

ANALYSIS OF SENSITIVITY AND UNCERTAINTY IN AN INDIVIDUAL-BASED MODEL OF A THREATENED WILDLIFE SPECIES

BRUCE G. MARCOT*

USDA Forest Service, Pacific Northwest Research Station, 620 S.W. Main Street, Suite 400,
Portland, Oregon 97208

E-mail: bmarcot@fs.fed.us

PETER H. SINGLETON

USDA Forest Service, Pacific Northwest Research Station, 1133 N. Western Avenue, Wenatchee,
Washington 98801

E-mail: psingleton@fs.fed.us

NATHAN H. SCHUMAKER

US Environmental Protection Agency, Environmental Research Lab, 200 SW 35th Street,
Corvallis, Oregon 97333

E-mail: schumaker.nathan@epa.gov

ABSTRACT. Sensitivity analysis—determination of how prediction variables affect response variables—of individual-based models (IBMs) are few but important to the interpretation of model output. We present sensitivity analysis of a spatially explicit IBM (HexSim) of a threatened species, the Northern Spotted Owl (NSO; *Strix occidentalis caurina*) in Washington, USA. We explored sensitivity to HexSim variables representing habitat quality, movement, dispersal, and model architecture; previous NSO studies have well established sensitivity of model output to vital rate variation. We developed “normative” (expected) model settings from field studies, and then varied the values of ≥ 1 input parameter at a time by $\pm 10\%$ and $\pm 50\%$ of their normative values to determine influence on response variables of population size and trend. We determined time to population equilibration and dynamics of populations above and below carrying capacity. Recovery time from small population size to carrying capacity greatly exceeded decay time from an overpopulated condition, suggesting lag time required to repopulate newly available habitat. Response variables were most sensitive to input parameters of habitat quality which are well-studied for this species and controllable by management. HexSim thus seems useful for evaluating potential NSO population responses to landscape patterns for which good empirical information is available.

KEY WORDS: Individual-based model, HexSim model, sensitivity analysis, uncertainty analysis.

1. Introduction. The response of rare or threatened species to real or potential landscapes with fragmented habitat is often assessed by use of individual-based models (IBMs) that simulate habitat selection, movement, reproduction, and

*Corresponding author. Bruce G. Marcot, USDA Forest Service, Pacific Northwest Research Station, 620 S.W. Main Street, Suite 400, Portland, Oregon 97208, e-mail: bmarcot@fs.fed.us

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mortality of individual animals in a landscape (Lamberson et al. [1994], Akçakaya et al. [2004], Heinz et al. [2006], Harrison et al. [2011]). When properly calibrated, IBMs can provide systematic and useful insights into processes including animal dispersal, exploration for resources, and habitat selection behaviors (Rupp and Rupp [2010], Latombe et al. [2011], Watkins and Rose [2013]), as well as of population vulnerability (Griebeler [2011]), disease transmission (Ramsey and Efford [2010]), and even plant population dynamics (Adams et al. [2011]). However, it is our experience that few sensitivity analyses have been conducted in a thorough, structured manner on IBMs, which prompted this study.

Sensitivity analysis of population models, including IBM type models, is highly useful for model application to management (Cross and Beissinger [2001], Aberg et al. [2009], Confalonieri et al. [2010], McElhany et al. [2010]). Managers may wish to know the degree to which model results arise from uncertainties in model parameters and architecture, or from potential behavior of the real-world system, and also which input parameters—especially those controllable or affected by management actions—have greater influence on outcomes.

One IBM used in a variety of species conservation projects is HexSim, a spatially explicit movement and dispersal modeling shell (Schumaker [2013]). HexSim runs on terrestrial landscapes tiled with regular hexagons and user-supplied details on habitat quality, species life histories, and other parameters. Recent applications of HexSim include analysis of habitat fragmentation effects on wolves (*Canis lupus*) in Manitoba (Stronen et al. [2012]) and on Ord’s kangaroo rats (*Dipodomys ordii*) in Alberta, Canada (Heinrichs et al. [2010]), and evaluation of threatened populations of Northern Spotted Owls (NSO; *Strix occidentalis caurina*) in a suite of hypothetical landscapes varying in absolute habitat area and size and spacing of old-forest habitat patches in the Pacific Northwest, USA (Marcot et al. [2013]). Heinrichs et al. ([2010]) included a brief summary of sensitivity analysis, reporting that extinction risk was largely insensitive to variations in population and habitat quality parameters, and most sensitive to decreases (but not increases) in vital rates of survival and reproduction. Other applications of previous versions of HexSim (known as PATCH) are many (see McRae et al. [2008]). HexSim is also being used in an ongoing study of how NSO populations could respond to various scenarios for managing fire, fuels, and vegetation in dry, fire-prone forests of the eastern Cascade Mountains in Washington and Oregon, USA (sites.google.com/a/pdx.edu/vegetation-fire-owl/; also see Singleton [2013]).

In a ground-breaking application, HexSim was recently used by U.S. Fish and Wildlife Service (USFWS) in a multimodel approach to map and designate critical habitat of NSOs for the species’ recovery (USFWS [2011, 2012]) under the U.S. Endangered Species Act (Schumaker et al. [2014]). The credibility, efficacy, and uncertainty of USFWS’ critical habitat designation for recovering NSO populations, and of the implications from other studies also using HexSim for managing NSOs and other species, lies, in part, in the validity of HexSim in realistically depicting

population response (size and trend). This entails ensuring that movement, habitat selection, and demographic parameters have been adequately identified and calibrated in the model, and further, that the basic response behavior and sensitivity structure of the model are known.

Sensitivity analyses have been conducted on few other IBMs and patch occupancy models (Curtis and Naujokaitis-Lewis [2008], Miller [2012]) and few have been published on HexSim. Rustigian et al. ([2003]) conducted sensitivity analyses of the PATCH model for a salamander species, but the algorithms used in HexSim have advanced over that earlier version.

The objective of our work was to develop methods for conducting a sensitivity analysis of an IBM and to explore in detail the sensitivity structure of a specific IBM model of NSO populations, which have been declining in recent decades largely from loss of habitat due to wildfire and logging and from competition with other species (Forsman et al. [2011], Clark et al. [2013], Yackulic et al. [2012]). The methods we present are general in scope and can be used for evaluations of other species and with other IBMs. Without a detailed sensitivity analysis, high uncertainty remains as to which variables of management control could most influence the outcome of population conditions (size, trend), and how the model can be made more reliable by identifying variables of major influence that could be prioritized for empirical study, particularly related to habitat quality as affecting successful reproduction, habitat distribution as affecting dispersal and colonization, and carrying capacity as affecting population recovery. Conducted correctly, sensitivity analysis has high practical value for prioritizing management actions and inventory, monitoring, and research activities.

