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Gude, Justin A.; Mitchell, Michael S.; Russell, Robin E.; Sime, Carolyn A.; Mech, L. David; and Ream, Robert R., "Wolf Population Dynamics in the U.S. Northern Rocky Mountains Are Affected by Recruitment and Human-Caused Mortality" (2012). *USGS Northern Prairie Wildlife Research Center*. 277.

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Population Ecology

Wolf Population Dynamics in the U.S. Northern Rocky Mountains Are Affected by Recruitment and Human-Caused Mortality

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ABSTRACT Reliable analyses can help wildlife managers make good decisions, which are particularly critical for controversial decisions such as wolf (*Canis lupus*) harvest. Creel and Rotella (2010) recently predicted substantial population declines in Montana wolf populations due to harvest, in contrast to predictions made by Montana Fish, Wildlife and Parks (MFWP). We replicated their analyses considering only those years in which field monitoring was consistent, and we considered the effect of annual variation in recruitment on wolf population growth. Rather than assuming constant rates, we used model selection methods to evaluate and incorporate models of factors driving recruitment and human-caused mortality rates in wolf populations in the Northern Rocky Mountains. Using data from 27 area-years of intensive wolf monitoring, we show that variation in both recruitment and human-caused mortality affect annual wolf population growth rates and that human-caused mortality rates have increased with the sizes of wolf populations. We document that recruitment rates have decreased over time, and we speculate that rates have decreased with increasing population sizes and/or that the ability of current field resources to document recruitment rates has recently become less successful as the number of wolves in the region has increased. Estimates of positive wolf population growth in Montana from our top models are consistent with field observations and estimates previously made by MFWP for 2008–2010, whereas the predictions for declining wolf populations of Creel and Rotella (2010) are not. Familiarity with limitations of raw data, obtained first-hand or through consultation with scientists who collected the data, helps generate more reliable inferences and conclusions in analyses of publicly available datasets. Additionally, development of efficient monitoring methods for wolves is a pressing need, so that analyses such as ours will be possible in future years when fewer resources will be available for monitoring. © 2011 The Wildlife Society.

KEY WORDS *Canis lupus*, harvest, human-caused mortality, Montana, Northern Rocky Mountains, population dynamics, recruitment, wolf.

Managing controversial species, including gray wolves (*Canis lupus*), presents unique challenges for wildlife professionals. Responsible conservation of these species must consider a variety of social, political, biological, and economic factors

(Mech 1995, Treves and Karanth 2003). The recovery and management of wolves in the U.S. Northern Rocky Mountains (NRM; Bangs et al. 1998) has resulted in a population that has exceeded minimum recovery goals (≥ 300 wolves and ≥ 30 breeding pairs; U.S. Fish and Wildlife Service [USFWS] et al. 2003) since 2002 in each of 3 federal recovery areas: the Northwest Montana Recovery Area (NWMT), the Central Idaho Experimental Population Area (CIEPA), and the Greater Yellowstone Experimental Population Area (GYEPA). The unadjusted minimum population count for the entire NRM recovery area in late 2010 was 1,614 wolves, compared to 101 wolves in 1995 following wolf reintroductions into the CIEPA and GYEPA.

Received: 22 November 2010; Accepted: 4 April 2011;
Published: 3 August 2011

Additional Supporting Information may be found in the online version of this article.

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Removal of wolves in the NRM (except for Wyoming) from the federal endangered species list in 2009 (USFWS 2009) transferred management authority from USFWS back to Montana and Idaho. Extant wolf populations in most of the world have been managed by human harvesting and/or lethal depredation control (Fritts et al. 2003). Similarly, Montana, Idaho, and Wyoming have developed wolf management plans that include some level of public harvest as well as depredation management (Mech 2010). Wolf populations only recently recovered in these states, and federal law requires that the populations be monitored closely for 5 years post-delisting to ensure they do not fall below required recovery levels. Thus, accurate assessments of population status and population response to harvesting programs are critical. Along with adequate fieldwork to obtain data, population modeling is a valuable part of this process. Accurate data and sufficient biological reality are vital for ensuring model inferences are reasonable.

One of the critical variables in the population dynamics and responses to harvest of canids is recruitment (e.g., Knowlton et al. 1999). Recruitment into wolf populations from both dispersal (Hayes and Harestad 2000, Adams et al. 2008) and reproduction (Fuller 1989) is known to have large effects on wolf population dynamics. Recruitment into wolf populations is also highly variable (Fuller et al. 2003). Wolf pack litter sizes consistently average 6 pups (Mech 1970), but pup survival and recruitment can be highly variable (e.g., Mitchell et al. 2008, Almborg et al. 2009). New packs are formed by maturing members of existing packs which disperse from natal packs, pair with opposite-sex dispersers, and produce pups (Rothman and Mech 1979). Both processes have been important to the recruitment of wolves into the NRM population, and have played roles in NRM wolf population dynamics (e.g., pup survival: Almborg et al. 2009; dispersal: Boyd and Pletscher 1999).

Recently, Creel and Rotella (2010) analyzed the effects of human-caused mortality on wolf populations by correlating wolf population growth with human-caused mortality rates. Creel and Rotella (2010) do not explicitly account for the contribution of variable recruitment to the relationship between human-caused mortality and wolf population growth, which is potentially problematic given the wide variability in successful reproduction and formation of new packs in the data they analyzed. Based on their analyses, Creel and Rotella (2010) concluded that sustainable human-caused mortality for NRM wolves was 0.224, which is substantially lower than conventional wisdom incorporated into wolf management plans (e.g., Montana Fish, Wildlife and Parks [MFWP] 2003) and previous scientific results (Fuller et al. 2003, Adams et al. 2008, Murray et al. 2010). They also predicted that wolf harvest in Montana would result in larger declines than previously predicted by Montana Fish, Wildlife and Parks (MFWP 2010).

