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Research Article

A Meta-Population Model to Predict Occurrence and Recovery of Wolves

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ABSTRACT Wolves (*Canis lupis*) have been recolonizing Washington since 2008. In an effort to guide recovery and management decisions for wolves, we created a spatially explicit meta-population matrix model using vital rates based on empirical data from other states in the northwestern United States to estimate probability of occurrence, terminal extinction rates, and potential recovery time. We applied an existing habitat model for Idaho, Montana, and Wyoming to the Washington landscape to determine the extent of probable habitat. We then simulated an evenly distributed metapopulation based on average size of pack territories reported in central Idaho where average probability of occurrence exceeded 40%. Using the program RAMAS GIS, we created a female-only, stage matrix model with dispersal using population metrics from central Idaho and northwestern Montana. Model simulations that begin in 2009 suggest Washington should reach its recovery goals in approximately 12 years (2021). We used the model to project recovery timeframes and the risk of declining below recovery objectives if management scenarios are considered during recovery. This model is also intended to be a versatile and adaptive tool for managers to project potential carrying capacity and the minimum viable population in the future when locally derived empirical data become available as wolves recolonize Washington. The model framework can be easily adapted to guide management decisions of wolves in other states (Idaho, Montana, Oregon, Wyoming) or countries and it can also provide a way to identify recovery thresholds (quasi-extinction) in other areas considered for recovery where no data are currently available. © 2015 The Authors. *Journal of Wildlife Management* published by Wiley Periodicals, Inc. on behalf of The Wildlife Society.

KEY WORDS *Canis lupus*, pack size, population viability, recolonization, survival, wolves.

Wolves (*Canis lupus*) were extirpated in the contiguous United States in the 1930s but began naturally recolonizing northwestern Montana from Canada in 1986. More wolves were re-introduced to Yellowstone National Park, Wyoming, and north-central Idaho as part of recovery efforts under the Endangered Species Act (ESA) in 1995 and 1996. Since 2008, wolves have begun re-establishing territories in Washington, after being absent from the landscape for over 70 years (Wiles et al. 2011). As a result, the Wolf Conservation and Management Plan was adopted by the Washington Fish and Wildlife Commission in 2011, which established guidelines for recovery objectives (15 successful breeding pairs for 3 consecutive years, with $\geq$4 pairs in each of the 3 recovery regions), mapped potential habitat where wolves would be expected to recolonize, reported on the social tolerance of wolves, and established a protocol for wolf removals when conflicts with livestock occur (Wiles et al. 2011).

We constructed a spatially explicit, wolf meta-population, stage matrix model (Caswell 2001) as part of the Plan, and reported on how that model was used to predict recolonization and recovery of wolves in Washington. Such matrix models were previously developed for brown or grizzly bear (*Ursus arctos*) recovery in British Columbia, Canada (Wielgus 2002), France, and Spain (Chapron et al. 2009), and cougar (*Puma concolor*) harvest management in Washington (Wielgus et al. 2013). Corsi et al. (1999) estimated wolf distribution in Italy for conservation planning. Theberge et al. (2006) and Patterson and Murray (2008) conducted population viability analyses on wolves in Algonquin Park, Canada; however, as far as we know, the model we present is the first population viability analysis for wolf recovery planning in the western United States.

Extensive spatial and demographic datasets have been collected on wolves recolonizing Idaho, western Montana, and Wyoming (Boyd and Pletscher 1999, Larsen 2004, Carroll et al. 2006, Oakleaf et al. 2006, Mitchell et al. 2008), but little to no data were available for Washington. Our

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objective was to use the existing empirical data to create a predictive model for wolf distribution and recovery in Washington (and adjacent states) to help evaluate the draft recovery objectives being considered. Specifically, we used a model of wolf occurrence probability (based partially on prey density), pack social structure (Vucetich et al. 1997), survival, and fecundity data to create landscape population models using the program RAMAS GIS (Akcakaya 2002). Although it would be beneficial to run simulations with multiple population viability analysis programs (Mills et al. 1996), we selected RAMAS GIS because of the capability to incorporate a ceiling density-dependent option for a territorial carnivore and geographic and demographic data in a population viability model. We then used the model to project time frames for potential recovery, and the probabilities of falling below recovery objectives or extirpation for different management scenarios.

STUDY AREA

Our study area was the state of Washington partitioned into the 3 recovery regions (Fig. 1) identified within the Wolf Conservation and Management Plan (Wiles et al. 2011). The Eastern Washington Recovery Region was east of highways U.S. 97, State Route 17, and U.S. 395. The North Cascades Recovery Region was north of Interstate 90 and west of highways 97 and 17. The Southern Cascades and Northwest Coast Recovery Region was south of Interstate 90 to the Oregon border and included Washington's Olympic Peninsula. Detailed descriptions of the state are presented in (McNab and Avers 1994).

