Relative influence of human harvest, carnivores, and weather on adult female elk survival across western North America

Jedediah Brodie[1]*, Heather Johnson[2], Michael Mitchell[3], Peter Zager[4], Kelly Proffitt[5], Mark Hebblewhite[6], Matthew Kauffman[7], Bruce Johnson[8]†, John Bissonette[9], Chad Bishop[2], Justin Gude[5], Jeff Herbert[5], Kent Hersey[10], Mark Hurley[4,6], Paul M. Lukacs[6], Scott McCorquodale[11], Eliot McIntire[12]‡, Josh Nowak[12], Hall Sawyer[13], Douglas Smith[14] and P.J. White[14]

[1]*Wildlife Cooperative Research Unit, University of Montana, Missoula, MT 59812, USA;* [2]*Colorado Parks and Wildlife, 415 Turner Drive, Durango, CO 81303, USA;* [3]*U.S. Geological Survey, Wildlife Cooperative Research Unit, University of Montana, Missoula, MT 59812, USA;* [4]*Idaho Department of Fish and Game, P.O. Box 25, Boise, ID 83707, USA;* [5]*Montana Fish, Wildlife, and Parks, 1420 E. 6th Ave., Helena, MT 59620, USA;* [6]*Wildlife Biology Program, University of Montana, Missoula, MT 59812, USA;* [7]*U. S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA;* [8]*Oregon Department of Fish and Wildlife, 1401 Gekeler Lane, La Grande, OR 97850, USA;* [9]*U.S. Geological Survey- Utah Cooperative Fish and Wildlife Research Unit, College of Natural Resources, Utah State University, Logan, UT 84341, USA;* [10]*Utah Division of Wildlife Resources, Salt Lake City, UT 84114, USA;* [11]*Washington Department of Fish and Wildlife, 1701 S 24th Ave, Yakima, WA 98902, USA;* [12]*Centre d'étude de la forêt, Laval University, Quebec, QC G1K 7P4, Canada;* [13]*Western Ecosystems Technology, Inc., 200 South 2nd St., Laramie, WY 82070, USA;* [14]*Yellowstone Center for Resources, P.O. Box 168, Officer's Row Bldg 27, Yellowstone National Park, WY 82190, USA;*

Summary

1. Well-informed management of harvested species requires understanding how changing ecological conditions affect demography and population dynamics, information that is lacking for many species. We have limited understanding of the relative influence of carnivores, harvest, weather and forage availability on elk *Cervus elaphus* demography, despite the ecological and economic importance of this species. We assessed adult female survival, a key vital rate for population dynamics, from 2746 radio-collared elk in 45 populations across western North America that experience wide variation in carnivore assemblage, harvest, weather and habitat conditions.

2. Proportional hazard analysis revealed that 'baseline' (i.e. not related to human factors) mortality was higher with very high winter precipitation, particularly in populations sympatric with wolves *Canis lupus*. Mortality may increase via nutritional stress and heightened vulnerability to predation in snowy winters. Baseline mortality was unrelated to puma *Puma concolor* presence, forest cover or summer forage productivity.

3. Cause-specific mortality analyses showed that wolves and all carnivore species combined had additive effects on baseline elk mortality, but only reduced survival by < 2%. When human factors were included, 'total' adult mortality was solely related to harvest; the influence of native carnivores was compensatory. Annual total mortality rates were lowest in populations sympatric with both pumas and wolves because managers reduced female harvest in areas with abundant or diverse carnivores.

‡Present address: Natural Resources Canada, 506 Burnside Road W, Victoria, BC V8Z 1M5, Canada
*Correspondence author. E-mail: jedediah.brodie@gmail.com
†Authorship alphabetical after B. Johnson.

4. Mortality from native carnivores peaked in late winter and early spring, while harvest-induced mortality peaked in autumn. The strong peak in harvest-induced mortality during the autumn hunting season decreased as the number of native carnivore species increased.

5. *Synthesis and applications.* Elevated baseline adult female elk mortality from wolves in years with high winter precipitation could affect elk abundance as winters across the western US become drier and wolves recolonize portions of the region. In the absence of human harvest, wolves had additive, although limited, effects on mortality. However, human harvest, and its apparent use by managers to offset predation, primarily controls overall variation in adult female mortality. Altering harvest quotas is thus a strong tool for offsetting impacts of carnivore recolonization and shifting weather patterns on elk across western North America.

Key-words: additive mortality, *Cervus elaphus*, climate change, compensatory mortality, harvest, predation, ungulate

Introduction

Global ecological change can make the management of harvested populations increasingly difficult. Altered environmental and human socioeconomic conditions can affect the demography (Hidalgo *et al.* 2011) and yield (Minns & Moore 1992) of harvested species. Mitigating these impacts (cf. Boyce *et al.* 2012) requires an understanding of how diverse ecological and human-related factors affect population dynamics, although such an understanding can be difficult to achieve.

