Management and Conservation Article

Survival of Colonizing Wolves in the Northern Rocky Mountains of the United States, 1982–2004

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ABSTRACT After roughly a 60-year absence, wolves (*Canis lupus*) immigrated (1979) and were reintroduced (1995–1996) into the northern Rocky Mountains (NRM), USA, where wolves are protected under the Endangered Species Act. The wolf recovery goal is to restore an equitably distributed metapopulation of ≥30 breeding pairs and 300 wolves in Montana, Idaho, and Wyoming, while minimizing damage to livestock; ultimately, the objective is to establish state-managed conservation programs for wolf populations in NRM. Previously, wolves were eradicated from the NRM because of excessive human killing. We used Andersen−Gill hazard models to assess biological, habitat, and anthropogenic factors contributing to current wolf mortality risk and whether federal protection was adequate to provide acceptably low hazards. We radiocollared 711 wolves in Idaho, Montana, and Wyoming (e.g., NRM region of the United States) from 1982 to 2004 and recorded 363 mortalities. Overall, annual survival rate of wolves in the recovery areas was 0.750 (95% CI = 0.728–0.772), which is generally considered adequate for wolf population sustainability and thereby allowed the NRM wolf population to increase. Contrary to our prediction, wolf mortality risk was higher in the northwest Montana (NWMT) recovery area, likely due to less abundant public land being secure wolf habitat compared to other recovery areas. In contrast, lower hazards in the Greater Yellowstone Area (GYA) and central Idaho (CID) likely were due to larger core areas that offered stronger wolf protection. We also found that wolves collared for damage management purposes (targeted sample) had substantially lower survival than those collared for monitoring purposes (representative sample) because most mortality was due to human factors (e.g., illegal take, control). This difference in survival underscores the importance of human-caused mortality in this recovering NRM population. Other factors contributing to increased mortality risk were pup and yearling age class, or dispersing status, which was related to younger age cohorts. When we included habitat variables in our analysis, we found that wolves having abundant agricultural and private land as well as livestock in their territory had higher mortality risk. Wolf survival was higher in areas with increased wolf density, implying that secure core habitat, particularly in GYA and CID, is important for wolf protection. We failed to detect changes in wolf hazards according to either gender or season. Maintaining wolves in NWMT will require greater attention to human harvest, conflict resolution, and illegal mortality than in either CID or GYA; however, if human access increases in the future in either of the latter 2 areas hazards to wolves also may increase. Indeed, because overall suitable habitat is more fragmented and the NRM has higher human access than many places where wolves roam freely and are subject to harvest (e.g., Canada and AK), monitoring of wolf vital rates, along with concomitant conservation and management strategies directed at wolves, their habitat, and humans, will be important for ensuring long-term viability of wolves in the region.

KEY WORDS *Canis lupus*, gray wolf, mortality, Northern Rocky Mountains, protected areas, survival.

Gray wolves (*Canis lupus*) were eradicated from the northern Rocky Mountains (NRM) of the United States by the 1930s (Young and Goldman 1944, McIntyre 1995). For the next 50 years, wolves were only occasionally reported and there was no functional wolf population in the area (U.S. Fish and Wildlife Service [USFWS] 1994). Reestablishment of wolves to northwest Montana (NWMT) began in 1979 through dispersal from Canada, and reproduction was first documented in 1986 (Ream et al. 1991, Pletscher et al. 1997). Wolves from Canada were reintroduced to central Idaho (CID) and Yellowstone National Park (YNP) in 1995 and 1996 to establish wolves in Idaho and the Greater Yellowstone Area (GYA; USFWS 1994, Bangs and Fritts 1996).

The Endangered Species Act (ESA) was passed in 1973 and wolves were listed in the contiguous United States in 1974. Wolf recovery plans were formulated for the NRM (ID, MT, and WY) in 1980 and 1987 and reintroductions

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to CID and YNP using wild wolves from Canada were recommended in an Environmental Impact Statement in 1994. Configured as a 3-segment metapopulation and one recovery area, the objective of the program was to restore wolves as a viable population to the NRM and return management to the affected States. Recovery plans included genetic exchange, either natural or artificial, between the 3 populations (USFWS 1994). Genetic exchange was assumed to be primarily natural because of the distance between recovery areas and dispersal capability of wolves (>500 km; Fritts 1983, Boyd and Pletscher 1999).

The minimum goal for restoration was to establish a metapopulation of ≥30 breeding pairs, with a breeding pair defined as an adult male and female wolf that raise 2 young to 31 December, and ≥300 wolves equitably distributed among the 3 core recovery areas for a ≥3 successive years (USFWS 1994). In addition to a minimum population requirement, each state needed a USFWS-approved management plan. Once this was achieved, wolves would be removed from the Endangered Species list and managed solely by the States of Idaho, Montana, and Wyoming, USA. These minimum population requirements were reached in 2002, but approved state plans were not completed until 2007. Wolf delisting occurred in 2008 but was remanded back to the USFWS after litigation for further consideration. Wolves were again delisted, except in Wyoming, in 2009.

The strategy for recovery was to nurture natural wolf immigration and to protect as endangered any population of wolves that became established in NWMT (USFWS 1987, 1994). Unlike NWMT, wolf restoration in CID and GYA called for reintroduction of wolves from Canada and management not as endangered but as experimental–nonessential, which allowed for more management flexibility in conflict situations (e.g., allowing ranchers to legally shoot wolves depredating on livestock) and less administration (e.g., no ESA Section 7 consultation).

Beginning in 1982, radiocollars were placed on wolves in NWMT to aid management and research (Ream et al. 1991, Pletscher et al. 1997). From 1995 to 1996, 35 and 31 wolves from Canada were reintroduced to CID and YNP, respectively (Bangs and Fritts 1996, Phillips and Smith 1996). All reintroduced wolves were fitted with radiocollars and survival was monitored. In all 3 areas annual radiocollaring efforts directed at wild-born animals continues. The annual proportion of the population collared ranged from 20% to 50% (Mitchell et al. 2008). We used radiocollar data from 1982 to 2004, a period of USFWS oversight for wolf management prior to proposed delisting and state management, to examine factors associated with wolf hazard.

The wolf population expanded rapidly in the 2 areas where wolves were reintroduced but more slowly where they had recolonized naturally (Bangs et al. 1998, Fritts et al. 2001). In 2004, 324 wolves were present in GYA, 452 in CID, and 59 in NWMT (USFWS et al. 2005).

The recovery plan for wolves in the NRM emphasized establishing successfully reproducing packs in core areas of secure habitat where wolf mortality would be minimal (USFWS 1987, 1994). The CID wilderness complex, YNP, Glacier National Park (GNP), and the Bob Marshall wilderness area (BMWA) of NWMT, and the extensive areas of multiple-use public land surrounding those areas, were selected to function as core areas–refugia for wolf recovery (USFWS 1987). All of these areas encompass large areas of public land where livestock grazing and motorized vehicle use, 2 factors contributing to higher rates of wolf mortality, are limited (USFWS 1994, Mitchell et al. 2008). Outside these core areas, habitat for wolves is less suitable and dominated by agriculture, and wolf protection accordingly is more tenuous. However, wolves were expected to be able to disperse between these 3 core recovery areas and survive in less secure habitat, facilitating connection between the 3 areas and thereby creating a large metapopulation (USFWS 1987, Pletscher et al. 1997, Boyd and Pletscher 1999). Critical to this plan was understanding if the 3 core areas functioned as presumed, or in other words that mortality outside core areas would not overwhelm source populations of wolves leading to population declines.

Human-caused mortality in the NRM strongly affects wolf population viability (Mitchell et al. 2008) as it does for other wolf populations (Fuller 1989, Adams et al. 2008, Person and Russell 2008). In addition, each NRM area differed in land status or ownership (e.g., park, wilderness, state, private, national forest) and management policy, so it was open to question how wolves would fare in each area. In general human access across the NRM is much greater than other areas where wolves have been studied (e.g., AK and Canada) even in wilderness areas (e.g., outfitter horse access for big-game hunting). Lastly, wolves in NWMT were managed as endangered, giving them greater legal protection than reintroduced wolves in CID and GYA.