We replicated the analyses of Creel and Rotella (2010) for the NRM wolf population, with 2 important changes. First, using the same modeling and evaluation methods as Creel and Rotella (2010), we explicitly evaluated the contribution of recruitment by comparing models of population growth

that include variation in recruitment to a model where population growth is affected only by human-caused mortality. Second, Creel and Rotella (2010) used all annual data from NRM wolves from 1999 to 2008, despite documented differences in monitoring effort over this period (USFWS et al. 2005:2, Mitchell et al. 2008:886, USFWS 2009:15136), and they did not use 2009 data (i.e., observations following the 2009 public wolf harvest). We use a revised data set for modeling; we included 2009 NRM data and excluded data for years with clearly reduced field monitoring. Including data from years with markedly lower field effort could result in misleading inferences because the lower index counts would be mistreated as changes in population sizes. Last, we also evaluated models of factors affecting both recruitment and mortality rates for wolves in the NRM. Using the results of these modeling exercises, we then estimated the impacts of human-caused mortality, including public wolf harvest seasons, on wolf populations in Montana. We evaluated the accuracy of our estimates compared to predictions of Creel and Rotella (2010) and field monitoring data, including 2010 data that were not used in modeling exercises.

STUDY AREA

The NWMT, CIEPA, and GYEPA federal wolf recovery area boundaries overlap the states of Montana, Idaho, and Wyoming (Mitchell et al. 2008). Lands in NWMT are primarily public or corporate-owned and managed for timber production. Wolves in NWMT were managed as an endangered population prior to federal delisting. Much of the CIEPA is federally designated wilderness; surrounding forested lands are a mix of public and private lands. Wolves in the CIEPA were managed as a nonessential, experimental population prior to federal delisting. Land ownership in the GYEPA is a mixture of public and private lands, and local land management emphasizes livestock production with the exception of Yellowstone National Park. Wolves were managed as a nonessential, experimental population in the GYEPA prior to federal delisting.

METHODS

State, federal, and tribal personnel monitored the status of wolf populations in the NRM using intensive field efforts. These agencies documented the minimum number of wolves, packs, and breeding pairs (USFWS 1994). Monitoring staff used field surveillance and public sightings to determine where wolf packs may exist. Intensive trapping in those areas during spring, summer, and fall, coupled with some aerial darting of wolves in winter, allowed staff to radio-collar wolves. Individual radio-collared wolves from each pack then facilitated repeated aerial and ground observations of wolves traveling with each radio-collared wolf (Mech 1973), to determine the size of each pack and whether it met the definition of a breeding pair. Efforts to monitor marked wolves were increased in December of each year to determine the size and reproductive success of each wolf pack. Approximately 30% of the known NRM wolf packs were monitored annually, and observations from monitoring these wolves were supplemented by agency track surveys and

public observations of wolf pack size for the remaining packs (USFWS 2009). Each December 31, the minimum population count in each recovery area, N_{MIN} , was calculated as the sum of the number of wolves observed in known packs. Documented wolves unaffiliated with packs were also added to N_{MIN} . The NRM wolf monitoring data are therefore not censuses and do not include adjustments for wolves that were missed in monitoring efforts; they are indices to population size (Johnson 2008).

We obtained data on N_{MIN} , mortality, and recruitment in each of the 3 NRM wolf recovery areas during 1999–2009 from annual reports made available online (e.g., USFWS et al. 2010). We adjusted N_{MIN} for each year when monitoring in subsequent years identified wolves that were present in the prior year (based on presence of yearling wolves) but had not been detected. When this situation occurred, it was documented in annual reports from subsequent years. To model wolf population growth (wolf λ), the imperfect detection of wolves could be compensated for by using adjustments to raw counts or minimizing variability in the difference between raw counts and the true population size by conducting surveys using the same methods on every occasion (Caughley 1974, Caugley et al. 1976, Johnson 2008). The latter method assumes N_{MIN} is an index to the actual population size, with a bias that is relatively constant from year to year, allowing accurate estimates of wolf λ . Adjustments to NRM wolf monitoring data to account for imperfect detection currently do not exist. Left with the latter approach to analyzing index data, we did not use N_{MIN} from the NWMT recovery area in 2003 and 2004 because permanent staff was not assigned to the monitoring program in NWMT in these years, and the wolf monitoring effort was reduced (e.g., USFWS et al. 2005:2). Consistent with Creel and Rotella (2010), for each sequential pairing of years in each recovery area except for 2002–2003, 2003–2004, and 2004–2005 in NWMT, we estimated an annual wolf λ by dividing N_{MIN} in year $t + 1$ by N_{MIN} in year t .

We tabulated annual summary figures for each recovery area on total known human-caused mortality, including illegal, accidental, livestock-depredation removals, and licensed public harvest for 2009, and other forms of human-caused mortality. This tally did not include unreported, illegal human-caused mortality, which was generally unknown. In some areas, unreported illegal mortality has accounted for a substantial portion of total wolf mortality (Person et al. 2008). Therefore, our human-caused mortality calculation represents an index to the actual human-caused mortality and is not a census of all human-caused mortality. Consistent with Creel and Rotella (2010) and due to the schedule of monitoring data summaries, for each year t , we calculated an annual human-caused mortality rate as that in year $t + 1$ divided by N_{MIN} in year t . Whereas most wolf mortality occurs following the wolf birth pulse and dispersal seasons, N_{MIN} is determined in December prior to and following these events annually. We did not have field data on N_{MIN} following the annual increase phase of NRM wolf populations, so we chose to

work with N_{MIN} from the preceding December while accounting for human-caused mortality that would occur prior to the next N_{MIN} publication. These calculations therefore express, as a proportion of N_{MIN} in year t , the number of wolves known to be removed by humans in year $t + 1$.