2. Methods. We used HexSim to develop normative (expected reference conditions, sensu Jay et al. [2011]) and sensitivity analysis (variation in expected conditions) model runs of IBMs of NSO populations. HexSim is a highly flexible simulation framework within which wildlife and plant models are constructed. HexSim models can range from extremely simple to highly complex, and from abstract and hypothetical to detailed and realistic. The software is designed on a “queuing theory” or sequential-event architecture (Gross et al. [2008]) for simulating terrestrial wildlife population dynamics ranging from simple to intricate. In creating a HexSim model, the user defines a temporal event space in which movement, survival, reproduction, and other events occur in a defined sequence for each time iteration. Most of these life history events in a HexSim model can be influenced by spatial attributes such as dispersion of habitat and barriers to dispersal.

2.1. Study area. We developed our model of NSO populations in HexSim v2.4 as a key part of a risk analysis to advise forest managers and decision-makers on potential effects on NSO populations from alternative scenarios for managing

vegetation, fire, and fuels on national forests of the eastern Cascade Mountains. We conducted model runs for the portion of the Okanogan-Wenatchee National Forest within the range of the NSO in the eastern Cascade Mountains of Washington, USA (Supporting Information Appendix A). This 1.62 million-ha area is characterized by complex, mountainous topography. Elevations range 240–2,750 m and the upper elevation limit of NSO nesting habitat in this landscape is approximately 1,600 m. Vegetation types occupied by NSOs in this area range from moist- to dry-mixed conifer forest (Lillybridge et al. [1995], Johnson and O’Neil [2001]). Within the study area, ongoing research on NSOs, including presence surveys and demographic monitoring, began in 1989 (Anthony et al. [2006], Singleton et al. [2010], Forsman et al. [2011]). Information from these efforts provided the empirical data for parameterizing our HexSim population models (Raphael et al. [2013], Singleton [2013]).

2.2. The normative model. HexSim operates by specifying parameters for selection and use of habitats across the landscape, and for survival, reproduction, and movement. NSO habitat in the model refers to conifer forest vegetation dominated by large diameter trees with closed canopies used by NSOs for nesting, roosting, and foraging (Singleton [2013]). The habitat map we used was derived from observed habitat characteristics at NSO nesting and foraging pair activity centers in Okanogan-Wenatchee National Forest (Singleton [2013]). Singleton ([2013]) used logistic regression to characterize topography (slope and topographic position) and vegetation (mean tree size, dominant tree species, and overstory canopy closure) at the NSO activity centers, and mapped three habitat use categories: poor habitat (areas currently used by NSOs less frequently than available within their elevation range: total 923,912 ha), moderate habitat (use approximately in proportion to availability: total 395,591 ha), and good habitat (use exceeding availability: total 117,737 ha).

Each 86.6-ha hexagon in the tiled HexSim habitat map, totaling 40,138 hexagons, was then assigned a habitat value based on the amount of good and moderate habitat within the hexagon. We used Singleton’s (2013) comparison of the total resource values from hexagons surrounding documented NSO activity centers to the analysis area landscape at two scales, to represent the breeding season core home range area in our HexSim model (6 hexagons, or approximately 500 ha) and annual home range (23 hexagons, or approximately 2,000 ha). Resource threshold settings, representing habitat quality levels contributing to establishment of an NSO territory, were set to reflect these patterns of habitat abundance around documented NSO activity centers. Also, high elevation areas (>1,800 m) without forest vegetation (predominantly alpine rock and ice) and a large lake (Lake Chelan) were considered to be barriers to NSO movement, and denoted in an NSO movement barrier map overlaid onto the habitat map (total 33,176 ha).

We parameterized the model with 15 input parameters (Table 1) representing female-only demography with 4 stage classes (juvenile, first-year, second-year, and

TABLE 1. Input parameters and values for the normative Northern Spotted Owl (NSO) model developed in HexSim. Sensitivity analyses consisted of varying each value $\pm 10\%$ and $\pm 50\%$ of their normative values. In the sensitivity analyses, where two parameters are included together in this table, we covaried values of both because they were linked within the structure of the HexSim model.

Parameter code	Parameter name in HexSim (unit of measure)	Description	Normative values
—	Initial population size (NSOs)	No. of adult female NSOs added to the simulation at time 0.	185
—	Number of time steps (years)	Duration of each replicate simulation.	150
—	Simulation seed (integer)	Random number generator's seed.	random
MaxRngArea,	Maximum range area (ha), Minimum	Upper limit on territory size. Lower	471, 250
MinRngRes ^a	range resource (unitless)	limit on territory habitat quality.	
HexRngEI ^a	Hexagons range-eligible if value at least (unitless)	Lowest habitat quality allowed for hexagons added to a territory.	30
ResTargs	Resource targets, by stage class (unitless)	Resource goal (habitat quality) used during territory construction.	1,035
ResTrtThMod,	Resource trait threshold—moderate,	Break-points used to place NSOs in	60, 70
ResTrtThHi	high (unitless)	resource (habitat quality) acquisition classes.	
PathLenBPro,	Path length bounds, minimum and	Bounds on uniform distribution used	250, 250
Path LenBDis	maximum (no. hexagons)	to select dispersal path lengths.	
MnResQualPrs,	Mean resource quality – for floater	Resource value (habitat quality)	40, 40
MnResQualDis	prospecting, and for floater dispersal and exploration (unitless)	sufficient to halt the dispersal process.	
RepulMinPrs,	Repulsion minimum—for floater	Resource value (habitat quality)	30, 30
RepulMinDis	prospecting, and for floater dispersal and exploration (unitless)	threshold at which dispersing NSOs exhibit absolute avoidance.	
MaxExplAPro,	Maximum explored area – for floater	Maximum permitted search area for prospecting NSOs.	92, 92
MaxExplADis	prospecting, and for floater dispersal and exploration (no. hexagons)		
MaxExplAHR ^a	Maximum explored area (no. hexagons)	Maximum home range area.	46
Barriers	Movement barriers	Movement barrier locations.	include

^a These 3 input parameters were also covaried in a set of sensitivity tests using HexSim's batch-model sensitivity analysis function.