Despite these differences, and based on research from NWMT during their colonization phase that indicated high survival among wolves there (Pletscher et al. 1997, Boyd and Pletscher 1999), we predicted that wolf survival would not differ between recovery areas nor threaten the NRM population because wolves were increasing most years (except for some yr in NWMT; USFWS et al. 2005). Because excessive levels of human-caused mortality were the primary reason wolves were extirpated, evaluation was important because delisting requires that the causes of endangerment be reduced to a level that no longer threatens the population (ESA of 1973). Survival data were also important beyond population counts because we could assess factors associated with high risk for wolves, which would inform management action. Further, sustainable survival rates for wolves are already known and indicative of population status (Keith 1983, Fuller et al. 2003, Adams et al. 2008), and because radiocollars were being used extensively as part of the recovery effort, we could easily use them for survival estimation comparing them to this larger data set, which would inform us about the status of our population. Therefore, our objectives were to determine demographic, behavioral, and anthropogenic determinants of wolf survival across the 3 recovery areas of the NRM.
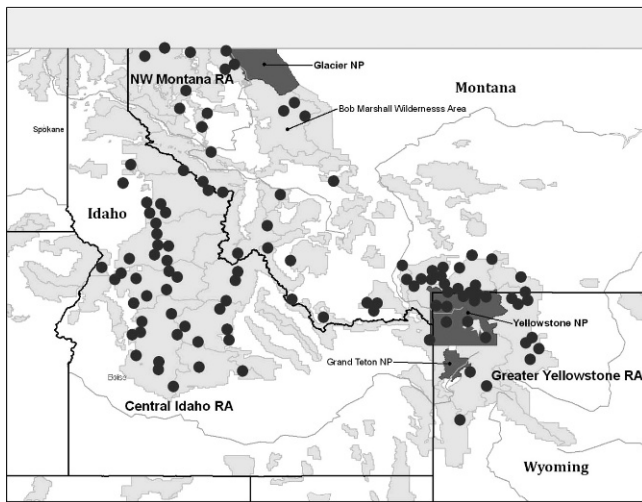
Figure 1. Location of wolf packs (black dots) in the northern Rocky Mountain study area (USA) in 2004. Note few packs in the Glacier National Park (NP)–Bob Marshall Wilderness Area portion of the northwestern Montana recovery area (RA) relative to Central Idaho and Greater Yellowstone Area.

STUDY AREA

Our large study area (>266,400 km^2) is difficult to characterize specifically because of wide local and regional variation (Fig. 1). Each of the 3 recovery areas is mountainous; a mountain–valley dichotomy prevails and this habitat is critical to supporting wildlife in the region. Many species of wildlife in this study area typically spend winter in the mountain valleys, where human population density is high, and summer in more remote mountains (Hansen et al. 2002). Ungulate seasonal movements follow this pattern, as do wolves, within their territorial constraints (wolves in the NRM are not migratory). Elevations ranged from about 200 m to 4,200 m; annual precipitation ranged from 25 cm to 150 cm. Temperatures ranged from −40° C to 35° C due to variation in elevation. Vegetation was dominated by coniferous forests of lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), subalpine fir (*Abies lasiocarpa*), Englemann spruce (*Picea engelmannii*), and whitebark pine (*Pinus albicaulis*), with quaking aspen (*Populus tremuloides*) and cottonwood (*Populus* spp.) at lower elevations. Willow (*Salix* spp.) was also common throughout the area. Grasslands, high mountain meadows, and shrub-steppe habitats were interspersed throughout the region. Each area had several major river systems and lesser watercourses creating the mountain–valley dynamic important to the vegetation

and summer–winter movement of ungulates and wolves. In general, winters were from October to April with most precipitation coming as snow, but increasing variability in snowfall and duration has been recorded (Wilmers and Post 2006; YNP, unpublished data).

Each wolf recovery area was centered on a large area of public land including National Parks, National Forest, and designated wilderness (Table 1). The NWMT recovery area encompassed GNP and the BMWA, comprising 11,770 km^2, and was surrounded by national forest lands, Blackfeet tribal, or private lands. The NWMT was the most fragmented recovery area and was interspersed with private lands mainly used for timber production (Table 1). The CID recovery area was about 53,000 km^2 of primarily national forest including 15,800 km^2 of wilderness, but there was also permitted grazing on public land. In the GYA recovery area, YNP occupied 8,991 km^2 in a 68,000-km^2 recovery area comprised mostly (62%) of public land (national forest, national wildlife refuges, and Bureau of Land Management areas).

Like physiographic features and climate, the potential prey of wolves varied across areas but was generally similar. Each area had a mix of elk (*Cervus elaphus*), deer (mule [*Odocoileus hemionus*] and white-tailed [*O. virginianus*]), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*), and pronghorn antelope (*Antilocarpa americana*). Bison (*Bison bison*) were unique to YNP and Grand Teton National Park. Primary prey for wolves varied across the region but was generally either elk or deer, although some wolves in YNP used bison as well (Smith et al. 2000). Most areas had the full complement of large carnivores, except that grizzly bears (*Ursus arctos*) were absent in the CID recovery area. Besides wolves, black (*U. americanus*) and grizzly bears, cougars (*Felis concolor*), coyotes (*Canis latrans*), and humans preyed on most of these ungulates. Livestock, mostly cattle and sheep, were also accessible to wolves throughout the year but were more vulnerable in summer. A more detailed description specific to each study area is presented in Mitchell et al. (2008).

METHODS

We captured and radiocollared wolves as adults, yearlings, and pups (>20 kg; usually >5 months of age) either by foot-hold trapping or helicopter darting and netting. Capture efforts in NWMT were almost exclusively foot-hold traps during May–October; capture in the Yellowstone area was almost exclusively darting in YNP November–February and a combination of trapping and darting outside (yr-round); Idaho was predominately trapping with some

Table 1. Land characteristics of the 3 wolf recovery areas (Central ID [CID], Greater Yellowstone Area [GYA], and northwestern MT [NWMT]) in the Northern Rocky Mountains of the United States. We based land characteristics and area for densities in 2004 on the intensive study area identified in Oakleaf et al. (2006) and on the average of 9-km^2 cells in each recovery area.

Recovery area	Wolf density (no./1,000 km^2)	% private	% federal	% forest	Human density (no./km^2)	Road density (km/km^2)
GYA	1.77	31.7	62.2	31.1	2.34	0.66
CID	3.03	23.2	72.4	47.3	2.64	0.60
NWMT	0.72	36.3	56.3	59.8	3.825	0.77

Table 2. Description of variables we used in analyses of wolf survival in northwestern United States (1982–2004).

Variable	Description and coding system
Demographic	
GENDER	Gender (M = 1)
AGECLASS[a]	Dummy variable representing age class (pup; yearling; ad; old ad [>9 yr])
AGEYEARS[b,c]	Age (yr)
Behavioral	
DISPERSER	Dummy variable representing dispersal status (disperser = 1)
BREEDING[b]	Dummy variable representing breeding status (current breeder = 1)
PACKMEMBER[b]	Dummy variable representing pack affiliation status (with pack = 1)
SMALLPACK[b]	Dummy variable representing small pack size ([pack size <5] = 1)
HOMERANGESIZE[b,c]	95% fixed kernel home range size (km^2)
Temporal	
YEAR[a]	Dummy variables representing each yr of the study (1982–2004)
SEASON[a]	Dummy variable representing each season of the study (Jan–Mar; Apr–Jun; Jul–Sep; Oct–Dec)
Anthropogenic	
ROADS[b,c]	Road density in home range (km^2)
HUMANS[b,c]	Human density in home range (km^2)
FEDERAL[b]	% of home range managed by Federal government
PRIVATE[b]	% of home range under private ownership
STATE	% of home range managed by the State government
CATTLE[b,c]	Cattle density in home range (km^2)
SHEEP[b,c]	Sheep density in home range (km^2)
PROTECTION[b]	Average protection status in home range, determined by Gap Analysis Program (GAP)
Habitat	
ELEVATION[b]	Average elevation in home range (m)/1,000
SLOPE[b]	Average slope in home range (°)
ELK[b]	Dummy variable representing elk as primary prey in home range (elk = 1)
MULEDEER[b]	Dummy variable representing mule deer as primary prey in home range (mule deer = 1)
FOREST[b]	% of home range covered by forest habitat
AGRICULTURAL[b]	% of home range covered by modified agricultural land
Other	
RECOVERYAREA[a]	Recovery area where the subject was resident
RECRUITMENT	Whether subject was recruited as part of representative vs. targeted capture efforts (representative = 1)
PACKSADJACENT[b]	No. of wolf packs adjacent to home range

[a] We developed variable by coding each category into a separate dummy variable.
[b] Available only for a subsample of subjects.
[c] Also includes separate variable representing quadratic relationship ($x + x^2$).

darting and netting (yr-round). Once captured, standard measurements and biological samples such as blood were obtained from each wolf and a very high frequency and occasionally a Global Positioning System radiocollar (Telonics Inc., Mesa, AZ and Televilt Inc., Lindesberg, Sweden) was attached. All radiocollars contained mortality switches that increased radio-signal pulse from approximately 55 beats/minute to approximately 110 beats/minute if a collar was stationary for 4 hours. Radiocollars in mortality mode were retrieved as soon as feasible, usually within 1 week, but some circumstances prevented quick recovery. Cause of death was determined through on-site exams or lab necropsies either because field exams were inconclusive or a law-enforcement investigation was involved. We focused specifically on wolf mortality-rate determinants; wolf cause of death in the context of risk is addressed in other research (D. Murray, Trent University, unpublished data).

Once collared, wolves were typically tracked from aircraft every 7–14 days, but often more frequently, as in YNP where wolves were sometimes tracked daily. When radio contact was lost with a particular wolf, search efforts ensued in the local area for several months. Coordinated high-elevation flights among recovery areas were also flown each year to look for missing wolves.

