Management and Conservation Article

Estimation of Successful Breeding Pairs for Wolves in the Northern Rocky Mountains, USA

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ABSTRACT Under the Endangered Species Act, documenting recovery and federally mandated population levels of wolves (*Canis lupus*) in the Northern Rocky Mountains (NRM) requires monitoring wolf packs that successfully recruit young. United States Fish and Wildlife Service regulations define successful breeding pairs as packs estimated to contain an adult male and female, accompanied by ≥2 pups on 31 December of a given year. Monitoring successful breeding pairs will become more difficult following proposed delisting of NRM wolves; alternatives to historically intensive methods, appropriate to the different ecological and regulatory context following delisting, are required. Because pack size is easier to monitor than pack composition, we estimated probability a pack would contain a successful breeding pair based on its size for wolf populations inhabiting 6 areas in the NRM. We also evaluated the extent to which differences in demography of wolves and levels of human-caused mortality among the areas influenced the probability of packs of different sizes would contain successful breeding pairs. Probability curves differed among analysis areas, depending primarily on levels of human-caused mortality, secondarily on annual population growth rate, and little on annual population density. Probabilities that packs contained successful breeding pairs were more uniformly distributed across pack sizes in areas with low levels of human mortality and stable populations. Large packs in areas with high levels of human-caused mortality and high annual growth rates had relatively high probabilities of containing breeding pairs whereas those for small packs were relatively low. Our approach can be used by managers to estimate number of successful breeding pairs in a population where number of packs and their sizes are known. Following delisting of NRM wolves, human-caused mortality is likely to increase, resulting in more small packs with low probabilities of containing breeding pairs. Differing contributions of packs to wolf population growth based on their size suggests monitoring successful breeding pairs will provide more accurate insights into population dynamics of wolves than will monitoring number of packs or individuals only.

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Because typically only 2 adults breed in each wolf (*Canis lupus*) pack, the pack is the reproductive unit in a wolf population (Mech and Boitani 2003). United States Fish and Wildlife Service (USFWS) recovery criteria for wolves in the Northern Rocky Mountains (NRM; Fig. 1) and management guidelines for Mexican wolves in the southwestern United States require monitoring "breeding pairs," defined by regulation as packs containing ≥1 adult male and 1 adult female with ≥2 pups on 31 December of a given year (USFWS 1994, 1996). The intent of this definition is to provide a demographic measure of successful reproduction and survival for any given pack, reflecting past success in recruitment of pups (sufficient for replacement of breeding ad) and the likelihood to breed successfully in the upcoming year (ad M and ad F present prior to the breeding season). In this context, the regulatory term "breeding pair" is somewhat misleading because any pack of wolves by definition contains 2 adults attempting to breed. We recommend, therefore, using the term "successful breeding pair" as an alternative, more precise term and will use it to refer to the USFWS regulatory term "breeding pair" throughout this paper.

The demographic recovery goal for gray wolves in the NRM is ≥30 successful breeding pairs, equitably distributed among the 3 recovery areas (Fig. 1) for 3 successive years, comprising a metapopulation of ≥300 wolves with genetic exchange between subpopulations (USFWS 1994). This goal has been exceeded consistently since 2002 and the USFWS has proposed delisting the NRM population (USFWS 2007*a*, *b*). Once delisting occurs, the USFWS will require Idaho, Montana, and Wyoming to maintain and document ≥10 successful breeding pairs annually and to estimate wolf population size and distribution within their state boundaries (USFWS 2006).

To date, documentation of successful breeding pairs in NRM has relied largely on federal funding to capture and

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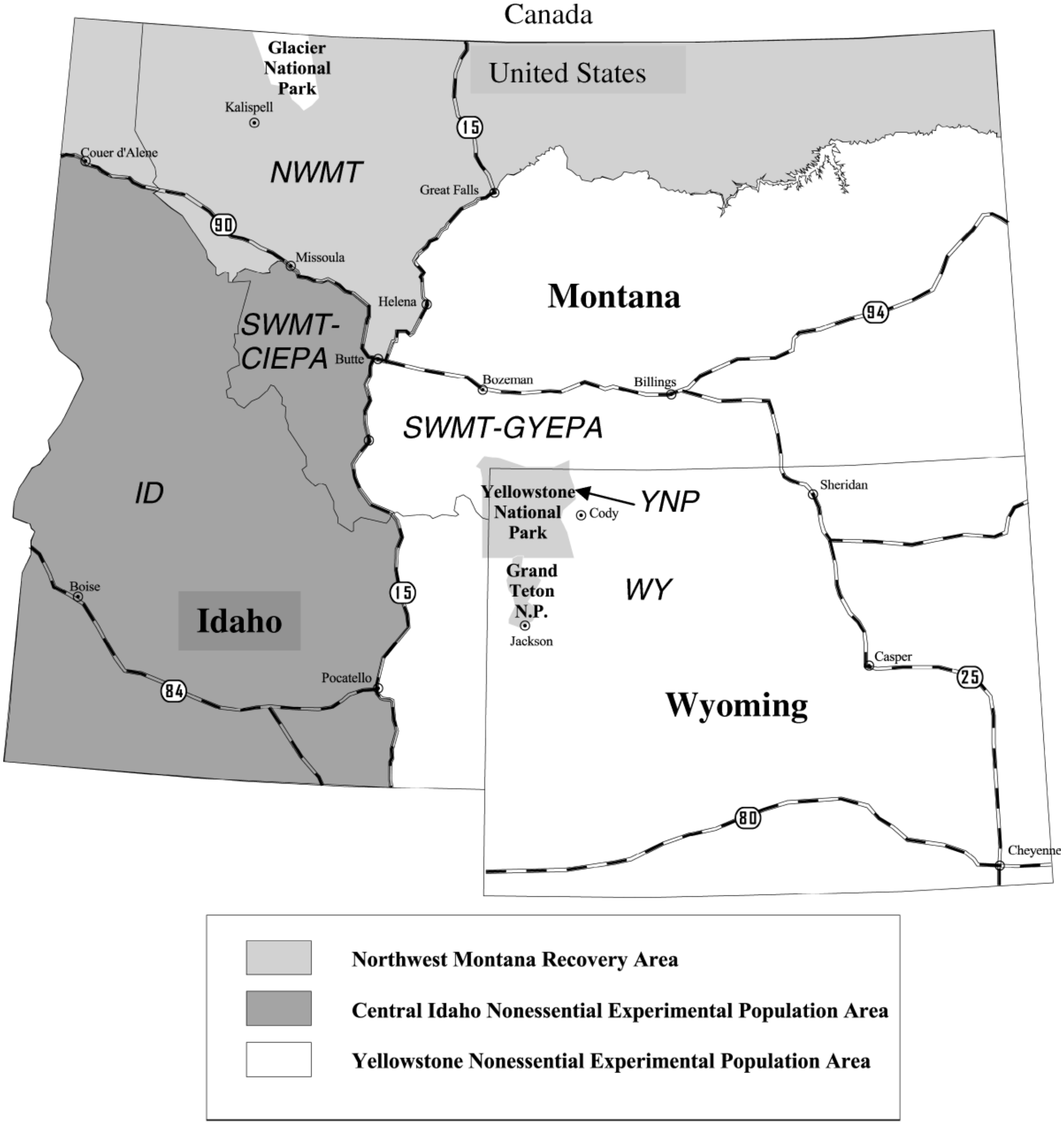

