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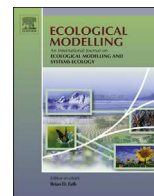
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# An individual-based model for southern Lake Superior wolves: A tool to explore the effect of human-caused mortality on a landscape of risk



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## ABSTRACT

Gray wolves (*Canis lupus*) have complex life-histories due, in part, to mating systems that depend on intra-group dominance hierarchies set within an inter-group (pack) social structure linked to philopatric territories. In addition to this spatially oriented social structure, mortality risk associated with interactions with humans varies spatially. We developed an individual-based spatially explicit (IBSE) model for the southern Lake Superior wolf population to better capture the life-history of wolves in a harvest model. Simulated wolves underwent an annual cycle of life-history stage-dependent mate-finding, dispersal, reproduction, and aging on a simulated landscape reflecting spatially explicit state and water boundaries, Indian reservation boundaries and ceded territories, wolf harvest zones, livestock depredation areas, and a spatial mortality risk surface. The latter 3 surfaces were linked to mortality events for simulated wolves. We assessed our IBSE model and conducted a sensitivity analysis of the most uncertain parameters with a categorical calibration of patterns observed at the individual, pack, population, and landscape level. We found that without recreational harvest, the Wisconsin wolf population grew to an average carrying capacity of 1242 wolves after 50 years and breeding pairs persisted for a mean 1.8 years. We simulated 6 recreational harvest scenarios with varying rates and timings of harvest and assessed effects on population size, pack sizes, age ratios, dispersal and immigration rates, and breeding pair tenures of the Wisconsin wolf population. The simulated harvest with rates of 14% which corresponded to the 2012 harvest in Wisconsin reduced the populations 4% in the first year of harvest and equilibrated to the pre-harvest population size after 20 years of harvest, on average. A 30% harvest rate across the simulation on average reduced the populations by 65% after 20 years with some populations going extinct before 100 years. In general, harvest increased the proportion of pups in the simulated populations and decreased breeding pair tenure. Targeted lethal control was more effective than harvest for reducing the number of wolves near known livestock depredation sites. Our model facilitates prediction of important population patterns that is simultaneously dependent on complexities associated with spatially structured life history and mortality.

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**Abbreviations:** IBSE, individual-based spatially explicit; SLS, southern Lake Superior referring to Wisconsin and the Upper Peninsula of Michigan; WHZ, wolf harvest zone.

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## 1. Introduction

Wildlife populations experience life history events that have seasonal and spatial patterns. Animals that live in areas with higher road density may have a higher risk of death by vehicle collision, and in many cases offspring enter the population as a birth pulse in the spring (Packard, 2003). This variability is important to consider when tracking changes in a population throughout the year and to understand how different mortality sources affect the population. However, many population-based models currently used often do

not capture the seasonal life history events that drive population dynamics (Gotelli, 1995). In these cases, individual-based modeling is an excellent way to integrate seasonal and spatial life history events to gain a better understanding of the population properties that emerge because of the decisions and behaviors of individuals (Grimm and Railsback, 2005; Macal and North, 2010).

Individual-based modeling is increasing in ecology to answer pragmatic questions and to explore ecological theories (Grimm and Railsback, 2005). In populations with complex social structures, population prediction can be especially difficult because individuals contribute differently to the population depending on their social role. Gray wolves (*Canis lupus*) have a social structure where breeding pairs and their offspring make up packs (Mech and Boitani, 2003). Because not all wolves are breeders, the population effect from the death of a wolf depends on that wolf's social status, the time of year, and the size of the population. The death of a pregnant female wolf would reduce population recruitment while the death of non-reproductive yearling would have no effect on population recruitment in the next year beyond its own contribution to overall mortality. Concerning the time of the year when a wolf death occurs, the death of a potential breeder before breeding season may or may not have a population effect depending on whether there is time for replacement of that breeder (Brainerd et al., 2008). All of these population effects are more pronounced at small population sizes because of demographic stochasticity and possible Allee effects (Berec et al., 2001). With individual-based models, individual differences can be modeled explicitly leading to a more realistic population model.

Individual-based models are sometimes used to understand the effect of various management actions (Grimm et al., 2005). Anticipating the need for removal strategies of problem wolves from the growing Minnesota wolf population, Haight et al. (2002) developed an individual-based model to test the effect of three wolf removal strategies and the combinations of multiple strategies. This individual-based model provided guidance to managers on wolf removal strategies by showing that proactive removal of wolves in areas near farms reduced depredations, removed fewer wolves than the reactive strategy, and was the least costly strategy (Haight et al., 2002). In another example, an individual-based spatially explicit (IBSE) model was used to understand the effect of social structure on canid populations and evaluate coyote management strategies (Conner et al., 2008; Pitt et al., 2003). This IBSE model showed that spatially intensive removal of coyotes was longer-lasting and more effective than random removal of coyotes (Conner et al., 2008). These examples demonstrate the utility inherent in individual-based models and their use as realistic, practical, and theoretical tools.

An IBSE model, though complex, makes explicit assumptions that enhance model transparency (Grimm, 1999). IBSE models require less abstraction than population-based models and this makes them easier to conceptualize by different groups of people. Stakeholders interested in an issue can include science in their discussions through IBSE models that simulate different management scenarios (Bousquet and Le Page, 2004). However, it is important that IBSE models used to make management decisions are well-documented. This documentation should include model assumptions, parameter values, model assessment, sensitivity analysis, and model predictions over a range of scenarios (Bart, 1995; Thiele et al., 2014).

We developed an IBSE model to explore the effects of human-caused mortality sources on wolves in the southern Lake Superior (SLS) region. The purpose of our model was to understand how wolf colonization and distribution in the SLS region was affected by roads, agriculture, and different mortality sources linked to the landscape, political boundaries, and management. Our model provided a visual and quantitative tool to understand and predict wolf

population growth in Wisconsin. The model also enabled evaluation of spatially structured harvest scenarios on the Wisconsin wolf population. The Ojibwe (also known as Chippewa) Indians of northern Wisconsin hold rights to harvest of living natural resources, including wolves, both on and off of their reservations independent of state regulations. The Ojibwe tribes have different population and zone objectives than does the State of Wisconsin and our IBSE model allowed for the reconfiguration of zones and harvest rates to assess harvest effects from the tribes' perspective. Specifically, our objectives were to: (1) build and document a plausible IBSE model of the colonization of the Wisconsin and Michigan wolf population from resident Minnesota wolves, (2) assess the model and conduct a sensitivity analysis of uncertain parameters using observed patterns at the individual, pack, population, and landscape levels, (3) use the model to explore the effects of different types and timing of human mortality sources that occurred on different parts on the simulated landscape, and (4) demonstrate the use of the IBSE model as a platform for evaluating management proposals.

