires additional employees to actively seek feral hogs from January through May. During the remaining months, harvesting is limited to convenient, and thus less frequent, harvesting. To reflect this recurring trend, we have an relatively low off-season harvest rate between months 6 and 12 , a much higher on-season harvesting rate from months 1 to 5. Since we have no data on harvesting outside of GSMNP, we only model harvesting within its boundaries. Let $Hrate$ denote the seasonal harvest rate given by

$$Hrate = \begin{cases} rate_1, & m = 1, \ldots, 5 \ \& \ r = 1, \ldots, 6 \\ rate_2, & m = 6, \ldots, 12 \ \& \ r = 1, \ldots, 6 \, . \\ 0, & r = 7, 8 \end{cases}$$

To find parameter values and assess the general harvest trend, we initially assume that $Hrate$ is uniform in space and only varies in time according to the season. After estimating parameter values, we then vary harvesting in time and space in order to more accurately model the system and evaluate the effects the Park's efforts have on the population.

The number of feral hogs harvested at time t in region $r = 1, ..., 6$ is denoted by

$$H_{r,t} = Hrate \cdot P_{r,t}. \tag{3}$$

The number of feral hogs that survive harvesting in each region continue on to the subsequent mast-dependent survival step.

The number of feral hogs that die due to natural causes is mast dependent and independent of piglet survival. We assume that there is an alternative food supply available (base food source) but that it is less desirable, less prevalent, and less nutritious than hard mast. Thus the feral hogs do not die when the primary supply is consumed, but they also do not survive as easily. These dynamics are captured by the previously mentioned scale function, paired with a constant, but significantly less, amount of the base food source. The adequacy of the food supply is also related to the current population as more feral hogs need more available mast.

The percent of feral hogs that do not perish due to natural causes is given by $Surv_{r,t}$, the survival rate in region r at time t. $Surv_{r,t}$ is dependent on the available mast in the region in the given month and has a minimum value of $Surv0$ given no available mast and approaches a maximum value of $SurvMax$ as mast availability increases. Since the percent that survive is dependent on mast availability, we first determine $Surv_{r,t}$ via the scale function,

$$Surv_{r,t} = F(M_{r,t}, Surv0, SurvMax, M_h), \tag{4}$$

and apply both the survival rate as well as the harvest rate to the existing population:

$$P_{r,t} \cdot (1 - Hrate) \cdot Surv_{r,t}. \tag{5}$$

Individuals that make it through harvesting and mast-dependent survival move on to the birth stage of the model.

2.3.2. *Birth.* Female feral hogs go into estrus as soon as they can and usually give birth in January (Singer [1981]). The number of piglets produced per population in our model depends on the following factors:

i. Percent of the population that are mature females: We assume that 50% of the population is female, but that only 90% are mature. This means that 45% of the population are able to give birth, denoted by B_F.

ii. Average litter size: Typical litter size is 3 to 8, so we will take it as 6, denoted by L_A (Singer [1981]).
iii. Percent that are pregnant: Even if a feral hog reproduced in the previous year, they can still go into estrus. In each regions, we assume there are enough males to impregnate nearly all the available females but that the actual number of the mature females that become pregnant is mast dependent (Stegeman [1938]) (Conversation with William Stiver, May 2012).
iv. Percent of the pregnant females that give birth: Inevitably, a portion of the females that become pregnant will not successfully give birth. This portion depends on the mast level during the pregnancy. In a low mast years, the percent of pregnant females that will come to term is very low compared to high mast years where a much larger percentage of pregnant females will give birth (Singer [1981]).
v. Percent of the litter that survives the first month: This also depends on current mast level and is comparable to the survival for the population in general, but lower as there is a higher mortality for piglets in the first 6 months.

The last three factors are heavily mast-dependent with inadequate mast causing production of far fewer births than when there is plentiful mast. Although the amount of mast available in each region in the months surrounding January determines these birth parameters, we use the amount of mast remaining in January in each region as an indication of the presence of mast before and after feral hogs give birth. Thus the percent of mature females that become pregnant is determined by the scale function and is dependent on the amount of mast available in each region in the month of January.

