An individual-based model for black bears in the southern Appalachians

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Abstract

We describe an individual-based model for black bears (\textit{Ursus americanus}) in the southern Appalachians, which consists of Great Smoky Mountains National Park (GSMNP), Cherokee (CNF), Pisgah (PNF), and Nantahala (NNF) national forests, and most of eastern Tennessee and western North Carolina. This model incorporates fall hard mast variation which determines black bear reproductive success and movement. We evaluated the model with existing empirical data on harvest, year-to-year variation, and reproductive dynamics. To demonstrate the potential use of the model for spatial control, we tested an alternative harvesting strategy in a subregion of the model to address concerns regarding potential bear-human encounters. This model has the capability to provide insight into the hard mast-driven dynamics of the black bear population and test the effectiveness of different harvesting strategies.
strategies.

*Key words:* Individual-based, Black bear, Hard mast, Spatial control, Harvest management, Bear-human encounters

1. Introduction

The establishment of Great Smoky Mountains National Park (GSMNP) in the mid-1930s created a protected environment for many over-exploited species. One of the species that benefited was the black bear (*Ursus americanus*), which became a source population for the surrounding region. GSMNP is surrounded by numerous small tourist towns and sprawling suburban areas, and the human population surrounding GSMNP has been increasing, particularly during the last three decades. This change in human population and increase in the black bear population has led to an increase in bear-human encounters and nuisance incidents (Delozier and Stiver, 2005).

There are two principal reasons bears leave GSMNP and other protected regions: to establish a home range and search for food. During summer, sub-adult bears leave their mothers and find areas where they can establish home ranges. Female offspring usually establish home ranges near those of their mother, whereas male offspring disperse further (Rogers, 1987; Costello, 2010). During the fall, bears may move greater distances searching for food to build up fat reserves for hibernation (Quigley, 1982; Carr, 1983; Rogers, 1987). Their primary fall food source in the southern Appalachians is hard mast, principally acorns (Beeman and Pelton, 1970; Eagle and Pelton, 1981; Brody and Pelton, 1988), which can vary from year to year. During years of hard mast failure, bears may move out of protected areas in search of
food. Variation in hard mast also affects female reproductive success. If a female is unable to gain sufficient weight, lactation may be insufficient to feed her litter, resulting in cub mortality during the denning period (Eiler et al., 1989).

Bear conflicts are not unique to the southern Appalachians. Throughout the range of the species, the successful recovery of black bear populations, coupled with urban sprawl, has resulted in increased nuisance activity (Timmins, 2005; Dente and Renar, 2005; Martin and Steffen, 2005; Ryan, 2005). The importance of public opinion on wildlife management practices is well documented (Decker and Chase, 1997), particularly if the public perceives a species as dangerous, and they may be less and management agencies may be less willing to promote conservation issues related to a particular species if the public perceives it as dangerous. One option wildlife managers have is to control wildlife populations through sport hunting, thereby reducing the populations and the potential for harmful interactions. However, information on optimal harvest strategies to carry out such controls is lacking.

Models are a powerful tool in the development of management strategies (Miller, 1992; Schoen, 1992; McCullough, 1996). Most of the models that have addressed black bear management have been deterministic Leslie-type models accounting for demographics (Yodzis and Kolenosky, 1986; Burton et al., 1994; McCullough, 1996). Such models are not able to address space explicitly and are therefore limited in their management implications. Wiegand et al. (1998) developed a spatially explicit simulation model to determine the risk of extinction of brown bears (Ursus arctos) in Spain. However, this model did not include intra-year dynamics of the bear population, which
is vital to assess management strategies.

Understanding the year-to-year dynamics of black bears, or any species targeted for management, is vital to developing an effective harvesting strategy. Harvest management, composed of effort, location, and time, is a spatial control problem. Each of the components of harvesting can affect the population in different ways. Therefore, a model must have enough detail to account for these effects. We address this issue by developing a spatially-explicit individual-based model (IBM) for black bears in the southern Appalachian region. IBMs involve modeling the life stages of each individual via a set of rules based on life history data of the organism (DeAngelis and Gross, 1992; Grimm and Railsback, 2005). To demonstrate the potential of the model, we explore the effects of fall hard mast on population dynamics and the effects of allowing hunting in a state-designated bear sanctuary on black bear abundance and potential bear-human interactions.

2. Model Description

This section follows the protocol for describing IBMs proposed by Grimm at al (2006).

2.1. Purpose

The main purpose of the model is to provide managers with a tool applicable for assessment of management activity impacts on the dynamics of the black bear population in the southern Appalachians. The model allows many facets of the population to be studied. This paper focuses on the description of the model, its evaluation, and an example of how the model can be used
as a tool for spatial control of harvesting to minimize potential bear-human encounters.