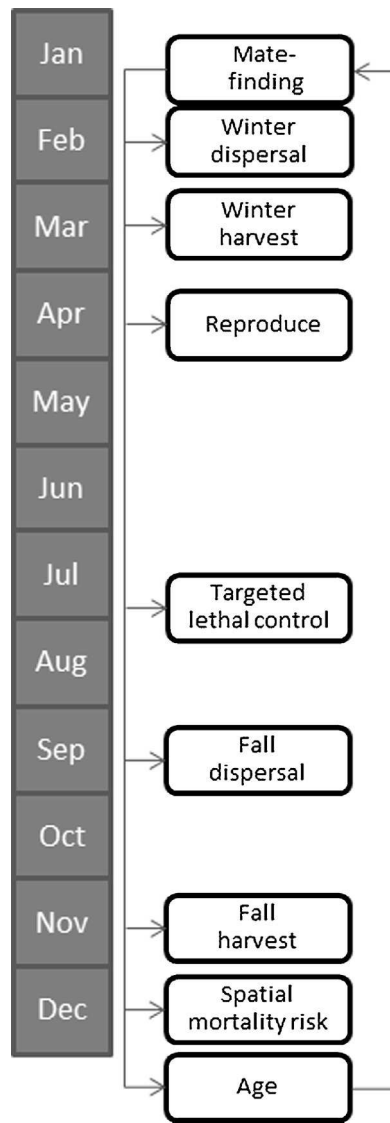
## 2. Materials and methods

### 2.1. Spatial mortality risk map

The IBSE model derived population parameters based on the collective behaviors and fates of individual wolves interacting with mortality risk that varied spatially. To create a spatial mortality risk component, we took a heuristic approach to scaling a simulated wolf's annual probability of mortality on the basis of road density and amount of agriculture in the SLS region (Wydeven et al., 2009b). The response variable was the dead ( $N = 195$ ) or alive ( $N = 15,134$ ) status of radio-telemetry locations for each of 195 wolves in Wisconsin's radio-telemetry database that were monitored consistently and found dead sometime during 1979–2012 (see Wydeven et al., 2009b for wolf capture, handling, radio-collaring, and tracking methods). We used logistic regression conditioned on a wolf's identity to remove unobserved individual heterogeneity (Gail et al., 1981).

We used roads and agriculture as predictors because these variables were selected from a suite of 16 variables (some highly correlated) in an analysis of the probability of wolf pack territory occupancy in Wisconsin by Mladenoff et al. (2009). We quantified road density ( $\text{km}/\text{km}^2$ ) and percentage of agriculture in 1 km buffers around each radio-telemetry location (see Appendix A for details on road and agriculture parameter derivation). We performed the conditional logistic regression in Program R (Version 3.0.1, R Development Core Team, 2013) using function 'clogit' in the 'survival' package (Therneau, 2013).

We divided a  $630 \text{ km} \times 554 \text{ km}$  landscape of the SLS region centered on Wisconsin into  $1 \text{ km}^2$  pixels, and obtained road density and percent agriculture covariates for each  $1 \text{ km}^2$  land pixel. Next, we obtained a fitted value for each land pixel from the conditional logistic regression model using Raster Calculator in ArcMap (Version 9.2, Environmental Systems Research Institute, 2009). These fitted values were the probabilities that an average wolf's radio-telemetry location would be a death location. Because the predicted probability values did not directly translate to annual mortality rates, we scaled these fitted values to reflect the annual mortality rate for wolves in Wisconsin (Wydeven et al., 2009b). The scaling reflected the estimated annual mortality rate for wolves in primary wolf range in Wisconsin (Stenglein, 2014). Therefore, the spatial mortality risk map reflected the majority of the annual probability of mortality for the simulated wolves (see Appendix A for details on spatial mortality risk surface model and use).



**Fig. 1.** Events of simulated wolves that occur during the calendar year in an individual-based spatially explicit model for wolves in the southern Lake Superior region, USA.

2.2. The IBSE model

We built an IBSE model of the SLS wolf population in NetLogo v. 5.0.1 (Wilensky, 1999) and describe it following the Overview, Design, and Details (ODD hereafter) protocol (Grimm et al., 2006, 2010). A full ODD description is provided in Appendix B and here we provide an overview of the overall structure and processes of our IBSE model. We assumed that observed population dynamics were primarily driven by the model rules that affected the behaviors and decisions of individual virtual wolves (hereafter, wolves). Wolves faced decisions on life stage events reflecting wolf phenology in the SLS wolf population (Fig. 1; Wydeven et al., 2009a). In addition to the phenomological realism, our model used the best-available data from the SLS wolf population to parameterize life stage events, including dispersal (Treves et al., 2009), litter size (Fuller et al., 2003), territory size, and pack size (Wydeven et al., 2009b).

Because of our interest in inferences about the SLS wolf population, and in particular the Wisconsin portion of that wolf population, we constructed a SLS landscape for simulated wolves (see Section 2.1). This particular SLS landscape focused our model

**Table 1**

Definitions and descriptions used in an individual-based spatially explicit model of wolves in the southern Lake Superior region, USA.

Definition	Description
Breeding pair	Two unrelated wolves of the opposite sex that resided on a pack territory and bred.
Breeding pair tenure	The number of years that the same breeding pair produced pups.
Breeding range	Areas of Minnesota, Wisconsin Wolf Management Units 1–5, and the Upper Peninsula of Michigan where the spatial mortality risk is <0.75.
Disrupted pack	Reproductive pack that lost at least 1 breeder to some mortality event.
Lone wolf	Wolf outside of breeding range or within breeding range but without parents or siblings within an 8 km radius.
Pack	2–12 wolves that resided on a pack territory.
Pack size maximum	The maximum number of wolves in pack above which there were not enough resources.
Single breeder	Wolf that was part of a breeding pair and remained on the breeding pack territory after death of its mate.
Targeted lethal control	Mortality event in Wisconsin that focused on killing wolves in depredation buffer areas.
Unrelated wolves	Wolves that were not parent–offspring, full siblings, or half-siblings.
Winter population count	Count of wolves in January of each year, after aging and before mate-finding.
Wisconsin winter population count	Count of the wolves in Wisconsin, but outside of the reservation, in January of each year.