We related wolf mortality risk to a variety of independent variables (Table 2; Oakleaf et al. 2006). We assessed variables not in Oakleaf et al. (2006) as follows: we categorized PACKSIZE (we considered <5 wolves a small pack and ≥5 wolves a large pack) by observing pack size during winter observations, which typically occurred multiple times per season. We based DISPERSER status of study animals on knowledge of the territory of the radioed wolf after collaring versus its pack affiliation prior to dispersal. We considered a subject animal as resident if it was traveling with pack-mates within its territory and a disperser if it left its established territory not to return. We did not know breeder status for all collared wolves, so we only used related variables when we positively knew breeding status for animals that we either frequently observed or determined to be a breeder through observation of lactation or later pedigree analysis.

Statistical Analysis and Modeling

Hazard modeling.—We right-censored wolves that either died of capture-related causes or whose radio signal

was lost (e.g., transmitter failure, collar loss, emigration from the study area) at their final monitoring date; we censored those that survived until the end of the study on 31 December 2004. We assessed determinants of wolf mortality using Andersen–Gill (AG) hazard models (Fleming and Harrington 1991, Andersen et al. 1993). Briefly, AG methods are analogous to better known Cox proportional hazard models except that AG methods are based on counting process methodology and have greater flexibility including allowing discontinuous risk intervals, which makes AG models particularly well suited for telemetry-based survival analysis using subjects having punctuated survival timelines (Johnson et al. 2004, Murray 2006). The AG method records subject survival time as a function of a binomial censoring variable (1 = failure, 0 = censored) relative to counting, risk, and intensity processes; the counting process is an indicator function equal to 1 when mortality occurs, the risk process is 1 when monitoring is ongoing, and the intensity process is a product of the risk process and hazard function $h(t)$ (Fleming and Harrington 1991, Hosmer and Lemeshow 1999). Integrating the intensity process over time yields the expected number of deaths at t, or the cumulative intensity process. In the resulting models, hazards associated with variables i and j are proportional through time and differ only multiplicatively by the exponential term involving the covariates [$h_i(t)/h_j(t) = \exp(\beta_1)$]. Thus, we can easily evaluate determinants of mortality risk in a subject population using the AG framework, and it follows that such hazard models are considered as semi-parametric because distribution of lifetimes and the baseline hazard function are unspecified and the hazard ratio does not depend specifically on time.

Fitting hazard models to a large set of candidate variables presents a variety of challenges, including dealing with inconsistent functional roles of some variables among groups of subjects or across space and time. We also contended with variables that were incomplete, served as proxies for other variables or survival determinants, or whose role on hazard was interactive. Accordingly, we conducted hazard modeling through a cautious approach that emphasized phenomenological relationships between variables and wolf hazard rather than a rigid approach focused on quantitative cause-and-effect relationships. We fit several families of AG models, with the first series (demographic models) involving demographic, behavioral, and temporal variables (Table 2) for all 711 wolves monitored during the study. Variables under consideration as potential mortality-risk determinants included both continuous and categorical (dummy) variables of which several were time-dependent and could be considered time-varying (i.e., interactive with time, see Table 2); we updated most time-dependent covariates annually (e.g., age, habitat variables) but we updated seasonally those related to wolf behavior (e.g., dispersal, pack size, breeding status). Our limited a priori knowledge of the functional relationship between time-dependent variables and wolf hazard justified using a variety of modeling frameworks to assess variable significance; we conducted analyses using the same variables as either time-

dependent or time-varying, and noted that results were usually qualitatively similar irrespective of variable classification scheme. Therefore, we inferred that the general relationships presented herein are robust and do not depend on variable relationships with time. In most cases we report results from the more conservative time-varying classification scheme.

The main demographic models under evaluation involved complete sets of independent variables (i.e., no missing data) such that we included all subjects in analyses; later models also included partially complete variables and, therefore, used a restricted set of subjects (see below). The first series of analyses pooled recovery areas into an all-inclusive model set, but because we detected area-specific differences in hazard, subsequent analyses considered recovery areas separately, which allowed us to examine determinants of wolf hazard both overall as well as in separate recovery areas with differing baseline habitat and prey availability, level of wolf protection, etc. The method by which we recruited subjects to the study had a profound influence on mortality risk, and this influence failed to conform to the proportional hazards assumption (see below). Therefore, we stratified most models according to subject recruitment method, later segregating demographic models by the RECRUITMENT variable specifically to evaluate hazard differences between groups. Stratification is an important process in hazard modeling and allows for calculation of a stratum-specific baseline hazard function where the assumption of hazard proportionality fails to be upheld (Hosmer and Lemeshow 1999).

The second series of models (habitat models) included spatially explicit behavioral, anthropogenic, and habitat variables associated with the 95% fixed-kernel home range of each subject (Table 2), along with other demographic and behavioral variables considered in the first series of models. We excluded temporal variables from this latter series because their evidence ratios generally were low and precision was poor. Habitat models were restricted to wolves with estimable home ranges and, therefore, excluded subjects that were either nonresident or dispersing or radiolocated too infrequently (<20 locations/yr; see Oakleaf et al. 2006) to estimate their home range. Approaches for dealing with wolf recovery areas and study recruitment method followed those described previously for demographic models. Because we re-estimated home ranges each year, we updated spatially explicit time-dependent covariates according to an annual schedule.

Testing hazard model assumptions.—We can easily test basic distributional and associated assumptions underlying AG models using martingale theory (Fleming and Harrington 1991, Andersen et al. 1993). The functional form of several continuous variables under consideration (e.g., AGEYEARS, ROADS, SHEEP) was not necessarily linear but could be quadratic (Johnson et al. 2004). We evaluated the most appropriate functional form of such variables by examining martingale residuals of fitted AG models against untransformed (x) and transformed ($x + x^2$) forms of each variable. We used the LOWESS regression yielding

approximately linear fit to select the most appropriate functional form (Cleves et al. 2003). The assumption of proportional hazards is critical to AG model fit, and we determined it primarily by assessing proportionality in plots of ln-transformed analysis time versus $-\ln[-\ln(\text{survival probability})]$ (Hougaard 2000, Therneau and Grambsch 2000). We assessed model goodness-of-fit by checking Cox−Snell residuals for a standard exponential distribution where the hazard function equals 1 for all t and, thus, the cumulative hazard for the residuals is linear at approximately $45°$ (Cleves et al. 2003). We conducted influence and leverage analysis by refitting best-fit candidate models with $n - 1$ observations and evaluating differences between the efficient score residual matrix and the variance−covariance matrix, relative to time (Cleves et al. 2003). We do not report the above diagnostics because test results were consistently favorable. Other assumption checking and diagnostic tests are outlined in the Discussion. We constructed hazard models using STATA (Stata Corporation, College Station, TX).

Given the many independent variables under consideration and the phenomenological approach we advocated when developing hazard models, we were unable to model all combinations and our analyses should be considered as exploratory. We examined 2-way interaction terms between all variables in model sets for significance (Hosmer and Lemeshow 1999). Multicollinearity is an important concern in any multivariate regression, but acceptance criteria are poorly identified especially for hazard models having many time-dependent covariates. We assessed variable multicollinearity by sequentially adding variables to our selected models and evaluating stability of the parameter estimates (Mitra and Golder 2002, Van den Poel and Larivière 2004); we considered our use of multimodel inferencing procedures (see below) to help mitigate against the influence of collinearity. We also further assessed inter-relationships between variables via standard collinearity diagnostics and appropriate thresholds (mean variance inflation factor [VIF] > 6.0; individual VIF > 10.0; tolerance < 0.10; condition no. > 30.0; Belsley et al. 1980). Where appropriate, we eliminated models including redundant variables from candidate sets to achieve independence.

We compared hazard models within each set using standard model-selection methods (Burnham and Anderson 2002), and we calculated Akaike's Information Criterion corrected for sample size (AIC_c), AIC_c differences (Δ_i), and AIC_c weights (w_i) to guide model selection. We used $\Delta_i <$ 10 for model evaluation, and $P < 0.10$ for all individual variables, to restrict our set of candidate models to a smaller number with high ecological plausibility. We considered models with $\Delta_i < 2.0$ to be indistinguishable from the best-fit model (Burnham and Anderson 2002). Variables that were not complete for all individuals (e.g., AGEYEARS, BREEDING, PACKMEMBER, SMALLPACK) were subject to restricted analysis where we selected the best-fit model for the complete data set and used a backward stepwise procedure to remove any nonsignificant ($P > 0.10$) variables. Using Δ_i, we then compared the best-fit model

with versus without the restricted variable to assess its significance. Throughout, we report model-averaged hazard ratios, unconditional variances, and weight of evidence for individual variables (Burnham and Anderson 2002). For time-dependent covariates the unit was hazard ratio per day, and we used 90-day and 365-day intervals to describe their influence on subject mortality risk. Where appropriate, we report annual survival rates as determined from a piecewise exponential model (Heisey and Fuller 1985, Hougaard 2000), after having first ascertained that the assumption of constant hazards within the time interval was upheld.