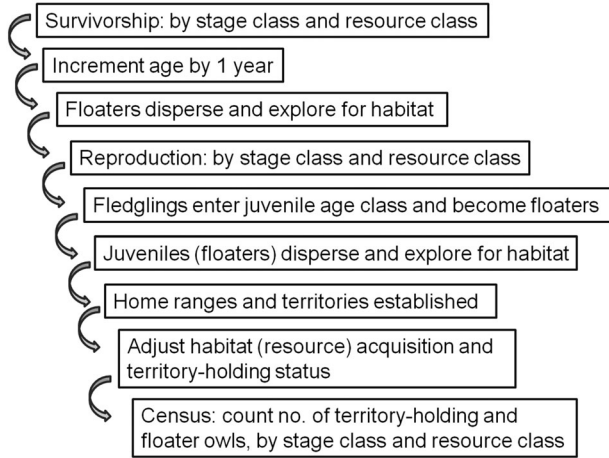


FIGURE 1. Annual event sequence of Northern Spotted Owls as modeled in HexSim. As an individual-based model, HexSim simulates survival, movement, habitat selection, reproduction, and mortality of individual organisms as incremental events during a given time step.

third-year and older); paired (territory-holding, nesting, reproductive adult) birds and unpaired (nonterritorial) “floater” birds; and 3 habitat quality (resource use) classes (low, moderate, high) based on analysis of empirical habitat selection behaviors (Singleton [2013]). We included consideration of floater birds because previous NSO HexSim modeling suggested that they could play an important role in population persistence (Marcot et al. [2013]). Movement in the normative model consisted of stochastic *dispersal* of juvenile NSOs, *prospecting* for high-quality habitat by which to establish a breeding territory, and *exploring* for habitat to establish a foraging home range (Table 1; Supporting Information Appendix B). Prospecting and exploration are handled in HexSim simultaneously, and all movement is influenced by habitat quality, distance and stopping criteria, and autocorrelation in the direction of individual movement path segments.

The event sequence for each simulated year includes stochastic survivorship and reproduction by stage and resource classes, and dispersal and floater movement to prospect for suitable unoccupied habitat and to establish territories and home ranges (Figure 1). Survivorship and reproduction schedules in the model draw from probability distributions calibrated to field data (Forsman et al. [2011]), and all movement events in the model are stochastic and bound by specified value ranges or algorithms parameterized to emulate known NSO movement dynamics (Marcot et al. [2013]).

We established *normative model* settings (Table 1) in HexSim calibrated to empirical data on NSO biology and habitat selection, and, for sensitivity analysis, we ran

TABLE 2. Response variables calculated from results of the HexSim simulations of Northern Spotted Owl (NSO) populations on Wenatchee National Forest, Washington, USA, with results from the normative model ($n = 25$ replications, each running 150 simulated years).

Variable code	Description	Values from the normative model, mean $\pm$ 1SD
EndMeanTerritories	Mean number of territory-holding adult female NSOs in the final decade.	187.3 ± 6.1
EndMinTerritories	Minimum number of territory-holding adult female NSOs over the entire simulation. ^a	161.4 ± 5.7
EndMeanFloaters	Mean number of nonterritory-holding floater NSOs in the final decade.	107.4 ± 7.7
EndMinFloaters	Minimum number of nonterritory-holding floater NSOs over the entire simulation. ^a	77.2 ± 5.00
SimLamb	Lambda calculated over the entire simulation period. ^a	1.022 ± 0.052

^aExcluding the initial (usually 50-year) start-up bias period.

the model on static, current habitat conditions (Singleton [2013]) to eliminate variation from changing landscapes. Input parameters used in our NSO HexSim model (Table 1) specified initial population size, model run time, and stochasticity, as well as a host of biological parameters pertaining to habitat extent, use of various levels of habitat quality to establish home ranges and breeding territories, and distances and geometries of movement through the landscape for dispersal, prospecting, and exploration of unoccupied habitat.

We ran simulations over 150-year periods, ignoring the first 50 years as the “start-up bias” or model equilibration phase (see Results below; also as determined by Singleton [2013] for each of 25 replicates per iteration). We calculated 7 response variables of population size and trend over the final 100-year simulation period (Table 2; Singleton [2013]). Response variables included mean and minimum numbers of breeding NSO territories and of nonbreeding, nonterritorial floater NSOs; and population trends (λ) of breeding NSO territories (N) across each full simulation period, calculated as simulation $\lambda = [\text{mean } N \text{ in the final decade}] / [\text{mean } N \text{ in the first decade}]$.

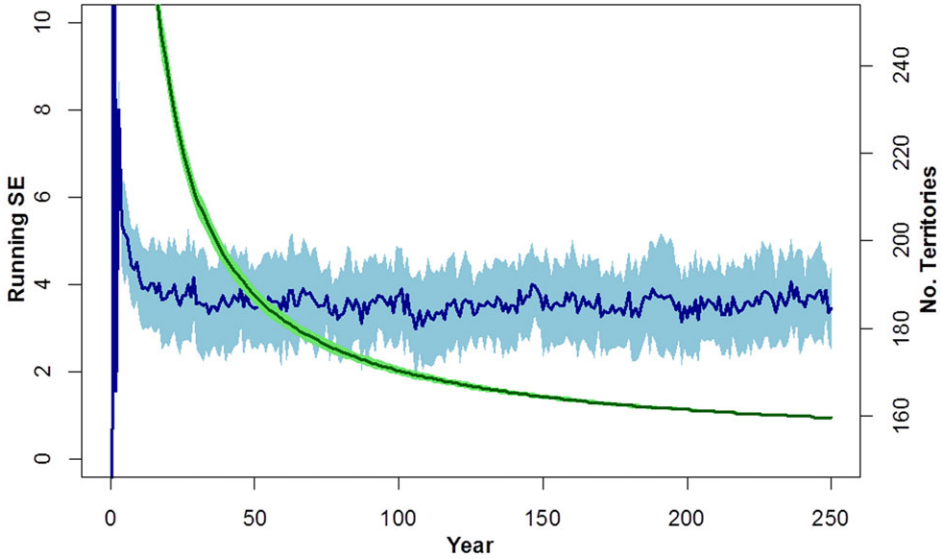


FIGURE 2. Results of running the Northern Spotted Owl (NSO) HexSim model under normative settings (Table 1) showing the mean and range of the number of NSO territories (dark blue line and light blue band) and the running standard error (SE) of NSO territories (green line) over simulation time, over 25 replicate runs.