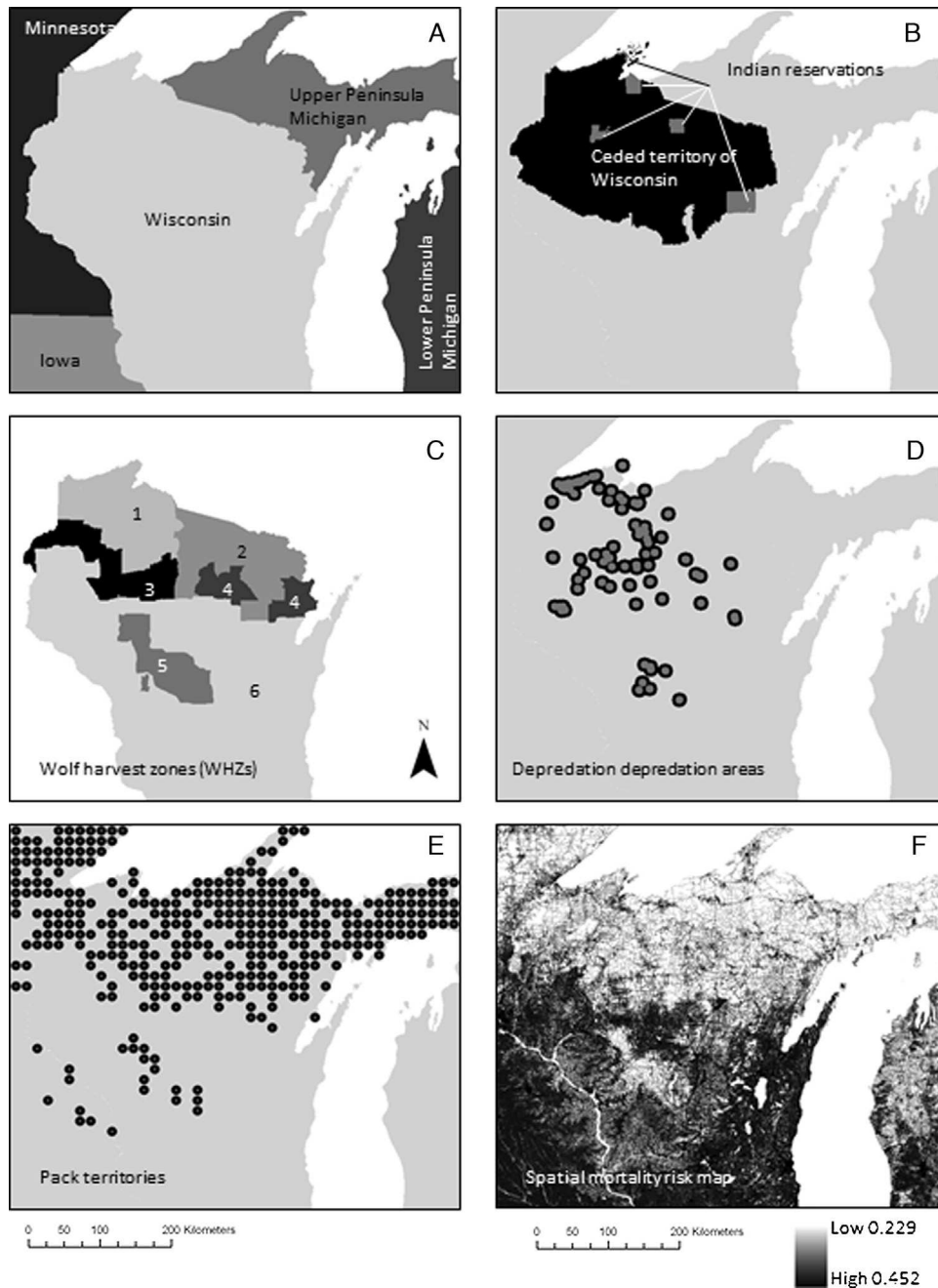
inference on the specifics of colonization and the interaction of different mortality factors for wolves in the SLS region. Despite criticism for the complexity of IBSE models (Grimm, 1999), the level of complexity we included in this IBSE model was necessary to address our questions about the SLS wolf population.

The IBSE model included four hierarchical levels of organization: individual wolves, territories (the location of packs), the wolf population, and the landscape (see Table B1 in Appendix B). Individual wolves were characterized by their spatial location and the state variables of sex, age, mother’s identification, father’s identification, and whether they were a member of a pack, an immigrant, a breeder, and a disperser. Breeder status, pack status, and genetic heritage (i.e., mother’s identification, father’s identification) were the primary determinants of wolf movement and behavior on the landscape.

Territories were the potential locations of packs and they were characterized by the state variables of pack size, pack members, number of breeders, and the litter size of the last litter. Territories were considered occupied if there were ≥2 wolves within the territory boundary. We defined territories as 15 km × 15 km patches of habitat where the center of the territory was in breeding range (Table 1, Fig. 2E). Based on this definition, the simulated landscape had 363 potential territories with 151 potential territories in Wisconsin.

Virtual packs of wolves (hereafter, packs) were identified as aggregates of 2–12 wolves located in discrete territories. Packs consisted of a breeding pair, their offspring of multiple generations, and any unrelated wolves that dispersed into the pack. Packs could also have a single breeder or no breeders if one or both breeders died. Wolves were identified as either a member of a certain pack or lone wolves. Lone wolves were wolves that were outside pack territories or wolves that did not have any full siblings within their territory. When within territories, lone wolves were considered part of the pack.

Each pixel in the 630 × 554 pixel landscape represented 1 km<sup>2</sup> and had values for: state boundaries (Minnesota, Wisconsin, Michigan, Iowa) or water (Fig. 2A), Ojibwe ceded territories of Wisconsin (a region where bands of the Ojibwe Indians may exercise treaty



**Fig. 2.** Landscape variables in an individual-based spatially explicit simulation for wolves in the southern Lake Superior region, USA, including: (A) state and water boundaries, (B) Indian reservation boundaries and the ceded territories in Wisconsin, (C) wolf harvest zones in Wisconsin, (D) locations of farms with chronic depredation problems and farms with a depredation in 2010 or 2011 surrounded by a 5 km buffer (light gray; depredation buffer) and a 10 km buffer (black), (E) centers of pack territories that denote 15 km  $\times$  15 km sections of habitat, and (F) a spatial mortality risk map.

rights to hunt and gather natural resources, Fig. 2B), Indian reservations (including 4 Ojibwe reservations in northwest Wisconsin and the Menominee and Stockbridge/Munsee reservations of northeast Wisconsin; Fig. 2B), Wisconsin wolf harvest zones (WHZs, Fig. 2C), Wisconsin chronic depredation farms, livestock depredation sites, and a 5 km buffer around depredation areas (depredation buffer, hereafter, Fig. 2D), pack territories (Fig. 2E), and the spatial mortality risk map (Fig. 2F).

The model incremented population dynamics in 1 year time steps designed to match wolf life history events during an annual cycle (Fig. 1). The simulation ran for 100 years or until all wolves were extinct. We describe briefly the processes that individual wolves stepped through in the model (Fig. 1, Appendix B). In each

year of simulation, wolves could search for mates (mate-finding), disperse (winter dispersal) and search for mates again, be harvested in winter (winter harvest), reproduce, experience a targeted lethal depredation control event (targeted lethal control), disperse (fall dispersal), be harvested in fall (fall harvest), face spatial mortality risk, and age (Fig. 1). Aside from the spatial mortality risk event and aging, not all wolves participated in or were affected by each event.

### 2.2.1. Mate-finding

Mate-finding was an action taken by lone wolves and single breeders and occurred  $\leq 2$  times per year (Fig. 1). Lone wolves would search for mates, have an opportunity to disperse if a mate was not found (see Section 2.2.2), and then search for mates a second time.

We defined single breeders as territorial breeding wolves whose mates died. We allowed single breeders to pair up by first allowing any subordinate, unrelated adult wolves of the opposite sex in their own pack to fill the vacant breeding position and by allowing any unrelated lone wolves of the opposite sex from up to 2 territories away to usurp the empty breeding position if breeders were unavailable within the pack. When both breeders died, the wolves in a pack could hold the territory until the breeding positions were filled (Brainerd et al., 2008). These vacant breeding positions were filled by new breeding pairs established from remaining lone wolves searching for each other, even if breeding vacancies happened in the current year. A lone wolf would search for an unrelated lone wolf of the opposite sex within 2 territories; if found, the male and female would move to the closest territory. They would form a breeding pair if the territory was unoccupied by another breeding pair. We chose a distance of 2 territories away for the mate-finding distance and tested the sensitivity of the model output to this parameter (see Sections 2.4 and 3.4; Appendix C).

