Appendix B

Assessment of Population Viability of Wolves in Oregon

This technical report to the Oregon Fish and Wildlife Commission presents results from an updated individual-based population model used to assess population viability of wolves in Oregon. The model uses wolf data collected in Oregon through July 2015.

Presented: November 9th, 2015

Suggested citation:
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EXECUTIVE SUMMARY

We present results from an individual-based population model (IBM) based on a peer-reviewed published model (Bull et al. 2009) used to assess the viability of the gray wolf (Canis lupus; hereafter, wolf) population in Oregon. When parameterizing our model, we relied on peer-reviewed published estimates of wolf vital rates. Our population model, the assumptions made in the model, and vital rates used in the model were obtained or supported by peer-reviewed published literature. We compared estimates of parameters used in our model to those observed in Oregon from 2009-2014 and concluded our model used to project future population growth was conservative compared to growth rates currently observed in Oregon. We used a starting population size of 85 wolves which was based on wolf population counts conducted by the Oregon Department of Fish and Wildlife (ODFW) through July 2015. This value is higher than reported end of year counts (ODFW 2015) because additional wolves that were present in Oregon at the start of the biological year (i.e., April) were documented after January 31, 2015. Consequently, results presented in this report differ slightly from those presented to the Oregon Fish and Wildlife Commission on April 24, 2015. We used linear regression models to determine the relative effect of model parameters on intrinsic population growth rates of wolves. We assessed population viability using two metrics: 1) the cumulative proportion of simulations that had fewer than 4 breeding pairs (defined as conservation-failure) and 2) the cumulative proportion of simulations that had fewer than 5 wolves (defined as biological-extinction).

Increased pup ($\beta = 0.045$), yearling ($\beta = 0.024$), and adult ($\beta = 0.019$) survival resulted in increased population growth rates. Population growth rates of wolves were most sensitive to environmental stochasticity, which we modeled through the use of a prey multiplier ($\beta = 0.088$). The increased environmental stochasticity incorporated in the model by the prey multiplier increased variation in survival rates of wolves by up to 20% annually, which caused this parameter to have a large effect on population growth rates. Increased levels of illegal ($\beta = -0.027$) and legal ($\beta = -0.028$) anthropogenic mortality had negative effects on population growth rates. Increased mean litter size had a positive effect on population growth ($\beta = 0.049$). Increased mortality rates for dispersing wolves had a negative effect on population growth ($\beta = -0.026$) while increased probabilities of dispersing wolves successfully establishing a territory had a positive effect on population growth ($\beta = 0.034$). Combined, these results highlight the importance of survival, reproduction, and human-caused mortality on population growth rates of wolves. Other parameters considered in our model had minimal effects on population growth rates or viability of wolves. Maintenance of high natural survival and reproductive rates of wolves while minimizing human-caused mortality will help ensure the long-term persistence of the species in Oregon.

Our baseline model indicated there was a 0.05 (95% CI = 0.01 – 0.09) probability of wolves falling below the conservation-failure threshold and a 0.01 (95% CI = 0.00 – 0.03) probability of falling below the biological-extinction threshold in the next 50 years. When we parameterized our model with vital rates required to match population growth rates observed in Oregon from 2009-2014, we did not observe any situations where the simulated wolf population fell below the conservation-failure or biological-extinction thresholds. Consequently, we contend future risk of conservation-failure falls between estimates from our baseline model (0.05 probability of conservation-failure) and our model parameterized with vital rates required to

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1 Peer-reviewed published literature is papers published in scientific journals or books that have been reviewed and deemed acceptable from a study design, analysis, and interpretation standpoint by one or more peers prior to being published.
match observed population growth rates of Oregon’s wolves from 2009-2014 (0.00 probability of conservation-failure). Regardless of model parameterization, our results suggested it is extremely unlikely wolves in Oregon will be at risk of extirpation over the next 50 years.

**INTRODUCTION**

The Oregon Wolf Conservation and Management Plan (hereafter, Oregon Wolf Plan; Oregon Department of Fish and Wildlife [ODFW] 2010) outlines phases of wolf (*Canis lupus*) recovery and criteria for delisting wolves as required by Oregon’s Endangered Species Act (ESA). In January 2015, Oregon’s wolf population successfully reached population objectives for Phase I to allow ODFW to propose that the Oregon Fish and Wildlife Commission consider delisting of wolves from Oregon’s ESA (ODFW 2010). Quantitative models are commonly used to assess population dynamics and extinction risk of threatened and endangered species (Boyce 1992, Morris and Doak 2002) and can provide insight into the first and second delisting criteria outlined in the Oregon ESA:

1. “The species is not now (and is not likely in the foreseeable future to be) in danger of extinction in any significant portion of its range in Oregon or in danger of becoming endangered”; and
2. “The species natural reproductive potential is not in danger of failure due to limited population numbers, disease, predation, or other natural or human related factors affecting its continued existence”.

To address these delisting criteria, we modified a peer-reviewed quantitative model (Bull et al. 2009) to provide insight into dynamics of Oregon’s wolf population to help inform any future decisions regarding wolves and Oregon’s ESA.

To make accurate predictions of future population growth, quantitative population models should accurately reflect biological processes of the species being modeled. Individual-based models (IBM) were previously used to model wolf population dynamics (Vucetich et al. 1997, Haight et al. 1998, Nilsen et al. 2007, Bull et al. 2009) because they can most accurately represent the unique social and breeding structure of wolf populations. We modified an IBM developed to assess effects of management on wolf populations in Norway (Bull et al. 2009) to meet our needs to assess population viability of wolves in Oregon. Our modeling approach focused on determining effects of key biological processes, uncertainty in model parameters, and management actions on wolf population dynamics and viability.

**METHODS**

We used an IBM modified from Bull et al. (2009) to assess future population dynamics of wolves in Oregon. The primary modifications to the Bull et al. (2009) were to change the vital rate values of wolves in North America based on our literature review. The biggest modification we implemented in our model was to alter the way reproduction was handled in the model. Bull et al. (2009) assigned pairs of wolves a probability of producing a large or small litter and assumed all dominant females would produce pups each year. In our modified model, we assumed not all dominant females would produce pups in a given year, but litter sizes would be determined from a single distribution each year. We modified the Bull et al. (2009) to include two types of catastrophes (see description below) and allowed dispersing wolves to leave Oregon and have increased risk of mortality during dispersal (see description below). All of these additional modifications provided increased reality to the model and would provide a more
conservative view of wolf population growth. Other than these minor changes, our code used to implement the model was identical to the peer-reviewed model developed by Bull et al. (2009).

Our model incorporated 6 demographic processes that affected wolf populations that were modeled in the following order (Fig. 1): 1) survival and transition between age classes, 2) dispersal and emigration out of Oregon, 3) territory establishment by dispersing wolves, 4) immigration from outside Oregon, 5) anthropogenic mortality, and 6) reproduction. Our IBM included 5 distinct social classifications of wolves (Fig. 2) and transitions between social classifications were governed by distinct model parameters (Table 1).

Our IBM was coded and implemented in R (R Development Core Team 2012). To generate our results, we conducted 100 realizations of population growth over 50 years. We utilized 100 realizations of population growth because this allowed the confidence intervals to be acceptably narrow, but not excessively narrow to indicate a false sense of precision in our estimates of population viability Bull et al. (2009). We incorporated environmental stochasticity in our model by randomly drawing vital rate values from a uniform distribution with a predefined mean and standard deviation at each time step of the simulation (Table 1). Unless otherwise noted, vital rates were applied at an individual level, which inherently incorporated demographic stochasticity into our model. For each simulated population we tracked parameter values, population size and growth rates, and number of breeding pairs (i.e., pairs of wolves with ≥ 2 pups surviving the biological year) at each time step.