2.3. Sensitivity tests of model parameters. We ran two general categories of sensitivity tests: (1) tests of varying the values of NSO biological parameters, and (2) tests of general model architecture pertaining to evaluating dynamics of recovery from low population levels or deflation from high population levels.

In the tests of NSO biological parameters, we did not evaluate sensitivity to varying survivorship and reproduction, in part because these parameters consisted of complex, conditional matrices and not simple, single values. For example, the NSO survival rates varied stochastically as a function of stage class, resource use class, and other factors. Also, other analyses have already established high sensitivity of population size and trend to survivorship and reproduction (Lamberson et al. [1994], Marcot et al. [2013]). Many years of field study have provided estimates of NSO vital rates (survival and reproduction) with nearly unprecedented accuracy (Forsman et al. [2011]), and sensitivity to vital rate stochasticity can be analyzed separately (e.g., Wisdom et al. [2000], Aberg et al. [2009]). Instead, our analysis focused on lesser-known parameters pertaining to habitat quality, distribution, movement, and carrying capacity.

We first ran 10 sensitivity analysis scenarios (listed in Figure 3) in which the values of 15 input parameters (Table 1) were each varied by $\pm 10\%$ (which

		Sensitivity Analysis Scenario									
		Sens 01	Sens 02	Sens 03	Sens 04	Sens 05	Sens 06	Sens 07	Sens 08	Sens 09	Sens 10
HexSim NSO input parameters varied	MaxRngArea	X									
	HexRngEl		X								
	MinRngRes	X		X							
	ResTargs				X						
	ResTrtThMod					X					
	ResTrtThHi					X					
	PathLenBPro						X				
	MnResQualPrs							X			
	RepulMinPrs								X		
	MaxExplAPro									X	
	PathLenBDis						X				
	MnResQualDis							X			
	RepulMinDis								X		
	MaxExplADis									X	
	MaxExplAHR										X
Response variables: Abs [MaxHigh-MaxLow]	EndMeanTerritories	○ 12.5 ○	● 8.4 ●	● 191.9 ●	● 381.3 ●	● 378.3 ●	○ 1.3 ○	○ 31.5 ○	○ 0.8 ○	○ 3.0 ○	● 176.8 ●
	EndMinTerritories	○ 14.1 ○	● 4.9 ●	● 167.7 ●	● 368.6 ●	● 367.1 ●	○ 0.2 ○	○ 29.2 ○	○ 1.2 ○	○ 2.7 ○	● 164.6 ●
	EndMeanFloaters	○ 22.8 ○	● 2.9 ●	● 102.1 ●	● 287.1 ●	● 283.6 ●	○ 1.3 ○	○ 22.4 ○	○ 1.2 ○	○ 4.3 ○	● 103.5 ●
	EndMinFloaters	○ 16.4 ○	● 1.0 ●	● 74.7 ●	● 250.8 ●	● 251.3 ●	○ 1.0 ○	○ 17.0 ○	○ 2.0 ○	○ 3.2 ○	● 84.5 ●
	SimLamb	○ 0.003 ○	○ 0.004 ○	● 0.643 ●	○ 0.001 ○	○ 0.033 ○	○ 0.018 ○	○ 0.016 ○	○ 0.008 ○	○ 0.018 ○	○ 0.058 ○
Response variables: Abs [High-Low]	EndMeanTerritories	○ 0.8 ○	○ 0.6 ○	● 21.4 ●	● 63.1 ●	● 65.7 ●	○ 1.3 ○	○ 1.9 ○	○ 1.8 ○	○ 0.9 ○	● 28.1 ●
	EndMinTerritories	○ 2.4 ○	○ 0.1 ○	● 17.6 ●	● 63.9 ●	● 63.1 ●	○ 0.5 ○	○ 1.4 ○	○ 2.6 ○	○ 0.6 ○	● 26.9 ●
	EndMeanFloaters	○ 2.8 ○	○ 1.7 ○	● 2.5 ●	● 36.9 ●	● 40.5 ●	○ 2.4 ○	○ 0.9 ○	○ 0.2 ○	○ 2.5 ○	● 18.5 ●
	EndMinFloaters	○ 0.2 ○	○ 0.8 ○	● 2.4 ●	● 38.0 ●	● 33.6 ●	○ 0.2 ○	○ 0.0 ○	○ 0.2 ○	○ 0.6 ○	● 14.4 ●
	SimLamb	○ 0.001 ○	○ 0.003 ○	● 0.010 ●	● 0.014 ●	● 0.010 ●	○ 0.006 ○	○ 0.008 ○	○ 0.001 ○	○ 0.005 ○	○ 0.003 ○

FIGURE 3. Results of running 10 sensitivity analysis scenarios in HexSim, selectively varying 15 input parameters by $\pm 10\%$ (high, low) and $\pm 50\%$ (maximum high [MaxHigh], maximum low [MaxLow]) of their normative values (Table 1). The X's denote which input parameter was varied in each scenario. Numbers are the absolute differences of each response variable outcome; higher values denote greater sensitivity. The circles are blackened by 20% increments (see key) of the normalized value of each sensitivity analysis scenario's response variables, that is, their relative sensitivity outcome across each row. As an example from scenario Sens 10, EndMeanTerritories was 176.8 territories greater under the MaxHigh value of the input variable MaxExplAHR than under its MaxLow value. This outcome compares to all other scenarios in the same row as $100 \cdot (176.8 / 0.8) / (0.8 / 381.3) = 46\%$, for which its "tornado" circle icon is half filled (see key). In this way, sensitivity of each response variable to each scenario could be directly compared as a percentage of the overall variation in the response.

resulted in "high" and "low" outcomes, respectively) and $\pm 50\%$ ("maximum high" and "maximum low" outcomes) of their normative values in a test of nominal range sensitivity (sensu Morgan and Henrion [1990]), and we recorded the values of each response variable averaged over 25 replicate runs. Initial model tests confirmed that 25 replications provided fully stabilized variance in response variable outcomes (Singleton [2013]). The 15 input parameters pertain to NSO population size,

parameters affecting colonization and home range area as influenced by habitat quality, and movement and dispersal as influenced by habitat distribution. We then calculated the absolute difference between high and low, and between maximum high and maximum low (H and L , respectively), outcomes for each response variable outcome n , and presented these differences in a pie-dot version of “tornado diagrams” that depict the relative sensitivity of each response variable to each input parameter (Goodwin and Wright [2004]). Relative sensitivity was calculated on a 0–100% scale as $(\frac{n}{L})(\frac{L}{H}) \cdot 100$ (see Figure 3 for example).