### 2.2.2. Winter dispersal

Wolves of any age dispersed after a first round of mate-finding if they were not part of a breeding pair, were not single breeders, and were not part of a pack. Dispersing wolves chose a random direction and dispersed a distance drawn from a log-normal probability distribution with mean = 3.918 and SD = 1.005 on the log scale (Treves et al., 2009). According to this distribution, wolves dispersed an average of 50 km. The wolves that dispersed outside of the SLS region into Canada (beyond extent of the model) were considered emigrants. An equal number of immigrants were then generated and entered the simulation in randomly chosen locations in breeding range. We chose the number of immigrants equal to the number of emigrates and tested this assumption in a sensitivity analysis (see Sections 2.4 and 3.4; Appendix C). Wolves that entered the simulation as immigrants were given a random age (1–12) and random sex assignment, pack membership if they arrived in an occupied territory, status as an immigrant, and no mother and father identification numbers. The immigrants represented wolves that entered the SLS region from Canada, and did not represent wolves that moved from one area of the SLS region into another area of the SLS region (e.g., wolves from Minnesota that moved into Wisconsin were not considered immigrants).

### 2.2.3. Reproduce

Females in breeding pairs would reproduce each year producing a single litter. Litter sizes were drawn from a normal distribution with mean = 5.406 and SD = 0.790 reflecting the mean and standard deviation of litter sizes from North American studies (Fuller et al., 2003). We rounded the value drawn from the distribution to the next whole number to represent litter size as a whole number of pups. We tested the influence of a discrete distribution (Poisson) for litter size in a sensitivity analysis (see Sections 2.4 and 3.4; Appendix C). Wolves born into the simulation were given age 0, a random sex assignment, a membership into their current pack, and their mother's and father's identification numbers.

### 2.2.4. Targeted lethal depredation control

The Wisconsin portion of the simulated wolf population was exposed to targeted lethal depredation control during summer when the Wisconsin winter population count was  $\geq 350$  wolves, and every year thereafter, to align with what was actually observed in Wisconsin (Ruid et al., 2009; Wydeven et al., 2009b). Targeted lethal depredation control events removed 10% of the wolves calculated from the Wisconsin winter population count primarily from the depredation buffer (Fig. 2D). In the IBSE model, we removed 90%

of the targeted lethal depredation control quota from the depredation buffer and restricted to areas outside of Indian reservations. If there were not enough wolves within the depredation buffer, then wolves were removed from an additional 5 km buffer around the depredation buffer to fill the quota (Fig. 2D). The remaining 10% of the quota (1% of the Wisconsin winter population count) were removed from random locations in Wisconsin outside of Indian reservations. We chose for most (90% of the lethal depredation control quota) of lethal depredation control events to focus in the depredation buffers because most depredations are related to livestock loss and they occur in very specific locations, like the chronic depredation farms and known depredation sites that we used in our model (Olson, 2013; Ruid et al., 2009; Wisconsin Department of Natural Resources, 1999).

### 2.2.5. Fall dispersal

We used a threshold pack size of 12 wolves as a trigger for a second type of dispersal to model resource limitation in the pack (Fig. 1). This number was based on the observations that maximum pack sizes in Wisconsin were 12 wolves from 1980 to 2007 (Wydeven et al., 2009b). In the model, packs with >10 non-breeding pack members would assign a number of members in excess of this non-breeder pack maximum to disperse out of the pack. The individuals were chosen randomly from among the non-breeding pack members. For example, if there were 12 non-breeding pack members, the model would randomly select 2 of them to disperse out of the pack. These dispersers were assigned a random direction and dispersed a distance of kilometers drawn from a lognormal distribution (3.918, 1.005). Dispersers died unless they arrived in an occupied territory with <12 wolves, a vacant pack territory, or other land area.

### 2.2.6. Fall harvest and winter harvest

We initiated harvest when the winter population count was  $\geq 844$  wolves in Wisconsin because this was the population size observed during winter of 2011–2012 before the first actual harvest (MacFarland and Wiedenhoef, 2013). Harvest quotas were calculated as user-determined percentages of the population harvested per WHZ times the winter population count in each WHZ. We chose a constant harvest level for Minnesota and Michigan and harvest quotas in these states were calculated as the percent harvest multiplied by the previous winter's population count. In most cases, harvest occurred as a fall harvest after dispersal and before the spatial mortality risk event. However, in some cases, a percentage of the harvest was allocated as a winter harvest which occurred early in the calendar year, after mate-finding and before reproduction. Wolves were chosen randomly for harvest. We did not expect that harvest rates would be different for different age and sex classes because mortality rates overall do not vary by age (for wolves >6 months old) and sex class (Wydeven et al., 2009b).

### 2.2.7. Spatial mortality risk

The spatial mortality risk event scaled an individual wolf's probability of mortality to the spatial mortality risk map (Appendix A). Each wolf was assigned a number from Uniform distribution (0, 1) and if this number was less than the spatial mortality risk value at their location (1 km<sup>2</sup> pixel), they would die. We chose for spatial mortality risk to occur once per year in the winter because this is when actual wolves in Wisconsin experience their highest mortality rates (Stenglein, 2014).

### 2.2.8. Age

At the end of the calendar year, all wolves aged 1 year, and wolves died if they were >12 years old (Fig. 1).

**Table 2**  
Overview of calibration criteria and patterns for a categorical calibration model assessment of an individual-based spatially explicit model of wolves in the southern Lake Superior region, USA. See Appendix C for more details.

Hierarchical level	Calibration criterion	Weight, points	Reference	Fitting criteria (number of criteria)
Landscape	Occupied territory	High, 6	Wydeven et al. (2009a, 2009b)	Increase in amount of occupied territory over time from 2 measures (2)
Wolf population	Population growth rate	High, 6	Wydeven et al. (2009a, 2009b)	Average annual growth rate, and whether growth rate slowed in recent years (2)
Wolf population	Age structure	Low, 2	MacFarland and Wiedenhoft (2013)	Age structure in year 30 from 2 measures (2)
Wolf population	Population size	High, 6	Wydeven et al. (2009a, 2009b)	Population size in year 28, and minimum population increase between 2 time periods (2)
Territory	Pack size, number, and composition	Low, 3	Wydeven et al. (2009a, 2009b), Mech and Boitani (2003)	Number of packs and average pack size in year 28, & proportion of unrelated wolves (3)
Individual wolf	Average age	Low, 1	MacFarland and Wiedenhoft (2013)	Average age of wolves in year 30 (1)
Individual wolf	Survival probability	Medium, 8	Wydeven et al. (2009a, 2009b), Stenglein (2014)	Average survival of wolves in different age classes (4)
Individual wolf	Dispersal probability	Medium, 2	Treves et al. (2009)	Highest dispersal rate in yearling age class (1)

### 2.3. Model assessment

We used components of pattern-oriented modeling and model ‘evaluation’ (joining of evaluation and validation in assessing a model’s performance, reliability, and quality) to assess our IBSE model (Augusiak et al., 2014; Grimm and Railsback, 2012). The main purpose was to determine whether our model reproduced patterns at multiple scales that have been observed in actual wolf populations. Appropriate model assessment for complex systems requires assessing different patterns at multiple scales, because a complex model that is calibrated to reproduce a single pattern may not represent accurate patterns that emerge at different scales (Grimm and Railsback, 2012).

Categorical calibration is the approach that we used to assess whether our choice of parameters in the IBSE model led to acceptable model output (Thiele et al., 2014). We identified calibration criteria representing all 4 hierarchical levels in our model (i.e., landscape, wolf population, territory, individual wolf) on which we compared patterns in model output to observed data collected from actual wolf populations (Table 2, Appendix C). For each pattern we considered what was reproduced by the IBSE model compared to what has been observed in the SLS wolf population. When we did not have SLS wolf data to compare to the values of the IBSE model, we drew from other published data on wolves (Table 2). We assigned points to the calibration criteria based on an importance weighting and the number of patterns that were assessed (Table 2, Appendix C). We assigned a point when the pattern from the simulation fell within the range of plausible values (acceptance criteria) that we established from the literature (Thiele et al., 2014). We expected the model to score at least 90% of the points. We reassessed the model and our range of plausible values for any pattern that was not supported by the model.