We also obtained recruitment data from the annual wolf pack summary tables for each recovery area. For each year t , we calculated recruitment for each recovery area as the total number of wolves in newly discovered packs summed with the total number of young-of-the-year surviving to December 31 in existing wolf packs. Note that recruitment in this sense arises from both birth and the formation of new packs by dispersers. We explicitly included the contribution of dispersal by constructing our recruitment variable in this manner. Dispersers that contributed to the formation of new packs could either have dispersed into the population or within the population, and we had no way to make this distinction. Our recruitment calculation represented an index to the contribution of dispersal to recruitment that is likely inflated by including some wolves dispersing within the population. Further, field efforts undoubtedly missed some new packs and young-of-the-year in known packs, especially as the population grew in the latter years. This likely deflated our index of recruitment from the actual recruitment rate. Lastly, we tallied recruitment on December 31, after mortality had affected the population during the preceding year, including any wolves that were born or had dispersed into the population. Therefore, our recruitment calculation indexed net recruitment, after annual mortality, not births and pre-mortality immigration. Despite these limitations, we believe that our recruitment calculation reliably indexed the recruitment into each population. The index also relied on publicly available NRM information that is collected in most other wolf studies that follow similar monitoring methods, so it is transportable to other studies. Using the recruitment index, we estimated an annual recruitment rate as the recruitment in year $t + 1$ divided by N_{MIN} in year t . This calculation represented the number of new wolves documented in year $t + 1$ as a proportion of N_{MIN} in year t .

We fit 3 simple, a priori generalized linear models using wolf λ as the response variable to develop predictive models of wolf λ . These models represented the hypotheses that human-caused mortality alone affects wolf λ , that recruitment alone affects wolf λ , and that both human-caused mortality and recruitment affect wolf λ . We fit all models to pooled data across the 3 NRM wolf recovery areas. We fit models using a log link, assumed normally distributed errors, and compared relative support for the models using analysis of AIC_c (Akaike's Information Criterion adjusted for small sample size) and AIC_c weights (ω ; Burnham and Anderson 2002).

We estimated the sustainable human-caused mortality rate for models containing human-caused mortality as a covariate. We set wolf $\lambda \geq 1$ and solved for the human-caused mortality rate using the maximum-likelihood estimates of model covariates. We used the delta method to estimate uncertainty in our model-based predictions of the sustainable

mortality rate. We then compared our model-based predictions for the sustainable human-caused mortality rate to observations in the 1999–2009 NRM dataset, to evaluate the ability of our wolf λ models to correctly predict increasing and decreasing wolf populations. For reference, we also compared the Creel and Rotella (2010) model-averaged prediction of sustainable mortality, 0.224, to 1999–2009 NRM observations.

We then compared wolf λ model predictions to field observations in 2008–2010 to evaluate the absolute accuracy of our model-based estimates for wolf λ . We used each of these models to estimate wolf λ in Montana for 2008–2009 (Montana data were included with all other NRM data to generate our models), and to predict wolf λ for 2010, using data from the previous year. Wolf monitoring data for 2010 were not used in our model building exercises, but they were used to validate model predictions. We focused on predictions for Montana for these years because the MFWP implemented a simulation model to predict wolf λ for Montana beginning in 2008 (MFWP 2010), and Creel and Rotella (2010) subsequently compared their predictions to those from the MFWP simulation model for 2009 and 2010 in Montana. We also compared our wolf λ estimates for 2008–2010 to MFWP simulation model predictions (MFWP 2010) and to predictions by Creel and Rotella (2010). We used Figure 2 from Creel and Rotella (2010) to predict wolf λ for Montana based on the impact of human-caused mortality, consistent with the method recommended in Creel and Rotella (2010).

We estimated the human-caused mortality rate and the recruitment rate based on data from previous years in order to estimate wolf λ for 2008 and 2009, and to predict λ for 2010. We fit competing models of factors affecting the human-caused mortality rate and the recruitment rate, using a log link, and assuming normally distributed errors. We evaluated 4 human-caused mortality rate models representing 4 a priori hypotheses: 1) human-caused mortality is density dependent (i.e., an increasing function of N_{MIN} of the previous year), 2) human-caused mortality is a function of recovery area, 3) human-caused mortality is a function of recruitment, and 4) human-caused mortality is a function of the previous year's mortality rate. We evaluated 4 single-variable

recruitment rate models, representing 4 a priori hypotheses: 1) recruitment is density-dependent (i.e., a decreasing function of N_{MIN} of the previous year), 2) recruitment is a function of recovery area, 3) recruitment compensates for human-caused mortality rates (i.e., is an increasing function of human-caused mortality rates), and 4) recruitment is a function of the previous year's recruitment rates.

We evaluated both model sets (human-caused mortality and recruitment rates) using AIC_c and ω . We then used the top models identified by the respective AIC_c analyses to estimate human-caused mortality rates and recruitment rates. We used field-monitoring data collected from packs residing within the portion of each wolf recovery area overlapping Montana to make these estimates specific to Montana. To account for licensed public harvest in total human-caused mortality rates, we added the quotas for wolf harvest set by the MFWP Commission to the model-predicted value for the number of wolves that would be killed by humans from other causes (i.e., depredation removals, vehicles, known illegal) within the Montana portion of each federal recovery area. We therefore assumed that these quotas would be filled, and that this form of mortality would be fully additive to other forms of human-caused mortality. This is likely a conservative assumption that may match present circumstances more closely than future circumstances, as public harvest of NRM wolves becomes more common (Mech 2010). Additionally, wolf mortality due to public harvest may compensate for wolf mortality due to livestock depredation conflicts, but the degree of compensation of these 2 human-caused mortality sources is unknown. We conducted all analyses using R (R Version 2.9.0, www.R-project.org, accessed 16 Oct 2010).