Figure 1. Northern Rocky Mountain federal gray wolf recovery areas and state boundaries for Montana, Idaho, and Wyoming, USA, 1979–2005. We designated 6 analysis areas based largely on geography and administrative boundaries, each experiencing different levels of isolation, protection, management, and exposure to humans: Northwest Montana (Northwest Montana Recovery Area [NWMT]), Idaho (ID, the state of Idaho excluding the portion contained in NWMT), Yellowstone National Park (YNP), Wyoming (WY, the state of Wyoming excluding YNP), the portions of southwest Montana included in the Central Idaho Recovery Area (SWMT-CIEPA), and the portions of southwest Montana included in the Greater Yellowstone Recovery Area (SWMT-GYEPA).

collar members of known wolf packs, and radiotelemetry to obtain visual counts, to classify pack members according to age (e.g., pups vs. ad) and sex, to track packs to den and rendezvous sites, and to record known mortalities and dispersal events (USFWS et al. 2000–2006). Use of such techniques to monitor successful breeding pairs resident within the large NRM population (estimated ≥1,020 individuals in 104 packs ≥4, 71 of which contained successful breeding pairs; USFWS et al. 2006) are becoming cost-prohibitive as the population continues to grow. Further, reduction of federal funding following delisting will sharply curtail the intensive monitoring techniques used to date. Methods for estimating successful breeding pairs in the absence of direct visual counts obtained using radiotelemetry are needed to ensure recovery objectives for the NRM wolf population continue to be met prior to delisting and to provide a reliable monitoring tool for state agencies following delisting.

Whereas determining pack composition required to meet USFWS criterion for a successful breeding pair can be difficult in the absence of radiotelemetry, verification of pack presence and size in winter is more easily accomplished in the NRM (e.g., through aerial surveys, track surveys). Assuming all verified packs with ≥4 wolves contain successful breeding pairs, however, would be misleading. Pack size should strongly affect the likelihood of meeting the successful breeding pair criterion; levels of pup and adult mortality should have a disproportionate influence on small packs than on large ones.

The relationship between pack size and probability of a pack containing a successful breeding pair has not been developed empirically for gray wolves. This relationship is likely to vary geographically across the distribution of the species, influenced by a variety of factors. Pack size varies with the demography of a population; rapidly growing, expanding populations tend to have small pack sizes, whereas established populations with slow growth rates can have relatively large pack sizes where food resources are abundant and predictable (Hayes and Harestad 2000, Fuller et al. 2003; D. Cluff, Department of Environment and Natural Resources, NT, personal communication), although pack sizes in these populations can decrease once food is limiting (Hayes and Harestad 2000, Fuller et al. 2003). Similarly, pack size should vary with lethal interactions with humans (e.g., control actions, poaching, vehicle or train collisions); high levels of human-caused mortality should reduce average pack size (Jedrzejewska et al. 1996, Fuller et al. 2003). Demographically, wolf populations across the NRM varied in date of establishment, size, and opportunities for expansion and growth. Human-caused mortality varied from near-complete protection in Yellowstone National Park to the experimental populations in Idaho and Wyoming where more forms of human-caused mortality were legal than for the endangered population in the Northwest Montana Recovery Area (NWMT; Bangs and Fritts 1996).

Our objective was to develop a monitoring tool for successful breeding pairs based on pack size that would be feasible and appropriate to the different ecological, budgetary, and regulatory context for NRM wolves that will follow delisting. To accomplish this, we estimated the probability a pack observed at the end of a year contained a successful breeding pair, based on its size, and would thus contribute to maintenance of federally mandated population levels. Also, because demographic conditions and levels of human-caused mortality for wolves are likely to influence successful breeding pair probabilities, and manipulation of these demographic conditions will be the primary tools available to managers following delisting, we evaluated the extent to which these factors explained variation in successful breeding pair probabilities across the NRM. Beginning in 1979 and each year thereafter, USFWS and cooperating partners compiled year-round monitoring data in December of each year, recording total number of known packs in the NRM, number of wolves observed in each pack, and whether each pack contained a successful breeding pair. We used these data to model probability of a pack containing a successful breeding pair for each of 6 analysis areas within the NRM that differed in wolf demography and levels of lethal interactions with humans. We hypothesized a monotonically increasing relationship between pack size and probability a pack contained a successful breeding pair that varied among analysis areas. We hypothesized that differences in these probabilities among analysis areas would be due to 1) an inverse relationship with population growth rate in the year prior to observation because small packs of a rapidly growing population should be more vulnerable to loss of breeding pair status, 2) a negative relationship with population density in the year prior to observation because of density-dependent effects on survival and reproduction, and 3) a negative relationship with extent of human-caused mortality over all years because of its direct (removal of breeders or pups) and indirect (reduction of pack sizes) effects.