Figure 1. The order in which 6 key demographic processes are implemented in an individual-based population model to assess population viability of wolves in Oregon.
Figure 2. Visual representation of the life cycle of wolves implemented in an individual-based population model to assess population viability of wolves in Oregon. The diagram represents probabilities of transitions between age- and social-classes of wolves. Parameters used in transition calculations are defined in Table 1.
Table 1. Parameter values used to predict future population growth of wolves in Oregon compared to values required to match observed growth rates of Oregon's wolf population from 2010-2014. Values used at each time step of the analysis were randomly drawn from a uniform distribution within the specified standard deviation (SD). Mean values are probabilities unless otherwise stated. All estimates used in our baseline model were obtained or supported by peer-reviewed literature.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Notation</th>
<th>Baseline model values</th>
<th>Values required to match growth rates observed in Oregon (2009-2014)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pup survival rate</td>
<td>$S_p$</td>
<td>0.68 0.15</td>
<td>0.75 0.05</td>
</tr>
<tr>
<td>Yearling survival rate</td>
<td>$S_y$</td>
<td>0.81 0.06</td>
<td>0.91 0.04</td>
</tr>
<tr>
<td>Adult (2 to 7-yr old) survival rate</td>
<td>$S_{ad}$</td>
<td>0.88 0.04</td>
<td>0.91 0.04</td>
</tr>
<tr>
<td>Old adult (8 to 9-yrs old) survival rate</td>
<td>$S_{old}$</td>
<td>0.63 0.11</td>
<td>0.85 0.05</td>
</tr>
<tr>
<td>Pup dispersal rate</td>
<td>$D_p$</td>
<td>0.15 0.05</td>
<td>0.15 0.05</td>
</tr>
<tr>
<td>Yearling dispersal rate</td>
<td>$D_y$</td>
<td>0.65 0.05</td>
<td>0.65 0.05</td>
</tr>
<tr>
<td>Non-breeding adult dispersal rate</td>
<td>$D_{ad}$</td>
<td>0.65 0.05</td>
<td>0.65 0.05</td>
</tr>
<tr>
<td>Proportion of dispersing wolves that survive</td>
<td>$M_d$</td>
<td>0.90 0.05</td>
<td>0.97 0.02</td>
</tr>
<tr>
<td>Proportion of dispersing wolves that leave Oregon</td>
<td>$E_d$</td>
<td>0.115 0.03</td>
<td>0.115 0.03</td>
</tr>
<tr>
<td>Probability of dispersing wolf establishing a territory</td>
<td>$T$</td>
<td>0.75 0.10</td>
<td>0.75 0.10</td>
</tr>
<tr>
<td>No. of immigrants arriving annually from outside Oregon</td>
<td>$I$</td>
<td>3 2</td>
<td>3 2</td>
</tr>
<tr>
<td>Pregnancy rate for dominant females</td>
<td>$P_{ad}$</td>
<td>0.95 0.02</td>
<td>0.95 0.02</td>
</tr>
<tr>
<td>Litter size</td>
<td>L</td>
<td>5 3</td>
<td>5 3</td>
</tr>
<tr>
<td>Proportion of wolves removed by illegal mortality</td>
<td>$IM$</td>
<td>0.05 0.03</td>
<td>0.02 0.01</td>
</tr>
<tr>
<td>Proportion of wolves removed by legal mortality</td>
<td>$LM$</td>
<td>0.05 0.03</td>
<td>NA NA</td>
</tr>
<tr>
<td>Prey index multiplier (adjustment to survival rates)</td>
<td>$Pr$</td>
<td>1.00 0.10</td>
<td>1.00 0.10</td>
</tr>
<tr>
<td>Density dependent threshold (no. of wolves)</td>
<td>$CC$</td>
<td>1,500 NA</td>
<td>1,500 NA</td>
</tr>
<tr>
<td>Probability of population wide reduction in survival</td>
<td>$S_{cas}$</td>
<td>0.01 NA</td>
<td>NA NA</td>
</tr>
<tr>
<td>Probability of pack-specific reproductive failure</td>
<td>$R_{cas}$</td>
<td>0.05 NA</td>
<td>0.05 NA</td>
</tr>
</tbody>
</table>
Model Parameters

Currently, Oregon has minimal vital rate information to parameterize a population model, and the potential for sampling bias or error from small sample sizes (i.e., observed data does not match the expected outcome) could cause inappropriate conclusions to be reached by using this information. Furthermore, estimated vital rates from protected wolf populations that are colonizing or recovering are unlikely to match those of established wolf populations (Ballard et al. 1987, Hayes and Harestad 2000, Fuller et al. 2003). Oregon’s wolf population is transitioning from a recovering to established population. Vital rates used in our IBM were obtained from peer-reviewed published literature that presented results from studies conducted primarily in established wolf populations. Consequently, whenever possible, we compared vital rates observed in Oregon to those reported in peer-reviewed published literature to determine the degree to which vital rates used in our model were representative of those observed in Oregon since 2009. In general, most vital rates used in our baseline model were conservative compared to those observed in Oregon from 2009-2014. Using conservative vital rate estimates allowed us to err on the side of caution (e.g., the precautionary principle; Myers 1993, Meffe et al. 2006) and prevent overly optimistic conclusions of wolf population viability.

Starting Population Size.– We utilized minimum count data collected by ODFW to determine our starting population size and structure prior to wolves producing pups in April 2015. These counts were higher than final survey numbers reported at the end of 2014 (ODFW 2015) because ODFW identified additional wolves after the report was submitted. Based on wolf survey information collected through July 2015, a minimum of 85 wolves were present in Oregon at the start of April. We acknowledge additional, undocumented wolves may be present in Oregon, but we relied on known individuals when developing our model. Counts identified 16 pairs or packs of wolves in addition to 3 individual wolves present in Oregon. Whenever possible, we used known data to assign pack, age, social class, and sex of wolves and randomly assigned these attributes when unknown. Newly documented pairs of wolves were assumed to consist of a male and female and both individuals were assigned dominant-adult status.

Survival.– Baseline survival rates of wolves used in our model represented survival in the absence of anthropogenic mortality (e.g., poaching, management removals). We adjusted survival rates reported in peer-reviewed literature to account for anthropogenic mortality using the following approach: 1) determine the overall mortality rate (1 – survival rate), 2) estimate the anthropogenic mortality rate as the product of proportion of total mortalities caused by humans and the overall mortality rate, and 3) sum the estimated anthropogenic mortality rate and the reported survival rate. As an example, Smith et al. (2010) reported an annual survival rate of 0.750 with 54% of mortality attributable to legal or illegal actions by humans. The anthropogenic mortality rate was 0.135 (1-0.750 × 0.540), which resulted in a ‘natural’ survival rate of 0.885 (0.750 + 0.135). In instances where authors directly reported cause-specific mortality rates (e.g., Wydeven et al. 1995), we summed reported survival and anthropogenic mortality rates to obtain an adjusted estimate of survival. After adjusting survival rates reported in peer-reviewed literature (Table 2) to account for human-caused mortality we arrived at a survival rate of 0.88 (± 0.04 SD) of adult wolves (2-7 years old; S_{ad}) for use in our model.

Using the largest sample size of radio-collared wolves reported in peer-reviewed published literature, Smith et al. (2010) reported that yearling wolves had a 54.9% higher risk (1.0012365 = 1.549) of mortality than adult wolves over 365 days. We adjusted the mean survival rate of 0.88 for adult (2-7 years) wolves by the increased hazard rate reported by Smith et al. (2010) to calculate a survival rate of 0.81 for yearling wolves (S_{y}; 1-[(1-0.88) × 1.549]; Table 1).
This may present an overly pessimistic view of resident yearling wolf survival, because yearlings have high dispersal rates (Gese and Mech 1991) and dispersing wolves were found to have higher risk of mortality (Smith et al. 2010). In our model, we utilized a separate mechanism to account for increased mortality of dispersing wolves (see below) and we recognize our estimates of yearling survival may be negatively biased. Senescence, observed through decreased survival at older ages is common for large mammals (Loison et al. 1999, Gaillard et al. 2000, Clark et al. 2014), but this phenomenon is not well documented in peer-reviewed published literature on wolves. To account for the potential of senescence, we used an annual survival rate for wolves > 7 years old of 0.63 as reported by Cubaynes et al. (2014), which we adjusted to 0.67 for use in our model ($S_{\text{old}}$) to account for anthropogenic mortality. Wolves ≥ 10 years of age had a survival rate of 0.00 in our model. While free-ranging wolves can live longer than 10 years, most wolves are typically no longer reproductively active after this age (Fuller et al. 2003, Kreeger 2003) and will contribute little to population growth and viability.

Estimates of non-pup survival used in our model were lower than observed to date in Oregon. Using known-fate survival analysis (White and Burnham 1999) on a sample 23 of wolves radio-collared in Oregon from 2009-2014, we estimated an annual survival rate of wolves > 6 months old of 0.91. Three collared wolves died during this timeframe, one of which was removed by ODFW and an additional wolf was illegally shot resulting in 66% of mortality being attributable to humans. Adjusting survival rates to account for anthropogenic mortality results in a survival rate of 0.97, which is substantially greater than the adult (0.88) and yearling (0.81) survival rates used in our model.

Table 2. Annual survival rates and human-caused mortality rates of non-pup wolves reported in peer-reviewed literature. Survival rates were estimated from known fates of radio-collared wolves unless otherwise noted. Adjusted survival rates represent survival rates on non-pups in the absence of human-caused mortality.

<table>
<thead>
<tr>
<th>Source</th>
<th>Reported survival</th>
<th>Human-caused mortality rate</th>
<th>Adjusted survival rate&lt;sup&gt;a&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adams et al. (2008)</td>
<td>0.79</td>
<td>0.09&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.89</td>
</tr>
<tr>
<td>Cubaynes et al. (2014)</td>
<td>0.80</td>
<td>0.04&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.84</td>
</tr>
<tr>
<td>Fuller (1989)</td>
<td>0.62</td>
<td>0.26&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.88</td>
</tr>
<tr>
<td>Hayes and Harestead (2000)</td>
<td>0.84</td>
<td>0.02&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.86</td>
</tr>
<tr>
<td>Peterson et al. (1984)</td>
<td>0.67</td>
<td>0.26&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.93</td>
</tr>
<tr>
<td>Smith et al. (2010)</td>
<td>0.75</td>
<td>0.14&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.89</td>
</tr>
<tr>
<td>Webb et al. (2011)&lt;sup&gt;d&lt;/sup&gt;</td>
<td>0.62</td>
<td>0.34&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.96</td>
</tr>
<tr>
<td>Wydeven et al. (1995)</td>
<td>0.61</td>
<td>0.28&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.89</td>
</tr>
<tr>
<td>Wydeven et al. (1995)</td>
<td>0.82</td>
<td>0.04&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.86</td>
</tr>
<tr>
<td>Mean</td>
<td>0.72</td>
<td>0.16</td>
<td>0.88</td>
</tr>
</tbody>
</table>

<sup>a</sup> Sum of reported survival and human-caused mortality rate.