In our model, we assume births only take place in January, denote m^* to be the month of January (Singer [1981]). When $m = m^*$, a percentage of the population in each region are pregnant females. Of those pregnancies, a portion actually come to term and produce piglets and then a fraction of the births survive their first month of life and are added into the general population. Denote the number of piglets produced by each individual in the region r at time t by $BR_{r,t}$. The value of $BR_{r,t}$ is the product of the birth rate with the average litter size and number of mature females. Since the birth rate is highly dependent on mast availability, the exact level is determined by the scale function:

$$BR_{r,t} = \begin{cases} B_F \cdot L_A \cdot F(M_{r,t}, BR0, BRMax, M_h) & m = 1 \\ 0 & m \neq 1. \end{cases}$$

The total number of births in each region will then be a product of $BR_{r,t}$ and the number of adult feral hogs that have lived through both survival stages. This value can immediately be added into the general population since the birth rate only includes piglets that survive. Let $SH_{r,t}$ denote the surviving feral hog population in region r at time t, which is composed of all individuals that have lived through the survival stage as well as any new births into the population given by

$$SH_{r,t} = P_{r,t} \cdot (1 - Hrate) \cdot Surv_{r,t} \cdot (1 + BR_{r,t}).$$

2.3.3. *General and seasonal movement.* The reasons feral hogs move throughout GSMNP can be characterized in two ways: between areas of the Park searching for food as well as making use of the topography of the Park by moving up in elevation during the spring and down in elevation in the fall (Singer [1981]). The movement toward higher elevations takes place in the warmer months and is caused by the decline in mast availability paired with increasing temperatures in lower elevations. The movement toward lower elevations is a result of mast becoming available in these regions at the end of the summer. Independent of this seasonal movement, the food-based movement is hard mast dependent (Scott and Pelton [1976]; Singer [1981]).

General movement of the feral hogs refers to the movement between the various regions independent of the intrinsic characteristics of the region themselves or time of year, but instead as a result of food availability. Each month a percentage of the population will move out of each region depending on the mast availability in each region. Lower food levels increase the percent of feral hogs moving out of that region where high levels of food results in limited movement. The specific level of general movement in each region is governed by the scale function. We assume that the local population density is low enough that it does not directly impact movement, but rather indirectly impacts general movement through mast availability. Feral hogs moving out of a region move to a neighboring region proportional to shared boundary length, captured in this connectivity matrix:

$$BL = \begin{pmatrix} 0 & 0 & 0 & 0.106 & 0.316 & 0.20 & 0 & 0.378 \\ 0 & 0 & 0.189 & 0.055 & 0 & 0.20 & 0.555 & 0 \\ 0 & 0.366 & 0 & 0 & 0.006 & 0.20 & 0 & 0.428 \\ 0.044 & 0.031 & 0 & 0 & 0 & 0.20 & 0.725 & 0 \\ 0.093 & 0 & 0.001 & 0 & 0 & 0.20 & 0 & 0.706 \\ 0.017 & 0.157 & 0.073 & 0.326 & 0.427 & 0 & 0 & 0 \\ 0 & 0.316 & 0 & 0.684 & 0 & 0 & 0 & 0 \\ 0.141 & 0 & 0.107 & 0 & 0.751 & 0 & 0 & 0 \end{pmatrix}, \tag{6}$$

where $BL_{i,j}$ is the percent of feral hogs moving out of region i that will move into region j. The matrix BL is a connectivity matrix derived from the proportion of shared boundary between regions.

For example, since $BL_{2,4} = 0.055$, this implies that region 2 shares a boundary with region 4 and that the length of their shared boundary constitutes 5.5% of the total boundary of region 2. As a result, when general movement takes place, 5.5% of feral hogs moving out of region 2 will move into region 4. All entries of $BL_{i,j}$ that are 0 imply that regions i and j do not share a boundary.

There are several clarifications that must be made regarding general movement as it relates to this matrix. First, recall that region 6 is the high-elevation region, which does not contain any hard mast producing trees. Since general movement is entirely mast-driven, in practice, we limit the amount of general movement from the lower elevation regions 1–5 to region 6 by allowing only 20% of all feral hogs marked to move from each interior region to move up to region 6. To ensure rows of BL sum to 1, the adjusted decrease in shared boundary length between each interior region with region 6 was redistributed to the other neighbors proportionally. Also reflected in BL is that all interior regions border region 6 while the two exterior regions do not.

Seasonal movement takes place when the population changes their location based on elevation from March through June and again in August (Singer [1981]).