2.2. State Variables and Scale

State variables for the model can be divided into two groups: those for each individual bear and those for the landscape (Table 1). The region was divided into 450-m x 450-m cells with an extent of 620 x 390 cells. This spatial resolution was chosen because it was large enough to reduce the effects of the low circuitous nature of bear movements (Quigley, 1982; Carr, 1983), yet small enough to capture day-to-day variation. Various map layers were used in the model (Figure 1) to allow for population analysis of various spatial subdivisions, including GSMNP and national forest regions, sanctuary and non-sanctuary lands, and human-populated areas.

2.3. Process Overview and Scheduling

In simplest terms, the black bear life cycle can be described by seasonal activities: summer mating, fall foraging, winter denning and birthing, and spring emergence. To capture within-season details, we modeled the population with processes on two temporal scales, daily and seasonal time steps. Daily time step components are shown in Figure 2. Reproduction and denning were modeled as seasonal events. A more detailed discussion of the two temporal scales is presented in the Submodel section.

2.4. Design Concepts

2.4.1. Emergence

Population-level dynamics emerge from the individual responses to food availability, which influence movement and reproductive success.
2.4.2. Adaptation

The model assumes bears adapt their movements based on two factors: food availability and proximity to older bears. These factors are described in detail in the movement submodel.

2.4.3. Sensing

Individual bears can sense the amount of food available around them up to their maximum daily movement range. They also are aware of other bears in the vicinity (see Submodel section).

2.4.4. Interaction

Two forms of direct interaction between individuals are included in the model. Mating occurs during the summer and is determined by males finding nearest females that are in estrus. Bear movement is partially determined by interaction tolerances in which younger bears are less likely to go to a cell with older bears. These tolerances are differentiated by sex and described in detail in the movement submodel.

2.4.5. Stochasticity

All daily and seasonal event probabilities occur based on comparisons using a pseudorandom number generator. The inherent variation in the model was assessed for each scenario through 20 iterations of the model with different seeds for the pseudorandom number generator. The number of iterations was chosen based on a comparison of the 95% CI for population size in GSMNP which showed significant diminishing returns after 20 iterations.
2.4.6. Observations

The model can produce numerous data sets amenable for comparison to field observations. To evaluate the model, we used GSMNP population size, Tennessee and North Carolina harvest totals and the fraction of females mating and weaning. To test the potential impacts of alternative harvesting strategies, we examined total population size, number of bears in human populated areas, and spatial locations of bears.

2.5. Initialization

Although cubs are born in late winter, we assumed a June 1 start date for convenience in modeling reproduction because cubs who have been with their mothers for over a year become independent by this time and estrus has yet to begin. Individual bears were randomly placed in cells, within GSMNP and national forest boundaries, that had fewer than ten people per km$^2$. We estimated initial densities for each region based on empirical data from the late 1970s (bears/cell): 0.15 (GSMNP), 0.03 (CNF), 0.06 (PNF), and 0.08 (NNF) (Mclean and Pelton, 1994; Powell et al., 1997).

Because the data used to calibrate the model were from the late 1970s and early 1980s and the most reliable empirical data on the population dynamics are from 1990 to the mid 2000s (Clark et al., 2005), the model was initiated in 1980 but model results were not considered until 1990. The 10-year model initialization period also provided spatial and demographic heterogeneity in the population.
2.6. Submodels

2.6.1. Mast Layer

In the southern Appalachians, soft and hard mast are black bears’ principal food sources for most of the year (Beeman and Pelton, 1970; Brody and Pelton, 1988; Eagle and Pelton, 1981). Soft mast, which includes berries and other fleshy fruits, provides most nutrition during summer. Hard mast, which includes acorns and other dry fruits, provides vital nutrition during the fall. Bears use hard mast to gain fat reserves for the winter denning period. Fall hard mast failures occur, on average, every four to five years (Koenig and Knops, 2000). It has been hypothesized that years of above average soft mast abundance can compensate for hard mast failures (Inman and Pelton, 2002). There were no data on the variability of soft mast in the region, so a constant soft mast availability was assumed.

Hard mast availability was simulated using a vegetation map layer that included nine forest types and one non-forest type (urban). Kilocalories (kcal) of available food throughout the year were estimated for each vegetation class using data derived for the northwestern section of GSMNP in 1995 (Inman and Pelton, 2002). The available kilocalories were updated every 2 weeks throughout the year. Because 1995 was an average fall mast year (Inman and Pelton, 2002), the data were scaled to approximate maximum mast availability (Table 2). Mast availability per cell was estimated as follows:

\[
Calories(i, j)[t] = Calories(i, j)[t - 1] + Cal_{Max} * Cal_B * Mast_{level}
\]

(1)

where:
• $i, j$ designate the coordinates of the cell.