STUDY AREA

Subpopulations of gray wolves in the NRM were distributed across NWMT, the Central Idaho Experimental Population Area (CIEPA), and the Greater Yellowstone Experimental Population Area (GYEPA), overlapping state boundaries for Idaho, Montana, and Wyoming (Fig. 1). Wolf populations within each recovery area experienced different levels of isolation, protection, management, and exposure to humans, based largely on geography and administrative boundaries. Based on these differences, we delineated 6 analysis areas within the recovery areas: 1) Idaho, excluding the panhandle, 2) NWMT, 3) Southwest Montana within CIEPA (SWMT-CIEPA), 4) Southwest Montana within GYEPA (SWMT-GYEPA), 5) Wyoming outside Yellowstone National Park, and 6) Yellowstone National Park (YNP).

Idaho Excluding the Panhandle

Wolves were reintroduced to Idaho in 1995 and spread throughout central Idaho, occupying 44,410 km^2 by 2005 (Bangs and Fritts 1996). Overall population growth (λ) has been high since reintroduction (Table 1; Fig. 2A), resulting in the largest wolf population among the analysis areas. Though slowing in later years, λ in Idaho remained strongly positive (Fig. 2B). No packs were documented in the panhandle of Idaho through 2005 (Bangs and Fritts 1996, Bangs et al. 1998, USFWS et al. 2000–2006, Nadeau et al. 2006). Much of central Idaho was federally designated wilderness; surrounding forested lands were a mix of United States Department of Agriculture, Forest Service lands and private timber lands. Livestock grazing was the most common land use outside of wilderness areas. Wolves in Idaho were managed as an experimental population; the primary source of mortality was human-related, most of which was removal in response to wolf–livestock conflicts and poaching. Most human-related deaths of wolves occurred outside wilderness areas.

Northwest Montana

Wolves recolonized NWMT in 1979 and were generally confined to the mountainous portions in the northwest corner of Montana, occupying 18,623 km^2 by 2005 (Bangs and Fritts 1996, Pletscher et al. 1997, Bangs et al. 1998, USFWS et al. 2000–2006). Population growth was lower in

Table 1. Wolf population characteristics for 6 analysis areas, Northern Rocky Mountains, USA, 1979–2005. $\lambda =$ population growth rate; $M_H =$ percentage of total mortality of radiocollared wolves caused by humans.

Wolf analysis area[a]	Yr wolves established	No. packs from establishment to 2005	Pack size		λ	M_H	
			$\bar{x}$	SD		Estimate	n
ID	1995	175	6.95	2.31	1.36	0.77	97
NWMT	1979	124	5.15	2.54	1.17	0.72	134
SWMT-CIEPA	2000	17	5.14	1.05	1.56	0.87	47
SWMT-GYEPA	1999	31	6.31	1.38	1.37	0.87	47
WY	1996	51	7.25	2.27	1.56	0.71	38
YNP	1995	99	9.88	2.56	1.16	0.23	56

[a] ID = state of ID, not including the portion in the Northwest Montana Recovery Area; NWMT = Northwest Montana Recovery Area; SWMT-CIEPA = portion of MT included in the Central Idaho Experimental Population Area; SWMT-GYEPA = portion of MT included in the Greater Yellowstone Experimental Population Area; WY = state of WY, not including Yellowstone National Park; YNP = Yellowstone National Park.

NWMT (Table 1; Fig. 2A) than in most other areas, and trends in later years indicated relative stability (Fig. 2B). Lands in NWMT were primarily public or corporate-owned and managed for timber production. Valley bottom lands were generally privately owned. Wolves in NWMT were managed as an endangered population; human-caused mortality due to poaching and vehicle or train collisions exceeded legal removals.

Southwest Montana Within CIEPA

The first established wolf pack in SWMT-CIEPA was verified in 2000, presumably originating from Idaho dispersers. From 2000 to 2005, wolves spread east and south along the Montana–Idaho border, occupying 6,537 km^2 (Bangs and Fritts 1996, Bangs et al. 1998, USFWS et al. 2000–2006). The SWMT-CIEPA wolves had one of the highest λs (Table 1) and, though population size was small (Fig. 2A), growth in later years was one of the highest among the areas (Fig. 2B). Land ownership in SWMT-CIEPA was a mixture of public and private; local land management emphasized livestock production. Wolves were managed as an experimental population. The primary source of wolf mortality in SWMT-CIEPA was human-related, most of which was removal in response to wolf-livestock conflicts.

Southwest Montana Within GYEPA

The first established SWMT-GYEPA pack was verified in 1999, likely originating from YNP dispersers. From 1999 to 2005, wolves occupied 9,916 km^2 in the southwest corner of Montana near YNP (Bangs and Fritts 1996, Bangs et al. 1998, USFWS et al. 2000–2006). Wolf numbers in SMWT-GYEPA were relatively small (Table 1; Fig. 2A) and the population had stabilized after an initial period of rapid growth (Fig. 2B). Similar to SWMT-CIEPA, land ownership was a mixture of public and private, and livestock production was prevalent. As with SWMT-CIEPA, wolves were managed as an experimental population and removal following livestock conflicts was the primary source of human-caused mortality.

Wyoming Outside YNP

Wolves became established in Wyoming outside YNP in 1996 and occupied 15,040 km^2 in the northwestern corner of the state by 2005 (Bangs and Fritts 1996, Bangs et al. 1998, USFWS et al. 2000–2006). The population had one of the highest λs (Table 1) among the analysis areas though it remained relatively small (Fig. 2A); trends in later years suggested some slowing, though λ remained relatively high (Fig. 2B). Landownership was a mixture of public and private lands, and livestock production was also prevalent on both public and private lands. Wolves were managed as an experimental population and removal following livestock conflicts was the primary cause of wolf mortality.