There are two forms of seasonal movement: from the higher regions to the lower regions in the fall (August) and from the lower regions to the higher regions during the spring (March through June). Since the high to low movement culminates with the drop of the hard mast paired with decreasing temperatures, we assume all feral hogs will move down in elevation during the month of August (Singer [1981]). The low to high movement takes place from March through June as hard mast in the lower regions become depleted and temperatures increase (Singer [1981]). With this in mind, we have additional feral hogs move from each low region to the high region beginning in March at a rate that increases as we approach June. This ensures nearly all feral hogs reach the higher regions by mid-summer.

Although these movement patterns were derived from a previous study (Singer [1981]), a more recent telemetry study is currently being formulated by GSMNP that makes use of advanced collaring and tracking techniques (Stiver [2012a]). The data will be used to either confirm these movement dynamics or reshape our current assumptions.

The number of feral hogs moving out of region r at time t is denoted by $MH_{r,t}$. In practice, general movement and seasonal movement follow the same pattern of first deciding how many feral hogs will move out of each region, removing them from the surviving population and then redistributing them to neighboring regions.

General movement is less of a driver than seasonal movement thus general movement occurs only in the absence of seasonal movement. In months when there is only general movement, the percent of feral hogs moving out of each region, $Move_{r,t}$, is dependent on the mast level in the region, $M_{r,t}$. Using the scale function we have

$$Move_{r,t} = F(M_{r,t}, Move0, MoveMax, M_h), \tag{7}$$

from which the number of surviving feral hogs moving out of each region can be computed:

$$MH_{r,t} = Move_{r,t} \cdot SH_{r,t}. \tag{8}$$

During general movement, feral hogs marked to move out of lower elevation regions $1, 2, 3, 4, 5, 7, 8$, and travel to adjacent regions according to the proportions given in BL. However, movement from the high elevation region 6 to lower elevation regions is controlled differently. After spending the warmer months in region 6, at the end of August the entire upper elevation population simply moves regions $1, ..., 5$ proportional by boundary length. Otherwise, during general movement months, we employ a mechanism for region 6 that accounts for the low elevation region from which the feral hogs came. We achieve this by having feral hogs move down to one of regions $1, ..., 5$ weighted by the number of feral hogs that have moved out of each of those regions to the upper region over the past year. To achieve these movement patterns, we define $MP_{i,j}$ as the proportion of feral hogs moving out of region i and into region j as

$$MP_{i,j,t} = \begin{cases} BL_{i,j} & i \neq 6 \ \&\ m = 1, 2, 7, 9, 10, 11, 12 \\ MP^{*}_{j,t} & i = 6 \ \&\ m = 1, 2, 7, 9, 10, 11, 12 \end{cases},$$

where

$$MP^{*}_{j,t} = \begin{cases} BL_{6,j} & 1 \leq j \leq 5 \ \&\ m = 8 \\ \frac{MP^{*}_{6,t-1} + 0.2 \cdot MH_{j,t-1}}{\sum_{j=1}^{5} MP^{*}_{j,t}} & 1 \leq j \leq 5 \ \&\ m = 1, 2, 7, 9, 10, 11, 12 \cdot \\ 0 & j \geq 7 \end{cases}$$

The feral hogs marked to move from each region during general movement are then removed from the surviving population and then redistributed given by

$$\begin{aligned} P_{r,t+1} &= P_{r,t} \cdot (1 - Hrate) \cdot Surv_{r,t} \cdot (1 + BR_{r,t}) \\ &\quad - MH_{r,t} + \sum_{i=1}^{8} MP_{i,r,t} \cdot MH_{i,t} \text{ for } r = 1, \ldots, 8. \end{aligned} \tag{9}$$

Seasonal movement takes place from March through June when depleted mast supplies and increasing temperatures cause feral hogs to move from lower elevation regions $1, ..., 5$ to higher elevation region 6. During this time we calculate an initial number of feral hogs that will move out of the lower regions by applying the scale function and then add an additional increase to the general movement amount in each subsequent month. This results in feral hogs migrating in increasing proportions to the high elevation region in the center of the Park while allowing a small population to remain at a lower elevation. For the month of July, general movement then applies again as discussed previously. Since the understory is the only food source in the high elevation region, the scale function produces relatively high general movement rates in this month, which simulates the start of the migration back down to lower regions. Then, in August, hard mast falls from oak trees and draws remaining feral hogs back down to the lower the elevation regions. During this month we move all remaining feral hogs in region 6 to regions $1, ..., 5$ proportional to shared boundary length. Although the specific number of feral hogs moving to and from each region changes during this time from year to year, the proportions and distribution locations are deterministic and based on the specific month.