RESULTS

We developed 27 calculations of NRM wolf λ , human-caused mortality rates, and recruitment rates including 7 from NWMT, 10 from GYEPA, and 10 from CIEPA. Vital rates varied substantially in each recovery area in our dataset (Table 1). During 1999–2009, N_{MIN} increased from 63 to 319 (506%) in NWMT, from 118 to 455 (386%) in the GYEPA, and from 156 to 913 (585%) in CIEPA.

Table 1. Variation in wolf vital rates in the U.S. northern Rocky Mountains based on field monitoring data, 1999–2009.

Parameter	Recovery area ^a	Minimum	Maximum	CV ^b
λ^c	NWMT	1.02	1.35	0.10
λ	CIEPA	1.00	1.50	0.09
λ	GYEPA	0.97	1.33	0.14
Mortality	NWMT	0.06	0.45	0.53
Mortality	CIEPA	0.05	0.33	0.60
Mortality	GYEPA	0.08	0.27	0.37
Recruitment	NWMT	0.56	0.81	0.14
Recruitment	CIEPA	0.24	0.55	0.29
Recruitment	GYEPA	0.42	0.70	0.17

^a NWMT, Northwest Montana Wolf Recovery Area; GYEPA, Greater Yellowstone Experimental Population Area; CIEPA, Central Idaho Experimental Population Area.

^b Coefficient of variation.

^c Annual population growth rate.

Table 2. Model selection results for models representing the impact of human-caused mortality, recruitment (successful production of pups within packs and creation of new packs), and both on the annual wolf population growth rate, wolf λ , in the U.S. northern Rocky Mountains, 1999–2009.

Model	K^a	Adj. R^2 ^b	ΔAIC_c ^c	ω^d
Human-caused mortality and recruitment affect wolf λ	4	0.49	0.0	0.935
Recruitment affects wolf λ	3	0.33	5.5	0.060
Human-caused mortality affects wolf λ	3	0.20	10.3	0.005

^a Number of estimated model parameters.

^b R^2 adjusted for degrees of freedom.

^c Difference in Akaike's Information Criterion (adjusted for small sample size) from top model.

^d AIC_c model weight.

We found that NRM wolf λ is affected by both human-caused mortality and recruitment (Table 2). This model received approximately 16 times more support than the model indicating wolf λ is affected by recruitment alone, and 187 times more support than the model indicating wolf λ is affected by human-caused mortality alone. On the log scale, the top model contained an estimated intercept that did not differ from 0 (0.04, 95% CI: -0.10 to 0.18), an estimated negative slope for the effect of human-caused mortality (-0.49 , 95% CI: -0.83 to -0.14), and an estimated positive slope for the effect of recruitment (0.41 , 95% CI: 0.19 to 0.63 ; see Table S1, available online at www.onlinelibrary.wiley.com). The effect sizes for human-caused mortality and recruitment were similar, but inclusion of both covariates increased the adjusted R^2 value by 50% (i.e., $0.49/0.33$) over the model with recruitment alone and by 250% (i.e., $0.49/0.20$) over the model with human-caused mortality alone (Table 2).

Our top model of wolf λ , including effects of both human-caused mortality and recruitment, predicted that sustainable mortality (wolf $\lambda \geq 1$) is an increasing function of recruitment (Fig. 1). Over the range of recruitment rates observed in the NRM during 1999–2009, this model predicted that the sustainable human-caused mortality rate increased from 0.29 to 0.77. These sustainable mortality predictions correctly identified every wolf population increase in the NRM during 1999–2009, and correctly identified 1 of 3 observed

population declines (Fig. 1). Our model depicting only the effects of human-caused mortality on wolf λ predicted that sustainable mortality is 0.484 (SE = 0.12) regardless of recruitment. This model correctly identified every wolf population increase in the NRM during 1999–2009, and incorrectly identified all 3 observed population declines during this period (Fig. 1). The Creel and Rotella (2010) model-averaged prediction of sustainable mortality correctly identified 18 of 24 observed population increases in the NRM during 1999–2009 as well as 2 of 3 observed population declines (Fig. 1).

Our top NRM human-caused mortality rate model included a positive relationship of human-caused mortality with N_{MIN} in each recovery area, suggesting density dependence in human-caused mortality rates (see Table S1, available online at www.onlinelibrary.wiley.com). The top human-caused mortality model received more than 200 times more weight than the next most supported model (Table 3), and indicated that human-caused mortality rates were lowest in the GYEPA, higher in CIEPA, and highest in NWMT. The most supported human-caused mortality model also indicated that human-caused mortality increased in CIEPA, increased more rapidly in NWMT, and increased most rapidly in the GYEPA, with increasing N_{MIN} (Fig. 2).

We found considerable model-selection uncertainty for NRM recruitment rate models (Table 4). The top 2 models garnered all of the AIC_c weight. The top model