In long-lived wildlife species, adult survival typically has strong effects on population dynamics. Although adult survival rates in such species are often relatively stable through time (Gaillard, Festa-Bianchet & Yoccoz 1998), small changes in adult survival generally have much larger impacts on population growth rates than do equivalent changes in other vital rates (Pfister 1998; Morris & Doak 2002). Moreover, for ungulate populations that are hunted, wildlife managers influence population size via adult survival by manipulating harvest, particularly of adult females given their strong effects on population dynamics relative to males (Fujiwara & Caswell 2002; Morris & Doak 2002).

Numerous studies have assessed the impacts of single factors (e.g. harvest alone or a single native carnivore species) on adult survival of harvested species, but we have poor understanding of the relative influence of the suite of factors that have been found to influence survival (McCorquodale, Wiseman & Marcum 2003; Toigo *et al.* 2007, 2008; Bischof, Mysterud & Swanson 2008). This knowledge gap stems, in part, from difficulty in drawing inference from single-site studies about important drivers of survival, such as carnivore species richness (Salo *et al.* 2010; Griffin *et al.* 2011), hunting pressure (Biederbeck, Boulay & Jackson 2001; Vucetich, Smith & Stahler 2005), habitat quality (Melis *et al.* 2009), land-use (Cole, Pope & Anthony 1997) and weather (Hebblewhite 2005), which often have limited variability at a particular locality.

The population dynamics of elk are of particular concern across western North America because of their strong ecological impacts (Riggs *et al.* 2000; Kauffman, Brodie & Jules 2010) and economic importance (Manfredo *et al.* 2004). Yet, many of the factors that may drive adult elk survival, and thus potentially abundance, are changing across the region. Native carnivores such as wolves and grizzly bears *Ursus arctos* are recolonizing areas from which they had been extirpated, winters have been warmer with less snow (Mote *et al.* 2005), and summer temperatures are increasing in many areas (Westerling *et al.* 2006), potentially influencing elk habitat quality. Such changes highlight the importance of understanding the factors driving 'baseline' (i.e. non-human-related) elk mortality. In addition to baseline variation in elk demography, human harvest comprises an important source of elk mortality. Thus, it is increasingly important to understand the net impacts of abiotic, biotic, and human-related factors on adult elk mortality to effectively manage this species across wide geographical areas in the face of changing ecological conditions. Such knowledge may also inform managers of potential consequences to other harvested but less-studied species.

A better understanding of how to adapt harvest objectives to this suite of changes may help inform ungulate management across North America and Europe. For example, given the recent recovery of large carnivores, there is great uncertainty about whether newly established carnivore populations will cause ungulate declines. The impacts of carnivores on ungulate populations largely depend on the magnitude of predation-induced mortality, the sexes and stage classes that are killed, the degree to which predation is additive vs. compensatory, and on the cumulative impacts of carnivore mortality relative to human harvest (Bischof, Mysterud & Swanson 2008), factors that remain largely unknown. Therefore, developing ungulate harvest strategies in the face of recovering carnivore populations and changing ecological conditions is emerging as a critical management issue in many areas.

To address these issues, we examined factors related to adult female elk survival using a large-scale data set from the western U.S. and Canada. We estimated mortality rates of adult ($\geq$ 2-year-old) female elk across 45 populations to examine the relative influence of predation, weather, habitat, land-use and human harvest. We performed two classes of analysis to address different questions. First, we used proportional hazards analysis to assess how 'baseline' survival (i.e. not affected by human factors) is related to large-scale patterns in habitat conditions and carnivore distribution (objective 1). Second, we used analysis of cause-specific mortality to determine which factors, human and non-human related, were associated with proximate causes of death (objective 2). This analysis assessed both baseline survival and 'total' survival (incorporating human impacts). The proportional hazards analysis was intended to reveal broadscale, ultimate factors associated with adult female elk mortality, such as the effects of habitat quality or interactions between weather and predation, whereas the cause-specific mortality analysis provided information about proximate causes of death (mainly predation and harvest).