We ran the model 100 times for 50 years each and took the mean of those runs as the values used in the categorical calibration. In addition to the pattern filter, we plotted the number of wolves in Wisconsin and the number of pups in Wisconsin in the simulation compared to the observed population (Wydeven et al., 2009b). This time-series was more difficult to capture in the pattern filter, but was very important in understanding the correspondence between the IBSE model output and the growth of the actual wolf population. We visually inspected these time series for correspondence.

### 2.4. Sensitivity analysis

We conducted a local, one-factor-at-a-time sensitivity analysis of the uncertain parameters in the model. We determined our most uncertain parameters were mate-finding distance and immigration

rate, because these parameters are not easy to measure and study in actual wolf populations (Mech and Boitani, 2010; Wydeven et al., 2009b). We also included the choice of distribution for litter size in our sensitivity analysis. We ran our categorical calibration on each simulation in a one-factor-at-a-time sensitivity analysis and took the best simulation to be the one with all or the highest number of points (Appendix C). Any simulation that achieved a score of at least 90% was considered equal to the best model.

For each parameter that we varied, we ran the model 100 times for 50 years each and took the mean of those runs as the values used in the categorical calibration. We also plotted the time series of wolf population size and number of pups with the time series observed in the actual Wisconsin population to gauge correspondence between these time series.

### 2.5. Simulations

Simulations in the IBSE model served two purposes: (1) to show the effect of different sources, rates, and timings of mortality on population counts, structure, and distribution, and (2) demonstrate the use of the IBSE model as a platform for evaluating harvest management proposals. We ran 6 different simulations where we varied the intensity, location, and timing of harvest: (1) no harvest, (2) the 2012 Wisconsin harvest rates, (3) the 2012 Wisconsin harvest rates with 75% fall harvest and 25% winter harvest (long-harvest scenario), (4) the 2013 Wisconsin harvest rates, (5) 30% harvest across the entire simulation, and (6) a rate of Wisconsin harvest that would enable a stable to increasing wolf population (from pre-harvest numbers) in the ceded territories of Wisconsin (Table 3).

Each simulation consisted of 100 replications and started with 20 breeding pairs in 20 randomly chosen potential territories in Minnesota. In each replication, we tracked number and age structure of wolves, number of packs, number of wolves in the depredation buffer, number and age structure of harvested wolves, number of pups born, the proportion of disrupted packs because of harvest (the number of packs that lost at least 1 breeder because of harvest divided by the number of packs that bred prior to harvest), and dispersal and immigration rates. We recorded these quantities at the end of each year.

## 3. Results

### 3.1. Spatial mortality risk map

According to the model, an increase in road density and an increase in percent agriculture increased the probability that a location was a death location (Appendix A). The scaled spatial mortality



**Table 3**

Wolf harvest rates in wolf harvest zones (WHZ) of Wisconsin, Michigan (MI), and Minnesota (MN), USA with percent of harvest occurring in the fall before mating season for 6 wolf harvest scenarios.

Brief description	Motivation	WHZ 1	WHZ 2	WHZ 3	WHZ 4	WHZ 5	WHZ 6	MI	MN	Fall percent
No harvest	Baseline understanding of simulated wolf population without harvest	0	0	0	0	0	0	0	0	NA
2012 harvest	Harvest Wisconsin wolves by WHZ as was observed during 2012 harvest	9.0	9.4	19.4	18.5	14.7	47.5	7.0	14.0	100
2012 long harvest	Harvest Wisconsin wolves by WHZ as was observed during 2012 harvest, except extend 25% of the harvest into the winter after mating season	9.0	9.4	19.4	18.5	14.7	47.5	7.0	14.0	75
2013 harvest	Harvest Wisconsin wolves by WHZ as was proposed for 2013 harvest	21.4	16.6	66.4	48.0	23.6	90.9	7.0	14.0	100
30% harvest	Harvest all wolves with a 30% harvest rate which is the overall rate of wolf harvest proposed for the 2013 Wisconsin wolf harvest	30.0	30.0	30.0	30.0	30.0	30.0	30.0	30.0	100
Stable population harvest	Harvest Wisconsin wolves by WHZ at a low enough rate to maintain a stable to increasing wolf population in the ceded territories of Wisconsin	5.0	5.0	10.0	10.0	20.0	75.0	7.0	14.0	100

risk probabilities ranged from 0.229 to 0.452, and the average spatial mortality risk for simulated wolves was 26–27%, which was the same as the average annual mortality of 26% estimated for wolves in Wisconsin (Stenglein, 2014). There were no substantial differences in the spatial distribution of survival by age and sex class for wolves, so we assumed the same spatial mortality risk map for all wolves (Stenglein, 2014; Wydeven et al., 2009b). The risk map showed generally a lower probability of mortality in the northern and central forest regions of Wisconsin, the upper peninsula of Michigan, and the northeastern portion of Minnesota than elsewhere in the SLS (Fig. 2F).

3.2. The IBSE model

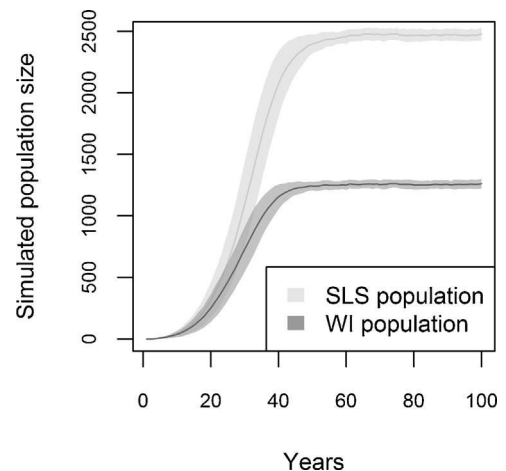
All of our simulated, non-harvested wolf populations persisted for 100 years. Populations that were not harvested stabilized at 1242 wolves (SD=34) in Wisconsin after 50 years and at 2453 wolves (SD=56) in the SLS region after 60 years (Fig. 3). Average winter pup:yearling:adult ratio after 50 years of simulation was 37:23:40, and mean breeder:nonbreeder ratio was 13:87. On average after 50 years, 45.9% (SD=4.3) of the packs that produced pups retained both breeders through the next winter count and the breeding pair tenure averaged 1.8 (SD=0.1) years.

3.3. Model assessment

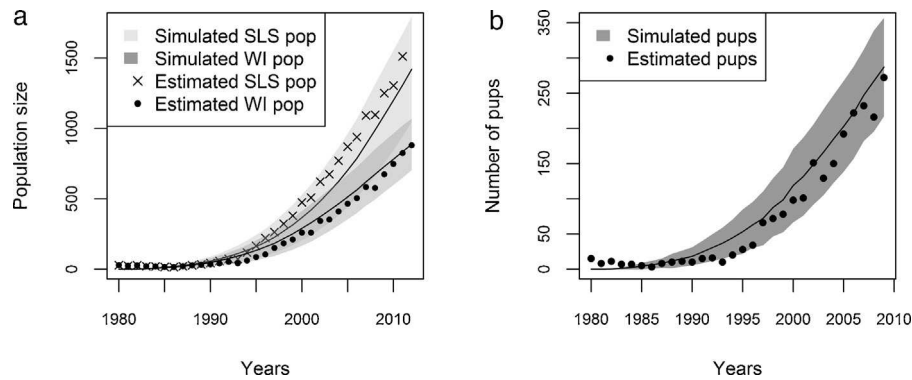
Estimated Wisconsin and SLS population counts were within 1 SD bands of the means of the projected population counts in all except the first 5 years of the simulation (Fig. 4A). Similarly, the winter pup counts in Wisconsin were within 1 SD of the estimated Wisconsin pup counts in all except the first 5 years of the simulation and in 1993 when the simulated wolf pup count was larger than the estimated wolf pup count (Fig. 4B).