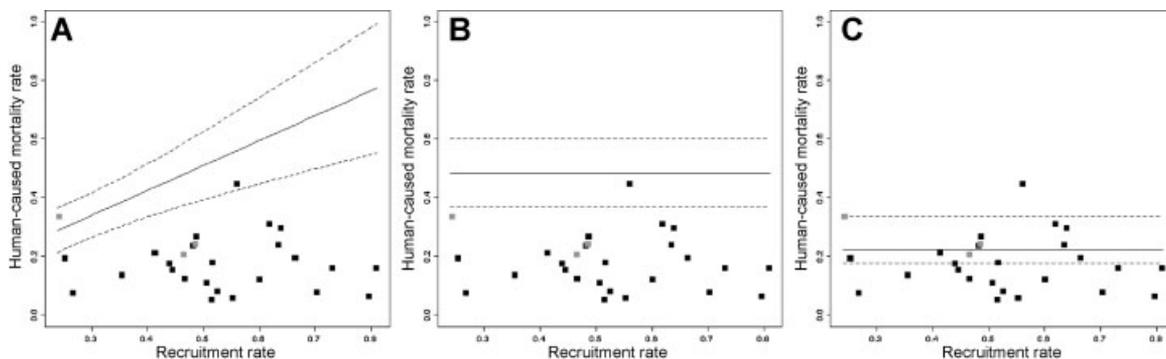


Figure 1. Predicted sustainable mortality ($\lambda \geq 1$) for wolf populations in the U.S. Northern Rocky Mountains from (A) our top model of wolf λ including effects of both human-caused mortality and recruitment, (B) our model depicting only the effects of human-caused mortality on wolf λ , and (C) the model-averaged prediction of sustainable mortality equal to 0.224 from Creel and Rotella (2010), which only considers the effects of human-caused mortality. Dashed lines in (A) and (B) represent one standard error, and dashed lines in (C) represent the model-averaged 95% CI reported in Creel and Rotella (2010). Points repeated on each panel are observed combinations of recruitment and human-caused mortality in the NRM 1999–2009. Black points are observed population increases and gray points represent the 3 observed wolf N_{MIN} (minimum wolf count) declines in our dataset, of 0.1%, 0.8%, and 2.9%. Predictions are accurate if the black points fall below the line representing the predicted sustainable mortality rate and gray points fall above the line representing the predicted sustainable mortality rate.

Table 3. Model selection results for models representing factors affecting human-caused mortality rates for wolves in the U.S. northern Rocky Mountains, 1999–2009.

Model	K^a	Adj. R^2 ^b	ΔAIC_c ^c	ω^d
Human-caused mortality is density-dependent, such that it increases with increasing size of the wolf population in each recovery area	7	0.51	0.00	0.992
Human-caused mortality differs by recovery area due to different social and livestock situations in each recovery area	4	0.07	11.04	0.004
Habitat available for wolves that does not lead to conflict with humans is full in each recovery area, so human-caused mortality increases with increases in wolf recruitment	3	−0.02	11.90	0.003
Temporal dependency drives human-caused mortality, so human-caused mortality is best predicted by the level of human-caused mortality in the previous year	3	0.19	12.50	0.002

^a Number of estimated model parameters.

^b R^2 adjusted for degrees of freedom.

^c Difference in Akaike’s Information Criterion (adjusted for small sample size) from top model.

^d AIC_c model weight.

was approximately twice as supported as the second model and indicated that recruitment was density dependent within each wolf recovery area. This model expressed that baseline recruitment rates were lower in CIEPA than in NWMT and the GYEPA, and that recruitment decreased with increasing N_{MIN} most rapidly in the GYEPA and least rapidly in NWMT (Fig. 3, see Table S1, available online at www.onlinelibrary.wiley.com). The second-ranked model indicated that recruitment rate was lowest in CIEPA and highest in NWMT, but was constant across observed N_{MIN} within in each area (Fig. 3).

We used estimates from the top NRM human-caused mortality rate model and model-averaged NRM recruitment rate estimates to evaluate effects of human-caused mortality and recruitment on Montana wolf λ in subsequent years. Our estimates for wolf λ in Montana and the MFWP simulation model predictions were similar and predicted wolf $\lambda > 1$, but contrasted with the Creel and Rotella (2010) predictions (Table 5). Estimates from our recruitment alone model and the predictions from MFWP simulation model for wolf λ in Montana for 2008–2010 were highest among the alternatives and higher than the observed wolf λ . The human-caused mortality alone model predicted lower Montana wolf λ than indicated by field monitoring data for 2008 and 2009, yet correctly predicted increasing wolf populations for 2008–2010. All predictions other than the Creel and Rotella

(2010) predictions were for larger wolf population growth than was observed in 2010. In contrast to the observed increasing wolf population in Montana during 2008–2010, Creel and Rotella (2010) predicted declining populations and were 25% lower than the Montana wolf λ observed in 2008, 28% lower than the Montana wolf λ observed in 2009, and 12% lower than the Montana wolf λ observed in 2010.

DISCUSSION

First principles of population ecology dictate that understanding the impact of human-caused mortality on animal populations requires explicit consideration of recruitment (Conroy and Kremenetz 1990, Mills 2007:290). Accordingly, we provide evidence that variation in recruitment (production of pups within established packs and the formation of new packs) into wolf populations must be explicitly considered to accurately evaluate impacts of human-caused mortality on wolf λ . This is consistent with population models that are used to predict the effects of harvest by humans on population growth or size for other species (e.g., mule deer [*Odocoileus hemionus*] and elk [*Cervus elaphus*]: White and Lubow 2002; waterfowl: Williams and Johnson 1995). The need to explicitly consider recruitment is also consistent with other findings indicating dispersal (Hayes and Harestad 2000, Adams et al. 2008) or production of pups (Fuller 1989) explains much of the variation in wolf

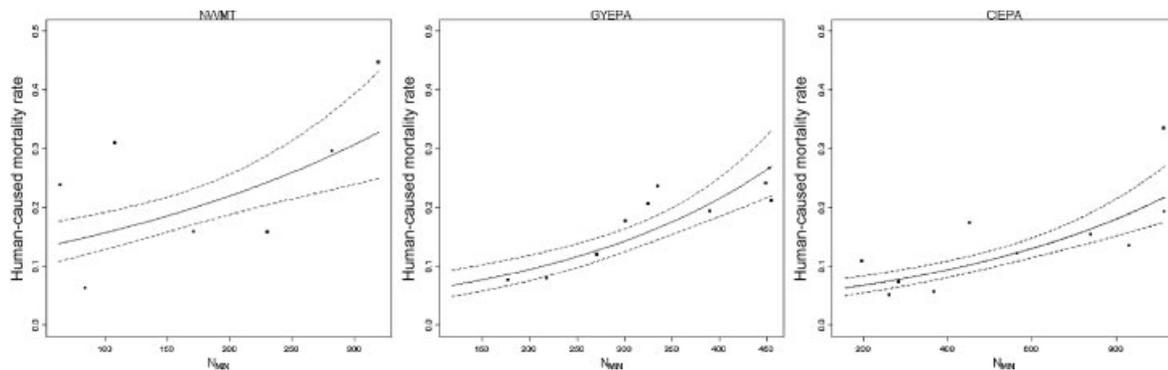


Figure 2. Predicted effects of minimum wolf counts, N_{MIN} , on human-caused mortality rates in each wolf recovery area in the U.S. northern Rocky Mountains, based on the top model of human-caused mortality rates, 1999–2009. Recovery areas included: the Northwest Montana Wolf Recovery Area (NWMT), the Greater Yellowstone Experimental Population Area (GYEPA), and the Central Idaho Experimental Population Area (CIEPA). Points are observations. Dashed lines represent 1 SE.