• $Cal_{Max} = Calories_{veg\_type}[month_t]/2$, represents the number of kilocalories of the vegetation type in cell(i,j) for the month of time $t$. It is divided by 2 because mast is replaced every 14 days in the model.

• $Cal_B$ is the proportion of the kilocalories available to bears. Between 70 - 90% of mast is used by birds and small mammals (Darley-Hill and Johnson, 1981; Steiner, 1996; Inman and Pelton, 2002). For the summer, we assume 30% is available, whereas only 10% is assumed to be available during the fall.

• $Mast\_level = \left(Mast_{year(t)} + \text{random\_unif}\right)/10$ represents the mast index value for that year. $Mast_{year(t)}$ ranges from 1 - 4. An index value of 1.0 represents a failure and 4.0 represents maximum mast production. Because no data were available on soft mast variation during summer, we assumed $Mast_{year(t)} = 3$. During a given masting event, not all trees produce the same amount of mast (Greenberg, 2000). Therefore, to allow for spatial variability, the actual index value in each cell is uniformly distributed between $[Index - 0.5, Index + 0.5]$. The number is then divided by 10 to represent the value as a proportion. For the data we represent in this paper, the following years were considered mast failure in GSMNP: 1992, 1997, and 2003.

Equation 1 does not represent the actual number of kilocalories in each cell. Instead, it is a metric of available food.
2.6.2. Movement

Bears have a hierarchical dominance structure in which older, larger males acquire home ranges that include the best food resources (Rogers, 1987; Powell, 1987). Older females have a similar advantage over younger females. Movement was modeled solely based on food availability and this hierarchical dominance structure. The model assumed bears move to cells with the most food. There are three components to bear movement: dominance, daily range, and seasonal territories.

Dominance was defined by age and differentiated by sex. A male could move into a cell if there were no older males within a one-cell radius, whereas females (and their cubs) could enter a cell if there were no older females in that cell (0-cell radius). The difference in this “tolerance” spacing between males (1-cell radius) and females (0-cell radius) is supported by data suggesting that females are more tolerant than males and often share home ranges with offspring (Quigley, 1982; Carr, 1983).

Each bear searched outwardly from its current cell. Males could move as far as four cells in one day, whereas females were limited to two (Quigley, 1982; Carr, 1983). If a bear was unable to find a suitable cell, it was randomly placed in one of the cells in its outer daily movement range. Because the cells are 450 m x 450 m, more than one bear can occupy the same cell. The movement rules allow for this because older bears can move to any cell despite the number of younger bears in it.

There are two seasonal movement patterns for black bears: Summer mating and Fall foraging. During the mating season, if a female is in estrus, the nearest adult male is moved to her cell to copulate. Once copulation occurs,
both male and female move to find food according to the above rules.

On June 1\textsuperscript{st} and September 1\textsuperscript{st}, positions of each sub-adult and adult are saved as a central location. As a bear moves closer to its maximum distance (eight cells for males, five for females) from this central location, the search region is skewed away from the maximum distance. For example, if a male is six cells east of its center, its search region in the x-direction was restricted to two cells to the east and four cells to the west (recall that males have a maximum search range of eight cells.). This implemented a restriction in uni-directional movement. When a bear reaches a cell at its maximum distance, the central location is reset to that point to allow for long distance movement, which has been observed in telemetry data (van Manen, 1994).

2.6.3. Update Food

The food bears eat during the year has been well studied (Beeman and Pelton, 1970; Eagle and Pelton, 1981), but the seasonal variation of the amount of food consumed is not as well documented. Because fall caloric intake is vital for reproductive success and the model only assumes variation in fall hard mast, the model keeps track of the food available during the fall only. A slightly modified version of Nelson’s (1980) monthly fall caloric intake estimates is used in the model. These values included (in kcal/day) 8,000 (Sept.), 10,000 (Oct.), 15,000 (Nov.), and 10,000 (Dec.). After movement, the corresponding amount of kilocalories was removed from the cell for each independent bear.
2.6.4. Update Food Reserve

Bear metabolic dynamics have been well documented (Brody and Pelton, 1988; Farley and Robbins, 1995; Hilderbrand et al., 1999; Maxwell et al., 1988; Pritchard and Robbins, 1990). Because most of the data are on bears in the western United States, which have a more carnivorous diet, we did not attempt to model the weight of each bear. Rather, the model keeps track of the net kilocalories stored.

\[
\text{Cal}_{\text{total}}(t) = \text{Cal}_{\text{total}}(t-1) + 0.4 \times \text{intake}(t) - (\text{cost}_{\text{mb}} + \text{cost}_{\text{move}}),
\]

where \( \text{cost}_{\text{mb}} = 142 \text{ kcal} \) is the daily metabolic energy loss (Eagle and Pelton, 1981; Brody and Pelton, 1988; Pritchard and Robbins, 1990; Farley and Robbins, 1995). The value 0.4 corresponds to the proportion of the consumed kilocalories that are converted to stored fat, also in kilocalories. It should be emphasized that this was an approximation to capture the general dynamics, not a specific estimate of actual kilocalories. Because of a lack of data on the actual metabolic cost of movement, we assumed \( \text{cost}_{\text{move}} = 1000 \text{ kcal} \).