We obtained a score of 32 out of 34 from the categorical calibration of our model, and therefore exceeded our minimum score for consideration of a best model. Our model assessment demonstrated correspondence between our base simulation and what has been observed in wolf populations for measures of occupied territory, population growth rate, population age structure, population size, proportion of adoptees in packs, average age of wolves, survival probability of wolves by age class, and dispersal probability (Appendix C).

The only patterns that were not passed in our model were related to pack number and pack size (Table 2, Appendix C). Specifically, the pack sizes in our model were consistently higher and



**Fig. 3.** The mean and standard deviation from 100 simulations of the Wisconsin (WI) and southern Lake Superior (SLS) wolf population sizes for 100 years of an individual-based spatially explicit simulation.



**Fig. 4.** Model assessment showing the mean and 1 standard deviation from 100 simulations of an individual-based spatially explicit model of (A) wolf population growth in Wisconsin (WI) and the southern Lake Superior region (SLS) plotted with the estimated population sizes from 1980 to 2012, and (B) number of pups in Wisconsin plotted with estimated number of pups in Wisconsin from 1980 to 2010.

the number of packs was consistently lower compared to what was observed in Wisconsin. However, the number of pups on average each year in the simulation tracked closely with the estimated number of pups in Wisconsin, and for our study this result was more important than a close correspondence between the average number of packs and average pack sizes (Fig. 4; Wydeven et al., 2009b). The discrepancy between the numbers of packs in the simulation compared to actual numbers of packs observed in Wisconsin was not a surprise to us in this assessment. We made the decision to model potential breeding pack territories based on rules about minimum distance between packs and a cutoff value from the spatial mortality risk map (Fig. 2F; Appendix B). We accepted the performance of our base model and were confident that our base model reproduced important patterns at multiple hierarchical levels (Grimm et al., 2005).

### 3.4. Sensitivity analysis

Compared to our base model, all simulations from our sensitivity analysis resulted in lower scores in the categorical calibration and less correspondence to the time series of wolf population size and number of pups (Appendix C). Also, none of the simulations met the criteria score for becoming a 'best model' (scored  $\geq 90\%$  of the points). Among the parameters that we tested, our analysis demonstrated that our model was most sensitive to choice of mate-finding-distance, less sensitive to choice of immigration rate, and not very sensitive to choice of litter distribution (Appendix C). Even when the categorical calibration score was high for a simulation in the sensitivity analysis, the correspondence of the time series of population count and number of pups in the simulation was quite divergent from the observed time series in the actual wolf population (Fig. C3 in Appendix C). Our choice of a mate search distance of 2 territories away, an immigration rate equal to emigration rate, and a normal distribution for litter size led to the model with the highest score from the categorical calibration and the closest correspondence to the observed growth of the wolf population and the number of pups (Fig. 4, Appendix C).

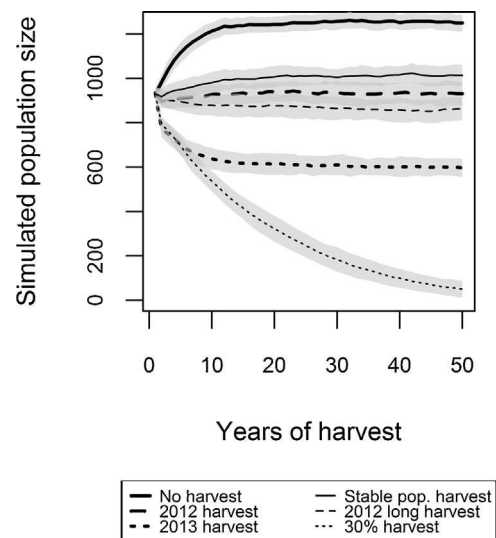
### 3.5. Simulations

Mean winter population count in Wisconsin after 100 years ranged from 19 (SD=25) to 1257 (SD=38) wolves depending on harvest scenarios. In the 30% harvest scenario, 14% of repetitions went extinct before 100 years, while all repetitions from all other scenarios persisted for 100 years. Harvest reduced the Wisconsin population size by an average of 1.2% (SD=3.1) to 17.3% (SD=2.9) in the first year, and  $-9.2\%$  (SD=6.3) to 94.7% (SD=3.9) in the 50th year (Fig. 5). The only harvest simulation that resulted in population

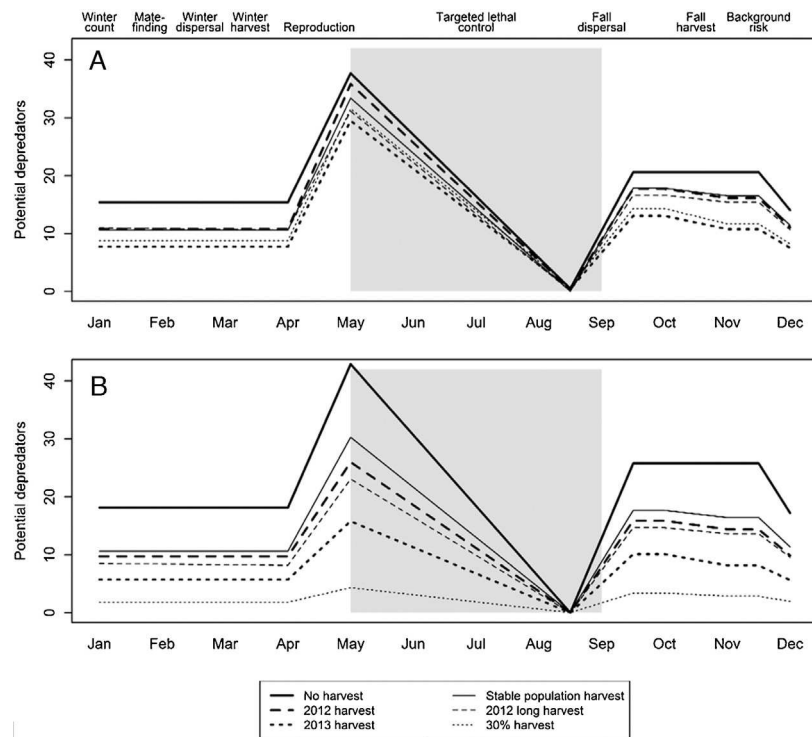
growth after 50 years was the stable population harvest scenario that had a goal of a stable to increasing population in the ceded territories (Fig. 5).