<sup>b</sup> Mortality rate calculated as the product of overall mortality rate (1-survival) and proportion of mortalities caused by humans.

<sup>c</sup> Human-caused mortality rate directly reported by authors.

<sup>d</sup> Apparent survival rates estimated from mark-recapture data.
Estimates of survival of wolf pups from birth to 6 months are highly variable and are usually estimated by comparing pup counts at den or rendezvous sites to *in utero* fetal counts of harvested females. Based on a review of peer-reviewed published literature (Table 3), we determined mean survival rates of wolf pups from birth to 6 months, determined from pup counts, were 0.73. Estimation of survival using pup count data assumes that pups are counted with a detection probability of 1.0, which is unrealistic and this method will likely produce negatively biased estimates of survival over the first 6 months of life. In general, radio-telemetry studies have indicated pup survival is similar to adult survival during months 7-12 after birth (Peterson et al. 1984, Fuller 1989, Adams et al. 2008). Consequently, we used 6 month survival rate of adults (~0.94), calculated as the square root of annual survival, to approximate survival of pups from ages 7-12 months. We used the product of summer survival rates times the 6 month survival rate of adult wolves as the annual estimate of pup survival ($S_p$) in our baseline model ($0.73 \times 0.94 = 0.68$; Table 1).

**Table 3.** Survival rates of wolf pups from birth to six months reported in peer-reviewed literature. Unless otherwise noted, survival was estimated by comparing pup counts six months after birth to *in utero* litter sizes. Annual survival rates calculated as the product of 6 month survival rates of pups and 6 month survival rates of adult wolves used in our model (0.88).

<table>
<thead>
<tr>
<th>Source</th>
<th>Survival from birth to 6 months</th>
<th>Annual survival$^a$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fuller (1989)$^b$</td>
<td>0.58</td>
<td>0.55</td>
</tr>
<tr>
<td>Mills et al. (2008)$^c$</td>
<td>0.83</td>
<td>0.78</td>
</tr>
<tr>
<td>Fritts and Mech</td>
<td>0.57</td>
<td>0.53</td>
</tr>
<tr>
<td>Fuller and Keith (1980)</td>
<td>0.69</td>
<td>0.65</td>
</tr>
<tr>
<td>Adams et al. (2008)</td>
<td>0.81</td>
<td>0.76</td>
</tr>
<tr>
<td>Hayes and Harestead (2000)$^d$</td>
<td>0.80</td>
<td>0.75</td>
</tr>
<tr>
<td>Petersen et al. (1984)</td>
<td>0.80</td>
<td>0.75</td>
</tr>
<tr>
<td>Ballard et al. (1987)</td>
<td>0.82</td>
<td>0.77</td>
</tr>
<tr>
<td>Mech et al. (1998)$^e$</td>
<td>0.91</td>
<td>0.85</td>
</tr>
<tr>
<td>Hayes et al. (1991)$^f$</td>
<td>0.48</td>
<td>0.45</td>
</tr>
<tr>
<td>Mean survival</td>
<td>0.73</td>
<td>0.68</td>
</tr>
</tbody>
</table>

$^a$ Annual survival is the product of survival from birth to 6 months and the 6 month survival rate of adult wolves used in our model.

$^b$ Survival rate reported was estimated over 8 month period using pup counts. Monthly survival rate was 0.9135 and survival over six months was 0.58.

$^c$ Survival was estimated with implant transmitters from Jun-Nov. Used monthly survival rates from this period to estimate 6 month survival rate.

$^d$ Survival estimated on an annual interval. Used the square root of reported survival rates to estimate survival from birth to 6 months.

$^e$ Survival estimate over first 4 months of life. Extrapolated to 6 months.

$^f$ Heavily exploited wolf population.
We compared the pup survival rates used in our model to pup count data collected in Oregon during winter surveys conducted from 2009-2014. During this time frame, 30 potential reproductive opportunities were documented. Of these 30 potential reproductive opportunities, 3 were censored because final pup counts were not completed. Assuming wolves give birth to an average of 5 pups per litter (Fuller et al. 2003), we calculated a total of 135 pups born from these 27 reproductive opportunities. Minimum pup counts conducted in December of 2009-2014 indicated a minimum of 82 pups across all years. Using this information we arrived at a minimum observed survival rate of 0.61 (95% CI = 0.53 – 0.69), which is lower but within in the range of the pup survival rate used in our model (0.68 ± 0.15; Table 1).

When implementing our model, annual survival rates were independently calculated for each age class by randomly drawing a survival rate from a uniform distribution with a predefined mean and standard deviation (Table 1). Survival rates of wolves were age-specific and were not influenced by social status of the individual (e.g., survival rates for a 4-year old sub-dominant adult were identical to survival rates for a 4-year old dominant adult). Survival rates were modeled at an individual level, with each individual having an independent probability of survival at each time step.

**Density-dependence.**— When populations surpassed a predefined population threshold, annual survival rates, regardless of age, were multiplied by the ratio of the threshold population size and current wolf population size. The specified threshold was implemented to account for the importance of density-dependence on population dynamics (Morris and Doak 2002), but does not represent an expected number of wolves in Oregon in future years. When implemented in our model, the density-threshold represents an arbitrary biological threshold where wolves begin to self-regulate through intraspecific strife or are limited by available prey.

Larsen and Ripple (2006) created a habitat suitability map for wolves in Oregon and found that a maximum of 1,450 wolves could occupy Oregon. This value increased to 2,200 wolves if industrial timberland in western Oregon was classified as suitable wolf habitat. Fuller et al. (2003) provided the following equation to estimate expected wolf densities:

\[
\text{Wolves/1,000 km}^2 = 3.5 + 3.27 \times U
\]

, where \( U \) is the ungulate biomass index (km\(^2\)). Using an estimated elk (\( Cervus elaphus \)) population of 128,000 elk distributed across 151,500 km\(^2\) of summer range habitat (ODFW, unpublished data) and assigning each elk a biomass value of 3, results in a value of \( U \) of 2.53 (128,000 \( \times \) 3/151,500). Based on this value maximum wolf densities were estimated to be 11.79 wolves/1,000 km\(^2\) of summer range elk habitat. This would result in a total population of 1,780 wolves within 151,500 km\(^2\) of elk summer range habitat in Oregon. Carbone and Gittleman (2002) provided the following equation to estimate wolf densities based on available primary prey biomass:

\[
\text{Number of wolves} = 0.62 \times \text{primary prey biomass}
\]

, where primary prey biomass is scaled per 10,000 kg. Currently, Oregon’s elk population is approximately 128,000 with each elk weighing on average 217 kg (ODFW, unpublished data). This results in approximately 2,777.6 \( \times \) 10,000 kg of primary prey biomass available to wolves across Oregon and a maximum population estimate of approximately 1,722 wolves.

Both the Fuller et al. (2003) and Carbone and Gittleman (2002) equations produce similar estimates of wolf population size and fall within the range reported by Larsen and Ripple (2006). However, these estimates were calculated under the assumption wolves will not cause reductions in prey populations. To account for this possibility, we used a conservative density-threshold (CC) of 1,500 wolves in our model. Again, it should be noted, the density-threshold represents
an estimate of maximum potential wolf population size, not a management objective for wolves in Oregon.

*Prey multiplier.–* Wolf-prey interactions can influence wolf densities and population dynamics (Fuller et al. 2003). We lacked sufficient data to explicitly model wolf-prey interactions and instead used a simplified approach described in the peer-reviewed published paper by Bull et al. (2009) where a stochastically generated a prey multiplier value (Pr) was used to represent changes in either prey abundance or vulnerability (e.g., increased vulnerability during severe winters). The prey multiplier represented environmental stochasticity in our model. At a value of 1.0, the prey multiplier represented baseline prey availability or vulnerability. Each year of the simulation, the prey multiplier had a 1 out of 3 chance of increasing, decreasing, or remaining the same, respectively. In years the prey multiplier increased or decreased, the maximum change was restricted to 0.10. The prey multiplier was bounded between 0.90 and 1.10 values generated outside this range were truncated to the maximum or minimum value. Survival rates used in the model were calculated as the product of randomly drawn survival rates and the prey multiplier after accounting for any density-dependent effects.