2.6.5. Mortality

There are numerous sources of mortality for black bear. Ideally, it would be best to explicitly model each type of mortality. However, limitations in understanding the mechanisms of these mortalities makes modeling them difficult. We restricted the model to three types of adult mortality: natural, harvest, and other.

Natural mortality included deaths due to disease and other non-interactive forms of mortality. This mortality is applied to every sub-adult and adult
bear daily and is estimated to be 0.00002 per day (McLean, 1991).

Because old age is not assumed to be part of this mortality type, this rate is constant for every individual. The model assumes 20 years as a maximum age for bears and removes all bears that reached that age. This assumption was made based on limited data on the typical life expectancy of bears in the southern Appalachians.

The “other” category incorporated poaching deaths plus other unknown sources of mortality. However, poaching has likely declined in recent decades. The model assumed that the probability of poaching was greater outside federal lands. The probability was 0.0002 in GSMNP and national forests and 0.002 outside these areas (Mclean and Pelton, 1994). This mortality was implemented daily for all independent bears.

As mentioned previously, North Carolina and Tennessee had different hunting seasons. Western North Carolina had a constant season across all counties, from late October into mid-November, followed by the last two weeks of December. The Tennessee harvest season varied among counties, but we modeled the state season for all counties together; a one-week season at the end of September and a two-week season in early December.

Both states had a mosaic of bear sanctuaries where harvesting is prohibited (Figure 1). Harvesting was also prohibited in GSMNP. To approximate the size restrictions in harvesting (75 lbs in TN and 50 lbs in NC), we assumed bears three years and older can be harvested. Also, females with cubs were not harvested. Harvest rates were estimated at 12% for each state (Mclean and Pelton, 1994). The resulting daily harvest rates of 0.006 and 0.004 for Tennessee and North Carolina, respectively. These harvest rates
were implemented daily during each of the respective hunting seasons. In 2006, Tennessee introduced a longer archery season which was incorporated in the model by adjusting the dates of hunting and effort.

Cubs were not subjected to the mortalities mentioned previously. We assumed that mortality of a mother would result in mortality of her cubs. Cub-specific mortality was modeled during the denning period and spring. If a female did not consume enough calories to endure the denning period and early spring, she lost her cubs. This was modeled by decreasing the stored calories during denning based on the following equation:

\[
Cal(t) = Cal(t - 1) - \text{cost}_{mb} - 400 \times \text{num\_cubs},
\]

where \(\text{cost}_{mb} = 51 \text{ kcal}\). If \(Cal(t) < 80,000 \text{ kcal}\), then all cubs were lost. As before, this equation was estimated from data (Farley and Robbins, 1995), but it was primarily used to capture the dynamics of lactation costs of females.

2.6.6. Update State Variables

The update state variables function updated all the relevant state variables at the end of each day. These variables included age, denning days, days in estrus, and days weaning cubs. All the checks for timed variables occurred at this point. For example, if a female had mated, the gestation time was incremented by one. Once she reached the 220th day, she gave birth according to the probabilities mentioned in the next section.

2.6.7. Denning

Hibernation is a common strategy to survive winters in which food is in low supply (Watts et al., 1981). Winters in the southern Appalachian region
are not as long or as harsh as in the western U.S., resulting in a short hibernation period of approximately three and a half months. Bears usually enter dens from early December through mid-January. Consequently, for the model, den-entry dates were randomly assigned so that 70% of females entered dens during the first two weeks of December and the remaining 30% during the last two weeks. Males entered dens uniformly from the last two weeks of December through the first half of January. In the model, females denned for 110 days and males for 90 days (Eiler et al., 1989). These values were constant from year to year. Denning bears were not subject to harvesting or the “other” mortality function.

2.6.8. Reproduction

Reproduction in black bears is characterized by three distinct phases: mating, birth, and nursing. Mating occurs during the summer between mid-June and early August. Primiparity in females is most commonly age three, although two-year-olds have been observed mating. We assumed three years was the first age of reproduction. Starting dates for estrus were assigned to adult females without cubs on June 1st. The dates were distributed such that 30% started during the second half of June, 55% during the month of July and 15% during the first two weeks of August (Eiler et al., 1989). Females were in estrus for 14 days (Eiler et al., 1989) or until copulation took place. Once copulation had occurred, a gestation timer was started for the pregnancy. A 220-day gestation was assumed (Eiler et al., 1989) with all births occurring during the denning period. The model assumed a 75% probability for a successful birth to account for failed implantations. Litter sizes varied from one to four cubs with the following probabilities: $P(1) =$
$0.2, P(2) = 0.4, P(3) = 0.3, P(4) = 0.1$ (Eiler et al., 1989).