Some of these sensitivity analyses entailed covarying, as in deterministic joint analysis (Morgan and Henrion [1990]), 2 input parameters because of their connections within the HexSim model structure (Table 1) and to determine interaction effects by use of ANOVA tests. We also separately tested interaction effects of covarying 3 input parameters (see Table 1) by $\pm 10\%$ of their normative values by using the built-in sensitivity analysis function in HexSim. We selected the 3 parameters—minimum range resource, hexagon range value, and maximum explored area—out of the fuller set as representative of how the owls view and explore for habitat quality and establish territories. Our sensitivity metrics follow what Morgan and Henrion ([1990]) termed normalized sensitivity, based on being normalized by the percent variation on the input parameters.

In sensitivity tests of general model architecture, we varied simulation run time (number of time steps in each replicate), and initial population size (number of adult female NSOs at time step 0). We analyzed simulation run time and effects of overpopulation (initial numbers of NSO breeding females greatly exceed carrying capacity) and underpopulation (far less than carrying capacity) as free and forced responses (Reddy [2011]) by determining transition times for the running standard errors (SE) of each response variable to equilibrate to within 5% SE. The purpose of this analysis was to determine recovery time (to carrying capacity) from overpopulation and from underpopulation, and if the two recovery times differed. We varied the starting normative population size (187 NSOs) by initially overpopulating the landscape (with 500 NSOs; free response) and initially underpopulating the landscape (with 10 NSOs; forced response) and observing the time needed to decrease or increase, respectively, to the normative carrying capacity level. Results of these tests helped determine the temporal dynamic behavior of the model, to ascertain the start-up bias period during which the model was reaching relative equilibrium given its input parameters, and to provide insights into how quickly NSO populations can respond to an increase or decrease in carrying capacity when habitat remains stable.

3. Results.

3.1. The normative model. The normative model resulted in an average long-term population on Okanogan-Wenatchee National Forest of 187 NSO breeding

territories and 107 nonterritorial, nonbreeding floater NSOs, with a small degree of variation around the population average of not less than 161 breeding territories over the course of 100-year simulations (Table 2, Figure 2). Average long-term population trends were stable (Figure 2), with simulation $\lambda \approx 1.0$ (Table 2).

3.2. Sensitivity to varying Northern Spotted Owl biological parameters. In general, we found that numbers of NSO territories and floaters were most sensitive to variations in 4 parameters (MinRngRes, ResTargs, ResTrtThMod, and ResTrtThHi; see Table 1) representing habitat quality, and somewhat sensitive to 2 parameters (HexRngEl and MaxEplAHR) representing area explored for establishing home ranges (Table 3, Figure 3). There was consistently low sensitivity to other input parameters, notably the coefficients describing movement path length and dynamics (e.g., parameters PathLenBPro, PathLenBDis, RepulMinPrs, RepulMinDis; Figure 3, Table 1). We found that sensitivity patterns were consistent at the two levels of varying input parameters ($\pm 10\%$ and $\pm 50\%$; Figure 3). Interestingly, there were no significant main effects found for measures of NSO population trend (response variable SimLamb, Table 3).

We also ran 27 sensitivity analysis scenarios in which 3 input parameters (HexRngEl, MinRngRes, and MaxEplAHR) were first set to their normative values and then varied $\pm 10\%$, individually and in tandem. From these analyses, we found that numbers of NSO territories and floaters were most sensitive to the higher (+10%) value of MinRngRes and the lower (−10%) value of MaxEplAHR, whereas sensitivity of the 3 NSO population trend response variables was mixed among higher and lower values of all 3 input parameters (Figure 4). Results of ANOVA tests (Table 3) suggest that the response variables are not necessarily more sensitive to covariation of these 3 input parameters, particularly where increase of one parameter might offset the response generated by decrease of another parameter.

3.3. Sensitivity to general model architecture. Although we ran some simulations out to 500 years, it was apparent from the 150-year normative runs, based on the static distribution of current habitat, that population size and trend equilibrated ($SE < 0.05$) by year 50, with very small standard deviations and low stochasticity among replicates runs (Figures 2 and 3). These findings established that, for sensitivity tests and further project use, we could limit simulations to 150 years and dismiss the first 50 years as the period of start-up bias. The specific period of start-up bias might vary, however, with other species models, but in general is a characteristic of this type of time-dynamic simulation model.

We found that populations, following the start-up bias period, more quickly equilibrated to carrying capacity (187 NSOs) under the free response (Figure 5) than under the forced response (Figure 6) scenario. In the forced response scenario,

	INPUT PARAMETERS			RESPONSE VARIABLES				
Sensitivity Analysis Scenario	HexRngEl	MinRngRes	MaxEplAHR	EndMeanTerritories	EndMinTerritories	EndMeanFloaters	EndMinFloaters	SimLamb
Normative	→ 30 → 250 → 46			0.0	0.0	0.0	0.0	0
1	↓ 27 ↓ 225 ↓ 41			12.7	15.4	11.6	9.0	0.015
2	↓ 27 ↓ 225 → 46			3.0	2.8	2.0	0.6	0.027
3	↓ 27 ↓ 225 ↑ 51			19.3	17.4	7.1	8.8	0.015
4	↓ 27 → 250 ↓ 41			17.4	16.4	11.4	7.2	0.019
5	↓ 27 → 250 → 46			0.4	0.3	1.2	1.5	0.017
6	↓ 27 → 250 ↑ 51			10.3	13.5	5.4	6.6	0.029
7	↓ 27 ↑ 275 ↓ 41			31.8	28.8	14.0	8.6	0.007
8	↓ 27 ↑ 275 → 46			18.1	13.0	3.8	0.7	0.023
9	↓ 27 ↑ 275 ↑ 51			9.5	4.9	2.6	5.3	0.029
10	→ 30 ↓ 225 ↓ 41			11.4	11.6	10.8	9.0	0.004
11	→ 30 ↓ 225 → 46			5.9	4.8	0.8	0.8	0.006
12	→ 30 ↓ 225 ↑ 51			15.5	17.2	5.6	5.6	0.028
13	→ 30 → 250 ↓ 41			19.9	15.1	13.6	9.1	0.040
14	→ 30 → 250 → 46			0.2	1.0	0.7	0.0	0.012
15	→ 30 → 250 ↑ 51			10.8	12.0	5.1	6.2	0.024
16	→ 30 ↑ 275 ↓ 41			32.3	27.1	14.4	10.9	0.027
17	→ 30 ↑ 275 → 46			19.2	14.4	5.7	3.1	0.034
18	→ 30 ↑ 275 ↑ 51			6.5	2.6	4.0	6.5	0.022
19	↑ 33 ↓ 225 ↓ 41			14.0	11.4	12.6	7.8	0.013
20	↑ 33 ↓ 225 → 46			4.1	3.8	1.0	2.2	0.005
21	↑ 33 ↓ 225 ↑ 51			15.0	14.1	4.7	5.1	0.033
22	↑ 33 → 250 ↓ 41			17.9	16.8	12.0	8.5	0.025
23	↑ 33 → 250 → 46			3.2	1.4	3.8	0.3	0.030
24	↑ 33 → 250 ↑ 51			9.5	12.2	3.7	6.3	0.026
25	↑ 33 ↑ 275 ↓ 41			31.9	27.6	13.8	9.0	0.022
26	↑ 33 ↑ 275 → 46			15.2	13.8	0.2	3.0	0.012
27	↑ 33 ↑ 275 ↑ 51			6.2	3.2	3.4	4.6	0.024