Yellowstone National Park

Wolves were reintroduced to YNP in 1995 and 1996 (USFWS 2006) and occupied 8,201 km^2 by 2005 (Bangs and Fritts 1996, Bangs et al. 1998, USFWS et al. 2000–2006). The population was second largest among the analysis areas (Fig. 2A); λ was high in the years following translocation, but trends in later years showed evidence of stability, possibly decline (Table 1; Fig. 2B). The YNP wolves were managed as an experimental population, but lands within YNP were protected and relatively undeveloped; human-caused mortality was thus low compared to deaths caused by intraspecific conflicts. Yellowstone National Park wolves were the most intensively monitored segment of the NRM population.

METHODS

Pack Size and Successful Breeding Pair Status

In each of our analysis areas, radiocollared packs were monitored on the ground and from aircraft at routine intervals throughout the calendar year, from the time a collar was first placed in each pack. Some uncollared packs were monitored by ground tracking. To document breeding, Montana and Wyoming relied primarily on aerial and ground observations of pack denning in spring and composition during fall months. Because of dense forest cover and inaccessible terrain, documentation of breeding in Idaho relied less on aerial and ground observations in fall, instead counting pups each summer by visiting den and rendezvous sites and tracking their fates through subsequent monitoring, when possible. At the end of each calendar year, we used all available information to assess whether each pack in each analysis area satisfied the successful breeding pair

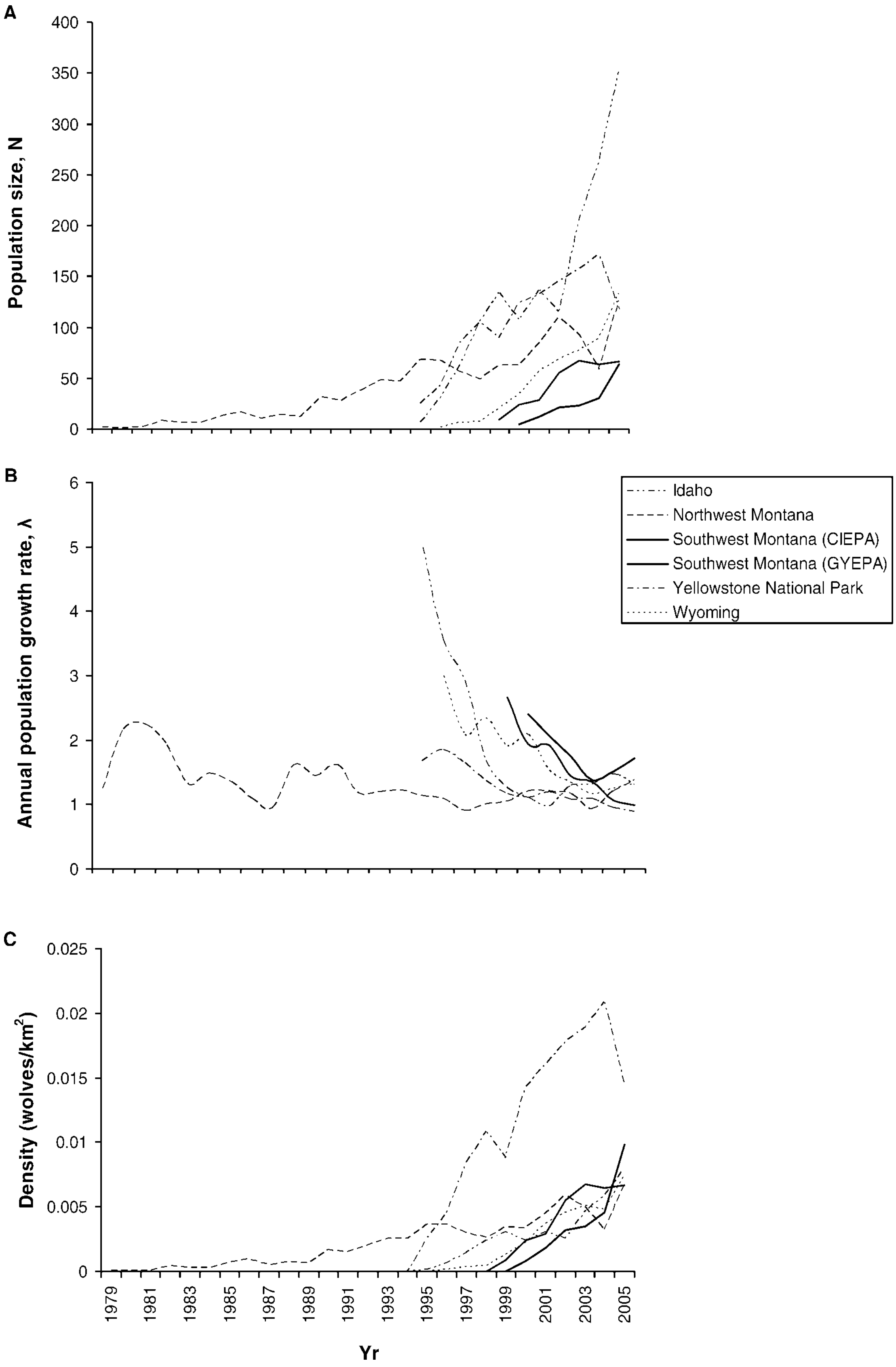

Figure 2. Population changes of wolves in 6 analysis areas over time, Northern Rocky Mountains, USA, 1979–2005. (A) Changes in population size (N); (B) changes in annual population growth rate, λ; (C) changes in density, D_t (N_t/cumulative, nonoverlapping area [km^2] occupied by wolves in an analysis area over all yr).

criterion set by USFWS. We determined a pack did not successfully produce pups if the pack did not localize, repeated ground and aerial surveys detected no auditory or visual sign of pups, or pups were known to have died or been killed. For packs where reproduction was known to occur but pup fates were unknown at the end of the year, we assigned successful breeding pair status conservatively with respect to pup survival, based on last known observation or on presence of pups in summer in Idaho. We excluded packs of unknown status from analyses. Monitoring effort in Montana 2003 was considerably lower than other years resulting in unknown breeding pair status for most packs, therefore we excluded data from Montana for 2003 from analysis. Otherwise, monitoring intensity of the NRM wolves was extremely high; data for each year approached a census for the NRM population, more so for early years than later ones. We assumed that undetected wolf packs, or pups within packs, and misclassified successful breeding pairs were few and would not change our results significantly had we detected and included them in our analyses.