We first determine how many feral hogs will be moving out of each region:

$$MH_{r,t} = \begin{cases} Move_{r,t} \cdot SH_{r,t} + \frac{m-2}{5}(SH_{r,t} - Move_{r,t} \cdot SH_{r,t}) & r \neq 6 \;\&\; 3 \leq m \leq 6 \\ 0 & r = 6 \;\&\; 3 \leq m \leq 6 \\ Move_{r,t} \cdot SH_{r,t} & r \neq 6 \;\&\; m = 8 \\ SH_{r,t} & r = 6 \;\&\; m = 8. \end{cases}$$

We again define $MP_{i,j}$ as the proportion of feral hogs moving out of region i and into region j which will account for the migration of feral hogs to upper elevations during the warmer months by increasing the proportion of feral hogs moving from regions $1, ..., 5$ to region 6 from March through June:

$$MP_{i,j,t} = \begin{cases} BL_{i,j} & 1 \leq i, j \leq 8 \;\&\; m = 8 \\ MP_{i,j,t-1} + \frac{m-3}{5} & 1 \leq j \leq 5 \;\&\; j = 6 \;\&\; 3 \leq m \leq 6 \\ MP_{i,j,t-1} - \frac{m-3}{5} \cdot \frac{BL_{i,j}}{\sum_{r \neq 6} BL_{i,r}} & 1 \leq j \leq 5 \;\&\; j \neq 6 \;\&\; 3 \leq m \leq 6 \\ BL_{i,j} & i \geq 7 \;\&\; 3 \leq m \leq 6 \\ 0 & i = 6 \;\&\; j \neq 6 \;\&\; 3 \leq m \leq 6. \end{cases}$$

Then, feral hogs moving out of each region are removed from the surviving population and redistributed during seasonal movement given by:

$$\begin{aligned} P_{r,t+1} &= P_{r,t} \cdot (1 - Hrate) \cdot Surv_{r,t} \cdot (1 + BR_{r,t}) \\ &\quad - MH_{r,t} + \sum_{i=1}^{8} MP_{i,r,t} \cdot MH_{i,t} \text{ for } r = 1, \ldots, 8. \end{aligned}$$

3. Parameter estimation. Feral hog population dynamics vary across space. The dynamics of a specific feral hog population greatly depends on the local environment. Most research conducted on the feral hog population in GSMNP is outdated and thus many of the parameter values are unknown. Our metapopulation model contains the following eight unknown parameters as described in Table 4 $Surv0$, $SurvMax$, $BR0$, $BRMax$, $Move0$, $MoveMax$, $rate_1$, and $rate_2$.

It is important to note that all the above parameters, except $rate_1$ and $rate_2$, are mast dependent and thus get updated each month using the scale function. With this in mind each "0" value will not ever be achieved due to a constant amount of available the base food source and each "Max" value shown above are approached asymptotically as a result of the rational form of the scale function.

We wish to find the parameter values that, when used in our model, produce harvest levels that best match the available harvest data. We use data from 1989 through 2000 since the harvesting strategies that took place during this time period were most consistent.

More specifically, the problem can be stated as

$$\underset{x}{\text{Minimize}}\ J(x) = \frac{\sqrt{\sum_y \sum_r (H_{r,y} - H^*_{r,y})^2}}{\sqrt{\sum_y \sum_r (H^*_{r,y})^2}},$$

where r represents all interior regions, y is the year ranging from 1989 to 2000, x represents all possible parameter values, $H^*_{r,y}$ is harvest data from region r in year y, and $H_{r,y}$ is the computed harvest from region r in year y.

In addition, we need to make sure that the parameters reflect conditions found in the Park. Specifically, minimum survival rate should be significantly less than maximum survival rate and on-season harvesting produces much higher yields than off-season rates. As a result, the above problem is also restricted by the following linear constraints order to ensure that the resulting values reflect these trends and the parameters are ordered correctly:

$$\begin{aligned} \tfrac{11}{10} Surv0 &\le SurvMax \\ BR0 &\le BRMax \\ MoveMax &\le Move0 \\ \tfrac{3}{2} rate_2 &\le rate_1 \end{aligned} \tag{10}$$

All parameters were constrained within the interval $[0, 1]$.

To solve the above optimization problem, we made use of the Global Optimization Toolbox from MATLAB$^{\text{TM}}$. Since our model contains a large number of

TABLE 4. A list and description of parameters found in the model.