METHODS

Habitat Occurrence Probability

Spatially explicit habitat models and probability of occurrence models have been derived to predict habitat suitability in areas not yet recolonized by wolves (Larsen 2004, Carroll et al. 2006, Oakleaf et al. 2006). These models were applied to the Washington state landscape and were reported in the Wolf Conservation and Management Plan for Washington (Wiles et al. 2011). We used the model developed by Oakleaf et al. (2006) to estimate relative probabilities of occurrence to spatially predict the areas of Washington likely to be inhabited by wolves. Model parameters included human, elk (*Cervus elaphus*), and domestic sheep densities, and forest cover where:

$$\text{Log } P_{\text{wolves}} = -4.457 + (0.057)\text{ forest cover} + (-0.87)\text{ human density} + (1.351)\text{ elk} + (-1.735)\text{ sheep density}$$

(Oakleaf etal. 2006)

Oakleaf et al. (2006) included cattle, white-tailed deer (*Odocoileus virginianus*), and mule deer (*Odocoileus hemionus*) in the analysis but reported these variables were not a significant improvement (likely due to collinearity) over elk in predicting recolonization of wolves in Northwest Montana, Idaho, and Wyoming.

We used the National Land Cover Data (30-m resolution; Homer et al. 2007) to develop a map for the percent of forest cover in Washington (Fig. 1). We isolated the forest cover

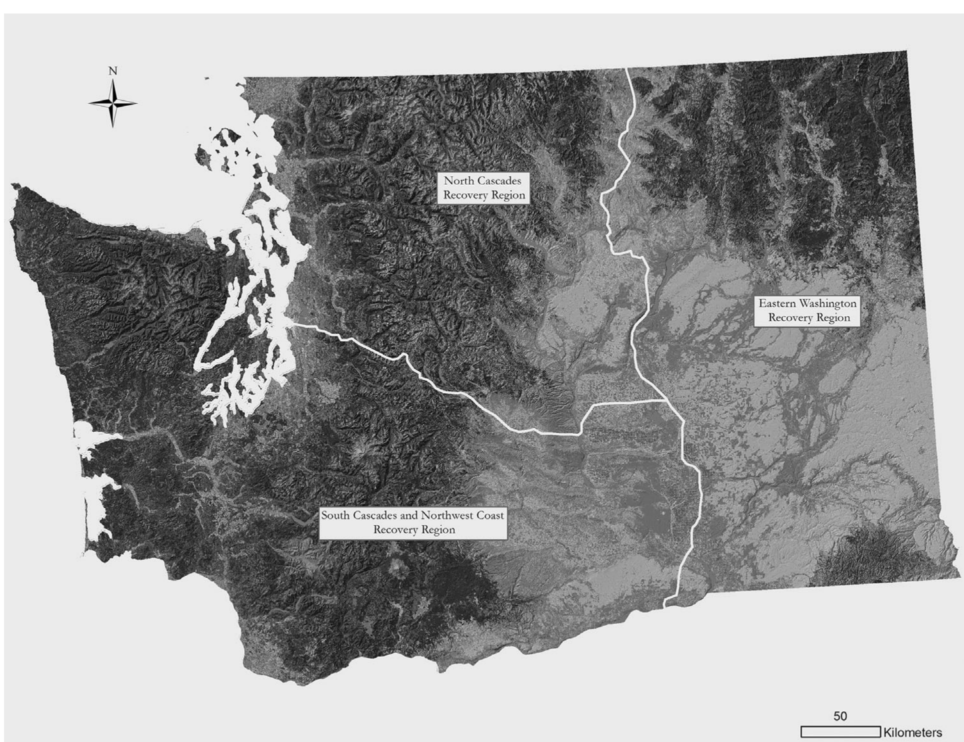

Figure 1. Wolf recovery regions identified in the 2011 Wolf Conservation and Management Plan for Washington (Wiles et al. 2011) and landscape cover types in Washington, USA with the Columbia Basin shrub-steppe and agriculture as light gray and forest cover as dark gray.

types, overlaid a 9-km^2 grid (Oakleaf et al. 2006), and created a new raster calculating the percent forest cover within each grid cell. We obtained human population data from the 2,000 U.S. Census Bureau survey data. We converted the data from census block groups to the number of people/km^2. We then created a raster layer of human population density for each 9-km^2 grid.

Elk density data were based on harvest statistics provided by Washington Department of Fish and Wildlife. All known harvest from the general and permit only seasons for each game management unit (GMU), divided by the area of each GMU (Oakleaf et al. 2006), and then averaged over a 3-year period (2003–2005) to estimate an index of relative density for elk. Oakleaf et al. (2006) averaged harvest over a 5-year period; however, significant changes in Washington's GMU and permit boundaries allowed only a consistent average of 3 years. The GMU areas averaged $1,190 \pm 1,057$ km^2 and we allocated the 9-km^2 grid cells that overlapped multiple GMUs the relative density of elk in the GMU containing the majority of the area.