The 2012 harvest scenario achieved a mean 4.1% (SD=2.9) population reduction in the first year, similar to the estimated reduction of Wisconsin's actual wolf population of 3.1% after the 2012 hunt (based on midpoints of 847.5 wolves in 2011/2012 and 821.5 wolves in 2012/2013 during winter population counts). Compared to the 2012 harvest scenario, the 2012 long-harvest scenario (included harvest in winter) had less population reduction in the first year of harvest (mean =  $-1.7\%$ , SD = 3.1), but more population reduction every year thereafter (Fig. 5). Variation in population reduction was always higher in the 2012 long harvest scenario compared to the 2012 harvest scenario presumably because harvesting mated females in the long-harvest scenario resulted in reproductive loss for an entire pack.

The 2013 harvest scenario achieved a mean 17.3% (SD=2.9) population reduction in the first year, similar to the estimated reduction of Wisconsin's actual wolf population of 17.9% after the 2013 hunt (based on midpoints of 821.5 wolves in 2012/2013 and 674.5 wolves in 2013/2014 during winter population counts). At a 30% constant harvest rate (i.e., 30% harvest scenario), the simulated wolf populations had a similar reduction of 24.9% (SD=4.0) in the



**Fig. 5.** The average and 1 standard deviation of estimated wolf population sizes in Wisconsin, USA, under 6 harvest scenarios for 50 years of harvest using an individual-based spatially explicit model of wolves in the southern Lake Superior region, USA.



**Fig. 6.** The number of simulated wolves in the depredation buffer in Wisconsin from an individual-based spatially explicit model for southern Lake Superior wolves, USA, from 6 harvest scenarios throughout the simulated year after (A) 1 year and (B) 20 years of harvest. The gray shaded area shows when the majority of the depredation events occur in Wisconsin (Olson, 2013).

population after 5 years of harvest, but then continued to decline and sometimes went extinct (Fig. 5).

After 5 years of harvest, there were 1–3% more pups in the winter population for all scenarios that had harvest (Table D1 in Appendix D). Average pack size increased with time in the no harvest scenario, and decreased with harvest by 0.6–1.7 wolves per pack (7–22% reduction) after 5 years of harvest (Table D1 in Appendix D). The percentage of breeding pairs that bred for  $\geq 1$  year decreased 3–12% after the first year of harvest compared to the no harvest scenarios (Table D1 in Appendix D). Average tenure of breeding pairs was 1.8 years in the no harvest scenario, and decreased to 1.5 in the 30% harvest scenario after 5 years of harvest (Table D1 in Appendix D).

The sequence of the life history events during each simulated year affected the number of wolves located in the depredation buffer areas (Figs. 1 and 6). In all harvest simulations (including the no harvest simulation) after the first and twentieth years of harvest, targeted lethal control was the most important factor in reducing wolves in the depredation buffer reactively and corresponded to the time of year when most depredations occurred (Olson, 2013; Fig. 6). This result was not surprising because the rules for targeted lethal control directly removed wolves in the depredation buffer zones (see Section 2.2.4, Appendix B). The second most important source of mortality for wolves in the depredation buffer was spatial mortality risk. In the simulation, fall harvest reduced the number of wolves in the depredation buffer, but the effect was smaller because harvest was not directed into depredation buffer areas (Fig. 6). The largest increase in wolves in the depredation buffer during the simulated year occurred because of reproduction and then fall dispersal (Fig. 6).

#### 4. Discussion

We built, documented, and assessed an IBSE model of the colonization and population dynamics of SLS wolves. Our approach enabled modeling dynamics associated with the complex life

history of wolves relating to pack structure, breeding status, age, sex, kin relationships, and location with respect to other wolves and features on a particular landscape. Our IBSE model was used by managers at Wisconsin Department of Natural Resources prior to the 2012 and 2013 harvest seasons to explore how different harvest scenarios may impact Wisconsin's wolf population (Wolf harvest rule to Natural Resources Board, July 2012 board meeting), and the model-estimated population reduction we predicted matched observed reduction following the 2012 and 2013 wolf harvest when evaluated in single year simulations. The model underestimated the observed population reduction when the 2012 and 2013 harvest seasons were modeled sequentially, which may be because we did not include a lag in breeder replacement after breeder loss (Brainerd et al., 2008). The Great Lakes Indian Fish and Wildlife Commission (a natural resources management agency of the Ojibwe Indians) used our IBSE model to explore the effect of harvest on the wolf population defined by the ceded territories of Wisconsin. They developed a harvest scenario with the goal of a stable to increasing wolf population in the ceded territories of Wisconsin because of the spiritual importance of wolves to the Ojibwe people (David, 2009; Stenglein and Gilbert, 2012). Harvest rates of 5–20% in WHZs 1–5 and 75% in WHZ 6 led to a stable population size of 1000 wolves after 20 years of harvest and an average harvest of >90 wolves per year. These uses demonstrate the utility of an IBSE model that multiple agencies and members of the public can use and understand.

Correspondence of our IBSE model to observed Wisconsin's wolf data at the individual, population, and landscape level was vital. Our model closely aligned with actual wolf population and pup counts documented in Wisconsin and the SLS region from 1985 to 2012. Our IBSE model began with a few wolf packs in Minnesota that recolonized Wisconsin and Michigan for each simulation. This pattern of recolonization was influenced by the corridor of patchy habitat on the SLS landscape between Lake Superior to the north and agricultural areas to the south (Mladenoff et al., 1995,

1999). The landscape configuration required simulated wolves in Minnesota to disperse east to find breeding range and increase their population size. This simulated recolonization allowed for the development of simulated pack structure and a realistic distribution of wolves across the simulated SLS landscape.

The IBSE model generated at least 3 emergent components of wolf biology for wolves in the SLS region. First, the simulated unharvested wolf population reached a carrying capacity that we can compare to other estimates of carrying capacity from the literature. Van Deelen (2009) fit growth curves to the SLS wolf data from 1985 to 2007 and estimated a carrying capacity of 1321 (95% CI: 1215–1427) wolves with ~650 wolves as the carrying capacity for Wisconsin alone. The equilibrium population size from our IBSE model suggests that an unharvested wolf population would stabilize at nearly double the level previously estimated by Van Deelen. Second, simulated wolves had a limited perception neighborhood for mate searching. We calibrated the IBSE model using a mate search distance of 2 territories away and when we varied this parameter in our sensitivity analysis we found less correspondence to observed patterns in the Wisconsin wolf population for other mate search distances. Therefore, we suggest 2 territories (30 km) as a realistic biological perception neighborhood for mate searching in the SLS region, which is similar to the perception neighborhood of ~20–40 km used for wolves in the Greater Yellowstone Ecosystem, USA (Hurford et al., 2006). This perception neighborhood may change due to landscape configuration, environmental factors, and proximity to other conspecifics (Berec et al., 2001; Hurford et al., 2006).

Third, we documented social effect of harvest in a simulated wolf population. Our IBSE model is one of the first models that can infer effects of human-caused mortality on social structure of packs (see also Haight et al., 2002; Haight and Mech, 1997). Wolves exist in packs consisting of a breeding pair and multiple generations of offspring, and exploitation may disrupt pack structure and lead to a higher proportion of pups (Fuller et al., 2003; Rutledge et al., 2010). We documented these effects of harvest in our IBSE simulation because harvest increased the proportion of pups in the population and caused more disruption in packs by killing breeders and decreasing the average tenure of breeding pairs. The mechanism in the model to produce this result was harvest mortality that was homogeneous by WHZ. A change in the composition of packs or the loss of a breeder could have cascading effects that were not well captured in our model (Brainerd et al., 2008). Our IBSE model did not include explicitly a lag effect of breeding pairs reestablishing once one or both breeders were lost, which is a phenomenon documented in wolves (Brainerd et al., 2008). Therefore, our IBSE model may underestimate the social effect of harvest on the wolf population and thus overestimate potential population growth following removal of wolves.