Name	Value	Description
A_r	13–55	Area of region r in thousands of acres
δ	0.08	Monthly food loss percentage due to decay and competitors
C_P	5000	Calories consumed per feral hog per day
M_h	$150,000$	Half saturation mast constant
B_F	0.45	Percent of population that are mature females
B_P	0.95	Percent of female population that are mature and can give birth
L_A	6	Average size of a litter
$Surv0$	0.88	Survival factor if there is no mast
$SurvMax$	0.97	Survival factor as mast approaches a maximum level
$BR0$	0.27	Percent of population that give birth and whose piglets survive the first month given no mast
$BRMax$	0.89	Percent of population that give birth and whose piglets survive the first month as mast approaches a maximum level
$Move0$	0.51	Percent of feral hogs moving with no available mast
$MoveMax$	0.16	Percent of feral hogs moving as mast approaches a maximum level
$rate_1$	0.35	On-Season harvest rate, from January through May
$rate_2$	0.15	Off-Season harvest rate, from June through December
$Surv_{r,t}$	0.88–0.97	Percent of feral hogs that survive in region r at time t. Mast dependent
$BR_{r,t}$	0.27–0.89	Percent of population that give birth and whose piglets survivethe first month in region r at time t. Mast dependent
$Move_{r,t}$	0.16–0.51	Percent of feral hogs that move out of region r at time t

complicated implicit functions, we employed a method that did not require input of any derivatives. Furthermore, given the overwhelming number of possible parameter combinations, we needed our local solver to work in concert with an algorithm that would test a large number of starting points. Thus, we chose to use the MultiStart Algorithm with fmincon as its local solver.

The MultiStart Algorithm was most appropriate for our problem as it allowed us to test a large number of evenly distributed starting points and stores all local solutions in a manageable way using the built-in manymins function. The MultiStart Algorithm generates uniformly distributed random starting points within the given bounds and passes them one-by-one to the local solver, fmincon, which attempts to find a local basin of attraction relative to each given start values. Any solution that is found is then stored increasing order of objective function output for later review using the manymins function.

The fmincon local solver was most appropriate for our problem as it accepts smooth, nonlinear objective functions, is a derivative-free solver, and allows enforcement of the linear inequality constraints and bounds given in (10). Instead of inputting a derivative, fmincon approximates the gradient numerically in order to move toward the basin of attraction given each starting point. In all of our trials, the exit flag produced by fmincon indicated that a convergent run occurred.

4. Results and discussion.

Recall that the initial population in the model is set using harvest data in each region from 1988 paired with a presumed yearly harvest rate. Due to the fact that our goal was to determine parameters based on how well they produced harvest numbers that matched our data, the initial population being used in the model greatly affected the computed harvest rates. In changing the initial population one also runs the risk of altering various parameter values. Due to this potential sensitivity to initial values, the previously stated optimization problem was run with the following differing initial populations: 454, 774, 1410, and 2924. These values were obtained the same way initial conditions were described previously except by assuming different uniform harvest rates.

After the initial population was set in each scenario, the optimal harvest values were then included in the parameter estimation.

After a number of exploratory runs of the MultiStart Algorithm with fmincon as a local solver, it became obvious that there were a great number of viable solutions that both satisfy the constraints and produce comparable error outputs. These initial trials also imparted some intuition about the appropriate range for each parameter. This allowed us to repeat our process with more confined constraints to improve the speed and accuracy of the results.

With the above in mind, given each of the four initial populations, we used 500 starting values and tested both the less constrained as well as more constrained bounds. In all 500 trials, a convergent local solution for all eight parameters were

TABLE 5. Results optimizing over all parameters for different initial population values. In the table, P_0 is the initial population value used in the optimization procedure. The average value and variance for the results of each initial population are also shown.

P_0		$Surv0$	$SurvMax$	$BR0$	$BRMax$	$Move0$	$MoveMax$	$rate_1$	$rate_2$
454	Mean	0.867	0.959	0.712	0.975	0.695	0.015	0.982	0.575
	Variance	0.00006	0.00001	0.03	0.002	0.002	0.0009	0.001	0.003
774	Mean	0.863	0.965	0.460	0.749	0.636	0.068	0.685	0.369
	Variance	0.0003	0.0001	0.01	0.02	0.008	0.001	0.003	0.005
1410	Mean	0.859	0.955	0.575	0.738	0.515	0.059	0.393	0.190
	Variance	0.00004	0.00001	0.005	0.002	0.005	0.004	0.0006	0.0006
2924	Mean	0.845	0.963	0.508	0.728	0.620	0.111	0.206	0.090
	Variance	0.0002	0.00003	0.007	0.004	0.006	0.001	0.0001	0.00007

found. Of these 500 values we only considered those within 20% of the lowest error output. As a result, we were able to narrow down the values to more reasonable candidates from which an average was calculated, as shown in Table 5.