Probability of Packs Containing a Successful Breeding Pair

We used logistic regression (Proc LOGISTIC; SAS Institute 2000) to estimate probability ($\hat{P}$) a pack of size i contained a successful breeding pair based on pack size for each of the 6 analysis areas. Because some of the same packs were observed over multiple years, we assessed lack of independence in our data by calculating ratio of deviance to degrees of freedom for our data set; a ratio >1 indicates overdispersion and lack of independence among observations (SAS Institute 2000). We assessed model fit using the receiver operating characteristic (ROC) statistic (Hosmer and Lemeshow 2000). A ROC $= 0.5$ indicates the model does not discriminate among the data. A ROC between 0.7 and 0.8 indicates acceptable discrimination, between 0.8 and 0.9 indicates excellent discrimination, and >0.9 indicates outstanding discrimination (Hosmer and Lemeshow 2000).

Factors Influencing Probability of Packs Containing a Successful Breeding Pair

To identify factors that could influence probability a pack of size i contained a successful breeding pair, we regressed deviance residuals from the logistic regression analyses against population growth rate for the year before observation (λ_{t-1}; Fig. 2B), relative wolf density for the year before observation (D_{t-1}; Fig. 2C), and percent of total mortality caused by humans (M_H) over all years, as well as all possible combinations of these characteristics (Proc GENMOD; SAS Institute 2000). We calculated D_t as [N_t/(cumulative, nonoverlapping area [km^2] occupied by wolves in an analysis area over all yr)]. Our estimate of D_t was based on area occupied by wolves in each analysis area over all years and was thus suitable only for tracking relative patterns in the NRM; trends in D_t over time represented how the growing wolf population in each analysis area filled the area (measured through 2005) available to it. We estimated cumulative, nonoverlapping area occupied by wolves by calculating 95% kernel utility distributions using all telemetered wolf locations within each analysis area over all years (Worton 1989; Seaman and Powell 1996). We calculated M_H for each wolf analysis area based on percentage of known mortalities of collared wolves that were due to control actions, documented poachings, or vehicle and train collisions from 1999 to 2004 (2005 data were unavailable at the time of this writing). The number of radiocollared wolves was too small (D. Guernsey, National Park Service, personal communication) to estimate M_H separately for SWMT-CIEPA and SWMT-GYEPA so we pooled data between the 2 areas to estimate a common M_H between them. Similarities in proportions of public lands and livestock densities suggest assuming human-caused mortality was similar between the 2 areas was reasonable (Montana Natural Resource Information System 2006). Because deviance residuals varied between and within pack sizes and we were interested in variation within pack sizes, we included pack size as a variable in each model to control for variation among pack sizes. We generated a null model (i.e., pack size only) to evaluate relative strength of λ_{t-1}, D_{t-1}, and M_H. We assessed fit of our global model using Pearson's correlation coefficient (R^2; Burnham and Anderson 2002).

We evaluated the models of deviance residuals using Akaike's Information Criterion (AIC; Burnham and Anderson 2002). Because our data consisted of packs observed over multiple years, we used Monte Carlo simulations to estimate the variance inflation parameter ($\hat{c}$) and used it to calculate quasi-AIC (QAIC; AIC modified for overdispersion in the data; Burnham and Anderson 2002) for our analyses. We considered all models with ΔQAIC ≤ 4 to be viable, with greatest confidence in models with ΔQAIC ≤ 2 (Burnham and Anderson 2002). We assessed model weight and model likelihood for each model; we calculated variable importance for each of the independent variables (excluding pack size) and used model-averaged coefficients to estimate relative contribution of each variable to model fit over all models (Burnham and Anderson 2002).

RESULTS

From 1979 to 2005, 497 observations of annual pack size and successful breeding pair status were recorded for 203 packs in the 6 analysis areas (see Bangs and Fritts 1996, Bangs et al. 1998, USFWS et al. 2000–2006). Average pack sizes were smallest in NWMT and SWMT-CIEPA and largest in YNP, ranging from 5.14 (±1.05 SD) to 9.88 (±2.56; Table 1). Percentage of total wolf mortality (M_H) attributable to humans varied among wolf analysis areas (Table 1). Unsurprisingly, M_H was lowest for YNP. The M_H was highest for the 2 SWMT areas combined; all other areas had high values of M_H but approximately 10–15% lower than those for SWMT (CIEPA and GYEPA; Table 1).

Probability of Packs Containing a Successful Breeding Pair

Logistic regression generated models relating pack size to probability of a pack containing a successful breeding pair

Table 2. Logistic regression models of probability of a wolf pack containing a successful breeding pair (i.e., containing $\geq$1 ad M, 1 ad F, and $\geq$ 2 pups) based on pack size for 6 analysis areas, Northern Rocky Mountains, USA, 1979–2005. Each model is a logit, which we used to estimate probability of a pack containing a successful breeding pair ($\hat{P}$) through the transformation: $\hat{P} = e^{\text{logit}}/(1 + e^{\text{logit}})$. n = number of wolf packs used to generate models.

Wolf analysis area[a]	n	Model logit	ROC[b]
ID	175	−0.90 + 0.38 (pack size)	0.72
NWMT	124	−2.09 + 0.49 (pack size)	0.76
SWMT-CIEPA	17	−6.32 + 1.22 (pack size)	0.84
SWMT-GYEPA	31	−2.51 + 0.49 (pack size)	0.72
WY	51	−2.07 + 0.47 (pack size)	0.78
YNP	99	−1.70 + 0.43 (pack size)	0.81

[a] ID = state of ID, not including the portion in the Northwest Montana Recovery Area; NWMT = Northwest Montana Recovery Area; SWMT-CIEPA = portion of MT included in the Central Idaho Experimental Population Area; SWMT-GYEPA = portion of MT included in the Greater Yellowstone Experimental Population Area; WY = state of WY, not including Yellowstone National Park; YNP = Yellowstone National Park.