RESULTS

During 1982–2004, we monitored survival of 711 radio-collared wolves across the 3 recovery areas. Animals monitored during 1982–1994 were exclusively from NWMT, whereas those tracked during 1995–2004 also included individuals resulting from reintroductions in GYA and CID (Table 3). Number of individual animals monitored by year initially was low in NWMT and even after 1995 generally remained below numbers for GYA and CID. Numbers of monitored wolves in the GYA and CID increased steadily post-1995 and peaked at the end of the study period in 2004, whereas in NWMT monitored wolves and the wolf population did not increase (Table 3). Notably, number of wolves monitored in all 3 areas increased after 2004 (E. E. Bangs, United States Fish and Wildlife Service, unpublished data). One animal marked in YNP emigrated to Utah, whereas another emigrated from YNP and ultimately died in Colorado; we right-censored both wolves after they left GYA. Most wolves (51.1%) died during the study whereas 26.0% survived until study completion (31 Dec 2004). We censored at the last known live signal wolves either succumbing to unknown fate due to radio-signal loss (21.4%) or dying of capture-related causes (1.5%). Overall, during our study wolves died from legal control (30.0%; $n =$ 363 deaths), illegal mortality (24.0%), natural causes (11.8%), other causes (e.g., vehicle accidents, strife; 21.4%), and unknown causes (11.8%). Overall, annual survival rate of wolves across all recovery areas was 0.750 (0.728, 0.772; $n = 363$ deaths).

Computed as a hazard rate, the method by which we recruited wolves into the study influenced risk of death, with those obtained through targeted sampling having consistently higher risk than the representative sample (log-rank test: $\chi^2_1 = 42.89$, $P < 0.001$; Fig. 2). Overall, 47.3% ($n =$ 579) of wolves recruited through representative sampling and 64.9% ($n = 134$) of those recruited via targeted sampling died during the study. The RECRUITMENT variable failed to conform to the assumption of proportional hazards ($\chi^2_1 = 5.24$, $P = 0.022$) and we therefore stratified it in subsequent analyses. The proportion of animals that we recruited via representative sampling differed among recovery areas (GYA: 88.0% [$n = 299$], CID: 79.0% [$n =$ 219], NWMT: 73.1% [$n = 193$]; $\chi^2_2 = 17.995$, $P < 0.001$), and in each recovery area wolves recruited via targeted sampling had higher mortality risk (GYA: $\chi^2_1 = 31.954$, P < 0.001; CID: $\chi^2_1 = 5.444$, $P = 0.020$; NWMT: $\chi^2_1 =$

	Greater Yellowstone Area				Central ID				Northwestern MT			
Yr	No.	Alive	Dead	Censored	No.	Alive	Dead	Censored	No.	Alive	Dead	Censored
1982									1	1	0	0
1983									0	0	0	0
1984									1	1	0	0
1985									4	4	0	0
1986									6	5	1	0
1987									11	7	4	0
1988									13	11	1	1
1989									20	14	6	0
1990									21	19	1	1
1991									23	12	7	4
1992									23	22	1	0
1993									38	25	13	0
1994									34	16	12	6
1995	20	18	2	0	15	12	2	1	27	17	8	2
1996	39	31	8	0	32	30	1	1	20	11	7	2
1997	45	29	15	1	36	33	1	2	22	13	8	1
1998	46	34	8	4	51	43	6	2	29	17	10	2
1999	54	45	6	3	59	45	11	3	38	25	12	1
2000	59	44	11	4	61	41	15	4	33	15	16	2
2001	92	71	15	6	61	41	11	9	36	31	5	6
2002	105	76	12	17	62	38	16	8	43	22	11	10
2003	133	100	27	6	70	46	6	18	27	16	5	6
2004	156	94	38	24	100	71	20	9	27	23	3	1

16.290, $P < 0.001$; Fig. 3). Overall, mortality rates tended to be higher in NWMT than in the remaining recovery areas (using GYA as reference; CID: $z_1 = 1.55$, $P = 0.12$; NWMT: $z_1 = 2.87$, $P = 0.004$). The recovery area variable conformed to the proportional hazards assumption (global $\chi^2_2 = 2.62$, $P = 0.27$), so we conducted subsequent analyses either with recovery areas pooled or by separate recovery area. Because we monitored only 6 (0.84%) subjects in multiple recovery areas (0.34% of total radio-days), we considered recovery area as a fixed variable.

Pooled Recovery Areas

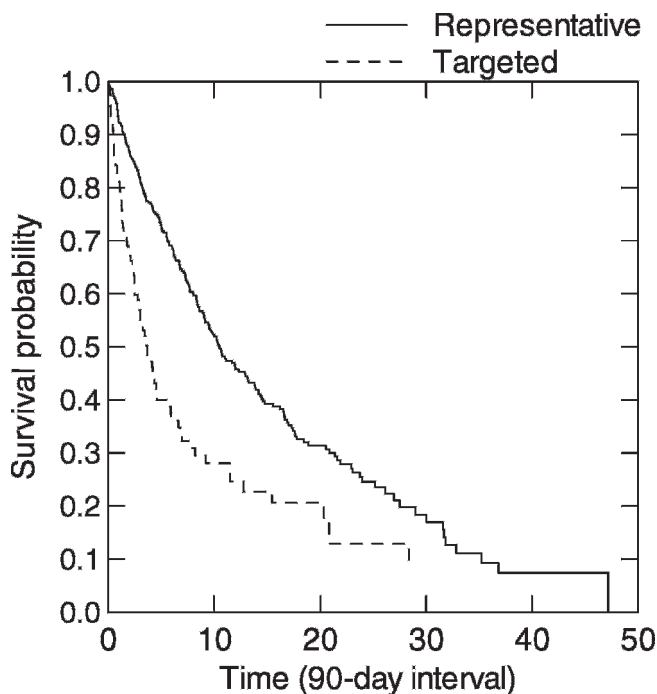Using RECRUITMENT as stratum and a dummy variable (MONTANA) to isolate subjects from NWMT, we

Figure 2. Kaplan–Meyer survivorship probability for wolves in northwestern United States (1982–2004) relative to whether subjects were radiomonitored as part of standard sampling (representative sample) or following focused capture efforts in response to livestock depredation or other problems (targeted sample). The origin (time = 0) corresponds to time of recruitment to the study.
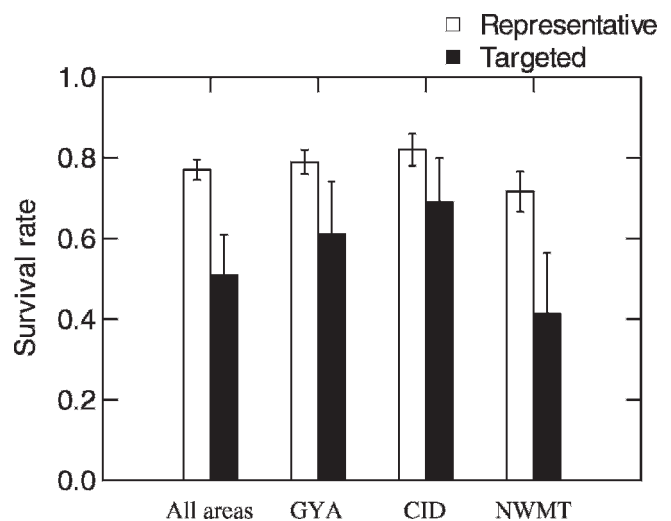

Figure 3. Annual survival rate (±95% CI) for wolves in western United States (1982–2004) by recovery area (GYA: Greater Yellowstone Area; CID: central Idaho; NWMT: northwestern Montana; $n = 711$ wolves, 363 deaths). Wolves were radiomonitored either as part of standard sampling (representative sample) or following focused capture efforts in response to livestock depredation or other problems (targeted sample).

Table 4. Candidate Andersen–Gill hazard models for wolves in northwestern United States (1982–2004), generated from models using demographic, behavioral, and temporal variables (see Table 2 for coding scheme). Sample sizes vary depending on whether models include all recovery areas (subjects = 711, deaths = 361), or are restricted to Greater Yellowstone Area (subjects = 269, deaths = 142), central Idaho (subjects = 175, deaths = 89), or northwestern Montana (subjects = 192, deaths = 130). We provide model parameter number (K), Akaike's Information Criterion corrected for sample size (AIC_c), AIC_c difference (Δ_i), and AIC_c weight (w_i). Likelihood ratio chi-square and P indicate goodness-of-fit for each model relative to the best-fit model. Individual parameter estimates for each model were significant ($P < 0.10$), and we provide only models with $<10\ \Delta_i$. All models were stratified according to whether subjects were recruited to the study for standard monitoring purposes (representative sample) versus following livestock depredations or other perceived problems (targeted sample).