Table 4. Model selection results for models representing factors affecting recruitment (successful production of pups within packs and creation of new packs) rates for wolves in the U.S. northern Rocky Mountains, 1999–2009.

Model	K^a	Adj. R^2 ^b	ΔAIC_c ^c	ω^d
Recruitment is density dependent, declining with increasing size of the wolf population in each recovery area.	7	0.60	0.00	0.63
Recruitment differs by recovery area due to differing spatial juxtapositions affecting immigration and different limiting factors on successful production of pups.	4	0.47	1.04	0.37
Recruitment is best predicted by the recruitment in the previous year, because wolf populations in each recovery area are rapidly growing.	3	0.35	15.31	0.00
Recruitment increases with human-caused mortality, compensating for the limiting effect of human-caused mortality.	3	-0.03	17.39	0.00

^a Number of estimated model parameters.

^b R^2 adjusted for degrees of freedom.

^c Difference in Akaike's Information Criterion (adjusted for small sample size) from top model.

^d AIC_c model weight.

population dynamics. Variation in recruitment also explains much of the variation in other populations of large carnivores harvested by humans (e.g., cougars [*Puma concolor*]: Cooley et al. 2009 and black bears [*Ursus americanus*]: Mitchell et al. 2009). Whereas the analyses of Creel and Rotella (2010) implicitly included both recruitment and human-caused mortality by calculating wolf λ as N_{MIN} in year $t + 1$ divided by N_{MIN} in year t , they only explicitly considered human-caused mortality as a predictor of wolf λ . Our results show that explicitly treating recruitment as a predictor variable produces more parsimonious and better fitting models (Table 2). Predictions of wolf λ arising from our models including recruitment did not differ markedly from our human-caused mortality alone model in the range of data we considered (Table 5). Inclusion of recruitment in models of wolf λ , however, shifted the paradigm of predictions about the impact of human-caused mortality on wolf λ to include the context of variable recruitment rates. Predictions of sustainable wolf mortality (i.e., the human-caused mortality rate where wolf $\lambda \geq 1$) become a function of recruitment (Fig. 1); therefore, the potential impacts of human-caused mortality on wolf λ in general are dependent on recruitment rates.

The primary reason for the absolute differences in predictions arising from our models and those of Creel and Rotella

(2010; Table 5) is the use of a different dataset. Even though the human-caused mortality alone model (created using the same model construct as Creel and Rotella 2010) did not garner much AIC_c weight in our analyses of wolf λ , this model predicted increasing wolf populations, in contrast to the Creel and Rotella (2010) declining predictions. Further, our prediction of the sustainable human-caused mortality rate arising from our human-caused mortality alone model was substantially higher than that predicted by Creel and Rotella (2010; Fig. 1). The primary reason for these differences was the omission of wolf monitoring data collected in NWMT during 2003–2004 in our analyses. These observations comprise the most dramatic annual changes in N_{MIN} seen in any of the NRM wolf recovery areas since wolf recovery in the region began in the early 1980s and had substantial leverage on the slope of the regression lines estimated by Creel and Rotella (2010). This was a period when permanent monitoring staff in NWMT left the program for other positions. Wolf monitoring in NWMT in 2003–2004 was thus conducted either by seasonal staff or opportunistically by permanent personnel who also had monitoring duties in other geographic areas (e.g., USFWS et al. 2005:2). Monitoring effort during this period was therefore considerably less than in other years and portions of the NRM we considered. The apparent declines in N_{MIN}

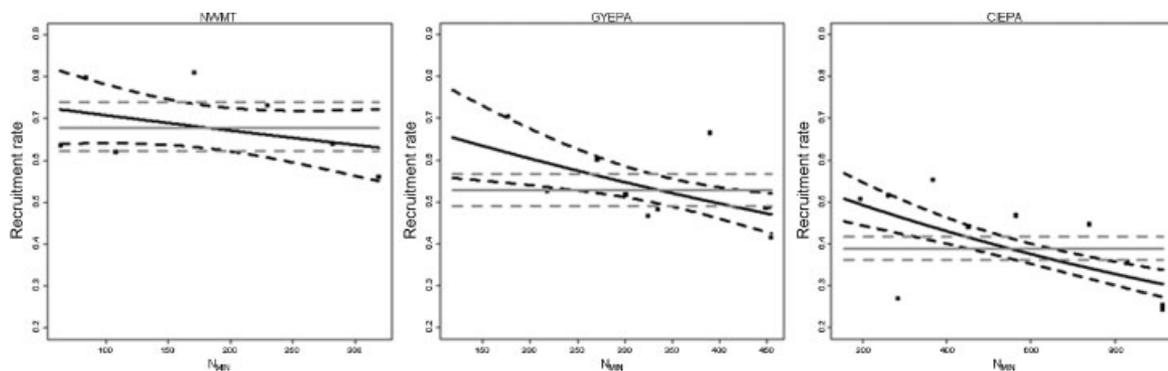


Figure 3. Predicted effects of minimum wolf counts, N_{MIN} , on recruitment (successful production of pups within packs and creation of new packs) rates in each wolf recovery area in the U.S. northern Rocky Mountains, based on the top models recruitment rates, 1999–2009. The top model is displayed in black and indicates declining recruitment with increasing N_{MIN} in each recovery area. The second ranked model is displayed in gray and indicates recruitment differs among recovery areas. Recovery areas included: the Northwest Montana Wolf Recovery Area (NWMT), the Greater Yellowstone Experimental Population Area (GYEPA), and the Central Idaho Experimental Population Area (CIEPA). Dashed lines represent 1 SE. Points are observations.

