SUPPLEMENTARY APPENDIX. Methods for modeling Northern Spotted Owl dispersal.

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METHODS

Spatially-explicit dispersal model. We used HexSim (version 1.2.1.5), a spatially-explicit, individual dispersal simulation modeling shell developed by N. Schumaker (www.epa.gov/hexsim/), to model NSO population response to artificial landscapes with varying habitat cluster size and spacing dimensions and varying proportion of the total landscape in habitat. HexSim is the current generation of the model previously called PATCH. Applications of PATCH to a variety of habitat and species evaluation projects have appeared in at least 20 peer-reviewed articles (e.g., Rustigian et al. 2003, Schumaker et al. 2004). In our use of HexSim, reproduction and dispersal were represented as stochastic events. Events of reproduction, dispersal, exploration, establishing a territory (where appropriate), and survival were conducted for each simulated year, and locations of territorial and non-territorial (floater) individuals (females) were tracked and tallied for each time period (year).

Landscape scenarios. A HexSim map consists of a tiled plane of hexagons. In our simulated landscapes, each hexagon was a single patch which was either fully suitable NSO habitat or fully unsuitable, and represented 1,800 ha (4,559 m side-to-side width) which is the median amount of habitat used by a breeding pair of NSOs (USFWS 2008).

The two variables in our simulated landscapes were habitat cluster size and spacing between habitat clusters. A habitat cluster consisted of contiguous hexagons of habitat that would provide for multiple pairs of NSOs. Habitat clusters were shaped to be as compact as possible within the hexagon configuration. Using ArcInfo Workstation (ESRI 1982-2008), we developed 31 artificial landscapes representing combinations of NSO habitat cluster size (4, 9, 25, 36, and 49 owl pairs) and edge-to-edge cluster spacing (7, 15, 29, 52, 74, and 101 km), and an all-habitat landscape (Supplementary Appendix Table 1). We selected these habitat cluster sizes and spacing values to bracket and best match those used by LNVM and as needed for consideration by FWS, and also to include an all-habitat landscape as a control condition. We held the total amount of habitat constant and varied the size of the overall landscape to accommodate the cluster size and spacing parameters. This also served to vary the total proportion of habitat throughout the landscape, which we related to population persistence.

Supplementary Appendix Table 1. Characteristics of the 31 simulated landscapes varying northern spotted owl (NSO) habitat cluster size and spacing as used in the HexSim simulation model.

	Habitat cluster size		Spacing between habitat clusters		Landscape parameters				
Habitat scenario	Hectares of NSO habitat per cluster	No. suitable NSO sites (hexagons) per cluster	Km	No. hexa-gons	Total no. of habitat clusters	Total no. suitable NSO sites (suitable hexes)	Total area of suitable NSO habitat (ha)	Total no. hexagons	Percent of landscape in suitable NSO habitat
1	7,200	4	7	2	441	1,764	3,175,200	7,056	25%
2	7,200	4	15	4	441	1,764	3,175,200	15,876	11%
3	7,200	4	29	7	441	1,764	3,175,200	39,900	4%
4	7,200	4	52	12	441	1,764	3,175,200	98,784	2%
5	7,200	4	74	17	441	1,764	3,175,200	176,800	1%
6	7,200	4	101	23	441	1,764	3,175,200	308,112	1%
7	16,200	9	7	2	196	1,764	3,175,200	4,900	36%
8	16,200	9	15	4	196	1,764	3,175,200	9,604	18%
9	16,200	9	29	7	196	1,764	3,175,200	21,714	8%
10	16,200	9	52	12	196	1,764	3,175,200	49,980	4%
11	16,200	9	74	17	196	1,764	3,175,200	86,829	2%
12	16,200	9	101	23	196	1,764	3,175,200	147,378	1%
13	45,000	25	7	2	72	1,800	3,240,000	3,528	51%
14	45,000	25	15	4	72	1,800	3,240,000	5,832	31%
15	45,000	25	29	7	72	1,800	3,240,000	11,336	16%
16	45,000	25	52	12	72	1,800	3,240,000	23,408	8%
17	45,000	25	74	17	72	1,800	3,240,000	38,407	5%
18	45,000	25	101	23	72	1,800	3,240,000	62,248	3%
19	64,800	36	7	2	49	1,764	3,175,200	3,136	56%
20	64,800	36	15	4	49	1,764	3,175,200	4,900	36%
21	64,800	36	29	7	49	1,764	3,175,200	9,016	20%
22	64,800	36	52	12	49	1,764	3,175,200	17,640	10%
23	64,800	36	74	17	49	1,764	3,175,200	28,512	6%
24	64,800	36	101	23	49	1,764	3,175,200	45,248	4%
25	88,200	49	7	2	36	1,764	3,175,200	2,916	60%
26	88,200	49	15	4	36	1,764	3,175,200	4,356	40%
27	88,200	49	29	7	36	1,764	3,175,200	7,650	23%
28	88,200	49	52	12	36	1,764	3,175,200	14,364	12%
29	88,200	49	74	17	36	1,764	3,175,200	22,765	8%
30	88,200	49	101	23	36	1,764	3,175,200	35,442	5%
31	5,891,400	3,273	0	0	1	3,273	5,891,400	3,273	100%