[b] Receiver operating characteristic; ROC = 0.5 indicates poor fit, 0.7 < ROC < 0.8 indicates acceptable fit, 0.8 < ROC < 0.9 indicates excellent fit, ROC > 0.9 indicates outstanding fit (Hosmer and Lemeshow 2000).

for each of the 6 analysis areas (Table 2). The ratio of deviance to degrees of freedom was 0.94, therefore no correction for overdispersion in the data was required. Sample size varied considerably among analysis areas, from $n = 18$ packs in SWMT-CIEPA to $n = 175$ in Idaho (Table 2). Model fit was acceptable for all wolf analysis areas, except for SWMT-CIEPA and YNP, which had excellent model fit (Table 2).

The relationship between pack size and probability of containing a successful breeding pair varied among the analysis areas (Fig. 3). Probability curves for NWMT, Wyoming, and YNP were very similar (Fig. 3). The lowest probabilities for a pack size of 4 were predicted for SWMT-CIEPA and SWMT-GYEPA ($\hat{P}$ = 0.19 and 0.37, respectively; Fig. 3), though curves otherwise differed considerably; curve slope for SWMT-GYEPA approximated slopes seen for other areas, whereas slope for SWMT-CIEPA was considerably steeper (Fig. 3). The highest probability of a pack of 4 containing a successful breeding pair was predicted for Idaho ($\hat{P} = 0.66$).

Factors Influencing Probability of Packs Containing a Successful Breeding Pair

We estimated $\hat{c}$ for residual deviance of probabilities that packs contained successful breeding pairs for different pack sizes to be 1.87, suggesting a lack of independence (though not enough to infer unacceptable model structure, i.e., $\hat{c} \geq 4$; Burnham and Anderson 2002). We therefore used $\hat{c}$ to calculate QAIC for our analysis to adjust for overdispersion in our data (Burnham and Anderson 2002). Fit of the global model to the residuals was good ($R^2 = 0.79$). The model including pack size, λ_{t-1}, and M_H ranked highest in our analysis (QAIC = −397.48), with model weight = 0.52 and model likelihood = 1 (Table 3). The next highest-ranking model was the global model (pack size, D_{t-1}, λ_{t-1}, and M_H), with ΔQAIC = 1.49, model weight = 0.25, and model likelihood = 0.46. Models containing pack size and M_H and pack size, D, and M_H had 2 < ΔQAIC $\leq$ 4 with small model weights and likelihoods (Table 3). All other models had ΔQAIC > 4 with model weights and likelihoods approximately equal to zero. The null model ranked last among models (Table 3).

All models with ΔQAIC $\leq$ 4 included M_H and its variable importance was 1.00 and its model-averaged coefficient estimate was −2.25 (95% lower CI [$\mathrm{CI_L}$] = −2.61, 95% upper CI [$\mathrm{CI_U}$] = −1.89). The 2 top-ranked models

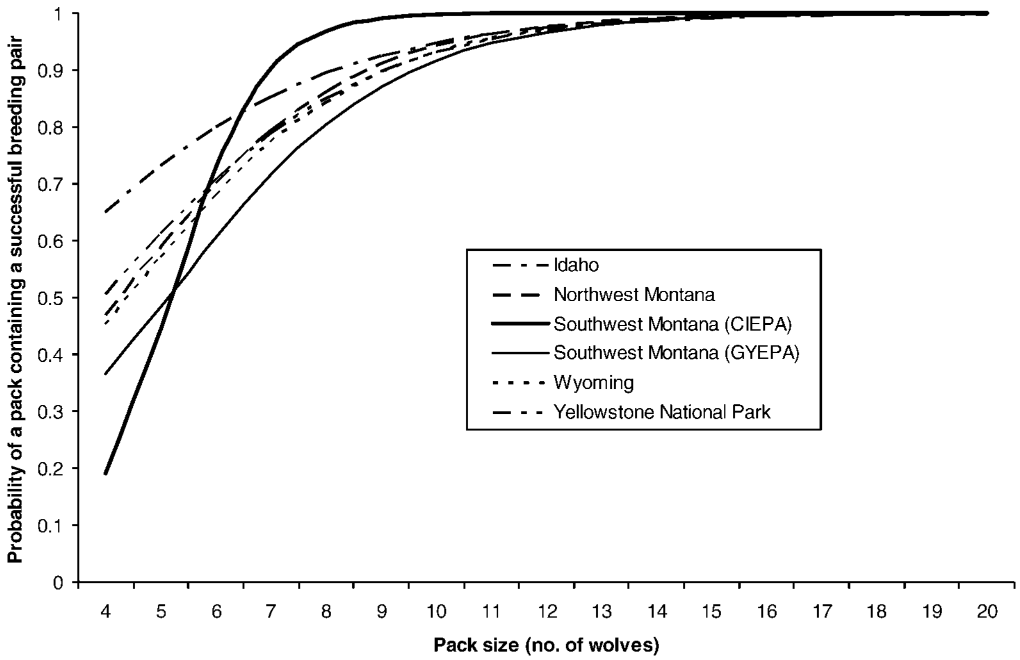

Figure 3. Probability of a pack of wolves containing a successful breeding pair (i.e., containing $\geq$1 ad M, 1 ad F, and $\geq$ 2 pups) based on pack size for 6 analysis areas, Northern Rocky Mountains, USA, 1979–2005, estimated using logistic regression.

Table 3. Factors influencing the probability a wolf pack of size i contained a successful breeding pair (i.e., $\geq$1 ad M, 1 ad F, and $\geq$ 2 pups), for 6 analysis areas, Northern Rocky Mountains, USA, 1979–2005 ($n = 497$). Models depict extent to which demographic characteristics and human-caused mortality among analysis areas explained residuals from logistic regression of successful breeding pair status on pack size.[a] We calculated quasi-Akaike's Information Criterion (QAIC) using $\hat{c} = 1.87$ to adjust for overdispersion in the data.