*Dispersal and Emigration.–* We assumed dominant wolves would maintain their territory and breeding positions until their death. In the event that both dominant animals in a pack died, all remaining pack members would disperse. This approach was partially used for simplicity of model implementation, but was also supported in peer-reviewed literature (Fuller et al. 2003). For example, Brainerd et al. (2008) found that in instances where both breeding wolves were lost, 85% of packs dissolved, and only 9% of packs reproduced the following year. Sub-dominant wolves that survived the year had a probability of dispersing from their existing territory, which was dependent on age and breeding status (Table 1). Age-specific dispersal rates used in our model (Dp, Dy, Dad) were obtained from literature (Potvin 1988, Fuller 1989, Gese and Mech 1991). We assumed non-breeding adults had similar dispersal rates as yearlings (Fuller et al. 2003). Survival rates of dispersing individuals were reduced (M₉) to account for increased mortality risk of wolves during dispersal (Table 1; Peterson et al. 1984, Fuller 1989, Smith et al. 2010). Smith et al. (2010) found dispersing wolves had a 38.9% higher risk of mortality over 365 days than resident wolves. After accounting for this increased risk, survival rates of dispersing adult wolves would be 0.83 with the ratio of dispersing versus resident adult survival rates of 0.94 (0.83/0.88). To be conservative, we lowered this value to 0.90 (± 0.05 SD) for use in our model, which is interpreted at 10% of dispersing wolves die during the dispersal process.

We used a spatial simulation to estimate emigration rates using peer-reviewed published estimates of dispersal distances of wolves (Fritts and Mech 1981, Fuller 1989, Gese and Mech 1991, Wydeven et al. 1995). We generated 10,000 random dispersal paths that started at a random location within summer range elk habitat (i.e., potential wolf habitat). We simulated dispersal paths using correlated random walks with the movement.simplecrw function in the Geospatial Modeling Environment (Beyer 2012) by selecting a random bearing from a uniform distribution (0 - 359°) and a random dispersal distance from normal distribution with a mean of 75 km (± 30 SD). We calculated emigration rates (E₉) as the proportion of simulated dispersal paths that terminated outside Oregon. Mean emigration rates were estimated to be 0.115 (Table 1). We estimated a standard deviation of the mean values calculated from 100 bootstrap samples that each contained 100 random dispersal paths. The estimated standard deviation of the mean of
these 100 samples was 0.03. Emigration was effectively treated as additional mortality in our model (i.e., these individuals were removed from the simulated population).

**Territory Establishment.**—Dispersing wolves ≥ 2 years old were assigned a probability of establishing a territory. Boyd and Pletscher (1999) found that 57% of dispersing wolves successfully found a mate the next breeding season after they dispersed. This value equates to the joint probability of two wolves establishing a territory. Independently, the probability of a dispersing wolf establishing a territory (T) would be 0.75 (√0.57), which we used in our model. Wolves that did not successfully establish a territory remained in the pool of dispersers until the following year. Those individuals that successfully established territories would first fill vacant alpha positions of the correct sex in established packs. If no alpha positions were available at established packs, dispersing wolves would then establish a new territory and maintain that position until they died or a mate joined them at the territory.

**Immigration.**—We assumed wolves from the extant Rocky Mountain wolf population would be available to immigrate into Oregon. For model simplification, we assumed the wolf population outside Oregon was unstructured and would produce a steady, but limited, stream of immigrants. We assumed 3 wolves (± 2 SD) would immigrate (I) annually into Oregon from surrounding populations. We assumed all immigrating wolves were sub-adults because a review of peer-reviewed literature indicated this age class is most likely to engage in dispersal behavior (Fuller 1989, Gese and Mech 1991, Fuller et al. 2003). Individuals arriving in the Oregon population were randomly assigned a sex assuming parity among dispersers (Gese and Mech 1991).

**Anthropogenic Mortality.**—Anthropogenic mortality was incorporated in the model under two forms: legal and unauthorized mortality. Unauthorized mortality represented all sources of anthropogenic mortality (e.g., poaching, vehicle-killed individuals) excluding mortalities authorized by ODFW under current laws. Legal removals included any administrative removals authorized by ODFW (e.g., livestock damage, human safety, incidental take). Anthropogenic mortality was modeled using a two-step process where unauthorized mortality was modeled first and followed by legal mortality. A proportion of the total population that remained after accounting for natural mortality events would be removed each year by each anthropogenic mortality source (Table 1). Anthropogenic mortality was applied independent of age, social status, or pack membership. Effectively, this approach treats anthropogenic mortality as a reduction in survival. For example, using an annual adult survival rate of 0.88, survival rates would be reduced to 0.79 (0.88 × 0.95 × 0.95) if 5% of the population was removed for both legal and unauthorized mortality, respectively.

From April 2009 to March 2015, ODFW has collected 54 wolf-years of data from radio-collared individuals. During this time, 1 radio-collared wolf was illegally killed and 1 radio-collared wolf was removed by ODFW, for a removal rate of 0.02 for each mortality source (ODFW, unpublished data). Due to the potential bias of radio-collared wolves being avoided by poachers, we increased the illegal mortality (IM) value to 0.05 (± 0.03 SD). To be conservative and allow for the potential of increased levels of lethal control actions, we used a value of 0.05 (± 0.03 SD) for legal mortality (LM) of wolves in our model (i.e., between 2-8% of wolves would be randomly removed from the population each year for management related actions).

**Reproduction.**—Only established wolf packs with a dominant pair of adults were allowed to reproduce. We were unable to find peer-reviewed estimates of pregnancy rates of dominant females in published literature; however, it is biologically unrealistic to assume all pairs of wolves successfully give birth to pups each year (i.e., female do not always become pregnant).
We assumed pregnancy rates of dominant females ($P_{ad}$) would be 0.95 ($\pm 0.02$ SD; Table 1). While evidence exists of multiple females producing pups within a pack, this is a rare occurrence and usually only occurs in extremely large packs (Mech 1999), and we assumed only one litter of pups would be born in packs with a dominant pair. The number of pups produced by pregnant females ($L$) was drawn from a uniform distribution ranging from 2-8 (Table 1) based on a review of literature (see summary in Fuller et al. 2003).

Catastrophes. – We included two catastrophes in our model. The first was modeled at the pack level as the probability of a pack having complete reproductive failure within a year ($R_{cas}$). Probability of reproductive failure was independent among packs and years. This approach was used to simulate the potential effects of diseases (e.g., canine parvovirus), which are known to negatively affect pup survival and recruitment (Mech and Goyal 1993, Almberg et al. 2009), where most or all pups die when exposed to the virus (Mech et al. 2008). We assumed complete reproductive failure had a probability of occurrence of 0.05 within each pack during each year of the simulation (i.e., one out of 20 litters will be subjected to complete reproductive failure). Packs that had complete reproductive failure were assigned a litter size of 0 (i.e., even if pups were produced they would all die before 1 year of age).

Our second catastrophe was modeled at the population level, where each year of the simulation there was a probability of a population wide reduction in survival ($S_{cas}$). This approach was used to represent extremely rare, range wide events that may affect wolf populations (e.g., disease, abiotic conditions, prey population crashes). We used a mean interval of 100 years between disturbance events, with each year having an independent probability of a disturbance event occurring. During years where a catastrophe event occurred, survival rates of all wolves in the population were reduced by 25%.

Assessment of Population Viability

We assessed population viability using two measures. The Oregon Wolf Plan defined a threshold of 4 breeding pairs for 3 consecutive years as a guideline to consider delisting wolves from the Oregon ESA (ODFW 2010). Consequently, we defined “conservation-failure” as a simulated population that fell below 4 breeding pairs. For each simulated population, we determined which time-step, if any, that the population dropped below the conservation-failure threshold. Simulated populations that dropped below the conservation-failure threshold were considered failures in all remaining time steps. We calculated risk of conservation-failure as the cumulative proportion of simulated populations that had < 4 breeding pairs.

We used a threshold of < 5 wolves as our metric of “biological-extinction”. In simulations with < 5 wolves, the extant population would effectively be extirpated and immigrants from outside sources would be maintaining the Oregon population. For each simulated population, we determined the time-step, if any, that the population dropped below the biological-extinction threshold. Once the population dropped below this threshold it was determined to be biologically-extinct for all remaining time steps. We calculated biological-extinction rates as the cumulative proportion of simulated populations that < 5 wolves.

Model Validation

To validate our baseline model, we conducted a set of 100 realizations of population growth over 5 years, where the starting population size was the number of wolves present in Oregon at the end of 2009 ($N = 14$ wolves). We calculated the mean number of wolves and breeding pairs from simulations and compared these values to population counts conducted by ODFW from 2010-2014. Survival rates used in our baseline model were more conservative than observed in Oregon from 2010-2014. Consequently, we conducted a second set of simulations.
where we parameterized our model with vital rates required to match observed population growth rates in Oregon from 2009-2014 (see Table 1 for differences between vital rates in the two scenarios). Using observed vital rate values in our model would allow us to determine if our overall model structure allowed accurate estimation of population growth under known conditions.