Model	K	AIC_c	Δ_i	w_i	χ^2	P
All recovery areas						
MONTANA + PUP + YEARLING + DISPERSER + (YR 2004)	5	3,543.1	0	0.889	59.10	<0.001
MONTANA + PUP + DISPERSER + (YR 2004)	4	3,548.6	5.5	0.057	51.54	<0.001
MONTANA + PUP + YEARLING + DISPERSER	4	3,548.8	5.7	0.051	51.33	<0.001
MONTANA + YEARLING + DISPERSER + (YR 2004)	4	3,552.3	9.3	0.009	47.77	<0.001
Greater Yellowstone Area						
DISPERSER + (YR 2002)	2	1,165.8	0	0.917	25.91	<0.001
DISPERSER + (YR 2004)	2	1,171.6	5.6	0.055	20.27	<0.001
DISPERSER	1	1,172.9	7.0	0.029	16.93	<0.001
Central ID						
YEARLING + (JUL–SEP) + (YR 2004)	3	656.8	0	0.582	19.92	<0.001
YEARLING + (JUL–SEP)	2	658.1	1.4	0.295	16.41	<0.001
YEARLING + (YR 2004)	2	662.1	1.4	0.039	12.37	0.002
YEARLING + (JAN–MAR)	2	662.2	5.5	0.037	12.25	0.002
(JUL–SEP) + (YR 2004)	2	663.6	6.9	0.018	10.87	0.004
YEARLING	1	663.8	7.0	0.017	8.62	0.003
(JUL–SEP)	1	664.6	7.9	0.11	7.76	0.005
Northwestern MT						
PUP	1	932.4	0	0.711	22.65	<0.001
PUP + (APR–JUN)	2	934.0	1.9	0.289	22.91	<0.001

determined that a range of variables influenced wolf mortality risk. For analyses including all recovery areas, the best model had a high degree of plausibility ($w_i = 0.889$; Table 4) and model variables had high weight of evidence (Table 5). Subjects from NWMT were 1.63 times more likely to die than their counterparts in other recovery areas. Wolf hazards also were influenced by demographic and behavioral variables, with the PUP, YEARLING, and DISPERSER variables each associated with increased mortality risk (Table 4). Daily hazard ratios for time-varying covariates tended to be high. For example, the DISPERSER variable was associated with 8.4% higher mortality risk/90 days ($1.0009^{90} = 1.084$) and 38.9% higher risk/365 days (Table 4). Wolves also experienced higher mortality in 2004. Inclusion of a single 2-way interaction term (MONTANA × PUPS) in the best-fit model improved fit ($\Delta_i = -11.437$; all other interaction terms: $\Delta_i > 2.061$), but small sample sizes precluded robust variance estimation for the PUP variable in this particular model.

Annual survival rate for pups (estimated from autumn to spring monitoring) was 0.398 (0.273, 0.579; 95% CI; $n = 23$ deaths) for NWMT compared to 0.756 (0.635, 0.899; 95% CI; $n = 3$ deaths) and 0.889 (0.777, 1.000; 95% CI; $n = 10$ deaths) for GYA and CID, respectively. Annual survival rates for nonpups (yearlings and ad) were 0.680 (0.643, 0.740; 95% CI; $n = 107$ deaths), 0.771 (0.737, 0.806; 95% CI; $n = 131$ deaths), and 0.789 (0.750, 0.829; 95% CI; $n = 86$ deaths) for NWMT, GYA, and CID, respectively. The proportional hazards assumption was upheld by the best-fit model pooling

Table 5. Model-averaged hazard ratios, unconditional variances, and weight of evidence [$w(E)$] for individual variables in Andersen–Gill models of wolf mortality risk in northwestern United States (1982–2004). We generated model sets from best-fit models using demographic, behavioral, and temporal variables (see Table 2 for coding scheme). Sample sizes vary depending on whether models include all recovery areas (subjects = 711, deaths = 361) or are restricted to Greater Yellowstone Area (subjects = 269, deaths = 142), central Idaho (subjects = 175, deaths = 89) or northwestern Montana (subjects = 192, deaths = 130). All models were stratified according to whether subjects were recruited to the study for standard monitoring purposes (representative sample) versus following livestock depredations or other perceived problems (targeted sample). Hazard ratios >1.0 indicate increased mortality risk.

| Variable	Hazard ratio	SE	Lower 95% CI	Upper 95% CI	$w(E)$
All recovery areas					
MONTANA	1.6274	0.1840	1.2669	1.9880	1.000
DISPERSER	1.0009	0.0002	1.0006	1.0013	1.000
PUP	1.0050	0.0013	1.0025	1.0076	0.991
(YR 2004)	1.0004	0.0002	1.0001	1.0007	0.949
YEARLING	1.0014	0.0005	1.0004	1.0023	0.944
Greater Yellowstone Area					
DISPERSER	1.0015	0.0003	1.0009	1.0022	1.000
(YR 2002)	0.9990	0.0004	0.9982	0.9997	0.917
(YR 2004)	1.0004	0.0002	1.0000	1.0009	0.055
Central ID					
YEARLING	1.0026	0.0009	1.0011	1.0045	0.970
(JUL–SEP)	1.0009	0.0003	1.0003	1.0015	0.907
(YR 2004)	1.0006	0.0003	1.0000	1.0012	0.640
(JAN–MAR)	0.9993	0.0004	0.9986	1.0001	0.037
Northwestern MT					
PUP	1.0081	0.0016	1.0050	1.0112	1.000
(APR–JUN)	0.9994	0.0003	0.9998	1.0000	0.289
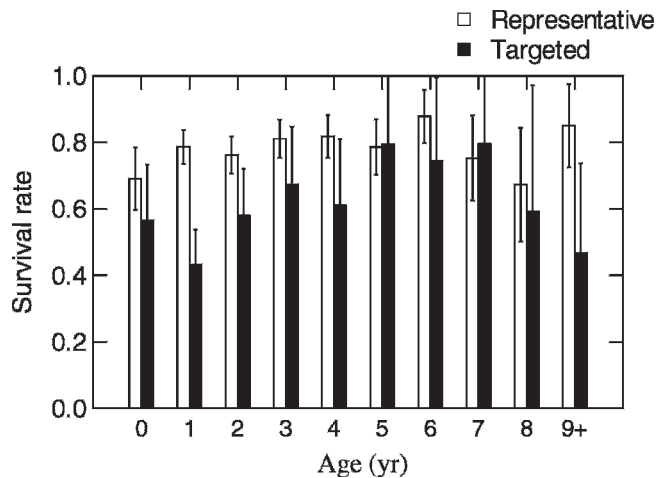
Figure 4. Annual survival rate (±95% CI) for wolves in western United States (1982–2004) by age (n = 618 wolves, 307 deaths). Wolves were radiomonitored either as part of standard sampling (representative sample) or following focused capture efforts in response to livestock depredation or other problems (targeted sample). Survival rates of 0-aged animals (pups) were largely restricted to autumn and winter of their first year (northwestern MT) or winter-only (Greater Yellowstone Area, central ID).

recovery areas (without interaction term; global $\chi^2_5 = 3.96$, $P = 0.56$, all variables $P > 0.20$), independent variables were not strongly correlated (mean VIF = 1.03; all individual VIF < 1.03; all tolerance > 0.960; condition no. = 2.67), and goodness-of-fit tests indicated high concordance between the set of models and the data.

Next, we restricted our analysis to wolves whose precise age was known (86.9% of subjects, n = 711; 85.0% of deaths, n = 361), and replaced PUP and YEARLING from the above best-fit model with the continuous linear variable representing age (AGEYEARS). This variable failed to improve model fit (Δ_i = 13.126), indicating that discrete differences in mortality risk were restricted primarily to pups (representative sample) or pups and yearlings (targeted sample) and that adults did not have marked fine-scale variability in hazards (Fig. 4). A similar analysis restricted to wolves whose current breeding status was known (77.9% of subjects, 66.5% of deaths) did not provide additional explanatory power when we added BREEDING to the best-fit model (Δ_i = 2.175). However, when we restricted the analysis to wolves whose status with respect to pack membership (PACKMEMBER) was known (76.1% of subjects, 63.2% of deaths), the model replacing the dispersal status dummy variable with the variable isolating wolves that were solitary did improve model fit (Δ_i = −7.080; hazard ratio: 1.0008 [1.0004, 1.0013; 95% CI]). Dispersers tended to be solitary, but DISPERSER and PACKMEMBER variables had acceptably low collinearity (mean VIF = 6.65; all individual VIF < 6.65; all tolerance > 0.150; condition no. = 5.474). Thus, we surmised that pack membership likely was a more important determinant of wolf mortality risk than was dispersal status. Yet, even when wolves belonged to a pack the actual size of the group apparently influenced mortality risk; an analysis restricted to animals known to be in a pack and whose pack size could be approximated by a dummy variable (SMALLPACK; 50.9% of subjects, 39.1% of deaths) revealed that mortality risk was elevated among animals belonging to smaller packs (Δ_i = −4.257; hazard ratio: 1.0007 [1.0003, 1.0011; 95% CI]).