Model	Log(L)[b]	K[b]	QAIC	ΔQAIC	Model wt	Model likelihood
Pack size, λ_{t-1}, M_H	380.99	5	−397.48	0.00	0.52	1.00
Pack size, D_{t-1}, λ_{t-1}, M_H[c]	381.48	6	−395.99	1.49	0.25	0.46
Pack size, M_H	376.61	4	−394.79	2.69	0.14	0.26
Pack size, D_{t-1}, M_H	377.72	5	−393.98	3.50	0.09	0.17
Pack size, D_{t-1}, λ_{t-1}	339.97	5	−353.61	43.88	0.00	0.00
Pack size, λ_{t-1}	335.48	4	−350.80	46.69	0.00	0.00
Pack size, D_{t-1}	296.07	4	−308.65	88.84	0.00	0.00
Pack size (null)	290.38	3	−304.57	92.92	0.00	0.00

[a] D_{t-1} = annual wolf density for the previous yr (N_{t-1}/cumulative, nonoverlapping area [km^2] occupied by wolves in an analysis area over all yr), λ_{t-1} = annual population growth rate for the previous yr, M_H = % of total mortality caused by humans.

[b] Log(L) = log likelihood; K = no. of parameters.

[c] Fit of global model was $R^2 = 0.79$.

included λ_{t-1}, and its variable importance was 0.77; the model-averaged coefficient estimate for λ_{t-1} was −0.10 (95% $\mathrm{CI_L} = -0.16$, 95% $\mathrm{CI_U} = -0.03$). D_{t-1} was included in 2 models with ΔQAIC $\leq$ 4 (Table 3) and had low variable importance at 0.34. The model-averaged coefficient estimate for D_{t-1} was 1.43 (95% $\mathrm{CI_L} = -1.07$, 95% $\mathrm{CI_U} = 3.92$).

DISCUSSION

United States Fish and Wildlife Service recovery criteria for wolves in NRM and management guidelines for Mexican wolves in the southwestern United States require monitoring successful breeding pairs, defined by regulation as a pack containing $\geq$1 adult male and 1 adult female with $\geq$2 pups on 31 December of a given year (USFWS 1994, 1996). In order for wolves to be (and to remain) delisted in the NRM, the states of Montana, Idaho, and Wyoming are required collectively to maintain a minimum of 30 successful breeding pairs (USFWS 2006). With delisting and the passage of management responsibilities from federal to state agencies, funding for intensive monitoring of the growing NRM wolf population is likely to decline while logistical challenges increase. Further, intensity of wolf management and hunting of wolves is expected to increase following delisting (Idaho Department of Fish and Game 2003, Montana Wolf Management Advisory Council 2003, Wyoming Game and Fish Department 2003); effects of these practices on successful breeding pairs are unknown but likely to increase the difficulty of monitoring. State managers therefore require a robust means of estimating the number of successful breeding pairs for wolf populations based on data obtainable through less intensive monitoring (e.g., pack size). To meet this need, we used monitoring data collected for the recovering wolf population in the NRM to estimate the probability that packs of different sizes would contain successful breeding pairs. To inform estimation of successful breeding pairs following delisting, we also evaluated the extent to which demographic conditions and human-caused mortality in each area influenced successful breeding pair probabilities for packs.

As we hypothesized, the relationship between pack size and probability that a pack contained a successful breeding pair increased monotonically, but variably, across all analysis areas. Our analyses suggest that this variation is likely due to the influence of human-caused mortality and the unique demographic context for each wolf analysis area. Consistent with our hypotheses, evidence for the negative effects of human-caused mortality was strongest, followed by an inverse effect of annual population growth rate. Our results suggest probability that a pack contains a successful breeding pair is lowered for small packs by increasing levels of human-caused mortality and that a more equitable distribution of this probability across all pack sizes is associated with lower population growth rates. In YNP, where human-caused mortality was lowest, population density was high, and recent population growth was near zero, probabilities that packs contained breeding pairs were the most evenly distributed across pack sizes, though still increasing monotonically. By contrast, the small populations of SWMT (CIEPA and GYEPA) that had high growth rates but also had high rates of human-caused mortality showed that smaller pack sizes had little likelihood of containing successful breeding pairs. Effects of population density on probability a pack would contain a successful breeding pair were small and uncertain (95% CI for coeff. estimate included zero) but could not be discounted entirely. The estimated negative effect of density was consistent with our hypothesis, but support was equivocal.

Interestingly, the very different wolf populations of NWMT, Wyoming, and YNP showed nearly identical probability curves, with the highest probabilities that small packs would contain successful breeding pairs among analysis areas (excluding ID). The NWMT and YNP populations were relatively stable, whereas the Wyoming population was growing rapidly, but all 3 areas had the lowest proportions of human-caused mortality among analysis areas. This suggests human-caused mortality has more influence than population growth on whether small packs contain successful breeding pairs. This inference is supported when probabilities for successful breeding pairs for NWMT and SWMT-CIEPA populations are compared. Both populations had the smallest average pack sizes among the wolf management areas, but the NWMT wolves experienced one of the lowest rates of human-caused mortality whereas the SWMT-CIEPA wolves experienced one of the highest (Table 1); packs of 4 wolves in SWMT-CIEPA were <50% as likely to contain a successful breeding pair as those in NWMT (Fig. 3; Table 3).

The Idaho wolf population was highly robust, exhibiting large population size, high growth rates, relatively modest effects of human-caused mortality, and the highest probabilities for small packs containing a successful breeding pair. In addition to abundant habitat and prey populations in Idaho favorable to wolves, we hypothesize the dynamics we observed were largely due to the rugged and vast expanses of roadless wilderness areas and other undeveloped lands managed by the United States Department of Agriculture, Forest Service in central Idaho. Though not affording the degree of protection of YNP, Idaho's interior likely serves to insulate the core of the Idaho wolf population, with most human-caused mortality occurring outside of undeveloped Forest Service lands (Nadeau et al. 2006), possibly explaining the high probabilities for Idaho packs to contain successful breeding pairs, where pup survival may have been higher than seen in other areas. Alternatively, unlike Montana and Wyoming, Idaho based its documentation of successful breeding pairs where pup fates were unknown on assumed survival of pups counted in summer. Thus, our estimates of probabilities packs would contain successful breeding pairs for Idaho could be biased slightly high because pup mortality that occurred prior to winter counts in other areas may not have been fully accounted for in Idaho's counts of successful breeding pairs.