FIGURE 4. Results of 27 sensitivity analyses covarying 3 values each of 3 input parameters (see Table 1). Under the input parameters, arrow directions denote normative values (yellow horizontal arrows), and +10% (green upward arrows) and -10% (red downward arrows) of the normative values. Values under the response variables are absolute differences between their normative model values (Table 2) and the results from the input parameter values. Horizontal bars represent the value in each cell, normalized for each response variable (yellow for population size variables, blue for population trend variables); high values and longer bars denote greater relative sensitivity of the response variable to the values of the input parameters in that row.

TABLE 3. ANOVA results on sensitivity tests of covarying three input parameters (Table 1) in the HexSim Northern Spotted Owl (NSO) model, on numbers of NSO territories and floaters (Table 2). Values are F -ratios and p -values in parentheses. Greater levels of statistical significance (smaller p -values) suggest greater sensitivity of the response variable to the input parameters.

Source (input parameters)	df	Response variable				
		EndMean Territories	EndMin Territories	EndMean Floaters	EndMin Floaters	SimLamb
HexRngEl	2	12.30 (0.198)	4.91 (0.304)	0.66 (0.656)	2,423.56 (0.014 ^b)	0.05 (0.952)
MinRngRes	2	50,595.12 (0.003 ^b)	1,673.36 (0.017 ^b)	50.59 (0.099 ^a)	5,673.22 (0.009 ^b)	1.92 (0.455)
MaxExplAHR	2	76,539.92 (0.003 ^b)	3,667.66 (0.012 ^b)	2,940.95 (0.013 ^b)	625,064.48 (0.001 ^b)	1.96 (0.451)
HexRngEl x	4	157.80 (0.060 ^a)	1.45 (0.547)	13.49 (0.201)	598.72 (0.031 ^b)	0.77 (0.683)
MinRngRes						
HexRngEl x	4	16.70 (0.181)	3.76 (0.367)	3.80 (0.365)	1,739.74 (0.018 ^b)	0.82 (0.668)
MaxExplAHR						
MinRngRes x	4	218.53 (0.051 ^a)	11.30 (0.219)	0.59 (0.738)	208.83 (0.052 ^a)	1.02 (0.622)
MaxExplAHR						
HexRngEl x	8	160.50 (0.061 ^a)	4.17 (0.363)	10.92 (0.230)	2,209.93 (0.016 ^b)	1.78 (0.525)
MinRngRes x						
MaxExplAHR						

^a $p < 0.10$.

^b $p < 0.05$.

populations did not reach carrying capacity until approximately year 75, whereas they settled down to carrying capacity in the initially overpopulated free response scenario by year 25. However, under both forced and free response scenarios, populations reached steady-state conditions at carrying capacity by year 150, with statistically significant, slightly lower minimum population levels (response variable Ending Minimum Territories, Figure 7; ANOVA $F = 8.3646$, $df = 74$, $p < 0.001$) and slightly higher trends (response variable Simulation Lambda, Figure 7; ANOVA $F = 22.485$, $df = 74$, $p < 0.001$) over the full simulation period under the free response scenario. We also hypothesize from these results that, as initial population size approaches carrying capacity, the difference in recovery time between over- and underpopulation levels would converge.

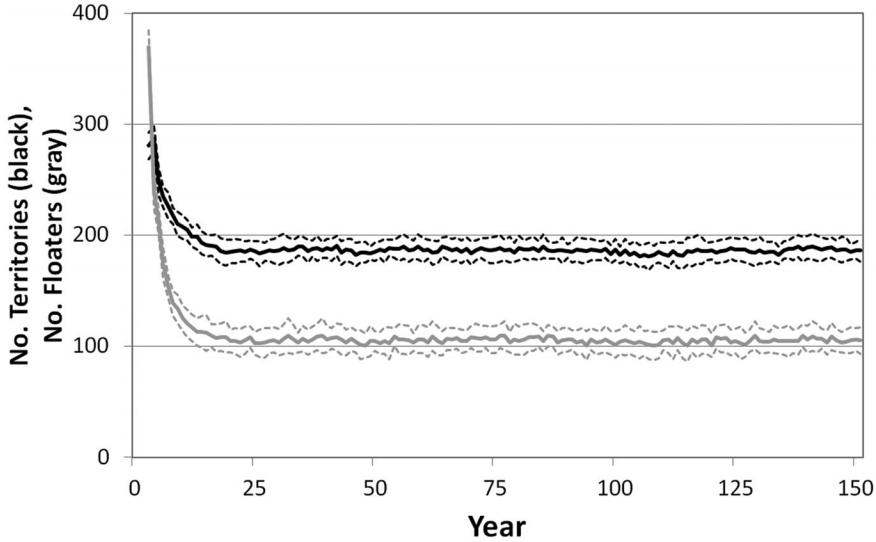


FIGURE 5. Results of running the Northern Spotted Owl (NSO) HexSim model under a “free response” scenario in which the landscape is initially greatly overpopulated by NSO territories and then allowed to equilibrate. Solid lines are mean values, dotted lines are ± 1 SD, over 25 replicate runs.

4. Discussion.

4.1. Implications for Northern Spotted Owl modeling and management. We identified that NSO population size and trend are sensitive largely to parameters representing habitat quality, and less sensitive to NSO movement distance and dispersal behavior. This is good news for the manager who may be concerned about uncertainty, in that habitat quality is well studied and better known than are other parameters in the model, particularly regarding owl movement dynamics. This suggests confidence in model outcomes if the habitat quality parameters are accurate and correctly depicted in the model structure. Further, habitat quality is a factor that, to an extent, can be controlled through management of vegetation, fire and fuels, and patterns of land ownership. This outcome is important also because, in general, much of conservation planning is focused on evaluating the implications of landscape patterns, such as resulting from alternative reserve designs or conservation strategies, on population processes.