We calculated the density estimate for domestic sheep from 1997 to 2002 United States Department of Agriculture statistics by dividing the number of sheep/county by the area (km^2), excluding any national parks or wilderness areas where sheep would not be allowed. Domestic sheep may be grazed in separate counties from the locations of the ranch where they are tallied so potential interactions with wolves may be different than the relative densities used in the analysis. Further investigation of range allotments may be needed to better understand this impact. We used the Spatial Analyst extension in ArcGIS 9.1 to calculate the model predictions to create a map with a 9-km^2 grid (Oakleaf et al. 2006) of the habitat occurrence probabilities and distribution of potential wolf habitat for Washington.

Hypothetical Pack Territories

Starting with the statewide habitat occurrence probability map as the extent of the outer boundary, we first generated hypothetical pack territories (Fig. 2, circles) across the state. We created circles 933 km^2 in area (radius of 17.2 km), which was the reported pack territory size for wolves in central Idaho (U. S. Fish and Wildlife Service [USFWS] 1999) and saturated the entire area of Washington with these potential territories. In each row, we aligned circles side by side at their midpoint and alternating rows aligned at the radius of the circle. We overlaid the hypothetical packs with the wolf occurrence probability layer (Wiles et al. 2011) and calculated the average probability of occurrence for wolves

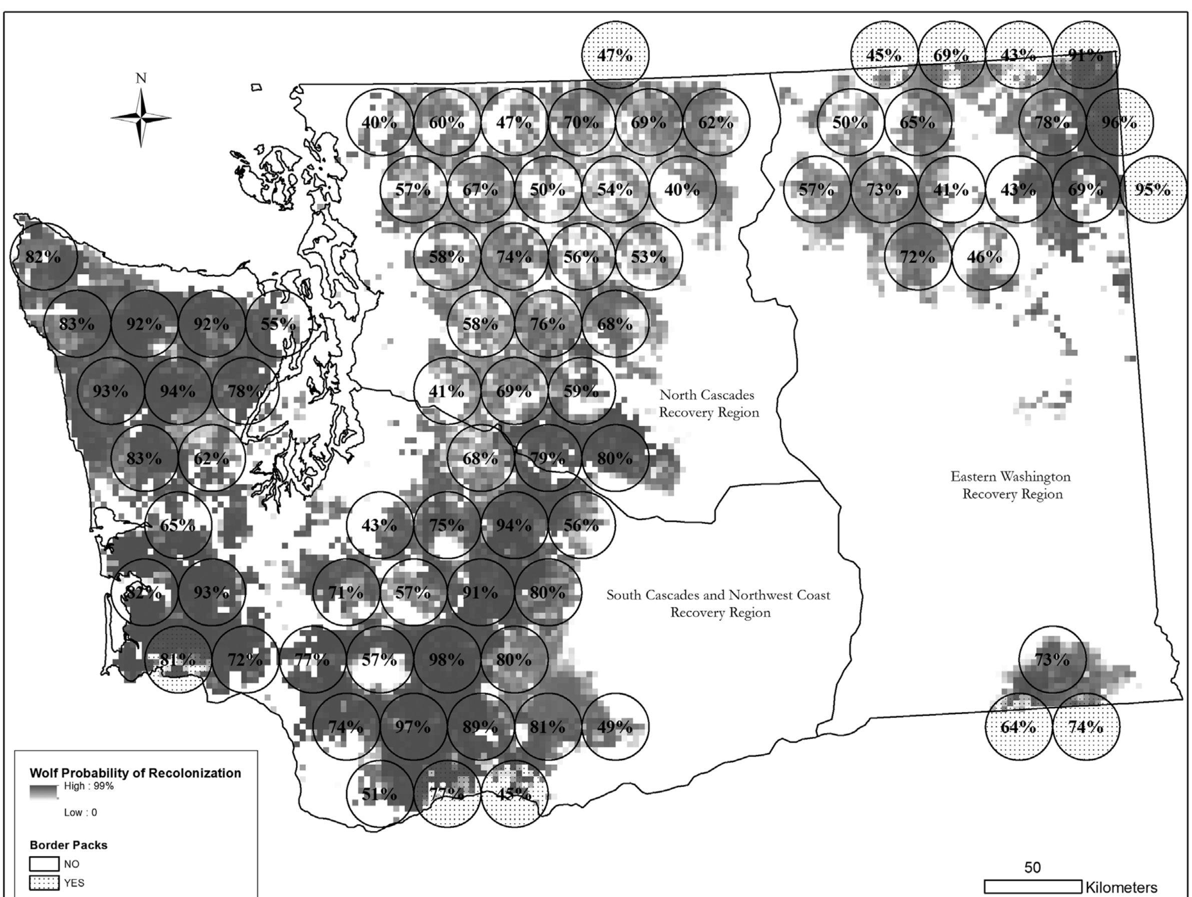

Figure 2. Hypothetical wolf pack territories displaying the probability of wolf occurrence (>40%) for each pack territory in Washington, USA based on model components described by Oakleaf et al. (2006). These territories and probabilities of occurrence are the foundation for the dispersal function in a population viability analysis for wolves in Washington.