Materials and methods

We compiled data on the fates of radio-marked adult female elk from state wildlife management agencies in Colorado, Idaho, Montana, Oregon, Utah, Washington and Wyoming (Table S1, Supporting information). We also used data from Yellowstone National Park (USA) and the Ya Ha Tinda elk population (Alberta, Canada). In total, we compiled survival data from 45 populations that spanned more than 13 degrees of latitude and 14 degrees of longitude (Fig. 1). In all study populations, elk were captured following approved animal care protocols and were fitted with VHF- or GPS-collars. Collared animals were monitored using ground or aerial telemetry every 3–90 days

(median = 22·5 days). When mortality signals were detected, carcasses were investigated an average of 14 days later. Even though sampling methodology varied among study populations, we were able to group mortality data into categories shown in Table S2 (Supporting information). Investigators used puncture marks, scat, tracks and other signs to determine whether elk had been killed by particular carnivore species. Harvest mortality included take from firearm and archery seasons as well as tribal hunts, illegal harvest and wounding loss. Other causes of death included accident, injury, road kill, disease and winter kill (i.e. starvation). If death could not be attributed to a specific cause, it was categorized as 'unknown'. Some investigators recorded animal age at time of capture, but some did not, so we were unable to incorporate age as a covariate; the limitations of this are discussed below. Data limitations also precluded us from assessing population density as a covariate, although, in ungulates, adult survival is less affected by density than is any other vital rate (Bonenfant *et al.* 2009).

PROPORTIONAL HAZARDS ANALYSIS

To determine the ultimate factors driving 'baseline' (non-human-related) elk survival (objective 1 above), we employed Cox proportional hazards models (Hosmer, Lemeshow & May 2008) to assess the relative influence of carnivores, habitat conditions and weather, while censoring harvest-induced mortalities. Individuals were also censored from the analysis following emigration from a given study area, collar failure or termination of the study. Local biologists determined whether each elk population was sympatric with 'well-established' pumas and wolves. In the proportional hazards analysis, we treated *study population* as a random effect on model intercepts using a shared frailty term (Hosmer, Lemeshow & May 2008). We treated *puma* and *wolf* as binary, indicating whether or not each species was well established in a given population. Only eight populations had well-established grizzly bear populations, so we did not explicitly assess the impacts of grizzly bears on adult female elk survival. Nearly, all of the populations (42 of 45) were hunted, so we did
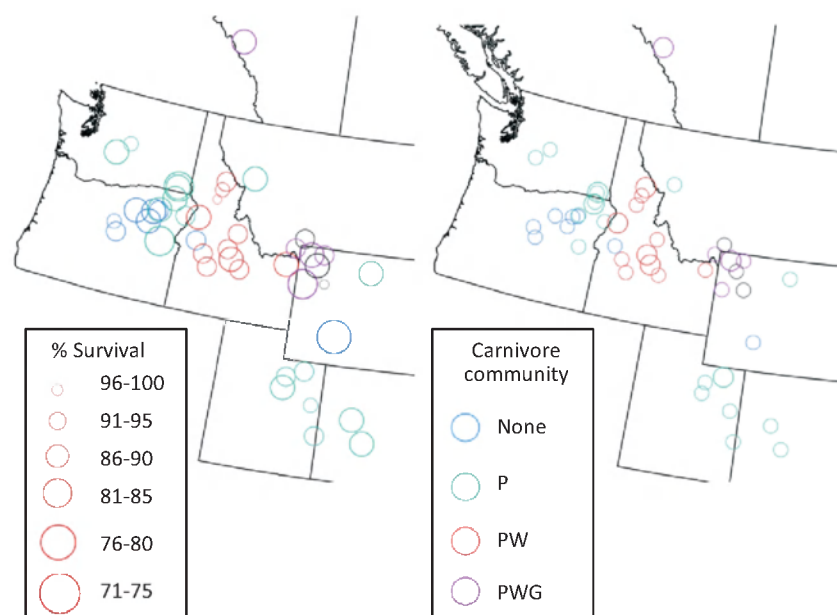

Fig. 1. Maps of study region showing total survival (left panel) and baseline survival (right panel). In both panels, circle size corresponds to survival rate and circle colour corresponds to carnivore community where P = 'well-established' puma populations, PW = well-established puma and wolf populations, and PWG = well-established puma, wolf and grizzly bear populations.

not include harvest as a binary covariate in the proportional hazards analysis, although we did assess its impacts using the cause-specific mortality analysis below.

We generated two landcover metrics thought to influence elk habitat quality. We used relocations from individuals to create minimum convex polygons (MCPs) representing the seasonal ranges of each population. For each population, we estimated the proportion of its range covered by conifer and broadleaved forest (averaged, for each forest type, between summer and winter MCPs) using data from the U.S. Geological Survey (USGS; http://gapanalysis.usgs.gov/data/land-cover-data/). We used these forest types as an index to habitat quality; forest could enhance elk survival by providing cover, and broadleaf forest also provides forage for elk (Kauffman, Brodie & Jules 2010).