We also found that the forced response takes substantially longer to reach NSO population equilibration than does the free response, suggesting that colonizing vacant habitats is relatively time consuming. This made sense biologically, as birds would more quickly die out if suitable, unoccupied habitat was not available as under the overpopulated conditions of the free response scenario, than birds being able

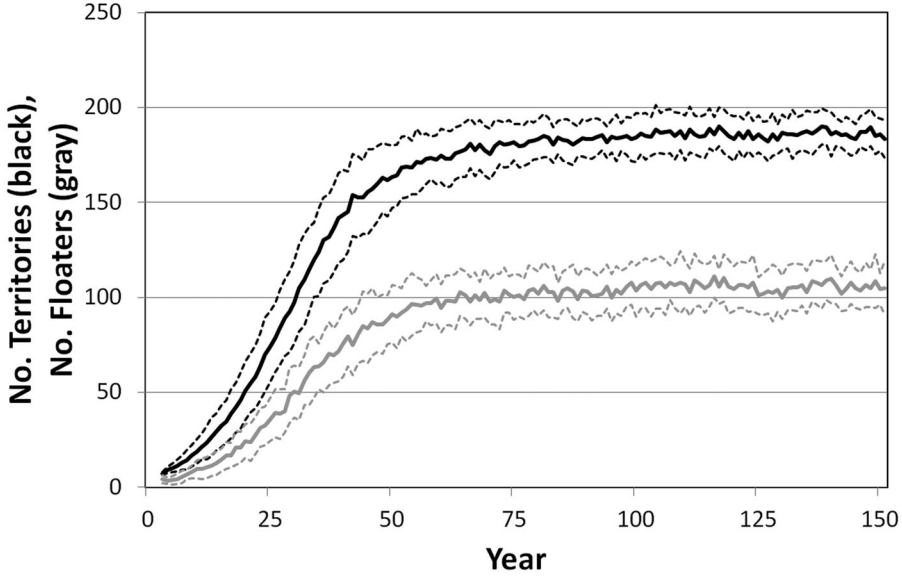


FIGURE 6. Results of running the Northern Spotted Owl (NSO) HexSim model under a “forced response” scenario in which the landscape is initially greatly underpopulated by NSO territories and then allowed to equilibrate. Solid lines are mean values, dotted lines are $\pm 1SD$, over 25 replicate runs.

to disperse, prospect, and explore for habitat across unsuitable environments with dispersal barriers, as with the underpopulated conditions of the forced response scenario. The implications of this are to provide more realistic expectations for lag times of NSO population expansion to discover and occupy habitats newly available from forest growth or from elimination of their primary competitor. Also, the lack of significant effects found for NSO population trend from the three-parameter variations (Table 3) is not unexpected. That is, over the long run times, the populations equilibrated to whatever carrying capacity was available under each scenario, given the variants in input parameters.

4.2. Additional sources of model variation, sensitivity, and uncertainty.

Several other causes of model variation and sensitivity have been analyzed elsewhere, in particular effects of including or omitting NSO dispersal barriers on the landscape, effects of Barred Owls (*Strix varia*; a key competitor) on NSO population size and trend (Wiens et al. [2014]), potential contribution of nonfederal lands as habitat (Singleton [2013]), and size and spacing of habitat blocks (Marcot et al. [2013]). Management essentially cannot control NSO dispersal barriers of elevation and large water barriers. On the other hand, controlling Barred Owls is an option being implemented under USFWS’ Northern Spotted Owl Recovery Plan

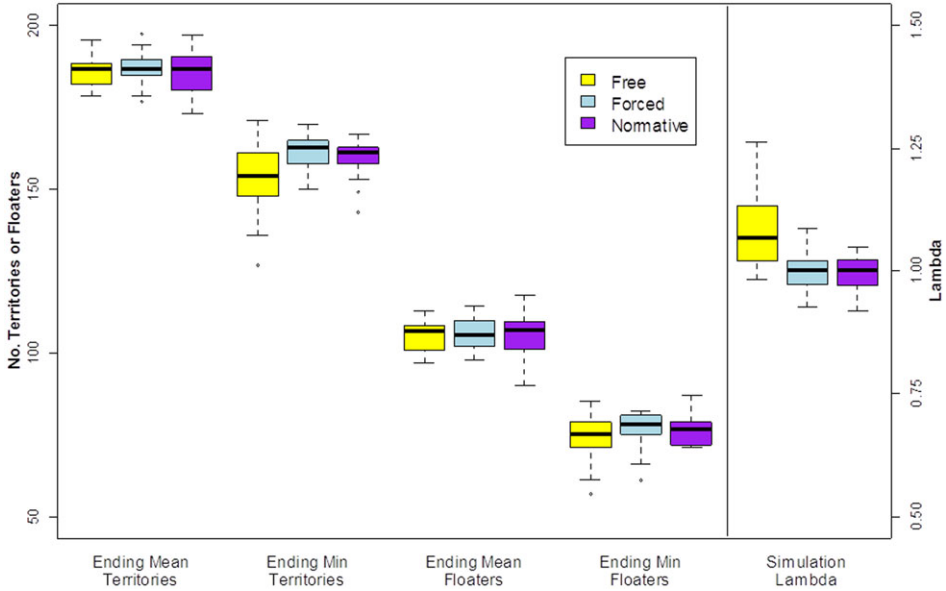


FIGURE 7. Results of sensitivity analysis in HexSim of number of Northern Spotted Owl (NSO) territories or floater (nonterritorial) individuals and population trend (response variables, Table 2) under free response, forced response, and normative model settings (varying the model only by the initial number of NSO territories). Results represent 25 replicate runs per scenario.

(USFWS [2011]). Research on Barred Owls within the modeling area included a radio-telemetry study conducted from 2003 to 2006 (Singleton et al. [2010]), and Singleton ([2013]) reported major adverse effects on NSOs from Barred Owls. We would anticipate that a two-species IBM model, such as including Spotted and Barred Owls in HexSim, might result in somewhat different sensitivity outcomes than from a single-species model, such as resulting from shifts in habitat and resource selection functions due to the presence of a strong competitor.