Table 1. Stage matrix for a population viability analysis for wolves in Washington, USA using parameter estimates (SD) from Northwest Montana (Smith et al. 2010). The top row represents fecundity rates for each stage class and the 3 lower rows are the transition probabilities.

	Pups 0–12 months	Juveniles 13–24 months	Young adults 25–48 months	Adults >48 months
Pups	0.00 (0.0)	0.35 (0.04)	1.04 (0.11)	1.04 (0.11)
Juveniles	0.81 (0.05)	0.00 (0.0)	0.00 (0.0)	0.00 (0.0)
Young adults	0.00 (0.0)	0.52 (0.04)	0.00 (0.0)	0.00 (0.0)
Adults	0.00 (0.0)	0.20 (0.01)	0.72 (0.05)	0.72 (0.05)

for each territory by averaging all the 9-km^2 grid cells within each of the territories (Fig. 2). Packs currently are established in areas of Washington with a mean of $75.8\% \pm 13.1\%$ ($n = 8$, range 49.6–91.0%) probability of wolf occupancy (Washington Department of Fish and Wildlife, unpublished data). We assumed packs would establish in the best quality habitat first so we buffered the probability range by 10% and included territories with an average probability >40% in the landscape population model. We identified packs in Washington that shared a portion of the territory with British Columbia or Idaho and had >40% occurrence probabilities as dispersal corridors or potential source populations.

We converted the centroid locations of the simulated pack territories with average probability of occurrence >40% to grids with a cell size of 1 km^2. We coded all the 1-km^2 grid cells that contained a centroid with a value of 1 and coded the remaining cells with a value 0 statewide; we imported this layer as the territory locations into RAMAS GIS to create a dispersal landscape for the metapopulation models. We then used the distance from the center of one pack territory to all others to estimate the dispersal-distance function in RAMAS GIS (Akcakaya 2002).

Landscape Population Model

Wolf populations comprise territorial social groups or packs (Mech and Boitani 2003). Each pack is generally composed of a single breeding pair but also may include pups of the year, pack members born from the previous years, or adopted members immigrated from other packs (Mech and Boitani 2003). As the number of members in a pack grows with each new litter of pups, the older siblings have a tendency to disperse to new areas to establish their own pack or may join another established pack (Boyd and Pletscher 1999).

We used probability of occurrence, survival, fecundity data, and knowledge of wolf pack social structure to create landscape-population models in RAMAS GIS to project potential recovery and probabilities for falling below recovery objectives or extirpation for different management scenarios in Washington. We created a female-only metapopulation (Akcakaya 2002) using a 4- stage matrix model in RAMAS GIS where we considered individual packs populations in a statewide metapopulation analysis. We used a female-only model for simplicity in the stage matrix (Wielgus et al. 2001) but extrapolated the results to numbers of both sexes using a male/female ratio of 50:50 (Mech 1970).

We created a stage matrix (Table 1) that incorporated transition equations from stage to stage (Fig. 3). Stages included pups (0–12 months), juveniles (13–24 months), young adults (25–48 months), and adults (>48 months) based on wolf social ecology (Mech and Boitani 2003). Fecundity of adult females was the product of average litter size observed in central Idaho (for successfully reproducing females) $\times$ percentage of successfully reproductive females (70%) $\times$ sex ratio (50%) $\times$ survival rate of adult females (Lambert et al. 2006). The model allowed 1 adult female to reproduce in each pack and 70% of the packs to successfully reproduce each year. We determined the percentage of successfully reproductive females annually by the ratio of packs with pups in December divided by the total number of packs for that year in a given recovery region (Smith et al. 2010, Mack et al. 2010). In the stage matrix, the fecundity of juveniles was 33% of young adult and adult females (Boyd and Pletscher 1999) because a portion of the juveniles could disperse from their natal pack territory, find a potential mate, and breed by age 2.

We used an average litter size of 4.1 pups/pack based on annual averages in Idaho (Nadeau et al. 2006, 2007, 2008, 2009; Mack et al. 2010) where litter size was determined by den site and rendezvous site inspections (Mitchell et al. 2008). We did not use data from northwestern Montana for average litter size calculations because they were based on aerial and ground observation during the fall months, rather than on den inspections, and may have been underestimated (Mitchell et al. 2008).