Separate Recovery Areas

We refined our hazard models by isolating each recovery area through separate analysis. In GYA, the best-fit model had high certainty compared to other candidates (Table 4). Model-averaged hazards indicated that the time-varying DISPERSER variable increased hazards by 14.4% (1.0015^{90} = 1.14444)/90 days and 72.8%/365 days, compared to residents (Table 5). Mortality rates in GYA appeared to be lower in 2002 and higher in 2004 than other years, although precision and weight of evidence for the latter variable were particularly low (Table 5). When we restricted the analysis only to animals whose pack membership status was known (19.7% of subjects, n = 30 4; 23.2% of deaths, n = 142), we found that models including PACKMEMBER versus DISPERSER were indistinguishable (Δ_i = −0.555; hazard ratio: 1.0015 [1.0007, 1.0023; 95% CI]), implying that the ultimate factor contributing to mortality risk in GYA was unclear. However, in analyses restricted only to wolves that were members of packs, we determined that the SMALL-PACK variable was associated with higher mortality risk (Δ_i = −3.355; hazard ratio: 1.0007 [1.0002, 1.0013; 95% CI]).

For CID, the best-fit candidate model had weak certainty, with several other candidate models having comparable Δ_i (Table 4). The YEARLING variable was present in each of the better models and had a high weight of evidence (Tables 4, 5); hazards for yearling wolves was 26.3% higher/90 days, and 2.580 times higher/365 days, than for nonyearling animals. Annual survival rate was 0.580 (0.395, 0.708; 95% CI) for yearlings (n = 29 deaths) and 0.812 (0.758, 0.854; 95% CI) for nonyearlings (n = 60 deaths). Mortality risk in CID was lower during 2002 and possibly higher in 2004 (Table 4). Restricted analysis for CID indicated that PACKMEMBER (86.5% of subjects, n = 221; 81.9% of deaths, n = 89) provided comparable explanatory power to the best-fit model excluding this variable (Δ_i = 1.136; hazard ratio: 1.0005 [0.9995, 1.0015; 95% CI]). Similarly, SMALLPACK failed to provide additional explanatory power (Δ_i = −0.487; hazard ratio: 0.9984 [0.9963, 1.0001; 95% CI]). Thus, we infer that neither pack membership nor pack size influenced mortality risk in CID.

For NWMT, the univariate model including PUP was the best fit, and both candidate models contained the PUP variable (Table 4). Based on their September–March survival rate, pups had 2.1 and 19.0 times higher mortality risk/90 days and 365 days, respectively, compared to nonpups (Table 4). Annual survival rate was 0.398 (0.273, 0.579; 95% CI) for pups (n = 23 deaths) and 0.690 (0.643, 0.740; 95% CI) for nonpups (yearlings and ad pooled; n = 107 deaths). Restricted analysis did not indicate that either PACKMEMBER (Δ_i = 8.102; 30.3% of subjects, n = 192; 23.6% of deaths, n = 130) or SMALLPACK (Δ_i = 2.441;

Table 6. Model-averaged hazard ratios, unconditional variances, and weight of evidence [w(E)] for Andersen–Gill models of wolf mortality risk in northwestern United States (1982–2004). We generated model sets for recovery areas pooled from best-fit models using demographic and behavioral variables (see Table 2 for coding scheme). We ran separate models depending on whether subjects were recruited to the study for standard monitoring purposes (representative sample) versus following livestock depredations or other perceived problems (targeted sample). Hazard ratios >1.0 indicate increased mortality risk.

	Representative					Targeted				
Variable	Hazard	SE	Lower 95% CI	Upper 95% CI	w(E)	Hazard	SE	Lower 95% CI	Upper 95% CI	w(E)
PUP	1.0060	0.0013	1.0035	1.0084	1.00					
DISPERSER	1.0009	0.0002	1.0005	1.0013	1.00	1.0011	0.0006	1.0000	1.0023	0.566
MONTANA	1.5020	0.1948	1.1202	1.8839	0.982	1.7281	0.3887	0.9663	2.4899	0.910
(DISPERSER × YEARLING)	1.0027	0.0009	1.0010	1.0045	0.638	0.9975	0.0015	0.9945	1.0004	0.397
YEARLING	1.0012	0.0006	1.0001	1.0023	0.318	1.0021	0.0011	1.0000	1.0042	0.571
GENDER	1.2342	0.1546	0.9655	1.5778	0.188	0.6491	0.1429	0.3689	0.9292	0.492

30.3% of subjects, 23.6% of deaths) influenced wolf hazards in northwestern Montana.

Subject Recruitment Method

Hazards models developed for subjects recruited via representative versus targeted sampling (all recovery areas pooled) revealed several similarities but also differences between groups of subjects. Hazard was consistently higher in Montana and among dispersers, and effect sizes also were comparable between groups (Table 6). However, pups only had higher mortality risk in the representative sample. Dispersing yearlings (DISPERSER × YEARLING interaction term) had higher and lower than average hazard in the representative and targeted samples, respectively, whereas risk was higher among males versus females in the representative versus targeted sample (Table 6). Restricted analysis indicated that for the representative sample BREEDING did not influence mortality risk ($\Delta_i > 1.199$). Although addition of the PACKMEMBER variable to the best-fit model for the representative sample provided equivocal results compared to the best-fit model ($\Delta_i = -1.669$; hazard ratio: 0.9989 [0.9978, 0.9999; 95% CI]), inclusion of SMALLPACK revealed negative effects of membership in small packs ($\Delta_i = -5.957$; hazard ratio: 1.0006 [1.0002, 1.0010; 95% CI]). For the targeted sample of wolves, none of the restricted variables were associated with hazards (all $\Delta_i > 1.710$) although statistical power was notably lower due to the smaller sample size. Thus, we infer that mortality risk patterns likely differed between the representative and targeted sample of wolves, but the particular association between covariates and mortality risk was largely equivocal in the latter group.

Habitat and Anthropogenic Variables

The next series of hazard models was restricted to 297 individuals (41.8% of total sample) that had a fixed home range with estimable habitat and anthropogenic variables. When we pooled recovery areas, 15 candidate models met our criteria for consideration ($\Delta_i < 10.0$, all $P < 0.10$) although 10 models had markedly low explanatory power ($w_i < 0.05$ and all $\Delta_i > 3.480$). Overall, 9 variables were associated with wolf hazard, with the MONTANA variable being present in all models and the PUP variable common

to most (Table 7). Wolf mortality risk also was negatively associated with the index of wolf density (PACKSADJACENT); parameter estimates for this variable indicated that on average, wolf mortality risk decreased by 2.7% (0.9997^{90} = 0.973)/90-day (10.4%/365-day) interval for each additional wolf pack with a home range that was adjacent to that of the subject in question (Table 7). Hazards tended to be higher among wolves at high elevations, in areas where agricultural cover was more abundant, and where forest cover was scarce. Wolf hazard was higher in areas where mule deer were the most common wild ungulate prey, as well as where cattle and sheep were more abundant (Table 7). Overall, the weight of evidence for most variables supported their strong association with wolf mortality risk (Table 7). All 2-way interaction terms were nonsignificant (all $P > 0.19$), and the best-fit hazard model satisfied the assumption of proportional hazards (global $\chi^2_4 = 1.00$, $P = 0.91$ all variables $P > 0.17$). Variables in the best-fit model set had acceptably low correlation (mean VIF = 1.77; all individual VIF < 2.83; all tolerance > 0.354; condition no. = 26.74), and all models had good fit. Analyses restricted to subjects with known breeding status (CURRENTBREEDING: 91.2% of subjects, $n = 297$; 84.4% of deaths, $n = 109$; $\Delta_i = 2.199$), known pack status (PACKMEMBER: 87.9% of subjects, 82.6% of deaths; $\Delta_i = 2.001$), and known pack size (SMALLPACK: 60.3% of subjects, 42.2% of deaths; $\Delta_i = 2.144$) failed to improve model fit.

For GYA, 15 models and 10 main variables were included in our candidate set, with 7 models having markedly low explanatory power ($w_i < 0.05$, all $\Delta_i > 3.210$). Notably, the best-fit model also had low explanatory power ($w_i = 0.214$), implying that several candidates were in contention. Model-averaged hazards indicated that the index of wolf density (PACKSADJACENT) was importantly associated with wolf hazards, with higher local wolf density correlating with reduced mortality risk (Table 7). Wolves with a higher percentage of their home range under State management, and also having more agricultural cover in their territory, also had higher risk in GYA. Several additional variables also were associated with higher hazards, but these tended to have low effect size and poor weight of evidence (Table 7). No demographic or behavioral variables were included in habitat-based hazard models for GYA, and current breeding

Table 7. Model-averaged hazard ratios and unconditional variances, and weight of evidence [w(E)] for Andersen–Gill hazard models, for wolves in northwestern United States (1982–2004) generated from models using demographic, behavioral, and habitat variables (see Table 2 for coding scheme). Habitat variables were available for a subsample of animals used in previous analyses, and sample sizes vary depending on whether models include all recovery areas (subjects = 297, deaths = 109), Greater Yellowstone Area (subjects = 139, deaths = 39), central Idaho (subjects = 89, deaths = 25), or northwestern Montana (subjects = 69, deaths = 45). All models were stratified according to whether subjects were recruited to the study for standard monitoring purposes (representative sample) versus following livestock depredations or other perceived problems (targeted sample). Hazard ratios >1.0 indicate increased mortality risk.