Our IBSE model demonstrated that the timing and location of mortality events affected the wolf population in different ways depending on wolf phenology. For example, extending harvest into the mating season resulted in more pack disturbance, higher population reduction, and more variability compared to the same amount of harvest restricted to the fall months. We suspect that this result is because some of the simulated female breeders were killed in the late harvest and this precluded pack reproduction for the year. The higher spatial mortality risk of mortality in agricultural areas and areas with high road density in Wisconsin led to higher background mortality rates outside of primary wolf range. The annual targeted lethal control removed the wolves in the depredation buffer areas and was the single-most important mortality event for maintaining low wolf populations in known depredation areas. Lethal control exerted only a short-term influence on the number of wolves in the depredation buffer area (wolf numbers increased in depredation buffer after fall dispersal), but coincided

with the time of year of when wolf depredations were occurring (Olson, 2013). After targeted lethal control, the general spatial mortality risk was more effective at reducing the number of wolves in the depredation buffer compared to harvest. All forms of harvests did somewhat reduce numbers of wolves that needed to be controlled in depredation buffer areas, and the effect was larger after more years of harvest. Harvests may have been a more important factor in reducing the number of wolves in these areas if WHZs were configured around areas of known high livestock depredation and harvest rates were high in these areas (Haight et al., 2002).

We highlight differences between political and biological boundaries for the SLS wolf population. The timing, level, and distribution of harvest affected the distribution, composition, and size of the wolf population. However, the most striking harvest effects occurred when Michigan and Minnesota wolves were harvested as intensively as Wisconsin's proposed 2013 harvest. Instead of Wisconsin's population stabilizing at some 600 wolves with the proposed 2013 harvest rates and Michigan and Minnesota harvesting at much lower rates, the wolves in the entire simulation plummeted. This is may be evidence of source-sink dynamics in our Great Lakes simulated landscape, and these dynamics become more apparent with increasing harvest (Pulliam and Danielson, 1991). When Wisconsin harvests at high levels compared to the Upper Peninsula of Michigan and Minnesota, Wisconsin likely becomes a population sink, with a source of wolves (mainly from the Upper Peninsula of Michigan) that supplement the diminishing Wisconsin wolf population. Wisconsin, Michigan, and Minnesota have a single wolf population, and the management decisions in one state affect the dynamics across this region.

An IBSE model is only as good as the parameter estimates that drive it. We were fortunate to have access to a long history of wolf research in the SLS region, and could derive the parameter estimates for our model from many sources (Mech, 1970; Mech and Boitani, 2003; Thiel, 1993, 2001; Wydeven et al., 1995, 2009a). We fit distributions to empirical data and our simulations drew from these distributions. However, some processes are not easy to parameterize in an IBSE model because of lack of information or complexity. Decisions for parameterization of each life history event were needed despite relatively poor understanding of these events. For example, general dispersal rates across age and sex classes for different times of the year are not well documented. In our simulation, we decided to not treat dispersal decision as a random draw from a distribution. Rather, we decided that dispersers were all wolves that fit certain criteria and these criteria changed depending on the time of the year. Also, we used a very simplistic understanding of pack structure based around an unrelated mated pair and their offspring of multiple generations, even though we know that inbreeding does occur occasionally in the wild (Mech and Boitani, 2003; Rutledge et al., 2010; Stenglein et al., 2011; Vonholdt et al., 2008).

Nonetheless, complex life histories largely preclude the use of simple phenomenological models especially for questions that are driven by controversial management actions such as the aggressive harvests being proposed for newly recovered wolf populations (Lebreton, 2005; Levins, 1966). Our IBSE model is a simplification of how we understand wolves to be interacting on the landscape, and simplification is inherent in modeling (Levins, 1966). It is not necessary for our model to be a perfect depiction of wolf life history, because our interest is in population-level questions and our model reflects wolf population growth and effects of harvest thus far. We advocate modeling, not as an endpoint, but as a step in an iterative process of integrating current knowledge, identifying critical information needs, and conducting research to advance our understanding and ability to predict population dynamics. For wolves, we see a main research need of understanding how harvest affects the

social structure of wolf populations and the behavior of individual wolves.

Although our IBSE model was calibrated to Wisconsin's annual population estimate for wolves, the count of wolves in the simulation by WHZ was not well aligned to the actual wolf population. In general, the simulation produces many more wolves in the North-eastern portion of Wisconsin and many fewer wolves in the central forest of Wisconsin compared to the actual distribution of wolves in Wisconsin. This is likely a reflection of random dispersal. Another place where we are unsure of the model is in the aggregate effects of harvest over time. In our simulations, we simulated a single harvest scenario and assessed correspondence in the 2012 and 2013 harvest scenarios as the percent reduction in the population in the first year of harvest under each scenario. Although the percent reduction under the two scenarios were both very similar to what was observed after each year's harvest, the results may not be so close when we simulate multiple years of harvest sequentially. In all harvest scenarios, the percent reduction is subdued in the population in subsequent years compared to the initial year of harvest. Therefore the aggregate and long-term effects of harvest may not be well captured by our IBSE model in its current form. It will be necessary to calibrate the model to the harvest years once we have more years of data from Wisconsin's harvested wolf population.

## 5. Conclusions

It is appropriate to view the Great Lakes wolf population as a single population that is managed jointly by Minnesota, Wisconsin, Michigan, the Ojibwe Indian tribes living in these states, and Ontario, Canada. It is clear from our model that the management decisions in one place affect the entire population. We highlight the annual Midwest Wolf Steward meeting that brings together managers, researchers, non-profit organizations, and other stakeholders to have important conversations about wolves in this region. We estimate that harvest rates well below the maximum modeled in this paper will be necessary to ensure long-term population viability.

We can use this model to evaluate potential changes in the WHZ configuration and the potential effects of zone changes on managing depredating wolves. A reconfiguration of the location and number of WHZs for harvest could be an effective way of managing wolf numbers. Smaller zones could be designated in areas where there is a high incidence of livestock depredations, and harvest rates could be much higher in these zones. Livestock depredation sites have been predicted from environmental variables, and this information could be used to delineated different WHZ (Olson, 2013; Treves et al., 2004). On the other hand, closing off some core areas to harvest could be an effective strategy for maintaining carnivore roles in functioning ecosystems (Ordiz et al., 2013). We can run these scenarios and others in our IBSE model to better understand how harvest zone configuration, variable harvest rates, and no harvest zones could affect wolf distribution, pack structure, population numbers and depredation control efforts.

We demonstrate the use of IBSE models in an adaptive management framework to assess the effects of harvest and exploitation of other wolf populations and populations of other large carnivores with the goal of better decision-making for management of populations. Adaptive management is an iterative decision-making process that is essentially an optimization problem to maximize an objective in the face of uncertainty (Walters and Hilborn, 1978). We demonstrated how our model could be optimized to meet an objective, by simulating a wolf harvest with a goal of a stable to increasing population. The process of developing an IBSE model is useful in itself to identify research questions, management needs, stakeholders, available data, and gaps in available data. Our model

has already been used effectively in the beginning stage of an adaptive management approach to wolf harvest in Wisconsin, and may continue to be used to inform harvest decisions and improve future management of wolves.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2015.01.022>.

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