Transition probabilities from stage to stage were the products of stage-specific survival rates (S) $\times$ percentage of that group moving to the next stage (Wielgus et al. 2001; Fig. 3). For example, the transition from juvenile (j) to adult breeder (af) in a pack was $S_j\,(0.72) \times 1 - S_{af}\,(0.28) = 0.20$ or the probability of a juvenile female surviving in a pack times the probability of a resident alpha adult female dying in a pack (Table 1). If there was >1 juvenile in the pack, and 1 transitioned to a breeder, the other juveniles in the pack

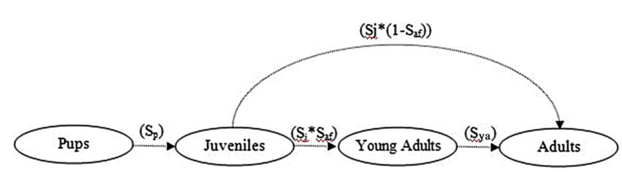

Figure 3. Life cycle graph for a stage matrix model included in a population viability analysis for wolves in Washington, USA. Stages include pups (0–12 months), juveniles (13–24 months), young adults (25–48 months), and adults (>49 months) with associated transition probabilities where S_p is annual survival rate of pups, S_j is the annual survival rate of juveniles, S_{ya} is the annual survival rate of young adults, and S_{af} is the annual survival rate of adult females.

transitioned into young adults based on the model stage classes. The transition from juvenile to disperser was S_j (0.72) $\times$ S_{af} (0.72) = 0.52 or the probability of a juvenile female surviving in a pack times the probability of a resident alpha adult female surviving in a pack. Transitions from young adults to adults, and adults moving on, were their survival rates.

We used survival rates from wolves in northwestern Montana rather than central Idaho because the topography, road densities, public access to national forest, and state and private forest land were comparable to much of Washington (i.e., lack of large roadless wilderness areas as in Idaho). Smith et al. (2010) reported the mortality factors affecting the survival rates of wolves in central Idaho, northwestern Montana, and the Greater Yellowstone area were legal control (30%), illegal mortality (24%), natural causes (11.8%), other causes including vehicle collisions or strife (21.4%), and unknown causes (11.8%) and we subsequently incorporated these factors in the model. We used adult survival data from 1987 to 2004 in northwestern Montana with the average weighted by the number of animals/year because sample sizes were small and unreliable from 1982 to 1986 (Smith et al. 2010). The survival rate for adult wolves from 1987 to 2004 in northwestern Montana was $0.72 + 0.05$, which was 9% lower than was observed in central Idaho (perhaps because of the relative paucity of large roadless wilderness in Montana). In northwestern Montana, poaching and vehicle or train collisions were the primary cause of mortalities while that population was listed as endangered (Mitchell et al. 2008) and vehicle mortalities appeared to be a significant cause of mortality for younger age classes of wolves in Italy (Lovari et al. 2007). We did not have empirical data on pup survival over the same time period in Montana, so we decreased the Idaho pup survival by the same percentage (9%) as the adult survival.

We built environmental and demographic stochasticity into our model by inputting the standard deviations observed from the central Idaho time series into the matrix model for fecundity and survival (Smith et al. 2010). We calculated the standard deviation of survival from the average annual survival for all years monitored for a given area.

In the model, density dependence affected fecundity and survival and pack size was based on a ceiling model where the empirically derived survival and fecundity rates were used until the carrying capacity (k) of each pack exceeded 4 females, at which time growth rates abruptly declined to 1.0. Carrying capacity for each pack was set to 4 combined female pups, juveniles, young adults, and adults and based on half (female only component) the average pack size (7.6 ± 2.2 wolves/pack) observed in central Idaho, northwestern Montana, and the Greater Yellowstone Area (Boyd and Pletscher 1999, USFWS 1999, Mitchell et al. 2008).

All dispersal-aged animals dispersed out of the pack of origin became breeders in the pack of origin, or died. In our model, we set the minimum age of reproduction at 2 years (22 months; Mech 1970) and mean dispersal age was 3 years (35.7 ± 20.2 months for M and F; Boyd and Pletscher 1999). Average dispersal distance for wolves was similar between sexes with an average distance of 95.5 km (113 km for M, 78 km for F) with a maximum dispersal distance of 840 km (Boyd and Pletscher 1999). We used these metrics to create a dispersal function in RAMAS GIS metapopulation modeling (Akcakaya 2002) and to develop a probability matrix of dispersal between hypothetical packs in Washington. We set large-scale landscape features that posed potential barriers to dispersal movements, such as the Columbia Basin (Fig. 1) and Puget Sound, to 0 in the dispersal matrix. We set the dispersal distance to 95 km and the maximum distance dispersed to 200 km to model a more typical dispersal pattern.