After den emergence, mothers nursed their cubs through the spring, summer, and the first part of fall. During the spring, the primary food source for bears are herbaceous plants, such as squawroot ($Conopholis americana$), which are generally low in nutrition. Cub mortality via low calories available to their mothers was still considered during this time. Equations 2 and 3 were used to account for the caloric decrease. Once summer began (June 1\textsuperscript{st}), it was assumed there was enough food for cub survival and caloric intake was no longer recorded.

Cubs are with their mother throughout the year and den with their mothers the following fall. By this time, cubs are no longer nursing and have developed their own fat reserves, and therefore, are not a metabolic burden to their mothers during denning. To model this phenomenon, cubs followed their mothers into denning and were abandoned the subsequent June 1\textsuperscript{st}. Those mothers were then assigned a new estrus date. All females that lost cubs, newborns or yearlings during the denning period (or spring) started estrus the following summer.

2.7. Implementation

The model was coded in C++ and compiled on a UNIX platform using g++. A model run involved 20 independent replications, each with different random number generator seeds. The resulting averages and 95\% confidence intervals were used to present the data (except for the spatial maps in which a single simulation was used to create the images).
3. Results

3.1. Model Evaluation

Three elements of a population that should be addressed when evaluating a model are magnitude, growth rate, and year-to-year variation. Given the large spatial extent and detailed demographic output, we considered all three elements.

We analyzed data from live trapped black bears in Great Smoky Mountains National Park using an open population estimator (Schwartz and Arnason, 1996) in Program MARK (White and Burnham, 1999) to estimate time-specific estimates of abundance. Figure 3 compares the 95% confidence intervals for the IBM (solid) and mark-recapture estimates for males and females in a sampling region in the NW quadrant of GSMNP. For males (A), both sets of data show large fluctuations in the population and an overall stable population. For females (B), both suggest smaller fluctuations and an overall increase in the population.

Figure 4 shows comparisons between empirical harvest data and model output. Because the model assumes a constant harvest rate and cannot capture the annual variation in hunting effort associated with hunter behavior, we took the three-year running average of the empirical data and compared it to the 95% confidence intervals for the model. Graph (A) shows the Tennessee harvest comparisons. The 1997 harvest data was a significant outlier relative to the rest of the harvest data. Because the model cannot capture that type of variation, we did not include it in the running average calculations. Although we did include it in the graph. The rapid increase in the number of bears harvested after 2005 in Tennessee is due to the addition of
an archery season and an extended dog-hunting season. The model incorporated these changes by adding the new time periods for harvesting and adjusting the harvest rate to account for the increased effort. Graph (B) compares North Carolina harvest data with the model. The results indicate that the model is capturing the magnitude of the harvest in both states.

The year-to-year variation in the population is driven by the effect of mast variation on reproductive success. Figure 5 compares model output with empirical estimates of female reproductive status during the denning period. The clear bars show the fraction of reproductively viable females that mated during the summer and are entering the denning stage. The hatched bars indicate the fraction of reproductively viable females that emerge from denning with cubs. The empirical data (*) indicate the fraction of visited den sites with cubs. Visits occurred during the late winter and early spring and averaged eight samples per year. Because the model is not designed to predict the exact timing of cub mortality during denning, we would only expect the empirical data to lie between the model bars.

3.2. Sensitivity and Robustness Analysis

Sensitivity analysis (SA) and robustness analysis (RA) are two methods for evaluating models. SA assesses how different parameter values affect model output. RA assesses if model output is consistent when parameter values are changed. If a parameter change causes a shift in magnitude, but maintains the overall dynamics (year-to-year changes) then the model is sensitive to changes, but robust. If a parameter change is not sensitive and not robust, it would imply that the overall magnitude is the same but there are differences in the year-to-year dynamics.
Figure 6 shows the SA and RA results for four sets of parameters that had the least empirical data. SA is depicted by the bars that show the average relative change in the GSMNP population compared with default values over time. RA was assessed by determining if the different parameter values caused any change in the year-to-year fluctuations. For example, if the default values for a three-year period involved growth, growth, and decline and the change in parameters resulted in growth, growth, and growth, the parameter change would be viewed as non-robust. Values that did produce changes are labeled with an asterisk (*).