The second column displays the lowest output of the objective function $J(x)$ in the given trial. The third column of the table indicated how many of the 500 starting points produced an error within 20% of the lowest error output and thus were considered when calculating the mean. The displayed mean values are very consistent between trials with the only values that are not clustered across trials being the harvest values, which are directly related to the initial population in a given trial. In fact, each harvest solution settled very close to the presumed harvest rates that set the initial value in the first place.

We chose the parameters from the third line in Table 5 because values were consistent across initial populations and Park officials believe that the current population of feral hogs in GSMNP is nearest to 1410 (Conversation with William Stiver, May 2012). Figure 3a illustrates the resulting computed harvest values when compared to the harvest data using these parameters. Keep in mind that harvest values were estimated using only the 1989 to 2000 data and that any similarities between computed harvest and harvest data past the year 2000 are an indication that the model is capturing historical population dynamics. Furthermore, since we have assumed the same uniform harvest rate in each region that only varies by season, the computed harvest values only capture the general behavior of the data rather than closely approximating it, as shown in Figure 3b. For the purposes of estimating the nonharvest parameters we only wanted to mimic general historical population trends and thus we were satisfied with the resulting values. We used these results to estimate values for the survival, birth and movement parameters.

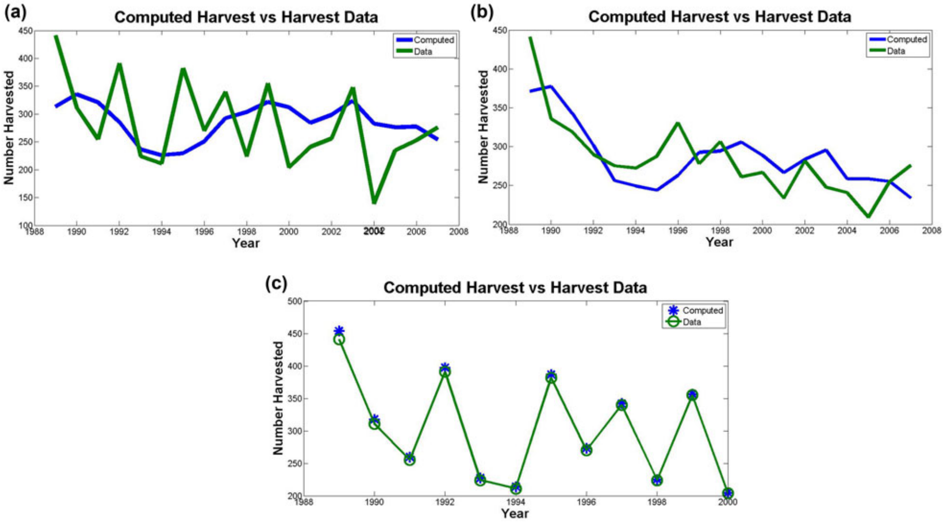

FIGURE 3. Each figure displays total computed harvest values produced by the model compared with the harvest data provided by GSMNP: (a) depicts a model simulation using parameter values obtained from the trials that used 1410 as an initial population. (b) displays the output from the same parameter values compared to a smoothed version of the harvest data where yearly values were derived from a three year average surrounding each data point. (c) was produced from a model simulation using yearly harvest values for each region and illustrates how we are able to accurately quantify historical harvest efforts.

In reality, the Park's harvesting levels and locations vary week-to-week or even day-to-day. In fact, when using the estimated nonharvest parameters in a similar optimization scheme but instead varying the harvest values by region and by year, we are able to match the harvest data nearly exactly as illustrated in Figure 3c. These harvest values more closely match historical efforts, and thus from our interest in evaluating the importance of the control program, the rest of our analysis will be based on this set of parameters.