The recovery of wolves in Washington is solely dependent on immigration from surrounding populations because no reintroductions have occurred thus far. Therefore, we included hypothetical pack territories defined as a border packs (Fig. 2) as the source populations for the immigration from British Columbia, Idaho, and Oregon. For the management scenario simulations, we included these packs in the model as contributing dispersal aged animals to other packs within the dispersal distance of the border pack territories. For the simulations where immigration was not included in the model, these border packs did not contribute wolves; however, dispersal still occurred between the hypothetical packs within the state.

Management Scenario Simulations

Before parameterizing the population viability analysis model, stakeholders had to decide on N (no. animals), P (probability of quasi-extinction), and T (simulation time; Akcakaya 2002). These metrics were predetermined by Washington Department of Fish and Wildlife and stakeholders when developing the recovery plan. We used the model to assess persistence of the recovery objectives established in the recovery plan (15 successful breeding pairs for 3 consecutive years, with $\geq$4 pairs in each of the recovery regions) by running 9 different scenarios with 100 simulations each for 50 years. Scenarios 1 and 2 (Table 2) evaluated the effects of immigration on persistence starting from 2 packs. Scenarios 3 through 5 (Table 2) evaluated the effects of immigration and a population cap on post-recovery persistence. Scenarios 6 through 9 (Table 2) evaluated the effects of introducing additional adult mortalities (presumably through lethal removal) and immigration on persistence at a regional and statewide level. The lethal removal management scenario removed 30% of all dispersal and adult age classes 1 time every 4 years in a recovery region after the delisting goals were met. The removal scenario was additive to the baseline mortality already incorporated in the model. The lethal management scenarios 6 and 8 assessed whether the recovery goals would be reached on a statewide level if wolves were removed in the Eastern Washington Recover Region once it had reached the recovery goal. The lethal management scenarios 7 and 9 assessed whether the northeast region would drop below recovery levels with 30% removals to the adult and dispersal population once every 4 years. For scenarios that assumed immigration, the model allowed dispersal to and from the existing border

Table 2. Results of scenarios modeling the persistence of wolf packs in the Eastern (EW), North Cascades (NC), and South Cascades and Northwest Coast (SC) Recovery Regions in Washington, USA using RAMAS GIS. We based parameters on a pack territory size of 933 km^2, survival data from wolves in northwestern Montana, USA, average pack size of 8 individuals with an average litter size of 4 pups, and an average dispersal distance of 95 km with a maximum dispersal distance of 200 km. Scenarios 1–5 estimated persistence of wolves at a statewide level and scenarios 6–9 estimated persistence at a regional and statewide level, but included management that removed 30% of all young adult and adult age classes every 4 years after the delisting goal in the Eastern Washington recovery region.

Scenario (100 simulations, 50 years)	Parameter[a]	Result	Conclusion and notes
1) Statewide population growth to 73 possible territories, starting with 2 occupied territories, assume immigration	Tx Mo Qx state	0 58 (49–65) 0	With immigration, wolves would maintain about 58 packs, with no risk (0%) of the population declining to extinction.
2) Statewide population growth to 73 possible territories, starting with 2 occupied territories, assume no immigration	Tx Mo Qx state	0.02 56 (0–64) 0.02	With no immigration, the population may grow to 56 packs, but there is a 2% chance it would decline to extinction.
3) Statewide population growth to 73 possible territories, starting with 23 occupied territories (distributed as 7 EW, 7 NC, 9 SC), assume no immigration	Tx Mo Qx state	0 56 (47–63) 0	Starting with the recovery objective (15 breeding pairs) met, wolves would likely persist if demographically significant immigration was stopped.
4) Start with 23 packs (distributed as 7 EW, 7 NC, 9 SC) to approximate recovery objective with >4 pairs in each recovery zone, no additional growth (i.e., population is capped), assume immigration	Tx Mo Qx state	0.03 19 (14–22) 0.93	Starting with the recovery objective (15 breeding pairs) met but further population growth is capped, the likelihood of needing to relist/falling below the statewide recovery objective is high (93%), even with continued immigration.
5) Start with 23 packs (distributed as 7 EW, 7 NC, 9 SC) to approximate with >4 pairs in each recovery zone, no additional growth (i.e., population is capped), assume no immigration	Tx Mo Qx state	<0.01 19 (15–23) 0.97	Starting with the recovery objective (15 breeding pairs) met but further population growth is capped and immigration is stopped, there is a 97% risk of having to relist/falling below the statewide recovery objective.
6) Start with recovery objective (5 breeding pairs) met in the EW recovery region, but not in the other 2 recovery regions; assume immigration, conduct management	Tx Mo Qx state	<0.01 58 (50–66) <0.01	Conducting wolf management in the EW recovery region after recovery objectives are met there, but before regional objectives are met in the other 2 regions, will not inhibit the ability to achieve recovery in all 3 regions over time.
7) Start with recovery objective (5 breeding pairs) met in the EW recovery region, but not in the other 2 recovery regions; assume immigration, conduct management	Tx Mo Qx region	<0.01 9 (6–12) 0.07	Conducting wolf management in the EW recovery region after recovery objectives are met there, but before regional objectives are met in the other 2 regions and with continued immigration, results in a 7% risk of falling below the recovery objective for Eastern WA; model assumed 1 of 5 pairs established in Blue Mountains.
8) Start with recovery objectives (5 breeding pairs) met in the EW recovery region, but not in the other 2 recovery regions; assume no immigration, conduct management	Tx Mo Qx state	<0.01 55 (41–62) <0.01	Conducting wolf management in the EW recovery region after recovery objectives are met there, but before regional objectives are met in the other 2 regions, will not inhibit the ability to achieve recovery in all 3 regions over time, even without immigration.
9) Start with recovery objectives (5 breeding pairs) met in the EW recovery region, but not in the other 2 recovery regions; assume no immigration, conduct management	Tx Mo Qx region	<0.01 8 (3–11) 0.48	Conducting wolf management in the EW recovery region after recovery objectives are met there, but before regional objectives are met in the other 2 regions and without any immigration from outside populations, results in a 48% risk of falling below the recovery objective for Eastern WA; model assumed 1 of 5 pairs established in Blue Mountains.