Sensitivity Analysis

Effects of Stochastic Parameters.– We used \( r \) (i.e., intrinsic rate of increase) as the dependent variable in a linear regression model where stochastically varying parameters and relevant interactions were used as independent variables. We conducted 200 realizations of population growth over a 5-yr period which resulted in 1,000 random combinations of parameter values and associated intrinsic growth rates (\( r \)). The sensitivity analysis was limited to a 5-yr span because allowing population simulations to last longer than 5-yrs could cause some simulations to reach the density-threshold of 1,500 wolves and confound the effect of parameter variation and density-dependence on \( r \). For each simulation, the starting population was assumed to be 120 wolves equally distributed among 20 packs. We used this starting population size because at extremely small population sizes (e.g., \( N < 10 \)) immigration of wolves could produce biologically unreasonable population growth rates (e.g., \( \lambda > 2.0 \)) and confound our ability to detect an effect of parameters on \( r \). Prior to running our regression model, all independent variables were standardized (standardized value = [observed value - mean value]/standard deviation) to allow direct comparisons between results. We used an alpha level of 0.05 to determine significance of parameters and the sign and slope of beta coefficients to determine the strength and relative effect of the parameter on \( r \).

Effects of Static Parameters.– Starting population size, density-threshold, and frequency of survival and reproductive catastrophes were static parameters in our model and the effects of these were not included in our regression analysis used to determine the relative effects of parameters on \( r \). Consequently, we conducted additional simulations where values of static parameters differed among simulations. Each simulation used 100 realizations of population growth over 50 years and was parameterized with baseline values except for changes in the static parameter of interest. We conducted 4 simulations to determine the effect of starting population sizes of 50 wolves, the known existing Oregon wolf population (\( N = 85 \); baseline value), 100 wolves and, 150 wolves. Simulations with starting populations of 50, 100, and 150 wolves were structured as follows: 1) each wolf belonged to a pack and each pack had 5 members with 2 of those members being dominant adults and 2) sex, age, and social class of remaining wolves were randomly assigned. To determine the relative influence of the density-threshold on population viability of wolves, we conducted a set of simulations where used a density-threshold of 100, 250, 500, 1000, and 1500 (baseline value) wolves. We conducted a set of 3 simulations where we investigated probabilities of individual pack reproductive failure of 0.05 (baseline value; once every 20 litters), 0.10 (once every 10 litters), and 0.20 (once every 5 litters). We investigated the effects catastrophic reductions in survival at year-specific probabilities of 0.01 (baseline value; once every 100 years), 0.02 (once every 50 years), 0.05 (once every 20 years), and 0.10 (once every 10 years).

Effects of lethal control of wolves

Legal, anthropogenic mortality is the parameter included in our model over which ODFW has the most control. To address the effects of varying rates of legal wolf removal on wolf population viability we conducted a set of 4 simulations where mean legal mortality rates and associated standard deviations varied among simulations while all other model parameters
were left at baseline values (Table 1). The following values were used as mean values (± SD) to represent legal anthropogenic mortality rates in the 4 simulations: 0.00 (± 0.00), 0.05 (± 0.03), 0.10 (± 0.06), and 0.20 (± 0.12). These levels of legal mortality rates were in addition to illegal mortality rates which were set at a mean value of 0.05 (± 0.03) during all simulations.

Our baseline model assumes legal removals will be implemented through random removal of individual wolves. However, the potential exists that lethal control actions could take place across entire wolf packs, rather than individuals. Consequently, we also conducted a simulation where legal removal of wolves would occur at a pack rather than individual level. We assumed the proportion of packs removed per year would be the same as the proportion of individuals removed in our baseline simulation (0.05 ± 0.03). After completion of simulations, we compared the results to the baseline simulation to determine what effect, if any, pack removal would have on population dynamics compared to individual removal.

**RESULTS**

**Model Validation**

Our baseline model resulted in underestimates of population size (Fig. 3a) and number of breeding pairs (Fig. 3b) compared to population count data collected in Oregon from 2010-2104. When our model was parameterized with survival rates of wolves observed from 2009-2014 (Table 1) the simulation results closely approximated observed population size and number of breeding pairs. Consequently, survival rates used in our baseline model are cautious compared to past survival rates in Oregon; however, the ability of the model to correctly predict past population dynamics when parameterized with observed survival rates suggests other parameters included in the model accurately portray wolf population dynamics in Oregon. Our baseline model predicted lower population growth compared to the model parameterized with survival rates observed from 2009-2014. This suggests our baseline model will underestimate wolf population growth and viability if survival rates from 2009-2014 are observed into the future.

**Assessment of Population Viability**

Using our baseline model, simulated wolf populations increased an average of 7% (i.e., \( \lambda = 1.07 \pm 0.17 \) SD) per year. Over the next 50 years, there was a 0.05 (95% CI = 0.01 – 0.09) probability of the population dropping below the conservation-failure threshold (Fig. 4). Most conservation-failures (3 out of 5) occurred within the first 10 years and by year 20, no additional populations passed the threshold. Of the five simulated populations that fell below the conservation-failure threshold, all eventually surpassed 4 breeding pairs in the future with these populations having 7, 20, 39, 84 and 194 breeding pairs in year 50 of the simulation, respectively. There was a 0.01 (95% CI = 0.00 – 0.03) probability the simulated population dropped below the biological-extinction threshold over the next 50 years. The single simulated population that dropped below 5 individuals recovered to 360 individuals by year 50.

Using observed survival rates of wolves from 2009-2014 in our population model resulted in no scenarios where wolf populations dropped below the conservation-failure or biological-extinction thresholds. Our baseline model may be more likely to represent future population dynamics of wolves, but may be overly pessimistic, especially in the near future, given recently observed survival rates of wolves in Oregon. Consequently, we contend future risk of conservation-failure likely falls somewhere between our baseline model (0.05) and our model parameterized with vital rates required to match observed population growth rates from 2009-2014 (0.00). Our model results suggest it is extremely unlikely (≤ 0.01 probability) wolves in Oregon will be at risk of extirpation over the next 50 years.
Figure 3. Comparison of (a) simulated mean population sizes compared to minimum population sizes observed in Oregon from 2009-2014 and (b) simulated number of breeding pairs to minimum number of known breeding pairs in Oregon from 2009-2014 using baseline simulation parameters (dashed line) or observed model parameters (solid line). Black dots represent observed wolf population size and number of breeding pairs determined from annual surveys of wolf populations conducted by ODFW. Polygons around simulated mean population sizes and number of breeding pairs represent 95% confidence intervals.
Figure 4. Estimates of cumulative probability of simulated wolf populations reaching the conservation-failure (< 4 breeding pairs) or biological-extinction (< 5 wolves) thresholds over the next 50 years in Oregon. Estimates were generated using our baseline model parameterization with 100 realizations of population growth over 50 years. Cumulative probabilities represent the cumulative proportion of simulations that crossed the threshold of interest.

Sensitivity Analysis

Effects of Stochastic Parameters.—Nine out of 17 stochastic parameters included in our baseline model had a significant effect on intrinsic growth rates as measured by \( r \), and no significant interactions between parameters were documented (Table 4). Most significant effects (Fig. 5) were directly or indirectly related to survival rates. Survival rates of pups (\( S_p; \beta = 0.045 \)), yearlings (\( S_Y; \beta = 0.024 \)), and adults (\( S_{ad}; \beta = 0.019 \)) were positively associated with \( r \). The prey multiplier (\( Pr \)) increased variation in survival rates of all age classes of wolves by up to 20% and resulted in the prey multiplier, which represented increased environmental stochasticity, having the greatest effect on \( r \) (\( \beta = 0.088 \)). Illegal (IM; \( \beta = -0.027 \)) and legal (LM; \( \beta = -0.028 \)) anthropogenic mortality were negatively associate with \( r \).
Table 4. Results of linear regression model used to estimate sensitivity of intrinsic growth rates of wolf populations in Oregon using an individual-based population model. Standardized regression coefficients with associated standard errors estimated from the full model are provided. Significance is determined as follows: *** = P < 0.001, ** = P < 0.01, * = P < 0.05, and NS = P > 0.05.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Standardized $\beta_i$</th>
<th>SE</th>
<th>P-value</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pup survival</td>
<td>0.045</td>
<td>0.007</td>
<td>0.000</td>
<td>***</td>
</tr>
<tr>
<td>Yearling survival</td>
<td>0.024</td>
<td>0.007</td>
<td>0.000</td>
<td>***</td>
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<td>Adult (2 to 7- yrs old) survival</td>
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<td>0.007</td>
<td>0.006</td>
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<td>0.411</td>
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<td>9-yr old adult survival</td>
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<td>0.007</td>
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<tr>
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<td>Adult dispersal</td>
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<tr>
<td>Proportion of dispersing wolves that die</td>
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<td>0.007</td>
<td>0.000</td>
<td>***</td>
</tr>
<tr>
<td>No. of immigrants arriving annually</td>
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<td>0.005</td>
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<td>Proportion of dispersing wolves that emigrate</td>
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<td>0.007</td>
<td>0.443</td>
<td>NS</td>
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<td>Proportion of dispersing wolves that successfully establish a territory</td>
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<td>0.006</td>
<td>0.000</td>
<td>***</td>
</tr>
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<td>Pregnancy rate for dominant females</td>
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<td>0.007</td>
<td>0.912</td>
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<tr>
<td>Mean litter size</td>
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<td>0.004</td>
<td>0.000</td>
<td>***</td>
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<tr>
<td>Prey index multiplier</td>
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<td>0.005</td>
<td>0.000</td>
<td>***</td>
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<tr>
<td>Illegal mortality</td>
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<td>0.000</td>
<td>***</td>
</tr>
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<td>Legal mortality</td>
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<td>0.000</td>
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<td>Pup survival × Prey multiplier index</td>
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<td>Yearling survival × Dispersal mortality</td>
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<td>0.012</td>
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<td>Adult survival × Dispersal mortality</td>
<td>0.003</td>
<td>0.011</td>
<td>0.785</td>
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Figure 5. Estimated effects of significant ($p < 0.05$) model parameters on intrinsic growth rates of wolf populations. Estimates were generated using baseline model parameterization. Results generated from 1,000 unique combinations of model parameters and associated intrinsic growth rates. Model parameters are standardized to allow direct comparison among parameters. Black line represents estimated regression line. Gray dots represent individual parameter estimates and associated population growth rate.
Increased mortality rates of dispersing wolves ($M_d; \beta = -0.026$) had a negative effect on $r$. This parameter negatively affected $r$ in two ways: 1) wolves were directly removed from the population and 2) fewer wolves were available to establish territories and contribute to population level reproduction. Increased probabilities of dispersing wolves successfully establishing a territory had a positive effect on $r$ ($T; \beta = 0.034$). Mean litter size ($L; \beta = 0.049$) was positively correlated with $r$. Pregnancy rates of dominant females ($P_{ad}$) were not significantly associated with $r$. We likely did not find a significant effect of pregnancy rates because of the high mean value (0.95) and low variation (SD = 0.02) used in our model.