Demographic rates. We parameterized HexSim with estimates from empirical studies on NSO biology, principally on stage-class survivorship and reproduction (Anthony et al. 2006) and stage-class dispersal (Forsman et al. 2002). We consulted directly with previous modelers Rollie Lamberson, Kevin McKelvey, and Barry Noon to ensure that our modeling approach best matched their modeling assumptions and methods, and with NSO biologists Robert Anthony and Eric Forsman to ensure correct model parameterization of vital and dispersal rates. To facilitate comparison among the various landscape configurations, we did not vary inherent vital and dispersal rates by habitat configurations (size and spacing of habitat clusters), nor were empirical data available by which to provide a basis for such variation.

Reproduction and survivorship. To parameterize HexSim, which we used as a female-only model, we summarized NSO stage-class specific reproduction *b* and survivorship *s* from a published meta-analysis that combined results from 14 demographic studies across the range of NSOs in Pacific Northwest, U.S. (Anthony et al. 2006), using 4 stage classes (Supplementary Appendix Table 2).

Supplementary Appendix Table 2. Northern spotted owl reproduction and survivorship rates used in the HexSim model.

		Reproduction		Survivorship		
Stage class	Stage class name	Reprod. class	Value[1]	Survival class	Average[2]	Stable
0	juvenile	b_0	0.000	s_0	0.442	0.442
1	subadult, 1-yr-old	b_1	0.078	s_1	0.814	0.814
2	2-yr-old	b_2	0.192	s_2	0.850	0.850
3	3-yr-old	b_3	0.348	s_3	0.856	0.882[3]

[1] Females born per female per year.

[2] Values derived from summary of empirical data for s_0 from A. Franklin (pers. comm.) and for s_1-s_3 from Anthony et al. (2006) (see text). These values result in population $\lambda = 0.95$.

[3] Value adjusted to achieve population $\lambda = 1.00$ (see text).

We calculated stage-class reproduction (no. females born per female per year) and annual survivorship as weighted means of values from NSO demographic study areas provided by Anthony et al. (2006), using their estimates of the reciprocal of standard error as weights and excluding data from one NSO demographic study area (Marin County) because of small sample size (R. Anthony, personal communication). The value of the first stage class survival, s_0, was not available from Anthony et al. (2006) and was provided by A. Franklin (personal communication).

We used the spreadsheet add-in program PopTools (Hood 2009) to calculate overall finite rate of population change, λ, from empirical estimates of mean reproduction and survival, in a standard Leslie matrix formulation:

$$\begin{pmatrix} s_0 b_1 & s_1 b_2 & s_2 b_3 & s_3 b_3 \\ s_0 & 0 & 0 & 0 \\ 0 & s_1 & 0 & 0 \\ 0 & 0 & s_2 & s_3 \end{pmatrix}$$

which led to $\lambda = 0.95$, or a declining population. Following the example from LNVM -- who modeled empirical estimates of vital rates that resulted in a declining population no matter the habitat amount and configuration, and vital rates adjusted to achieve a stationary population to better evaluate effects of habitat amount and configuration -- we then increased adult survival (s_3) in PopTools to achieve $\lambda = 1.00$, resulting in a "stationary population" configuration of vital rates (Table 2). We modeled each landscape scenario under the two sets of demographic vital rates representing average (declining) population conditions and stationary population conditions, thus, a total of 62 scenarios combining landscape designs and demographic vital rates.

Dispersal. In HexSim, dispersal paths (Fig. 1b) are generated stochastically based on both path length and autocorrelation of movement direction (Appendix). Path lengths can be constant for all individuals, or drawn from uniform or lognormal distributions. Dispersal consists of a series of steps from a hexagon to one of its six neighbors. Autocorrelation in movement direction is an important consideration in modeling dispersal (Bahn et al. 2008), and in HexSim may be varied between zero and 100%, the higher values representing more linear dispersal paths. Observed dispersal distances, measured straight-line from initial point to final point (referred to in the NSO literature as "final distance"), increase with both total path length and percent autocorrelation.