[a] Tx = probability of terminal extinction (the probability that the metapopulation will be extinct at the end of the duration, in this case 50 years). Mo = metapopulation occupancy (the average number and range of occupied territories during the 50-year period). It is assumed that 70% of occupied territories represent packs with successfully breeding females; Qx = the probability that the number of female adults and dispersers will fall below the recovery objective level at which relisting would be warranted; Qx region = the probability of quasi-extinction at recovery region level (<12 adult + dispersing females); Qx state = the probability of quasi-extinction at statewide level (<46 adult + dispersing females).

packs (Fig. 2), whereas for scenarios that assumed no immigration, the model did not allow dispersal to occur between any Washington packs and packs outside of Washington (border packs).

This model is applicable to a nearly infinite number of scenarios; however, we wanted to demonstrate the utility of the model and begin to assess the resiliency of the wolf packs to potentially high levels of mortality that might exist in a recolonizing population due to livestock interactions, disease, or other potential stochastic events. We assessed the parameters probability of terminal extinction (Tx; the probability that the metapopulation will be extinct in 50 years), metapopulation occupancy (Mo; the average number and range of occupied territories during the 50-year period), and quasi-extinction probability (Qx; the probability that the number of successfully breeding female adults will fall below the recovery objective of 15, where relisting would be warranted).

RESULTS

Our model, using demographic and pack size parameters from northwestern Montana, yielded a deterministic population growth rate of 1.23 compared to the observed growth rate of 1.22 in Montana (Sime et al. 2011). The stochastic growth rate for the model that included immigration was 1.18 ± 0.01 and 1.13 ± 0.03 for simulations excluding immigration. The simulated average pack size was 8.04 ± 5.4 wolves versus the observed wolf pack size of 7.6 ± 2.2 in Idaho, northwestern Montana, and Wyoming (Boyd and Pletscher 1999, USFWS 1999, Mitchell et al. 2008). The model predicted 6 breeding pairs in Washington by 2012 versus 5 observed breeding pairs in Washington by 2012 (Becker et al. 2013). Finally, the model predicted 12 potential packs representing 56 wolves in Washington by 2012 versus 10 packs and 51 wolves observed in Washington (Becker et al. 2013).

We ran simulations starting with 2 initial breeding pairs in 2009 (Becker et al. 2013). The model that included immigration from Idaho and British Columbia predicted Washington could reach its recovery goal of 15 breeding pairs including 4 in each recovery region within 12.0 ± 2.8 years (2021). Without immigration included in the model, recovery goals were predicted to take 21.3 ± 9.6 years (2030). As of 2015, no packs have been observed in the South Cascades Recovery Region. Persistent packs were predicted to establish in the South Cascades Recovery Region within 6.6 ± 3.2 years (2015) with immigration included in the model.

There was no risk of the population declining to extinction (with immigration, $Tx < 0.0$: Table 2, scenario 1) assuming wolves continue to recolonize Washington and to fill unoccupied habitat without increasing above the baseline mortality in the model. If no immigration occurs, the probability of extinction after 50 years increases slightly ($Tx < 0.02$; Table 2, scenario 2); however, the probability of extinction falls to 0 once the population reaches the recovery goal of 15 breeding pairs (Table 2, scenario 3). Once the population meets recovery objectives, if any further population growth is capped, the likelihood of falling below statewide recovery objectives is >90%, regardless of immigration assumptions (Table 2, scenarios 4 and 5).