Dispersal rates, regardless of age class ($D_p, D_y, \text{ and } D_{ad}$) had minimal effects on $r$ (Table 4). Both immigration ($I$) and emigration ($E_d$) did not have a significant effect on $r$. At most, our model limited the number of immigrating wolves to 5 per year (range = 1 – 5) and contributions to population growth from immigrants will be limited except for extremely small extant populations. We modeled emigration rates as a proportion of the dispersing wolves that survived and left the population each year. Consequently, emigration could contribute to reduced population growth rates when the number of emigrants is greater than the number of immigrants. This scenario is more likely to occur for large extant populations.

Effects of Static Parameters.—As expected, simulations with larger starting populations reached the density-threshold faster than those with smaller starting size (Fig. 6a). The risk of conservation-failure declined with increased starting population size (Fig. 6b). Using our baseline model, simulations that started with 150 and 100 individuals had no risk and a 0.01 (95% CI = 0.00 – 0.03) probability of conservation-failure over the next 50 years, respectively. At the current minimum known wolf population in Oregon, risk of conservation-failure (0.05; 95% CI = 0.01 – 0.09) was slightly higher than if 100 animals were in the population but substantially lower than if only 50 wolves (0.14; 95% CI = 0.07 – 0.21) occurred in Oregon. We did not observe a relationship between starting population size and biological-extinction risk as biological-extinction risk was $\leq 0.01$ over 50 years regardless of starting population size.

Unsurprisingly, mean maximum population sizes of wolves were larger for simulations with higher density-thresholds (Fig. 7a). The effects of varying density-thresholds on risk of conservation-failure over 50 years were similar for density thresholds between 250 – 1500 (range 0.03 – 0.05; Fig. 7b). In contrast, at a density-threshold of 100 wolves, risk of conservation-failure was much greater (0.64; 95% CI = 0.55 – 0.73), steadily increased over time, and never plateaued as observed in other simulations. This suggests that a population threshold of 100 wolves is insufficient to allow long-term persistence of $\geq 4$ breeding pairs. Regardless of the density-threshold used, maximum observed biological-extinction risk was $\leq 0.01$.

Increased frequency at which catastrophic reductions in survival rates occurred caused reduced population growth rates and reduced mean, maximum population size of wolves (Fig. 8a). Populations that were subjected to catastrophic reductions in survival at intervals of once every 100 or 50 years had a relatively low risk of conservation-failure (range = 0.05 – 0.06; Fig. 8b). Catastrophic reductions in survival at intervals of once every 20 (0.09; 95% CI = 0.03-0.15) and 10 (0.16; 95% CI = 0.09-0.23) years had moderate risk of conservation-failure compared to less or more frequent intervals. For all scenarios, biological extinction risk was $\leq 0.01$ over 50 years.
Figure 6. Estimated effect of variation in starting population size on (a) mean population size and (b) cumulative probability of conservation-failure (< 4 breeding pairs) over the next 50 years in Oregon. Current population size (N = 85) was the minimum wolf population size in Oregon as of April 1, 2015. Cumulative probability of conservation-failure represents the cumulative proportion of simulated populations that reached the conservation-failure threshold. All estimates generated using 100 realizations of population growth over 50 years using the baseline model parameterization.
Figure 7. Estimated effect of variation in density-threshold on (a) mean population size and (b) cumulative probability of conservation-failure (< 4 breeding pairs) over the next 50 years in Oregon. Cumulative probability of conservation-failure represents the cumulative proportion of simulated populations that reached the conservation-failure threshold. All estimates generated using 100 realizations of population growth over 50 years using baseline model parameterization.
Figure 8. Estimated effect of variation in interval between catastrophic reductions in survival of wolves on (a) mean population size and (b) cumulative probability of conservation-failure (< 4 breeding pairs). Cumulative probability of conservation-failure or biological extinction represents the cumulative proportion of simulated populations that reached the specified threshold. All estimates generated using 100 realizations of population growth over 50 years using baseline model parameterization.
Increased frequency of pack-specific reproductive failure reduced population growth rates and mean, maximum population size of wolves (Fig. 9a). Scenarios with reproductive failure once every 20 (0.05; 95% CI = 0.01 – 0.09) and 10 litters (0.05; 95% CI = 0.01 – 0.09) had similar risk of conservation-failure in the next 50 years (Fig. 9b). Risk of conservation-failure was almost 6 times greater at intervals of once every 5 litters (0.29; 95% CI = 0.20 – 0.38). These results highlight the importance of pup production on ensure population viability of wolves. Risk of biological-extinction was not strongly affected by interval of reproductive failure as all scenarios had a risk of biological-extinction ≤ 0.02.

Figure 9. Estimated effect of variation in intervals between reproductive failure on (a) mean population size and (b) cumulative probability of conservation-failure (< 4 breeding pairs) over the next 50 years in Oregon. Cumulative probability of conservation-failure represents the cumulative proportion of simulated populations that reached the conservation-failure threshold. All estimates generated using 100 realizations of population growth over 50 years using baseline model parameterization.
Effects of lethal control of wolves

Increased rates of legal mortality, while holding illegal mortality at baseline values, had a negative effect on population growth rates and mean, maximum population size of wolves (Fig. 10a). With a starting population of 85 wolves and at a legal mortality rate of 0.20, wolf populations declined. This suggested this rate of legal mortality was not sustainable over the long-term at least at a starting population of 85 wolves and additional illegal mortality of 0.05. At a mean legal mortality rate of 0.05, which was used in our baseline model, probability of conservation-failure was 0.05 (95% CI = 0.01 – 0.09; Fig. 10b) over the next 50 years. At a reduced mean legal mortality rate of 0.00, no simulated populations dropped below the conservation-failure threshold. Probability of conservation-failure increased to 0.40 (95% CI = 0.30 – 0.50) and 1.00, for mean legal mortality rates of 0.10 and 0.20, respectively, when combined with illegal mortality rates of 0.05. Combined, these results highlight the importance of minimizing anthropogenic mortality to benefit population viability of wolves. Probability of biological-extinction was relatively low for all simulations with mean legal mortality rates ≤ 0.10 (range = 0.00 – 0.07; Fig. 10c). In contrast, mean legal mortality rates of 0.20 resulted in an extremely high probability of biological extinction (0.90; 95% CI = 0.84 – 0.96), at least when combined with an illegal mortality rate of 0.05 and a starting population of 85 individuals. Larger populations will be able to sustain higher mortality rates because they will have a greater buffer between extant population size and thresholds of biological extinction.

It should also be noted, the levels of anthropogenic mortality used in our model are not directly comparable to mortality rates commonly reported in literature (i.e., \(1 - \text{survival rate}\)). Anthropogenic mortality rates as implemented in our model represent the proportion of wolves that would be removed from the population after accounting for natural mortality. For example, using a legal mortality rate of 0.10, an illegal mortality rate of 0.05, and a survival rate in the absence of anthropogenic mortality of 0.88, would result in an observed survival rate of 0.75

\[0.88 \times (1 - 0.10) \times (1 - 0.05)\]

The effects of legal removals on wolves reported above are predicated on a starting population of 85 wolves. At larger population sizes, wolves will have an increased buffer between extant population size and conservation-failure or biological-extinction thresholds and fewer simulations would be expected to cross these thresholds. This is particularly true for moderate levels of legal mortality (0.05-0.15) where populations are likely to increase on average, but without a sufficient buffer and under stochastically varying conditions, 2-3 consecutive years of negative population growth could push the population below a predefined threshold. This phenomenon is evident in our simulations because most conservation-failures occurred shortly after simulations started. By later years, population sizes had sufficiently increased that they were able to withstand several consecutive years of negative population growth without falling below the conservation-failure threshold.

