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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

Jennifer L. Stenglein[a,*], Jonathan H. Gilbert[b], Adrian P. Wydeven[c,1], Timothy R. Van Deelen[a]

[a] Department of Forest and Wildlife Ecology, University of Wisconsin – Madison, 1630 Linden Drive, Madison, WI 53706, USA
[b] Great Lakes Indian Fish and Wildlife Commission, P.O. Box 9, Odanah, WI 54861, USA
[c] Wisconsin Department of Natural Resources, 2501 Golf Course Road, Ashland, WI 54806, USA

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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.

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

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

* Corresponding author. Present address: Wisconsin Department of Natural Resources, 2801 Progress Road, Madison, WI 53716, USA. Tel.: +1 608 221 6334.
E-mail addresses: jennifer.stenglein@wisconsin.gov (J.L. Stenglein), jgilbert@glifwc.org (J.H. Gilbert), adrianwydeven@cheqnet.net (A.P. Wydeven), trvandeelen@wisc.edu (T.R. Van Deelen).
[1] Retired.

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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 (km/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 km × 554 km landscape of the SLS region centered on Wisconsin into 1 km^2 pixels, and obtained road density and percent agriculture covariates for each 1 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).