We parameterized HexSim with empirical data on stage-class specific dispersal distances reported from Forsman et al. (2002) as final distances of banded NSOs (Supplementary Appendix Table 3).

Supplementary Appendix Table 3. Final dispersal distances from banded northern spotted owls as summarized from Forsman et al. (2002) and used in the HexSim model expressed as number of hexagons (1 hexagon = 1,800 ha and is 4,559 m wide).

		Range of final dispersal distance (km)			Range of final dispersal distance (no. of hexagons)	
Stage class	Mean final dispersal distance (km)	Minimum	Maximum	Mean final dispersal distance (no. hexagons)	Minimum	Maximum
0	28.6	1.3	104.6	6.219	0.283	22.744
1	8.2	0.01	63.7	1.783	0.002	13.851
2	6.9	0.17	50.7	1.500	0.037	11.024
3	6.1	0.01	85.2	1.326	0.002	18.526

Dispersal distance and landscape exploration movement for each stage class were bound in HexSim by 0 km on the lower end and actual distances on the upper end. A uniform probability distribution was then used in the model to determine dispersal distance within these value bounds for a given simulated owl, resulting in the simulated dispersal distances being lognormally distributed arising from the stochastic exploration function within the model. We set spatial autocorrelation to a moderate value (50%) to avoid a completely random walk, that is, to constrain stochastic movement pathways without unduly impeding movement into adjacent hexagons, to match observed dispersal patterns of NSOs (Forsman et al. 2002).

Following each dispersal component (a more or less linear motion; see next section) of a HexSim movement was an exploration event (a local search). Exploration is the process whereby an owl would prospect for suitable vacant habitat to colonize. In this process, our simulated owls could search up to the number of hexagons representing the annual movement space for a given stage class. If a suitable site could not be located and colonized, then the disperser would remain a floater for that time increment, and in the next increment continue exploration for a suitable vacant hexagon.

We also parameterized HexSim with estimates of the proportion of each NSO stage class dispersing. This was a refinement over LNVM's approach which apparently presumed that 100% of each stage class dispersed if not part of a territorial pair. We assumed that 100% of juveniles (stage class 0) dispersed (E. Forsman, personal communication) and calculated annual percent of stage classes 1-3 dispersing to be 21.7, 14.4, and 4.4%, respectively, as sample-size weighted means among birds with various previous mate status (Forsman et al. 2002, see their Table 7).

HexSim model's dispersal and exploration functions. Movement routines in HexSim have two principal parts called *dispersal* and *exploration*. The dispersal component moves individuals across landscapes, but does not allocate resources to them. During exploration, individuals prospect for a vacant suitable site to colonize. Dispersal decisions are based strictly on habitat quality, whereas exploration behavior is influenced by both habitat quality and resource availability. Both dispersal and exploration involve taking individual steps between adjacent hexagons. Individuals never jump to non-adjacent target sites.

Each disperser is assigned a path length. Path lengths are the number of steps that the disperser will move. Path lengths can be constant, or can be drawn from uniform or lognormal distributions. Path length parameters are all specified as number of hexagons. The path length defines how many steps (from one hexagon to a neighbor) each individual will move during a given time increment.

Stopping conditions, if met, will cause an individual to stop its dispersal prior to moving the full path length. The dispersal stopping criteria are specified with a mean resource quality threshold that, if encountered over a specified number of sequential steps, will halt dispersal. The intent is that both the mean quality and amount of resource encountered (the number of steps the mean is taken over) will figure into decisions to abort the dispersal process. Because dispersal does not address resource availability, many dispersers may elect to stop in the same general location. In such cases, only a fraction may be successful at claiming a territory during exploration.

Dispersal behavior is controlled by three parameters: repulsion, attraction, and autocorrelation. Repulsion and attraction pertain to the degree to which a dispersing individual avoids or seeks, respectively, hexagons with particular habitat or resource attributes. The autocorrelation parameter makes dispersal paths more or less random. In the absence of repulsion and attraction, zero auto-correlation produces a uniformly distributed random walk of movement directions. At the other extreme, 100% auto-correlation results in straight-line movement trajectories. However, repulsion, attraction, and auto-correlation all work together to determine the dispersal path characteristics. In spotted owls, repulsion might be used to impose a degree of unwillingness to disperse across urban areas, whereas attraction might be used to draw owls towards patches of older forest. In our simulations, we provided for a slight attraction to habitat patches that would serve to increase the probability that owls would move to a habitat patch when starting from an adjacent, non-habitat hexagon. We did not use repulsion.