Table 5. Model predictions of minimum wolf population size and annual wolf population growth (wolf λ) in Montana, USA, based on several competing models. We also show observed values of minimum population size and wolf λ for comparison.

Year	Predicted minimum wolf population size							Predicted wolf λ						Observed values	
	Wolf quota ^a	HC ^b	R ^c	HC + R ^d	Model averaged ^e	Creel and Rotella (2010) ^f	FWP sim. ^g	HC ^b	R ^c	HC + R ^d	Model averaged ^e	Creel and Rotella (2010) ^f	FWP sim. ^g	Min. pop. size	Wolf λ
2008	0	486	504	491	492	371	509	1.15	1.19	1.16	1.17	0.88	1.21	498	1.18
2009	75	516	594	529	533	378	590	1.04	1.20	1.07	1.07	0.76	1.19	524	1.05
2010	0	583	629	594	596	498	666	1.11	1.20	1.13	1.14	0.95	1.27	566	1.08

^a Quota for public harvest established by the Montana Fish, Wildlife and Parks Commission within the boundaries of Montana. The quota setting process was begun during 2008, but the public harvest season was eventually not implemented in 2008 due to a federal court injunction. Public harvest was implemented in Montana in 2009. Public harvest was planned and approved for Montana in 2010, but due to the relisting of wolves in 2010 the season was not implemented.

^b HC model: human-caused mortality alone affects wolf λ .

^c R model: recruitment (successful production of pups within packs and creation of new packs) alone affects wolf λ .

^d HC + R model: human-caused mortality and recruitment affect wolf λ .

^e Model-averaged prediction, based on Akaike's Information Criterion (adjusted for small sample size) weights of the 3 models of wolf λ .

^f Creel and Rotella (2010) predictions approximated from their Figure 2.

^g Predictions previously described by Montana Fish, Wildlife and Parks (MFWP 2010).

in NWMT during these years, and the apparent increase in 2005 (when intensive monitoring resumed), were due to reduced monitoring effort during those 2 years (Mitchell et al. 2008:886, USFWS 2009:15136). Our exclusion of these data from analysis removed a strong but spurious inference of Creel and Rotella (2010) that was at odds with expert knowledge incorporated into wolf management plans (e.g., MFWP 2003) and previous research findings (Fuller et al. 2003, Adams et al. 2008, Murray et al. 2010), and produced estimates consistent with empirical monitoring observations of wolf $\lambda > 1$ for Montana in 2008–2010.

Our modeling also benefited from including monitoring data from 2009 (USFWS et al. 2010). Not only does the addition improve the precision of our inferences, the 2009 monitoring data were collected after the first regulated hunting season for wolves in Montana. Our calculations of wolf λ were thus influenced by the added hunting mortality for that year, coupled with monitoring results that suggested population growth in the GYEPA and NWMT and stability in the CIEPA. These calculations of growth or stability in a year with high human-caused mortality decreased our estimated effect size of human-caused mortality on wolf λ . Further, consistency between our estimates of wolf λ for Montana and monitoring observations for 2008–2010 suggests our models developed using all NRM data (with no public hunting in all but 1 year) were robust to the variation in human-caused mortality associated with a public hunt in Montana. Such validation is a prudent step before using model predictions to inform high profile decisions such as wolf harvest in the NRM immediately following the cessation of Endangered Species Act protections. We do not expect predictions generated by our models for future years will be accurate in every possible scenario. Nonetheless, predictions of our models for the wolf population in Montana in 2010 were close to the observed wolf λ and correctly predicted wolf $\lambda > 1$, despite the fact that we did not use 2010 data to develop our models. Our 2010 prediction may become more accurate if N_{MIN} for 2010 is increased in 2011. This may occur if wolf packs that were undetected in

2010 field monitoring are found with yearling wolves during 2011 field monitoring efforts (as was the case for some years and areas considered in our dataset). These (or similar) validation steps add credence to the usefulness of any predictive models for informing management decisions. Their absence calls into question the reliability of any model for prediction.

A comparison of our findings regarding the impact of human-caused mortality and recruitment on wolf λ to those of Creel and Rotella (2010) therefore raises 2 important points. First, models of NRM wolf λ that include recruitment as a covariate are more parsimonious and better fitting than those that do not (Table 2). Models of wolf λ including recruitment as a predictor variable also highlight that the impacts of human-caused mortality are dependent on recruitment rates, which are widely variable for wolves and other canids. Second, creating population models from population indices requires careful treatment and examination of the index data used to construct and validate the models. Familiarity with data sets (e.g., caveats or qualifications to raw numbers) is important to improving the quality and reliability of inferences. Effective consultation and collaboration with agency biologists who compile and publish public data is a critical step toward producing the accurate and reliable science essential for making good decisions about wildlife conservation, and for facilitating public understanding of those decisions. Insufficient attention to these principles can lead to misleading inferences and misguided policy recommendations.

Our findings that human-caused mortality and recruitment rates may be density-dependent in the NRM wolf populations may indicate that wolves in the NRM could be approaching capacity based on the amount of available suitable habitat (Oakleaf et al. 2006). This could lead to increases in human-caused mortality rates (Bangs et al. 2010) and intra-specific strife (Smith et al. 2010), and limit recruitment via mechanisms such as starvation and disease (Almberg et al. 2009). If the NRM wolf populations are stabilizing near biological carrying capacities or human social tolerance

levels, future wolf λ in Idaho, Montana, and Wyoming may decline from rates we observed.