Comparison of individual vs. pack removal.–Lethal control actions conducted through random removal of individuals or entire packs had little influence on mean population size over 50 years (Fig. 11a). Mean populations for both removal scenarios reached the density-threshold (\(N = 1,500\)) by the 50\textsuperscript{th} year of the simulation. Conservation-failure rates over 50 years were similar if individual wolves (0.05; 95% CI = 0.01 – 0.09) or packs (0.08; 95% CI = 0.03 – 0.13) were removed (Fig. 11b). Entire pack removal (0.01; 95% CI = 0.00 – 0.03) and removal of individuals (0.01; 95% CI = 0.00 – 0.03) resulted in similar estimates of biological-extinction risk over 50 years.
Figure 10. Estimated effect of variation in legal removal rates (proportion of wolves that would have survived the year otherwise) of wolves on (a) mean population size, (b) cumulative probability of conservation-failure (< 4 breeding pairs), and (c) cumulative probability of biological-extinction (< 5 wolves) over the next 50 years in Oregon when the starting population size was 85 wolves. Cumulative probability of conservation-failure or biological extinction represents the cumulative proportion of simulated populations that reached the specified threshold. All estimates generated using 100 realizations of population growth over 50 years using baseline model parameterization. For all simulations, unauthorized morality rates of 0.05 (± 0.03 SD) occurred in addition to varying levels of legal removal.
Figure 11. Estimated effect of individual versus pack level legal removal on (a) mean population size and (b) cumulative probability of conservation-failure (< 4 breeding pairs) over the next 50 years in Oregon. Cumulative probability of conservation-failure represents the cumulative proportion of simulated populations that reached the conservation-failure threshold. All estimates generated using 100 realizations of population growth over 50 years using baseline model parameterization. Pack level and individual removal rates were identical for each simulation (0.05 ± 0.03).
DISCUSSION

Our baseline model underestimated population growth rates of wolves compared to observed population counts conducted in Oregon from 2010-2014. This was a consequence of two factors: 1) our baseline model used lower survival rates than were observed from 2010-2014 and 2) at small population sizes demographic stochasticity can have a dramatic effect on population growth rates (Lande 1998, Fox and Kendall 2002). However, our model parameterized with survival rates of wolves radio-collared in Oregon from 2009-2014 allowed our model to track observed population growth rates during this timeframe. We contend these findings suggest our model structure is capable of accurately portraying population dynamics of wolves when survival rates used in the model are representative of current conditions. We used conservative survival estimates in our baseline model to ensure our PVA erred on the side of caution (i.e., precautionary principle; Myers 1993, Meffe et al. 2006). Consequently, our results represent a conservative view of population viability of wolves in Oregon.

If wolf populations in Oregon continue to follow vital rates observed from 2009-2014, our results indicated there would be no risk of conservation-failure or biological-extinction within the next 50 years. It is unlikely wolf populations in Oregon would continue to increase at observed population growth rates because established or exploited wolf populations do not increase as rapidly as protected or recovering populations (Ballard et al. 1987, Hayes and Harestad 2000, Fuller et al. 2003). Therefore, we contend results from our model parameterized with currently observed vital rates may present an overly optimistic view of wolf population dynamics moving forward in Oregon. Using our baseline model parameterized with vital rates obtained from a literature review, we documented a 0%, 3%, and 5% chance of conservation-failure over the next 5,10, and 50 years, respectively (Fig. 4). Most risk of conservation-failure occurs in the short-term (e.g., 15 years) because Oregon’s extant wolf population is close to the conservation-failure threshold and a few years of poor population growth could cause the population to decline below the threshold. Furthermore, during the first few years of our simulations, population sizes are small, which allows demographic stochasticity to have a greater effect on population persistence (Vucetich et al. 1997).

Our baseline model suggested risk of conservation-failure was lower for populations that started with 100 or 150 wolves compared to the current population size observed in Oregon (N = 85; Fig. 6). This is not an unexpected finding because larger populations, regardless of species, have a reduced risk of extinction and can withstand longer periods of reduced population growth. These results highlight the importance of creating a buffer between extant population size and conservation-failure thresholds to allow for potential years of negative population growth. Furthermore, increased modeled starting population size will minimize effects of demographic stochasticity and increase population viability. Based on observed population growth rates from 2009-2014 (mean $\lambda = 1.43$) and known reproduction in 13 groups of wolves in 2015, Oregon’s wolf population is expected to surpass 100 wolves by the end of the biological year. At this population size, risk of conservation-failure will effectively be eliminated ($\leq 0.01$).

In general, factors that influenced wolf survival had the greatest effect on intrinsic growth rates of wolves ($r$) in our simulation models. In our model, pup, yearling, and adult survival all had significant effects on intrinsic growth rates of wolf populations (Fig. 5). However, variation in pup survival had a greater effect on intrinsic growth rates than yearling or adult survival. While population growth rates of most large mammals are usually most sensitive to changes in adult survival, variability in adult survival, in the absence of high levels of anthropogenic mortality, is usually minimal compared to juveniles (Promislow and Harvey 1990, Gaillard et al. 2003).
The inherent variability in survival of juveniles causes this age class to have a disproportionate effect on population growth rates despite population growth rates being relatively insensitive to variation in this parameter. This does not discount the importance of adult and yearling survival on population growth and viability; rather it highlights the importance of minimizing annual variation and maintaining high survival rates of yearlings and adults.

Prey abundance and vulnerability are thought to influence wolf populations (Fuller and Keith 1980, Hayes and Harestad 2000, Vucetich and Peterson 2004). In our model, we did not explicitly model predator-prey relationships; rather, we used a prey multiplier value that increased stochastic variation in survival rates of wolves to simulate the effects of variation in prey abundance or changes in environmental conditions (e.g., snow depth) that influence vulnerability of prey over time. Effectively, the prey multiplier represented environmental stochasticity that allowed up to a 20% increase in variation in survival rates. Increased variability in survival (i.e., environmental stochasticity) will have negative effects on population growth rates and viability, regardless of the species of interest (Morris and Doak 2002). Consequently, it was expected that increased environmental stochasticity, modeled through our prey multiplier, had a negative effect on simulated wolf populations.

Anthropogenic mortality is the primary factor that influences dynamics of most wolf populations (Creel and Rotella 2010). Our model supported this conclusion because increased levels of anthropogenic mortality had a negative effect on intrinsic growth rates of wolves (Fig. 5). Furthermore, our simulation results indicated that increased rates of anthropogenic mortality resulted in increased risk of conservation-failure and biological-extinction when the initial population was 85 wolves (Fig. 10). Anthropogenic mortality is the parameter in our model over which ODFW has the most control and our results highlight that Oregon’s wolf population will continue to increase and become self-sustaining if anthropogenic mortality is limited.

Our baseline model used inputs of 0.05 for both illegal and legal anthropogenic mortality rates (i.e., 5% of wolves that do not die of natural causes will be removed by both illegal and legal mortality sources) and at this rate, risk of conservation-failure was low. If ODFW maintains mortality rates at or below this level, the wolf population is predicted to be at a low risk of conservation-failure (0.05) and biological-extinction (0.01). Sustained, high levels of anthropogenic mortality (e.g., 0.20) in a stochastically varying environment contributed to increased risk of conservation-failure in our simulations; however, this finding is predicated on our staring population size of 85 wolves. Larger populations would be able to sustain this level of anthropogenic mortality without reaching the conservation-failure threshold because there is an increased buffer between extant population size and the conservation-failure threshold. Our model suggested that total anthropogenic mortality rates (i.e., combined illegal and legal mortality) of 0.15 would result in an increasing population on average ($\lambda = 1.03$) but total anthropogenic mortality rates of 0.20 caused wolf populations to decline on average ($\lambda = 0.98$). Previous studies have indicated wolf populations can be sustained with mortality rates up to 0.25 - 0.30 (Adams et al. 2008, Creel and Rotella 2010, Sparkman et al. 2011). As implemented in our model, anthropogenic mortality rates of 0.20 would cause survival rates of adult wolves to be 0.70 (i.e., a mortality rate of 0.30) and the wolf population would decline slightly on average ($\lambda = 0.98$). Consequently, our model matches well with the results previous studies.