Ignoring landscape boundaries, each hexagon has six neighbors. Taking a single dispersal step involves selecting one neighbor and moving to it. Each neighbor is assigned a value PZ, where P is set based on autocorrelation, and Z reflects any repulsion or attraction. Hexagons can be either repulsive, neutral, or attractive. Autocorrelation probability values P range [0,1], and $0 \le Z < 1$ if a hexagon is repulsive, Z = 1 if it is neutral, and Z > 1 if a hexagon is attractive. Once PZ has been computed for each neighbor, the values are normalized by dividing each by the sum. Thus, each neighboring hexagon is ultimately assigned a probability that captures both auto-correlation and the influence of attraction or repulsion. To select a neighbor, a random number is drawn compared to the individual neighbor probabilities (the normalized PZ values). The larger a neighbor's probability, the greater the likelihood that it will be selected.

Auto-correlation is implemented by assigning higher likelihoods to directions that represent forward movement. HexSim therefore constantly tracts the direction of past movements. The abbreviations DA, AL, AR, BL, BR, and DB are used to label the neighbors that are directly ahead, ahead left, ahead right, behind left, behind right, and directly behind. These labels are relative to the forward direction. HexSim uses a “trend period” parameter to better define the forward direction. The trend period is a number of steps selected by the user, and HexSim tracks the forward direction for each step in this period. For example, if the trend period is set to 5, then the forward direction will be stored for each of the last 5 steps. The forward direction actually used to label the six neighbors (that is, locate DA, DB, etc) will be the direction that occurs most frequently over the trend period. The use of trend periods adds a kind of momentum to highly autocorrelated dispersal paths.

Once the DA, AL, AR, BL, BR, and DB labels have been attached to the appropriate neighbors, then each is assigned an autocorrelation probability, P. The equations used to assign P values are as follows:

$P(DB) = \alpha^4 / 6$,

$P(BL) = P(BR) = \alpha^2 / 6$,

$P(AL) = P(AR) = \alpha(2 - \alpha)^{2.467} / 6$, and

$P(DA) = 1 - P(AL) - P(AR) - P(BL) - P(BR) - P(DB)$,

where

$\alpha = 1 – (\text{percent autocorrelation}) / 100$.

These six autocorrelation probabilities are continuous and sum to one. The expressions for P(AL) and P(AR) are designed so P(DA) = P(AL) + P(AR) when the autocorrelation parameter is set to 50%. This is, of course, arbitrary. The formulas for P given above were selected because they satisfied the following four criteria: only a single autocorrelation parameter is required; all solutions must lie in [0, 1]; all solutions must be equal when $\alpha = 0$; P(DA) must be 1 when $\alpha =$ 100%. These functions were not based on any particular species' movement pattern, but instead were kept general so that a range of dispersal behaviors could be simulated..

Repulsion and attraction produce a coefficient (Z) which is multiplied by the autocorrelation probability, P. A single hexagon can be either repulsive, attractive, or neutral (neither repulsive or attractive), and this determination is based strictly on its quality score. HexSim hexagon quality scores are strictly non-negative. But attraction and repulsion minimum and maximum parameters can be assigned any real value . For hexagons with a score less than the maximum repulsion, Z is fixed at zero. As the hexagon's score increases from the maximum to minimum repulsion, Z increases linearly from zero to one. Z remains at one until the hexagon's score increases to the minimum attraction value. When the hexagon's score increases from the minimum to maximum attraction value, Z increases linearly with slope $1/\beta$, where β is the minimum attraction parameter. For hexagon scores greater than the maximum attraction, Z is fixed at χ/β, where χ is the maximum repulsion.

Finally, the probability of moving into each of the six neighboring hexagons is derived by normalizing the individual PZ values. Because the repulsion and attraction parameters may be set outside the range of observed hexagon scores, no hexagon may necessarily ever be fully repulsive or attractive. In fact, all hexagons may easily be set neutral.

The exploration process involves an intensive search for resources. A maximum explored area is specified, in hexagons. Individuals will not be allowed to explore more than this number of hexagons during any single exploration event. Users must also set an exploration goal, such as starting a new group (territory construction; in our use of HexSim, a "group" refers to a territorial female) or joining an existing group. Some goals have primary and secondary components. In these cases, if the primary goal cannot be met, then an attempt is made to attain the secondary goal. Because spotted owls do not form social groups, our simulated owls always attempted to start a new "group" (single-pair territory) and they did not have a secondary goal.