Alternatively, apparent density dependence in NRM recruitment rates could be due to saturation of monitoring capabilities in the most recent years as the NRM wolf population has continued to grow. Documenting recruitment requires monitoring both new packs and surviving young-of-the-year, both of which are difficult, expensive, and time-consuming to observe. Current monitoring efforts undoubtedly do not detect all recruitment or all human-caused mortality in NRM populations. The apparent decline in recruitment as wolf population sizes have increased in the NRM could be related to imperfect detection under existing monitoring methods and logistical constraints, especially in the most recent years in our dataset.

The best models in each of our analyses only explain approximately 50–60% of the observed variation in wolf λ , human-caused mortality rates, and recruitment rates, and our models were unable to correctly identify every population increase and decrease (Fig. 1). We expect the unexplained variation is at least partially due to sampling error resulting from imperfect detection of wolves in monitoring efforts. Random, stochastic variation in vital rates, variation in other vital rates (such as natural mortality or undocumented illegal mortality), and unconsidered structural variation in the vital rates we modeled also likely contributed to the unexplained variation. For example, conflict with livestock may limit wolf populations in some areas (Garrott et al. 2005), as may variation in prey density or the ratio of wolves to their ungulate prey (Eberhardt et al. 2003). We did not explicitly consider these variables in our simple analyses, but future work should include models incorporating these variables. Consideration should also be given to the variability in monitoring methods that produce estimates of prey density (Rabe et al. 2002, MFWP 2005), variation in available and selected prey species (Garrott et al. 2007), and to the scale at which wolf and prey data are assembled.

Due to unexplained variation, predictions from any of the models we considered will have limited accuracy at predicting wolf λ in any given year, and we acknowledge that considerable uncertainty remains regarding the impacts of human-caused mortality on wolf λ in the NRM. The contrasting results of Creel and Rotella (2010) and those we report can be viewed as alternative models for predicting wolf λ that embody some of this uncertainty. Using alternative models to predict parameters that will then be monitored is a tenet of formal adaptive management (Williams et al. 2007). Wolf management in Montana has been purposefully developed under the adaptive management paradigm (MFWP 2003, Nichols and Williams 2006). Monitoring over time will reduce uncertainty about wolf population dynamics and the effects of management actions on those dynamics via comparison of model predictions with field data. This will lead to more accurate predictive models, but more importantly to decisions that lead to management objectives with increased frequency. This process will be instrumental in quantifying the role of harvest in wolf population dynamics, and closing the reported knowledge gaps (Treves 2009).

MANAGEMENT IMPLICATIONS

When using models to inform decisions about wolf harvest, to make forecasts of wolf populations, or to draw inferences about patterns existing in wolf monitoring data, managers and researchers should explicitly consider both recruitment and human-caused mortality. Further, development of population models from index data should be done with careful consideration of the limitations of the index data, and shortcomings in those data should be acknowledged. Lastly, model predictions should be validated against monitoring data before they are used to make management policy recommendations. Our results, as well as those previously presented by MFWP (2010) meet these criteria, and we believe managers can take them into consideration when making decisions about public harvest policies for wolves.

High-quality wolf monitoring data will continue to be needed to develop predictive models that inform management decisions and to evaluate the usefulness of those predictive models for helping to achieve wolf management objectives. Monitoring of wolves in the NRM has been funded by the USFWS under the auspices of the Endangered Species Act, but that funding is uncertain once wolves are delisted. Even at current levels of funding, the intensive monitoring program has been unable to keep perfect pace with the growing NRM wolf population and has been unsuccessful at detecting all wolves and breeding pairs in the most recent years. Development of reliable wolf monitoring methods that are less expensive and field-intensive, and that account for imperfect detectability of wolves, is a pressing research need. Without an effort such as this, documentation of whether NRM wolf populations remain at or above minimum recovery criteria may still be possible, but future analyses of the sort presented here will not be as reliable.

ACKNOWLEDGMENTS

We dedicate this article to the hundreds of people who gave so much of their time, energy, and resources to collect the data that we used and to make the wolf recovery and conservation program in the Northern Rockies the success it has been since 1979. In particular, we acknowledge the contributions of M. Jimenez, D. Smith, J. Fontaine, T. Meier, D. Boyd, J. Holyan, C. Mack, V. Asher, L. Bradley, M. Ross, K. Laudon, J. Trapp, N. Lance, S. Nadeau, J. Rachel, I. Babcock, J. Husseman, and M. Lucid. Other employees and volunteers affiliated with the USFWS, the National Park Service, United States Forest Service, the United States Bureau of Land Management, United States Department of Agriculture Wildlife Services, academic institutions, Nez Perce Tribe, Blackfeet Nation, Confederated Salish, and Kootenai Tribe, Turner Endangered Species Fund, MFWP, Idaho Department of Fish and Game, and Wyoming Game and Fish also contributed greatly to the data set we used for our analyses. We are indebted to the citizens and private landowners of the region who reported wolves or wolf sign to agency personnel, which was often the first step in verifying a new wolf pack. We thank our pilots

for their interest, dedication, and years of safe flying. Finally, we thank the past and current members of the MFWP Commission for embracing adaptive management principles embodied in Montana's wolf plan and further utilizing science and predictive models to aid in their decisions on wolf harvest. Our work on this manuscript was funded by MFWP, the U.S. Fish and Wildlife Service, and the U.S. Geological Survey. Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government. K. Laudon and K. Proffitt provided valuable discussions that improved this manuscript. D. Pletscher, L. S. Mills, J. Rotella, S. Creel, 2 anonymous reviewers, and Associate Editor K. McKelvey provided constructive comments and criticism on previous drafts, and thereby improved this manuscript. Any shortcomings in this article, however, are not attributable to these individuals, and their efforts do not necessarily imply agreement with all aspects of this manuscript.

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Associate Editor: Kevin McKelvey.