Although the Park has had a control program in place for over 50 years, little is known about the effectiveness of their efforts. Since a significant amount of time and money is spent on the control program throughout the year, there is question to whether there should be fewer resources spent harvesting feral hogs in GSMNP. Using the yearly harvest values for each region we derived, we are in a unique position to evaluate what would happen if harvest efforts were reduced for a period. The values were shown to match the data very closely (see Figure 3c). To evaluate the effects of having applied a different level of effort from 1994 to 2000, we tested what would happen if the Park had either reduced or increased the harvest rates by 50% or 100%. The results are shown in Figure 4a and illustrate that historical Park efforts have been successful in limiting the size of the population. As

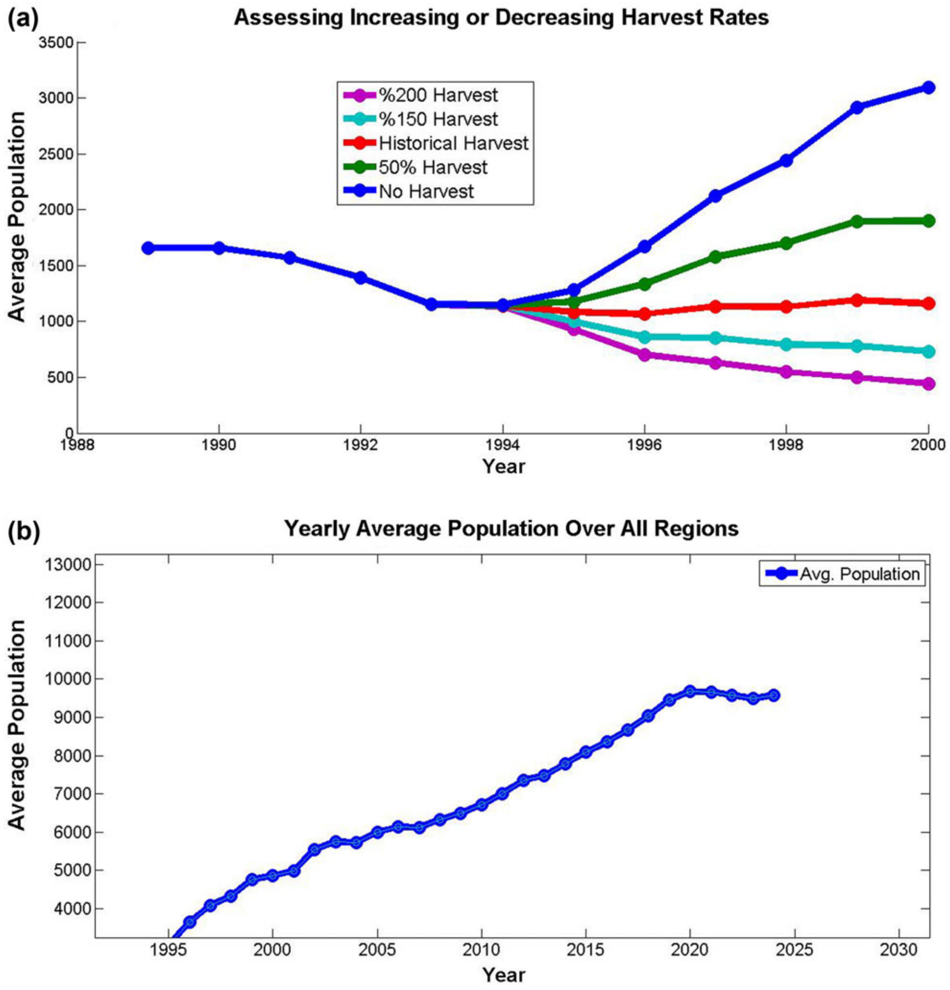

FIGURE 4. Both figures began with, and use parameter values derived from, an initial population of 1410. (a) shows the effects varying the estimated harvesting rates from 1994 to 2000. In just 6 years, decreasing the harvest rate can result in an increase in population by as much as 260%. The model shows that doubling the harvesting rate over 6 years could reduce the population by over 60%. (b) illustrates that without harvesting the population could increase to nearly 10,000 feral hogs.

Figure 4a shows, eliminating harvesting altogether for a 6-year period would result in an increase in the population by much as 260%. On the other hand, doubling harvest rates from 1994 to 2000 could have reduced the historical population by more than 60%. Supposing that the control program never existed and that instead the population was left to grow, the model levels off at a total population of nearly 10,000 individuals in and around GSMNP. This apparent carrying capacity is depicted in Figure 4b and was derived by a model simulation without harvest starting in 1988.