Variable	Hazard ratio	SE	Lower 95% CI	Upper 95% CI	w(E)
All recovery areas					
MONTANA	6.3129	2.1108	2.1758	10.4500	1.00
PACKSADJACENT	0.9997	0.0001	0.9996	1.0000	0.974
PUP	1.0064	0.0023	1.0019	1.0109	0.893
ELEVATION	1.0012	0.0005	1.0001	1.0022	0.849
AGRICULTURAL	1.0004	0.0002	1.0001	1.0008	0.374
MULEDEER	1.0007	0.0003	1.0001	1.0014	0.360
CATTLE	1.0010	0.0005	0.9999	1.0020	0.293
SHEEP	1.0016	0.0006	1.0005	1.0028	0.072
FOREST	1.0000	0.0000	1.0000	1.0000	0.025
Greater Yellowstone Area					
PACKSADJACENT	0.9997	0.0001	0.9995	1.0000	0.875
STATE	1.0002	0.0000	1.0001	1.0002	0.380
AGRICULTURAL	1.0004	0.0002	1.0000	1.0008	0.287
FEDERAL	1.0000	0.0000	1.0000	1.0000	0.129
PROTECTION	1.0005	0.0002	1.0001	1.0010	0.158
ROADS[a]	1.0012	0.0008	0.9996	1.0028	0.099
ELEVATION	1.0024	0.0011	1.0003	1.0046	0.076
PRIVATE	1.0000	0.0000	1.0000	1.0000	0.075
MULEDEER	1.0007	0.0004	1.0000	1.0014	0.073
CATTLE	1.0001	0.0000	1.0000	1.0002	0.064
Central ID					
MULEDEER	0.9997	0.0035	0.9900	1.0039	0.994
CATTLE	0.9941	0.0029	0.9884	0.9998	0.908
(MULEDEER × CATTLE)	1.0036	0.0011	1.0013	1.0058	0.811
SHEEP	1.0030	0.0014	1.0002	1.0057	0.046
ELEVATION	1.0007	0.0012	0.9984	1.0031	0.018
Northwestern MT					
PUP	1.0089	0.0049	0.9994	1.0185	0.774
PRIVATE	1.0000	0.0000	1.0000	1.0001	0.379
FEDERAL	1.0000	0.0000	0.9999	1.0000	0.216
FOREST	0.9999	0.0000	0.9999	1.0000	0.188
(PUP × PRIVATE)	0.9998	0.0001	0.9996	1.0000	0.142
CATTLE	1.0005	0.0002	1.0001	1.0009	0.113
SHEEP	1.0081	0.0045	0.9993	1.0168	0.099

[a] Quadratic relationship.

status, pack membership, and membership in a small pack were not related to hazards (all $\Delta_i > 2.085$).

For CID, 6 models and 6 variables were in the model set, with 4 models having low power ($w_i < 0.05$, all $\Delta_i > 5.741$). The best-fit model ($w_i = 0.811$) included variables MULEDEER and CATTLE, with the model-averaged estimates indicating an overall lower mortality risk within areas with higher mule deer and cattle numbers. However, the MULEDEER × CATTLE interaction term was significant, indicating that wolves had higher mortality risk in areas where both were abundant (Table 7). Annual survival rates, segregated according to the 50th percentile for

the MULEDEER × CATTLE term, were 0.920 (0.847, 0.958; 95% CI) versus 0.704 (0.640, 0.756; 95% CI) for the lower versus upper group, respectively. Additional spatially explicit variables related to mortality risk included SHEEP and ELEVATION; no demographic or behavioral variables were included in the candidate set of models (Table 7).

For NWMT, 12 models were considered as candidates with 4 having $w_i < 0.05$ (all $\Delta_i > 2.597$). As noted in demographic models, pups had higher mortality risk compared to nonpups (Table 7). Model-averaged hazards also were weakly associated with land management status (PRIVATE, FEDERAL), agricultural activities (CATTLE, SHEEP), and presence of forest cover in the home range. However, several variables had markedly low parameter estimates and large uncertainty. The significant PUP × PRIVATE interaction term indicated that pups had lower hazards where there was a high degree of private land ownership (Table 7).

DISCUSSION

Overall, we contend that annual wolf survival rates were likely adequate to sustain all 3 populations (Keith 1983, Fuller et al. 2003, Adams et al. 2008). When considered with even modest connectivity, whether natural or artificial, population viability is likely enhanced (USFWS 1994). Wolves in NWMT, however, were especially susceptible to human-caused mortality (E. E. Bangs, unpublished data) and in some cases mortality risk could have limited population growth rate. Indeed, population growth in NWMT was stationary or negative some years from 1995 to 2004 compared to the 2 other recovery areas where numbers increased concurrently (USFWS et al. 2005). Lower survival in NWMT was a finding contrary to our prediction of equal survival across recovery areas, and surprising given that wolves naturally recolonized this area, had a highest level of legal protection, and had been present for a longer period (Ream et al. 1991). This finding of lower survival in NWMT underscores the importance of metapopulation structure and refugia where populations function in a quasi-independent fashion, yet are sufficiently connected to allow for possible rescue effects (Levins 1969).

Our finding that wolf hazards were higher in NWMT was probably partly because GNP and BMWA did not function as high-quality wolf habitat (most of both areas are high in elevation and have low densities of potential prey during winter) and few wolves lived there (USFWS et al. 2005; Fig. 1). In contrast, CID and GYA were either inaccessible wilderness areas or, in the case of YNP, supported many wolves with high survival. For example, because most wolf mortality in our study area was of anthropogenic origin (E. E. Bangs, unpublished data) we considered that human access contributed negatively to wolf survival and that national parks (YNP) and remote wilderness areas (CID) where such access was limited or actively controlled are favorable to wolf survival. In NWMT, most wolves lived outside protected areas (Fig. 1), probably because year-round prey were scarce within those protected areas and more private land was present than in either CID or GYA

(Table 1). Thus, it is not surprising that wolves in NWMT had lower survival rates than their counterparts in other recovery areas.

In NWMT, poor survival was associated with cattle and sheep, low forest cover, and mule deer as primary prey; each of these factors is related to low-elevation habitat, private land, or agricultural activities. A habitat model by Oakleaf et al. (2006) also found less natural habitat available to wolves in NWMT. Agriculture per se was not unique to NWMT because all 3 recovery areas had substantial portions of land in agricultural use (Oakleaf et al. 2006), but NWMT was the most fragmented landscape (Table 1) with fewest wolves living in truly protected areas (Fig. 1). In contrast, both YNP and CID wilderness provided large areas of forested cover with abundant prey and protection from humans or infrequent human use.

In GYA, hazards were notably high among dispersers, suggesting that as wolves emigrated from YNP they encountered humans outside a park setting and, thereby, were subject to higher risk compared to YNP residents (Smith et al. 2007). In CID, yearlings had higher mortality risk, which, because most dispersing wolves tend to be yearling animals, likely identifies the same cohort of animals as those observed in GYA as being particularly susceptible to mortality when leaving protected areas (Adams et al. 2008, Person and Russell 2008). Pack membership increased survival, which probably acted to limit movements and retain wolves on a territory where conflicts were at least less than wandering wolves. Lower survival of dispersing and young wolves may only occur in exploited wolf populations because disperser survival is high in protected areas (Pletscher et al. 1997, Smith et al. 2007, Adams et al. 2008). Further support for this idea comes from differing survival rates for wolves collared due to livestock damage (targeted sampling) versus monitoring (representative) purposes. More wolves were collared in NWMT because of conflicts with livestock and these wolves had lower survival compared to wolves collared for monitoring purposes in the other recovery areas.

Pack density was highest in the northern reaches of YNP, which decreased mortality risk and is suggestive of positive density dependence, the opposite of NWMT in the early recovery period where there was low density and higher survival compared to our results (Ream et al. 1991, Pletscher et al. 1997). Further, our study found pack membership increased survival (but not breeding status), probably by reducing movement through high-risk areas both because of intraspecific mortality (territorial attacks) and livestock conflicts. But pack membership alone did not connote higher survival because in packs of ≤5 wolves survival was lower. These small packs were likely newly formed (and therefore small) and in marginal areas, or they were in chronically high risk areas and small because of control actions or illegal killing, and either cause would contribute to lower survival. For example, in GYA wolf packs outside YNP were smaller probably because of mortality associated with control actions, again suggestive of the source–sink dynamic that may be functioning in all of the recovery areas

(NWMT, and especially GNP and BMWA, may be a sink; USFWS et al. 2005). In YNP, anecdotal evidence also suggests that small packs were at a competitive disadvantage to larger packs and suffered more intraspecific death (the leading cause of mortality in YNP; Smith et al. 2007).