We did not evaluate directly the extent to which wolf dispersal among analysis areas influenced the patterns we observed because dispersal data were sparse. Nonetheless, we hypothesize dispersal played a role undetected in our analyses. Reintroduced wolf populations in YNP and Idaho likely provided dispersers into adjacent areas as they grew, possibly explaining the high population growth rates for SWMT-CIEPA and SWMT-GYEPA, in spite of high levels of human-caused mortality and low probabilities of small packs containing a successful breeding pair. Should dispersal from Idaho and YNP decline, population growth in SWMT-CIEPA and SWMT-GYEPA would be more influenced by the low probabilities that small packs contain successful breeding pairs. Though established originally by wolves dispersing from Canada, NWMT has at various times acted as both a source and a sink for dispersers (Boyd and Pletscher 1999). We consider it unlikely dispersal played a consistent role in the interaction between successful breeding pairs, population growth, and human-caused mortality in NWMT.

Conceivably, our estimates of successful breeding pair probabilities and the analyses based on them could have been biased by undetected packs or pups within packs, or by misclassified successful breeding pair status among packs. Whereas such errors may contribute to the unexplained variability in our analyses, we deem likelihood of bias to be low because 1) monitoring was sufficiently intensive to achieve a near-census of the population for most areas over most years, 2) monitoring methods were sufficiently similar across areas to ensure comparability of data, and 3) monitoring in all analysis areas incorporated multiple techniques (e.g., aerial tracking, radiotracking, ground-tracking, den visits) and multiple observations over time, reducing likelihood of systematic bias due to sampling error.

The applicability of our models to NRM wolf populations following delisting will require further evaluation (USFWS 2006). Whereas population growth rates of delisted populations could likely fall within the spectrum of values we modeled, human-caused mortality may not. Following delisting, increased control actions and implementation of regulated harvests may increase human-caused mortality beyond levels we evaluated; our results suggest this would increase the negative effect on successful breeding pairs in small packs that we observed. Because high levels of human-caused mortality also reduce average pack size for a wolf population, reduced probabilities of small packs containing successful breeding pairs could have important demographic consequences for NRM wolf populations following delisting (Jedrzejewska et al. 1996, Fuller et al. 2003).

Our models provide managers with the ability to estimate number of successful breeding pairs in a population given the distribution of pack sizes. Estimated number of successful breeding pairs, $\hat{\beta}$, for a population would be the sum over pack sizes $i = 4$ to k of the number of known packs of size i, n_i, multiplied by the estimated probability a pack of size i contains a successful breeding pair, $\hat{P}_i$ (e.g., from Fig. 3):

$$\hat{\beta} = \sum_{i=4}^{k} (n_i \cdot \hat{P}_i)$$

Uncertainty in the estimate of $\hat{\beta}$ can be estimated using back-transformed confidence intervals on $\hat{P}_i$. This standard method of calculating uncertainty requires calculating confidence intervals for the log-odds of $\hat{P}_i$ using the normal distribution approximation, and then transforming those intervals to the response scale (Neter et al. 1996). Confidence intervals for $\hat{\beta}$ could then be constructed using:

$$\hat{\beta}_L = \sum_{i=4}^{k} (n_i \cdot \hat{P}_{iL})$$

$$\hat{\beta}_U = \sum_{i=4}^{k} (n_i \cdot \hat{P}_{iU})$$

where $\hat{P}_{iL}$ and $\hat{P}_{iU}$ are the estimated lower and upper confidence bounds on $\hat{P}_i$. This method ensures that the estimated number of successful breeding pairs for each pack size i will range from zero to n_i, which would not be guaranteed if confidence intervals were calculated using the estimated variance of $\hat{P}_i$ directly. This method could be generalized to provide a specified level of confidence that $\hat{\beta}$ is above a certain threshold value (e.g., a state in the NRM could require that $\hat{\beta}_L > 10$ to be confident it is meeting its recovery criterion). Estimates of $\hat{P}_i$ could also be used to augment incomplete field data by estimating the number of successful breeding pairs among packs of unknown status.

MANAGEMENT IMPLICATIONS

Intensive control or regulated harvest of wolves could result in a large number of small packs that contribute little to population growth and whose successful breeding pair status is more vulnerable to stochastic events (e.g., loss of an ad) than is that of a larger pack, which may require managers to be cautious about management strategies that result in small pack sizes for populations near minimum recovery criteria. Further, our results suggest that number of packs and population size alone may be poor indicators of demographic vigor for a wolf population pressured strongly by humans; number of successful breeding pairs is likely a more biologically relevant metric to document achievement of recovery goals and to assess effects of management on wolf populations.

Given the logistical challenges of developing a data set needed to estimate successful breeding pairs empirically, managers could elect to use our models for wolf populations other than those we modeled. We generated our models using detailed data collected in geographic areas with different wolf population dynamics and levels of human influence. The variability we observed in the resulting models suggests that no one model would be appropriate to all wolf populations and that a model should be selected appropriate to the demography and regulatory framework of the wolf population of interest. We recommend the following matches between models and wolf population characteristics. Each represents a testable hypothesis suitable for further refinement in an adaptive management context.

1. Idaho: rapidly growing population with a protected core
2. SWMT-CIEPA: colonizing, rapidly growing population with high levels of wolf control
3. SWMT-GYEPA: heavily controlled population with low growth rate
4. NWMT–YNP–WY: stable population with low levels of wolf control, or where wolf control is balanced by recruitment

We caution that site-specific or episodic sources of mortality (e.g., disease) not included in our models could affect the accuracy of our predictions and should thus be considered by managers when and where these sources contribute strongly to wolf mortality.

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