3.2.1. Initial Population Size

The IBM starts with an initial population size of approximately 1,250 bears. The model was run with initial population sizes of 1,000 and 1,500 bears and compared with the default value. Over the 13-year period (1990 - 2002) in which data were collected, these alternative initial conditions resulted in less than a 5% change in the population averaged over time. The year-to-year dynamics of the population were not affected.

3.2.2. Fall Feeding Rates

In modeling the effects of fall mast failures on the reproductive success of females, a metric was established to track female caloric reserves. Although the daily consumption and metabolic and lactation costs were based on published data, some of the data were based on approximations. In particular, the daily consumption rates by Nelson (1980) may be controversial (E. Hellgren, pers. comm., 2004). The default rates correspond to an average of approximately 11,000 kcal/day. The model was run with four other
rates: 9,000, 10,000, 11,000, and 15,000. It was assumed that the rates were constant throughout the fall. The results show that 9,000 kcal/day leads to an essentially constant but low population size in which fall mast does not determine the population size (i.e., not robust). A constant consumption rate of 11,000 kcal/day was indistinguishable from the default rates. With a consumption rate of 15,000 kcal/day, the population decreased, on average, by 2% over the 13-year period. This was a result of bears needing more food than is available which effectively decreased the carrying capacity.

3.2.3. Movement and Interaction Tolerance

Movement in the IBM were based on food availability. Bears moved to the nearest cell with the most food. There were two components to this movement: daily movement range and interaction tolerance.

The default values for daily movement range were a 4-cell radius for males and a 2-cell radius for females (4/2). We compared the default values to 3 other sets of ranges: 2/4, 2/2, and 4/4. Female movement range was the most sensitive parameter, but the model was robust to those changes.

In modeling interaction tolerance, the model assumed a “safe” cell radius in which a bear can move into a cell. Results suggest that the model is highly sensitive to the female interaction value. There was a 25% drop in the population when the female interaction value was equal to 1 (default = 0). This increased spacing forced more females to emigrate from the park. This reduction in female bears resulted in a decreased effect of mast variation on the population (smaller density). Because data supports the smaller territorial association of female bears, the default assumptions provide a good representation of the system.
3.3. Example of Spatial Control

To look at the effects of alternative harvesting strategies on potential bear-human encounters, we projected a mast time series through 2022. In Figure 7, plot (A) shows the black bear population time series for the Pisgah bear sanctuary. The solid line corresponds to the base scenario in which we maintain the current harvesting regulations (no hunting in the sanctuaries) while the dashed line shows a scenario that allows hunting. Plot (B) shows the number of bears (summed over the year) in human-populated areas for the no hunting (circle) and hunting (asterisk) strategies. The high circle values correspond to fall mast failure years. Note that opening the sanctuary to hunting eliminated the bear-human encounters by decreasing the population to a sustainable level.

The model is also capable of displaying the spatial effects of alternative harvesting scenarios. Figure 8 shows the location of bears in a day in early November of a subregion of the model area. The subregion includes GSMNP, most of Nantahala National Forest, and a section of the Pisgah National Forest that is just west of Asheville, North Carolina, which contains the Pisgah bear sanctuary. The three maps show the spatial distribution of bears during a good (2014) and poor (2016) mast year for the base scenario. The black dots indicate at least one bear in that cell. Note the increase in bears outside GSMNP and in human populated areas (green) during the poor mast year. The third image shows how implementing a strategy that allows hunting in sanctuaries (e.g., Pisgah bear sanctuary, circled region), can have a significant effect on the number of encounters (there are no bears in human populated areas around the sanctuary). These are not meant to
suggest exact numbers or locations of bears during mast failure years, only
to represent a difference between abundant mast and mast failure years.

4. Discussion

4.1. Model Accuracy

We created an IBM of the black bear population of the southern Ap-
palachians to assist in the analysis of some of the growing concerns for this
population, particularly bear-human interactions. The flexibility of the IBM
allowed us to evaluate the model with the available empirical data sets. Based
on these evaluations, we conclude that the size, growth, and dynamics of the
model are realistic representations of population dynamics.

Despite the very encouraging evaluation results, the model has many
limitations. Two elements in the model with little empirical backing were
movement and caloric dynamics. We did not attempt to model all aspects
of bear movements explicitly. The movement rules in the model focus on
the effective movement dynamics for food consumption. Because there is
substantial home-range overlap among black bears (van Manen, 1994), the
spacing assumptions in the model seem to capture the general dynamics of
movement. The metabolic dynamics of reproductive females during fall are
a generalization of the actual dynamics. The lack of data for black bears
with similar diets and limitations in estimating mast availability led to these
simplifying assumptions. At some point between the onset of denning and
early summer movements, substantial cub mortality can occur, especially
after fall mast failures. Given the comparisons with empirical data not used
in developing the model or its parameters, we argue that our assumptions
are acceptable for applications of the model similar to the situations we investigate.