As previously mentioned, an IBM was recently constructed for feral hogs in GSMNP. Our project and Salinas et al. [2015] estimate a similar annual harvest rate, predict a similar population level and both emphasize the importance of the control program. Although based on similar data, the two models also differ in a number of ways. For instance, the IBM implements a density-dependent form of movement while the metapopulation model mimics believed movement patterns through mast-dependent and seasonal forms of movement. The distinctions in movement characteristics could account for the differences in estimated population growth and carrying capacity for feral hogs in GSMNP that the two models predict in the absence of harvesting. A telemetry study is currently being conducted by GSMNP where feral hogs are being tracked via GPS collars. Information from this project can be used to refine movement mechanisms in both models to best reflect the system.

The structure of the metapopulation model also allowed us to carefully estimate parameters against available data, providing an accurate global perspective of the system. Although both models allow acorn availability to influence mast-dependent responses in birthrates and movement rates, the metapopulation model is well suited to handle population level responses with limited empirical data and thus may better model survival. While the IBM reveals how individual behavior influences the population as a whole, the metapopulation model captures large scale dynamics and trends.

5. Conclusions and future work. We formulated a metapopulation model for feral hogs in GSMNP. The parameters in this discrete model (in space and time) were carefully estimated using data involving harvest (of feral hogs), hard mast, understory, and geographic size of the regions. Seasonal movement and appropriate demographic processes were included.

The structure of our model was shown to accurately estimate the amount of feral hogs harvested in the Park over the last 35 years. We can conclude that if the Park would reduce harvest levels in the future, the feral hog population can increase dramatically with an expected result of further habitat damage and negative impact on other species. Park officials recognize that these results emphasize the need to continue the control program. Seeing how their efforts has reduced the population also provides support for future funding.

The strong dependence of estimating harvest rates on an uncertain initial population is a limitation of our work. We used expert opinion from Park officials to guide our choices about the initial population levels and other features of the model. Also, though we only consider births in January, a second birth pulse in the summer has been documented in feral hogs in the event of extreme food conditions (Johnson et al. [1982]). This behavior was not deemed important to general dynamics and was thus not included in this model.

With the model in place, we are in position to make use of the available data to learn more about feral hog behavior in the GSMNP. More specifically, we intend to consider a cost-effective management strategy and analyze potential disease threats that feral hogs pose to the area. These endeavors will be aided further by new data resulting from ongoing related research and help guide control efforts.

One challenge in modeling feral hogs is that each population behaves differently depending on the local environment. Limited accessibility to most areas of the Park has deterred locating, tracking, eradication efforts, and the general study of the feral hogs in this region. However, three new grants were awarded related to feral hogs in GSMNP. Two of the grants provided funds to continue with a control and disease monitoring program in GSMNP that has provided the most current data for feral hogs locations (Stiver [2011, 2012b]). The third grant will fund a study in which the location and movement patterns of feral hogs in GSMNP and Big South Fork National River and Recreation Area. Feral hogs will be tracked using radio collars, which will provide more detailed information related to the movement of feral hogs throughout the Park (Stiver [2012a]). These unprecedented data about the movement and home range of feral hogs in GSMNP can be used to include more detailed movement structure in future models.

Since the implementation of the feral hog control program, over 13,000 harvest entries have been logged that can provide insight into the types of habitat in GSMNP that feral hogs prefer and can be used to determine potential locations of the invasive pest in the Park. Since the data we have are presence data only, they can be used to create a habitat suitability map via an Environmental Niche Factor Analysis (ENFA) or Maximum Entropy theory. Both approaches require only presence data and aim to find the relationship between known feral hog locations and environmental factors that drive the population.

This research related to feral hog dynamics in GSMNP provides the framework necessary to conduct additional analyses. To improve the efficiency of their efforts, we intend to use the model to consider an optimal harvest strategy. This may include specific regions, months, and strategies that will maximize harvest yields. A habitat suitability map will contribute to this process as it illustrates areas in the Park that have a high probability of containing feral hogs.

Another meaningful project related to feral hogs in GSMNP is to consider the threats and implications of feral hogs as a vessel for pseudorabies (Cavendish et al. [2008]). Pseudorabies poses significant threats for animals such as canines and commercial livestock (Cavendish et al. [2008]). Since feral hogs are currently the only reservoirs of pseudorabies, they are the only source of future outbreaks Stallknecht and Howerth [2001]. A disease analysis will involve a compartmental model with spatial and temporal elements while considering the possibility of pseudorabies suddenly appearing in far reaches of the Park as a result of illegal feral hog release by hunters.

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