Catastrophic reductions in survival of 25% had little effect on population growth rates and viability of wolves if the interval between occurrences was $\geq 50$ years (Fig. 8). Widespread, catastrophic events are impossible to predict and little can be done to directly mitigate their
effect. However, general tenants of population ecology provide insight into actions that can minimize their effects on population viability. The primary way to reduce effects of catastrophes on population viability is to maintain larger extant populations. Larger populations are more viable because they have a sufficient number of individuals to withstand population declines. In our model, catastrophic events occurred at the population level. This is likely a biologically unrealistic expectation because catastrophic events are likely to occur in geographic regions (e.g., Blue Mountains or Cascade Range) due to localized differences in environmental conditions. This geographic separation should reduce population level effects of catastrophic events because not all wolves would be subjected to the event in a single year. However, these smaller sub-populations would have a greater risk of localized extinction compared to the larger extant population. This highlights the importance of risk spreading through spatial distribution of wolves in ensuring the long-term viability of wolf populations.

Recruitment of pups into the adult population was a critical factor influencing population dynamics of wolves. While we did not directly include a recruitment parameter in our model, several factors that jointly influence pup recruitment had separate effects on wolf population growth and viability. Variation in mean litter size had a strong effect on intrinsic growth rates of wolves. Increased frequency of reproductive failure had a negative effect on population growth rates and viability. Finally, reductions in survival rates of pups had a negative effect on population growth rates of wolves. Pup production and recruitment affects wolf population growth and viability in two ways. At the end of the biological year, wolf pups typically represent a large fraction of the total wolf population (Fuller et al. 2003). Consequently, any reductions in pup recruitment will slow population growth rates of wolves in the short-term. In the long-term, reduced pup recruitment will affect the number of potential dispersing wolves in the population. Yearling wolves (i.e., recently recruited pups) are most likely to disperse and establish new territories (Gese and Mech 1991, Boyd and Pletscher 1999). Reduced pup recruitment will limit the number of potential dispersers in subsequent years, which should slow the rate of population growth because fewer dispersers will be available to establish territories and contribute to population level reproduction.

In our baseline model, we used a density-threshold value of 1,500 wolves. This value represented the biological phenomenon where population growth of wolves would be limited by availability of vulnerable prey (Fuller 1989, Mech et al. 1998, Fuller et al. 2003) or intraspecific mechanisms (Cariappa et al. 2011); however the ability of wolves to self-regulate through intrinsic mechanisms is thought to be limited (Keith 1983, McRoberts and Mech 2014). Varying the density-threshold value in our model had little effect on risk of conservation-failure at values \( \geq 250 \) wolves. Consequently, we contend our choice of a density-threshold value had minimal effects on our results.

The Oregon Wolf Plan (ODFW 2010) provides guidelines as to when lethal control of wolves can occur. Our results indicated increased levels of anthropogenic mortality negatively affect wolf population growth and viability. However, whether anthropogenic mortality was implemented at an individual or pack-level had little effect on our results. Caution should be used when implementing lethal control to address management concerns. For example, breeder loss can have a significant, negative effect on wolf population dynamics (Brainerd et al. 2008, Borg et al. 2015). Consequently, decisions regarding lethal removal of breeding wolves should be carefully considered.

Our analysis of wolf-population viability did not explicitly incorporate genetic effects. Genetic viability is a critical concern for any threatened or endangered population (Frankham et
especially for extremely small, isolated populations (Frankham 1996). Inbreeding is a potentially serious threat to the long-term viability for small, isolated populations of wolves (Liberg 2005, Fredrickson et al. 2007) but can be minimized through connectivity to adjacent populations. As few as 1-2 immigrants per generation (~5 years) can be sufficient to minimize effects of inbreeding on wolf populations (Vila et al. 2003, Liberg 2005). High levels of genetic diversity in Oregon’s wolf population are likely to be maintained through connectivity to the larger northern Rocky Mountain wolf population. Wolves are capable of long-distance dispersal (Fritts 1983, Boyd and Pletscher 1999, Wabakken et al. 2007) which should allow a sufficient number of immigrants to arrive in Oregon so long as sufficient connectivity is maintained between populations in adjacent states (Hebblewhite et al. 2010).

While our model did not account for genetic effects, we acknowledge the importance of genetics for isolated populations of mammals and recognize that genetic effects could become important if the Oregon wolf population becomes isolated from the remainder of the northern Rocky Mountain wolf population.

The IBM we used to assess wolf population viability in Oregon should provide a realistic biological representation of wolf population dynamics. However, our IBM does not have a spatial component and does not rely on habitat or other landscape features. Spatially-explicit models could provide a more biologically realistic representation of wolf population dynamics; however, spatially-explicit models require substantial amounts of data that is currently not available in Oregon to effectively parameterize the model. Habitat suitability maps have been developed for Oregon (e.g., Larsen and Ripple 2006), but these maps have not been validated and use of these maps would introduce another unknown source of error in population models. Furthermore, the effects of habitat on survival, reproduction, and dispersal of wolves in Oregon are unknown and it would be impossible to accurately model these effects without unwarranted speculation. For these reasons, we contend our non-spatial analysis of wolf population dynamics is currently the most appropriate approach to model wolf population dynamics and viability because it does not rely on unfounded assumptions that could lead to inappropriate conclusions.

We used our existing IBM to assess viability of wolves in the eastern Wolf Management Zone (WMZ) of Oregon (see ODFW 2010 for description of eastern WMZ). In this analysis, we restricted our starting population size to those wolves known to occur in the eastern WMZ as of April 1, 2015 (N = 76) and set the density threshold to 600 wolves compared to 1,500 wolves used in the statewide analysis. We selected the density-threshold for eastern WMZ using the equations following: Fuller et al. (2003) provided the following equation to estimate expected wolf densities:

\[
\text{Wolves/1,000 km}^2 = 3.5 + 3.27 \times U
\]

where U is the ungulate biomass index (km²). Using an estimated elk (*Cervus elaphus*) population of 66,000 elk distributed across 53,320 km² of summer range habitat in the eastern WMZ (ODFW, unpublished data) and assigning each elk a biomass value of 3, results in a value of U of 3.71 (66,000 × 3/53,320). Based on this value maximum wolf densities were estimated to be 15.64 wolves/1,000 km² of summer range elk habitat in the eastern WMZ. This would result in a total population of 834 wolves within 53,320 km² of elk summer range habitat in the eastern WMZ. Carbone and Gittleman (2002) provided the following equation to estimate wolf densities based on available primary prey biomass:

\[
\text{Number of wolves} = 0.62 \times \text{primary prey biomass}
\]

where primary prey biomass is scaled per 10,000 kg. Currently, the elk population in the eastern WMZ is approximately 66,000 with each elk weighing on average 217 kg (ODFW, unpublished data). This results in approximately 1,432.2 × 10,000 kg of primary prey biomass available to wolves across the eastern WMZ and a maximum population estimate of approximately 888 wolves. To be conservative, we used a density-threshold of 600 wolves in the eastern WMZ.

Remaining methods and parameter inputs for this analysis were identical to those used in the statewide assessment of wolf population viability (Table 1). As with the statewide analysis, we used two metrics to assess population viability: 1) conservation-failure, defined as the population dropping below 4 breeding pairs and 2) biological-extinction, defined as the population having fewer than 5 individuals.

Using our baseline model, simulated wolf populations increased an average of 6% (i.e., \( \lambda = 1.06 \pm 0.17 \) SD) per year. Over the next 50 years, there was a 0.06 (95% CI = 0.01 – 0.11) probability of the population dropping below the conservation-failure threshold (Fig. S1). Half of the conservation-failures occurred within the first 10 years and by year 20 no additional populations passed the threshold. Of the six simulated populations that fell below the conservation-failure threshold, all eventually surpassed 4 breeding pairs in the future with these populations having 22, 37, 61, 67, 72, and 88 breeding pairs by year 50, respectively. No simulated populations dropped below the biological-extinction threshold over the next 50 years. Risk of conservation-failure in the eastern WMZ was slightly higher, but not significantly different, than risk at a statewide level (0.06 vs. 0.05; Fig. S2). Our simulation results suggested risk of conservation-failure declined with increasing starting population size (Fig. 6), so it was not surprising that the slightly smaller starting population in the eastern WMZ (N = 76) had a slightly higher risk of conservation-failure compared to the statewide population (N = 85).
Figure S1. Estimates of cumulative probability of simulated wolf populations reaching the conservation-failure (< 4 breeding pairs) or biological-extinction (< 5 wolves) thresholds over the next 50 years in the eastern Wolf Management Zone of Oregon. Estimates were generated using our baseline model parameterization with 100 realizations of population growth over 50 years. Cumulative probabilities represent the cumulative proportion of simulations that crossed the threshold of interest.

Figure S2. Estimates of cumulative probability of simulated wolf populations reaching the conservation-failure (< 4 breeding pairs) over the next 50 years across the entire state or in the eastern Wolf Management Zone of Oregon. Estimates were generated using our baseline model parameterization with 100 realizations of population growth over 50 years. Cumulative probabilities represent the cumulative proportion of simulations that crossed the threshold of interest.
LITERATURE CITED


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2 All references cited in this document either reference 1) statistical software, 2) ODFW management plans, 3) peer-reviewed book chapters, or 4) peer-reviewed scientific publications.