Assuming recovery levels have been reached in the Eastern Washington recovery region, applying our hypothetical management actions (remove 30% of all disperser and adult age class wolves from a recovery region every 4 years) did not appear to inhibit the ability to achieve recovery in all 3 regions over time (Table 2, scenarios 6 and 8), regardless of immigration assumptions. However, the effects of immigration on achieving recovery goals were important at the local level.

Assuming the recovery objectives are met in the Eastern Washington recovery region but not the other 2 regions and management actions are applied, there would be 7% risk of declining below the recovery objectives for the Eastern Washington recovery region, with immigration in the model (Table 2, scenario 7). If immigration was not included in the model, the risk of declining below recovery objectives in the Eastern Washington recovery region alone increased to 48% (Table 2, scenario 8).

DISCUSSION

Wolves are currently recolonizing Washington and thus far the landscape metapopulation model we created in the short-term appears to be tracking similar to the observed population numbers and distribution (Becker et al. 2015). With 5 years of observed data, the predicted growth rates, pack sizes, breeding pairs, number of packs, and number of wolves generally tracked the observed numbers, although as with any model there is a degree of uncertainty with future predictions. Portions of Washington's landscape, particularly the east slope of the Cascades and Northeastern Washington, are similar to northwestern Montana with regards to topography, prey base, and the mosaic of wilderness, national forest, state lands, and private timber lands; therefore, we assumed that similar landscape and population metrics may apply for wolves recolonizing the state. Becker et al. (2015) reported the pack territory size in Washington ranged from 259 to 2,210 km^2 and averaged 754 km^2 with a small sample size ($n = 12$) so the territory size of 933 km^2 used in the model and based on central Idaho is larger than those observed in Washington. This may mean Washington could potentially have a few more packs than the model predicts if the potential habitat identified in Washington is used by wolves. The intrinsic rate of growth and pack size for our model versus the observed growth rates and pack size for northwestern Montana and central Idaho suggest that our model structure is appropriate.

The survival inputs in the model incorporate a baseline level of human-caused mortality (including a level of legal control) based on the recolonizing populations in northwestern Montana and central Idaho (Smith et al. 2010). The mortality levels due to depredation of livestock may be different in Washington because of the relatively few sheep grazing allotments. However, we ran several scenarios to assess the potential impacts of increasing adult wolf mortality due to management. Our models predicted that even when adding a 30% removal of the adult population every 4 years, there would be <1% chance that populations would fall below the recovery objective of 15 breeding pairs (Table 2). The results of the population persistence scenarios suggest that once Washington wolves reach recovery goals (15 breeding pairs), wolf populations would be relatively resilient to directed removals (e.g., lethal control or managed hunting season), assuming a low level of immigration from outside of the state. These results assume that the wolf population would fill unoccupied habitat.

Given that wolves are recolonizing Washington by natural dispersal, source populations are necessary to provide animals that can disperse into each of the recovery regions. Our modeling suggests that wolf populations are resilient; however, lethal management in neighboring jurisdictions or recovery zones that are saturated with pack territories could affect the rate at which the other recovery regions reach recovery objectives.

Population viability analyses are a tool that can provide managers with a forecast of how a specific management strategy can affect a population by predicting, within a confidence interval, a timeline and a population estimate, and can determine whether that population will grow or decline (Wielgus et al. 2001, Wielgus 2002, Theberge et al. 2006, Patterson and Murray 2008, Chapron et al. 2009). Because of the difficulties in replicating the natural world, a model is only as good as the components and the framework. Population viability analyses have been debated in the literature because of program capabilities (Mills et al. 1996), model structure (Vucetich et al. 1997), and how model components were derived (Patterson and Murray 2008). To avoid these pitfalls, we developed a model framework based on the social structure, behavior, and territoriality of wolves (Vucetich et al. 1997) and parameterized the model with demographic estimates and confidence intervals determined from long-term datasets from other western states. Nonetheless, all population viability analyses are accompanied by uncertainty and only used as guides for management rather than precise, accurate predictions.

MANAGEMENT IMPLICATIONS

Washington could reach its recovery goals by 2021 if landscape and population metrics remain similar to those in central Idaho and northwestern Montana. However, our model also suggests that if the wolf population reached the recovery levels statewide and were then capped at the recovery level (15 breeding pairs), there would be a 93% chance of falling below the recovery level with immigration included, and a 97% chance with no immigration (Table 2). Therefore, the recovery level identified in Washington's Wolf Conservation Plan of 15 pairs should not be used as a population target for management after recovery if managers want to reduce the risk of relisting wolves. As the RAMAS GIS model currently exists, it provides confidence in the recovery goals established in the plan to maintain a sustainable population of wolves in Washington over the next 20 years. In a broader context, this model could be applied to other jurisdictions that currently have wolves to understand how management affects population resiliency. In areas where wolves may recolonize, this model may be able to assist in predicting recovery timeframes and in the creation of recovery goals.

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