Other sources of model variation and sensitivity may pertain to the specific algorithms and code structure used in HexSim as compared to other IBMs. We support such multimodel evaluations (e.g., Ko et al. [2011]) as one way to evaluate sensitivity across different modeling platforms. Marcot et al. ([2013]) compared an earlier IBM to a HexSim analysis of NSO population response to various habitat patch sizes and spacing configurations, and found highly consistent results across the two models. This lends confidence to our modeling the behavior of NSOs to habitat dispersion.

Sources of model uncertainty, in addition to those discussed above, also pertain to the many assumptions that underlie such complex IBMs as HexSim. These include

assumptions relevant to the algorithms used in HexSim for movement dynamics (described in Marcot et al. [2013]). Also, we developed a female-only model which does not account for pair interaction and Allee (behavioral) effects on population vital rates, often associated with small population size and low density (Keitt et al. [2001]). Sensitivity of outcomes to these and other assumptions could be explored by developing alternative and more complex model structures in HexSim or other IBM modeling shells. However, increasing model realism entails greater model complexity and often many additional input parameters, and additional model complexity can confound interpretation of model results. At some point, sensitivity results may become more influenced by model complexity than by real-world dynamics.

Whereas some of the parameters we examined in this study are unique to HexSim, any spatially explicit IBM of a territorial species will have analogs. Our study will have obvious utility for developers of HexSim models, but a much broader spectrum of the research community should benefit as well. It has been uncommon for users of sophisticated population modeling platforms to perform sensitivity analyses of errors in model parameters that are less well known or understood than survival and reproduction rates, such as with parameters describing movement, exploration, and site selection. Our study focuses specifically on such extended sensitivity analyses and illustrates procedures that can be used with any complex simulation model.

4.3. Sensitivity analysis provides insights into uncertainty. Model sensitivity analysis can provide insights into four main aspects of uncertainty (Benke et al. [2008], Regan et al. [2002]). (1) Parameter value uncertainty pertains to uncertainty over the exact values of parameters and how they are represented such as by central tendency values, values depicting spatial variation, temporal variation, or inter-parameter relationship variation. We tested the implications of varying NSO biological parameters and discovered which response variables were most sensitive to input parameters, particularly input parameters not addressed in previous sensitivity analyses.

(2) Model structure uncertainty includes uncertainty over parameter selection, parameter relationships, and algorithms used. Model structure uncertainty is one facet of what is more generally called epistemic uncertainty (Regan et al. [2002], Aven [2003]), that is, uncertainty over how the system itself is structured and works. We tested the sensitivity implications of the general model architecture in part by determining the start-up bias period and through model dynamics of free and forced responses.

Other aspects of uncertainty include (3) inherent system variability which is the degree to which the system itself that is being modeled or analyzed, or parameters thereof, varies over space or time randomly or in response to conditions not included

in the model or analysis. Inherent system variability is sometimes referred to as aleatoric uncertainty (Aven [2003]). Additional experiments with our HexSim NSO model will provide insights into effects of inherent system variability, now that we understand and can parse out the sensitivity response from parameter value and model structure uncertainty.

A final area of uncertainty is (4) measurement error (observational error, experimental uncertainty) of input parameter values, of their correlations and relationships, and of algorithms used in the model. Measurement error tends to reduce precision and accuracy, and increases bias, of input parameter values and thus of the response variables and overall system response. Again, our sensitivity analyses of NSO biological parameters and model architecture revealed the most influential input parameters which would be prioritized for further study if needed to reduce their measurement error.

4.4. Other sensitivity analysis methods. Our particular analysis of model sensitivity is but one of a number of methods and metrics. For example, the sensitivity metric of Jørgensen ([1986], as used by Rustigian et al. [2003] on a PATCH model and by Pulliam et al. [1992] on another IBM) calculates sensitivity as variation in the response variables normalized by the absolute difference in the value of a single, given input parameter varied by $\pm 25\%$ of its normative value. We did not use this metric because our analyses pertained to covarying variables and because we wanted two levels of variation of the input parameters to test for consistency of sensitivity responses over a wider range of input values. We feel that our approach provides greater parity in comparing the influence of response variables with vastly different measurement units (e.g., numbers of territories versus population trend lambda values), and ours also accounts for covariation of input parameters.

Other sensitivity metrics also pertain to varying only a single parameter at a time, such as with Sobol's sensitivity analysis (Nossent et al. [2011]) and the Morris method (e.g., as used by Confalonieri et al. [2010], Vinatier et al. [2013]). Benke et al. ([2008]) conducted sensitivity analyses by combining differential error analysis and Monte Carlo simulation with stochastic and deterministic sensitivity analysis. Curtis and Naujokaitis-Lewis ([2008]) developed a program (GRIP) to conduct sensitivity analysis of spatial and nonspatial input parameters of population viability analyses from an IBM (RAMAS Metapop). McCarthy et al. ([1995]) used logistic regression; Saltelli et al. ([2000]) used global quantitative sensitivity analysis methods; Ravalico et al. ([2010]) used an approach called Management Option Rank Equivalence, which is a numerical optimization for decision analysis; and Neubert and Caswell ([2000]) applied formulas for analyzing sensitivity and elasticity of invasion speed to changes in demographic and dispersal parameters of invasive species. The performance of IBMs also depends on their time-step updating

algorithms and other aspects of the underlying structure and code (Caron-Lormier et al. [2008]). Beaudouin et al. ([2008]) demonstrated how IBM parameter values can be selected and calibrated based on empirical data by using sensitivity analysis. Clearly, many approaches are available and usually tailored to specific model constructs and evaluation needs. We developed our approach to best match the type and purpose of our NSO IBM model. If appropriate, as with multimodel analyses, conducting sensitivity analyses with different metrics and approaches also may provide useful insight into the degree and consistency by which model responses are influenced by input parameters.

5. Conclusions. We also have demonstrated an approach to analyzing sensitivity to variations in input parameter values and to model architecture and dynamics. In our NSO HexSim model, our findings provide support that NSO response seems most sensitive to parameters on habitat selection and resource use for which we probably have the best empirical data and understanding, which can be controllable by management, and which provides the most important information for conservation planning. We now have greater confidence as our specific model and its variants are used for planning conservation and recovery of NSOs, and that our approach can be applied for modeling of other threatened or imperiled species.

We provide a general framework and methodology for conducting sensitivity analysis of a specific IBM, HexSim that borrow from and extends existing approaches. Although specific results may vary with other IBMs depending on their structures and parameter relationships, this methodology will have value for other IBM-based studies, particularly applied to conservation assessment and planning.

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