4.2. Model Output

Models are often used for prediction. IBMs have the additional capability of filling gaps in data to elucidate mechanisms for population dynamics. Managers know that Fall hard mast variation is the main driver of black bear population dynamics in the southern Appalachians, and limited data suggests that fall mast affects movement and reproductive success. Our model was able to provide further insight into how fall mast affects the black bear population.

Figure 3 suggests a two-year decline in the population after a fall mast failure. The initial decline is caused by the movement of bears outside GSMNP to search for food. The fraction of these bears that return to GSMNP is unknown. The IBM can be used to extract life history data, like demographics, from these migrating bears and provide insight into how many of them return. The second decline is associated with the loss of cubs during the denning period following the mast failure. Because there is no new cohort, the population declines, which becomes evident the second year. Because most females will lose their cubs in years of severe mast failures, females are able to reproduce again in the following summer. These females, coupled with the females who just let their yearlings go, will all go into estrus that summer resulting in reproductive synchrony. This has been seen empirically (Figure 5). The effect is to produce a new large cohort three years after a mast failure. Because of mortality, this synchrony is dampened over time until the next hard mast failure. The IBM can be used to explore the long
term effects of these short shifts on the population dynamics.

4.3. Model Applications

We demonstrated how the model can be used to look at the effects of harvesting strategies on potential bear-human interactions. We focused on how opening a bear sanctuary (Pisgah) to hunting would not eradicate the population, but would maintain it at a level that would reduce potential bear-human encounters. The IBM can be used to address the effectiveness of individual sanctuaries with respect to size and location. For example, what is the minimum size for a sanctuary so that it can maintain a source population, or is an effective sanctuary size a function of its proximity to another sanctuary? More specifically, spatial control problems related to the location, magnitude, and timing of harvesting can be tested using the IBM.

Because of the versatility associated with IBMs, many other issues can be addressed with this model. For a long-term perspective, the model can be used to investigate how global warming might affect the black bear population via changes in mast production. The model can also give managers better insights into the population dynamics of the black bear population with emphasis on demographics and movement among regions.

5. Acknowledgements

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References


of extinction for the brown bear in the Cordillera Cantabrica, Spain. Ecol. Monogr. 68 (4), 539–570.


Figure 1: The eastern Tennessee and western North Carolina region used in the model.
Figure 2: Flow diagram for the model. Note that reproduction events take place in different compartments: Estrus (Update Indices), Mating (Movement), Gestation (Update Indices), and Births (Denning).
Figure 3: (A) 95% CIs for POPAN population estimate for males in the NW sampling region of GSMNP(Dash-dotted) and IBM output (solid line) and (B) corresponding female data.
Figure 4: Model comparisons with empirical harvest data (IBM (-), Data (*)): (A) Tennessee harvest and (B) Western North Carolina harvest. Upper and lower lines correspond to 95% confidence intervals for the IBM. Three-year running average was used for the empirical data. The clear dot in the Tennessee harvest data (1997) corresponds to an unusually high harvest year relative to its neighbors and was not used in the three-year running average.
Figure 5: Model output of the proportion of female bears that have mated during the onset of denning (solid bar) and proportion of female bears weaning by early summer (hatched bars). Empirical data on the proportion of females with newborn cubs based on den surveys are indicated by (*). If the empirical data falls between the solid and hatched bars, that proportion of females with cubs existed in the model at some point between the denning season and late spring.
Figure 6: Sensitivity and robustness analysis for four elements of the IBM. (A) Initial population size, (B) Fall feeding rate, (C) Daily movement range for each sex, and (D) Female "safe" cell radius. Bars indicate the average relative difference of new parameter values to default values for the GSMNP population. Asterisks (*) indicate that the new parameter values caused changes to in the year-to-year dynamics of GSMNP population. Change was defined as one or more differences in year-to-year dynamics (See text for more details).
Figure 7: Simulated time series of the Pisgah bear sanctuary (A) black bear population and (B) annual sum of bears in human-populated areas. The solid line / circles correspond to the base scenario of continuing the current practice of no hunting in the sanctuaries. The dashed line / asterisk correspond to an alternative scenario of allowing hunting in the sanctuaries. 2016 and 2022 correspond to mast failure years.
Figure 8: One-day snapshots in November of back bear locations in a subregion of the model that includes GSMNP, NNF and the southern part of PNF including the Pisgah bear sanctuary (circled region). The Base 2014 map shows bear locations during a good mast year under the current harvesting strategy. The Base 2016 map shows bear locations during a poor mast year under the current harvesting strategy. Note the increase in the number of bears in human populated areas. The Alt2 2016 map shows bear locations in a poor mast year under a strategy in which hunting is allowed in the bear sanctuaries (but not in GSMNP). Note the reduction in bears in human populated areas, particularly the region of the Pisgah bear sanctuary.
Table 1: State variables for the model divided into individual and landscape level designations.