The exploration process can be conducted using one of three exploration algorithms: uniform, greedy, and adaptive. These algorithms are the methods used to select which hexagon to explore. The starting point of each exploration is the individual's location, which is typically the end point of dispersal. As hexagons are explored, they are added to the current explored area. Only immediate neighbors of the already explored hexagons may visited. Thus, explored areas expand incrementally.

Under the "uniform" exploration algorithm, the closest unexplored neighbor to the exploration starting point will always be selected. Ties are settled randomly. This algorithm tends to produce roughly circular explored areas. Still, the landscape edges, excluded areas, and barriers must be respected. So the ultimate search area may not be a simple set of concentric rings.

The "greedy" strategy keeps track of every hexagon that has been explored, and every unexplored hexagon that touches an explored hexagon. The list of unexplored hexagons neighboring explored ones is prioritized at every step, and the best neighbor is always the next site to be explored. Again, landscape boundaries, excluded areas, and barriers are all taken into consideration.

The "adaptive" exploration strategy is a bit more complex. When it is used, individuals build up a list of already explored hexagons. To select a new site to explore, the adaptive strategy first picks a seed site from the list of already explored hexagons. This seed hexagon is selected probabilistically, based on quality. Then each of the seed hexagon's neighbors is considered for exploration. These neighbors are evaluated based both on their quality and on the number of previously explored neighbors they have. The reason for including the number of previously explored neighbors in the evaluation is that it helps keep the ranges compact. The number of explored neighbors is simply used as a coefficient for the hexagon score. Unexplored hexagons with 1, 2, 3, 4, 5, and 6 explored neighbors are assigned coefficients of 1.0, 1.2, 1.4, 1.6, 1.8, and 2.0, respectively. Finally the neighbor of the seed hexagon having the largest product of score and compactness coefficient is added to the explored area. The adaptive strategy is intended to provide a more sophisticated search than the uniform strategy, while not requiring the limiting assumptions of the greedy approach.

As the exploration process proceeds, individuals continually evaluate their explored areas to see if their goals can be met. When they can, the exploration will stop, and the resources claimed. When they cannot, the explorer will remain a floater.

Tests of model parameters and assumptions. Before conducting the full simulation runs, we first tested and resolved a number of aspects of HexSim model behavior to ensure correct model parameterization (denoted below in parentheses), including determining:

- the most appropriate means of varying landscape designs: viz., keeping the total number of habitat hexagons (approximately 1,800) and the total landscape area of habitat (approximately 3.2 million ha) as constant as the layout geometry would permit, rather than keeping the landscape area (total number of all hexagons) or the number of habitat clusters constant, so that the scenarios could vary in the proportion of the total landscape in habitat (Supplementary Appendix Table 1);
- minimum size of the modeled landscapes (>5 million ha or > 2,900 hexagons) so as to be large enough to avoid bias of boundary effects in the model;
- number of years to simulate in the model to achieve long-term stability of habitat occupancy under stable demographic and all-habitat conditions, determined by plotting running standard error of total occupied sites and noting the asymptote (100 years per run);
- number of model replicates to stabilize variation among model runs (20 replicates per scenario);
- number of simulated years required for the model to correctly initialize and to avoid start-up bias (5 years); and
- the appropriate statistical distributions of simulated dispersal distances (to match empirically reported findings).

We also verified that running the model with a fixed initial seed produced results comparable to using a random initial seed (the former approach providing results that could be duplicated).

Analysis of model outcomes. For each of the 62 modeled scenario combinations of habitat cluster size, habitat cluster spacing, and adult survivorship (λ), we used SPSS 16.0 (Norusis 2007) and SYSTAT (v. 11) (SYSTAT 2004) to summarize output from the HexSim model to produce statistics and graphs displaying (1) expected occupancy rates of habitat sites by (territorial female) NSOs and (2) realized λ, by 20-year time intervals (over 100 years), cluster size, cluster spacing, and proportion of the landscape in habitat. We calculated realized λ from the simulation runs as: $\lambda_{t+k} = N_{t+k} / N_t$, using several different time periods (decades) for t, and where N = total number of occupied sites (NSO pairs, excluding unpaired "floater" individuals) in the simulations at the given decadal time periods. Realized λ is thus the cumulative change in occupied sites from one or more decades before the end of the simulated time series to the end of that time series, and is calculated as the ratio of number of occupied sites at the end of the time period to number at the start of that period.

We summarized findings in terms of effects of habitat cluster size and spacing on short (20-year) and long (100-year) term trends of NSO populations, compared our results to those of LNVM, and considered general implications for habitat conservation guidelines for threatened species.

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