Our results contrast with early studies of wolves in NWMT (Ream et al. 1991, Pletscher et al. 1997, Boyd and Pletcsher 1999). Especially poor survival for NWMT pups is notable and may be partially due to time of collaring. In NWMT pups were typically collared in autumn when they were just large enough to support a collar. Calculations of survival then included autumn (a time potentially difficult for pups, especially if food is limiting) and overwinter mortality, whereas in CID and GYA pups were mostly collared in winter, making comparisons problematic. Regardless, these high mortality rates are suggestive of poor recruitment in NWMT compared to the other recovery areas and may be reflective of habitat quality (e.g., ungulate density and vulnerability to humans) compared to when wolves were colonizing the area (Ream et al. 1991). Adult survival from NWMT was higher during the colonization phase, which was probably due to low wolf density and more prey, but also because most wolves then lived within protected areas (GNP; Pletscher et al. 1997).

Our findings are not surprising in light of wolf studies elsewhere and are strongly supportive of the influence of human-caused mortality on wolf populations (Adams et al. 2008, Person and Russell 2008). Humans were important to survival of wolves in other regions and outside of protected areas dispersers had lower survival (Pletscher et al. 1997, Fuller 1989, Adams et al. 2008, Person and Russell 2008). This same dynamic appears to be operating across the NRM with no legal harvest but where human access and settlement is high compared to other wolf populations. Both CID and GYA have an area of overlay on secure habitat with adequate ungulate density contributing to high survival (Oakleaf et al. 2006). It is possible that once human harvest is allowed within the NRM this will substitute for mortality due to control and illegal take. This, however, is speculation because total mortality will still be important as harvest may be additive or partially additive.

Eventual harvest mortality will probably lower wolf survival across all 3 recovery areas, but without harvest there does not appear to be region-wide synchrony in survival. Lack of a region-wide trend enhances metapopulation structure for wolf recovery in the NRM allowing for population rescue if necessary. Wolf survival was low in 1999 in YNP but not in GYA due to disease, yet this was not the case anywhere else (Smith and Almberg 2007). Year and season were also not significant, except weakly in 2002 and 2004, suggesting lack of mortality synchrony region-wide, bolstering population stability in the event any one population should decline. Most wolves died of natural mortality in the core areas of CID and GYA (E. E. Bangs, unpublished data) and each population has different causes and rates, further strengthening wolf population viability in the NRM (USFWS et al. 2005, Smith et al. 2007).

Analytical Issues Potentially Influencing Results

We relied extensively on continuous-time survival analysis to elucidate patterns of wolf mortality risk. Such methods are bound by several important restrictions that may be particularly relevant in wildlife research (Murray 2006). Wolf recruitment to our study occurred either via standard capture efforts involving opportunistic radiotransmitter deployment (representative sampling) or specifically in response to livestock depredations or other perceived problems (targeted sampling). Deployment of transmitters through representative sampling usually was stratified across wolf packs within a recovery area, with a representative sample of packs monitored continuously in each area and <3 animals/pack typically monitored at any given time. Targeted sampling usually involved transmitter deployment near livestock grazing areas and included either solitary individuals or 1–2 members of a pack. Animals obtained through targeted sampling were recruited specifically to facilitate relocation in the event of further problems so that appropriate management actions (e.g., euthanasia, transplant) could be implemented. Thus, the latter sample was biased toward animals having higher mortality risk. Because recruitment method influenced wolf hazard and the RECRUITMENT variable did not conform to the proportional hazards assumption, in our main analyses we stratified AG models according to recruitment method. We also ran separate analyses for representative versus targeted subjects specifically to evaluate potential hazard differences between groups.

Wolf mortality risk often is correlated among pack members, implying that multiple transmitter deployments per pack could violate the assumption of independence. Robust variance estimation (clustering) adjusts hazards to reflect lack of independence (Hosmer and Lemeshow 1999), but we were limited in our ability to cluster because of the many wolf packs monitored (no. of packs: GYA: 57; CID: 65; NWMT: 53), lack of pack affiliation among many subjects (e.g., dispersers), and unknown pack affiliation status of many animals. However, because a subset of our analyses involved models with spatially explicit variables that were restricted to animals with known home ranges, we adjusted variances via clustering in a subset of analyses. Note that clustering improved model precision but did not alter our results qualitatively.

Subjects that we censored from analysis should represent a random sample of the population but could be biased toward those prone to dispersing or having defective transmitters. Censoring bias also could be incurred if wolves were killed illegally and their transmitters were destroyed intentionally at the time of death (Murray 2006). We minimized the influence of these potential confounds by searching for missing transmitters via wide-ranging telemetry flights conducted several times per year and intensifying local monitoring when specific radio frequencies went missing. The proportion of radiocollared wolves disappearing during the study was comparable among recovery areas (GYA: 20.4%, $n = 299$; CID: 23.3%, $n = 219$; NWMT: 19.7%, $P = 0.62$), implying that we likely detected emigrating animals at similar rates in all areas. Because we always deployed transmitters with new batteries (normal transmitter lifespan was approx. 3.5 yr with low known premature failure rate), the comparable duration of transmitter lifespan between censored versus uncensored animals (mean censored timeline: 661.9 [355.5; median] days, $n = 150$; mean uncensored timeline: 635.1 [370.0] days, $n = 561$) implies an absence of bias. In addition, differences in survival timelines were not related to gender or age class (all $P > 0.12$) despite the likely disparity in dispersal rates among these cohorts.

The proportion of dispersers whose signal was lost (31.4%, $n = 108$) differed from that for residents succumbing to a similar fate (18.1%, $n = 557$; $P = 0.002$). Also, we detected a relationship between anthropogenic factors and signal loss, where CATTLE, ROADS, and PRIVATE (all $P < 0.003$) each differed between fate unknown versus known dead or alive animals. However, in each case the odds ratio for the logistic regression model indicated reduced risk of signal loss in areas of high human activity, contrary to our a priori prediction (i.e., humans were responsible for lost signals due to tampering with the collar after a wolf was killed illegally), and likely implied reduced monitoring intensity (and higher signal loss and censoring) in remote areas of each recovery area. Thus, we consider that modest informative censoring was present in our sample and was associated principally with dispersal status rather than human-caused mortality.

Survival research requires that the time origin be clearly identified, which may be problematic in wildlife research where recruitment is staggered (left truncation) and early mortalities can be common (Pollock et al. 1989, Winterstein et al. 2002). To be comprehensive, our analysis included a sample of subjects monitored in Montana in the 1980s, but most animals were recruited to the study after releases in GYA and CID in 1995 (Table 2). We controlled for variable start times by isolating recovery areas in specific analyses, but analyses restricted to the 1995–2004 period did not differ qualitatively from those reported herein (D. Murray, unpublished data). Furthermore, inclusion of temporal variables (i.e., season, yr) in our models generally did not alter our findings qualitatively and parameter estimates associated with temporal variables tended to have low precision and poor weight of evidence. Thus we infer that the extensive left truncation in our study did not markedly alter our results.

If subjects are not monitored continuously in time, timing of death events may be imprecise and survival times may be artificially tied (Bunk et al. 1995, Murray 2006). In our study frequency of survival assessment varied both temporally and among the 3 recovery areas but generally occurred at <14-day intervals (E. E. Bangs, unpublished data). This level of discontinuity is characteristic of many survival studies involving large mammals and should impose limited loss of precision in death time assessment if mortalities were assumed to have occurred at the interval midpoint (Murray 2006). Yet, we used the Breslow approximation (Hosmer and Lemeshow 1999) to address tied failure times and consider that any lack of death-time precision should be

negligible relative to the overall duration of wolf timelines. Accordingly, the high relocation certainty and continuous nature of wolf survival timelines confirmed that continuous-time analytical methods were most appropriate (see Murray and Patterson 2006).

MANAGEMENT IMPLICATIONS

Unlike Canada and Alaska, where wolves have persisted and been harvested for decades, the NRM does not have large reservoirs of wolves away from areas of high human population density (Boitani 2003, Adams et al. 2008). Consequently management will need to be more intensive, both to resolve conflicts and to maintain wolf populations. As such, we offer these 3 management recommendations. First, we found that GNP and BMWA do not function as a large refugium from which wolves could emigrate into the surrounding area (USFWS 1987; Fig. 1). Therefore, increasing the survival of wolves around this area or in nearby Canada or CID would improve population status in NWMT by retention of resident animals or by emigration. Increasing survival here would involve reducing conflicts with livestock and reducing illegal killing. Second, we recommend that survival rates continue to be monitored if each segment of the NRM wolf population is not managed at high levels that are well above minimum recovery requirements. If the NRM wolf subpopulations are managed at lower levels, intensive monitoring of wolf survival rates is likely necessary. Further, our study found greater survival in wolves collared for monitoring purposes compared to those collared because of livestock conflict (representative vs. targeted), thereby emphasizing the need to monitor survival with the onset of legal human harvest to learn if harvest may be compensatory or additive. The source–sink dynamic we found depends on high survival somewhere in the region, so any change in management action must monitor survival in both sink and source areas. Third, higher wolf survival in some areas outside core recovery areas is necessary to maintain connectivity and natural dispersal. Because young or dispersing wolves had lower survival in both CID and GYA, and because managing age-specific harvest is not possible, we recommend harvest regulations that enhance opportunity for natural dispersal between recovery areas, especially linkages with GYA.

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