<table>
<thead>
<tr>
<th>State Variable</th>
<th>Units</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Individual Bears</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age</td>
<td>Days</td>
<td>Bear’s age in days</td>
</tr>
<tr>
<td>Sex</td>
<td>M/F</td>
<td>Determined at birth with 1:1 ratio</td>
</tr>
<tr>
<td>Location</td>
<td>(x,y)</td>
<td>Coordinates based on cell location</td>
</tr>
<tr>
<td>Denning flag</td>
<td>0/1</td>
<td>Flags a denning individual</td>
</tr>
<tr>
<td>Denning days</td>
<td>Days</td>
<td>Daily counter to determine den emergence (see text)</td>
</tr>
<tr>
<td>Estrus flag</td>
<td>0/1</td>
<td>Flags a female in estrus</td>
</tr>
<tr>
<td>Estrus days</td>
<td>Days</td>
<td>Daily counter to determine mating (see text)</td>
</tr>
<tr>
<td>Weaning flag</td>
<td>0/1</td>
<td>Flags a female weaning cubs</td>
</tr>
<tr>
<td>Fall caloric reserves</td>
<td>kilocalories (kcal)</td>
<td>Food intake minus kilocalories burned (see text)</td>
</tr>
<tr>
<td>ID number</td>
<td>Integer</td>
<td>Non-repeating integer values to ID individuals</td>
</tr>
<tr>
<td>Mother’s ID</td>
<td>Integer</td>
<td>ID of an individual’s mother</td>
</tr>
<tr>
<td><strong>Landscape cells</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>State</td>
<td>Integer</td>
<td>Tennessee or North Carolina</td>
</tr>
<tr>
<td>Region</td>
<td>Integer</td>
<td>GSMNP or one of the National Forests (see Figure 1)</td>
</tr>
<tr>
<td>Sanctuary</td>
<td>Integer</td>
<td>Identifies whether a cell can be hunted</td>
</tr>
<tr>
<td>Human population</td>
<td>( \frac{People}{km^2} )</td>
<td>Human population density</td>
</tr>
<tr>
<td>Vegetation class</td>
<td>Integer</td>
<td>Vegetation type for each cell (See Table 2)</td>
</tr>
<tr>
<td>Kilocalories</td>
<td>kcal</td>
<td>Kilocalories available minus amount consumed (see text)</td>
</tr>
<tr>
<td>Bear Population</td>
<td>Integer</td>
<td>The total number of bears in a cell</td>
</tr>
</tbody>
</table>
Table 2: Maximum kilocalories (x1000) available per cell for each month and vegetation type. January-May are not included because black bears eat mostly squawroot, which is not limiting and has not been measured in association with vegetation classes.

<table>
<thead>
<tr>
<th></th>
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</tr>
</thead>
<tbody>
<tr>
<td>None</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Spruce Fir</td>
<td>0.00</td>
<td>0.00</td>
<td>891</td>
<td>3,080</td>
<td>607</td>
<td>0.00</td>
<td>0.00</td>
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<tr>
<td>N. Hardwood</td>
<td>0.00</td>
<td>81.0</td>
<td>526</td>
<td>1,880</td>
<td>769</td>
<td>547</td>
<td>344</td>
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<tr>
<td>C. Hardwood</td>
<td>6480</td>
<td>830</td>
<td>324</td>
<td>5,060</td>
<td>5,630</td>
<td>4,780</td>
<td>3,360</td>
</tr>
<tr>
<td>Mesic Oak</td>
<td>81.0</td>
<td>283</td>
<td>405</td>
<td>3,680</td>
<td>4,050</td>
<td>202</td>
<td>0.00</td>
</tr>
<tr>
<td>Tulip Pop.</td>
<td>324</td>
<td>101</td>
<td>182</td>
<td>1,090</td>
<td>1,540</td>
<td>1,300</td>
<td>810</td>
</tr>
<tr>
<td>Xeric Oak</td>
<td>162</td>
<td>405</td>
<td>405</td>
<td>2,100</td>
<td>2,790</td>
<td>1,860</td>
<td>972</td>
</tr>
<tr>
<td>Oak-Pine</td>
<td>162</td>
<td>562</td>
<td>567</td>
<td>1,540</td>
<td>1,780</td>
<td>1,380</td>
<td>648</td>
</tr>
<tr>
<td>Pine</td>
<td>324</td>
<td>324</td>
<td>324</td>
<td>1,820</td>
<td>2,390</td>
<td>1,620</td>
<td>963</td>
</tr>
</tbody>
</table>