We hypothesized that survival could also be influenced by weather via winter severity (cf. Garrott *et al.* 2003) and/or summer habitat productivity (cf. Cook *et al.* 2004). We used the cumulative average snowfall from January to March of each study year as a metric of annual winter severity for each population; these data came from the PRISM Climate Group (http://www.prism.oregonstate.edu/index.phtml). We used mean cumulative summer normalized difference vegetation index (NDVI) as an index of habitat productivity (cf. Pettorelli *et al.* 2005). We used smoothed, weekly NDVI values of grassland cells within each elk range, using USGS-GAP land classification, from Advanced Very High Resolution Radiometer data from the USGS (http://earlywarning.usgs.gov/USphenology).

We tested 64 baseline mortality models representing all possible combinations of the six independent variables (*puma, wolf, conifer cover, broadleaf cover, summer NDVI, winter precipitation*). All continuous variables were standardized prior to analysis to have mean = 0 and variance = 1. All models also included *study year*, to account for changes in environmental conditions over time. We used multimodel inference to assess the effect of each variable on adult female elk survival by comparing model-averaged beta coefficients; variables were deemed important if the 95% confidence intervals of their model-averaged beta coefficients ($\hat{\beta}$) did not include zero.

CAUSE-SPECIFIC MORTALITY ANALYSIS

We assessed the relative influence of different mortality factors on proximate adult female elk survival using cause-specific mortality analyses. We used nonparametric cumulative incidence functions to estimate mortality rates from different causes under a competing risks framework, whereby mortality from one source precludes mortality from other sources (cf. Heisey & Patterson 2006). We then used linear models to measure the strength of the relationships between survival and each individual mortality factor (cf. Griffin *et al.* 2011). We generated a 'corrected slope' (model slope divided by intercept) that made the slope term relative to the absolute magnitude of mortality, as per Burnham, White & Anderson (1984). Additive vs. compensatory mortality for a given factor were indicated by corrected slopes of negative one and zero, respectively, with slopes between these values indicating partial additivity (Williams, Nichols & Conroy 2002; Murray *et al.* 2010); we examined linear models of additivity and compensation rather than threshold models as per Schaub & Lebreton (2004). Total mortality and mortality from any specific cause will often negatively covary

(Schaub & Lebreton 2004); nevertheless, our approach can elucidate the relative influence of different mortality causes on overall mortality (Murray *et al.* 2010; Griffin *et al.* 2011). We estimated the standard error (SE) of the corrected slope from the SE of the raw slope and model intercept using the delta method (Seber 1982).

We first evaluated only non-human-related mortality factors ('baseline survival') and then assessed whether harvest mortality had additive or compensatory impacts on 'total' elk survival relative to other factors. We also analysed correlations between rates of human-induced and baseline mortality factors. We generated smoothed daily hazard rates for elk and compared these rates across different large carnivore assemblages (cf. Griffin *et al.* 2011); the instantaneous hazard rate in these models is proportional to the daily odds of dying. All analyses were conducted in STATA 11.1 (StataCorp, College Station, TX, USA).

Results

Across our 45 study populations, we had data from 2746 individual adult female elk representing 9409 elk-years that included 1058 mortalities. All data were used in the cause-specific mortality analyses; only 8054 animal-years were used in the proportional hazards analysis, the rest were excluded because they occurred too long ago to reconstruct winter and summer weather estimates using the remote-sensing techniques discussed above. Total annual survival rates were highly variable across populations, whereas baseline survival rates were less variable (Fig. 1). Few deaths were directly attributable to weather, with only 14 mortalities (1·4% of total) assigned to either winter kill or malnutrition. The largest mortality factor was harvest (54·8% of all mortalities) followed by unknown causes (27·3%), wolves (6·8%) and pumas (6·0%). Baseline annual survival probabilities, from Kaplan–Meier analysis, ranged from an average of 0·950 (SE = 0·001) in populations without wolves or pumas, to 0·942 (0·004) with pumas only, to 0·934 (0·006) with pumas and wolves. No populations had wolves but no pumas. Baseline annual survival probabilities were 0·849 (0·005) and 0·946 (0·007) in harvested and unharvested populations, respectively.

PROPORTIONAL HAZARDS ANALYSIS

Of the six candidate variables in our proportional hazards analysis of baseline elk survival, the highest correlations occurred between *summer NDVI* and *proportion conifer cover* (Pearson's $R = 0.56$), suggesting little influence of collinearity problems (see Table 1 for the complete correlation matrix). In the top model, mortality rates for adult female elk increased in the presence of wolves and with increased *winter precipitation* (Tables S3 and S4, Supporting information). Using multimodel inference, however, only *winter precipitation* received unequivocal model support annual mortality increased with increasing winter precipitation (Fig. 2a). *Winter precipitation* was the only candidate variable to have a model-averaged beta

Table 1. Pearson's correlation coefficients among predictor variables in survival analysis; sampling units are animal-years

	Puma	Wolf	Conifer forest cover	Broadleaf forest cover	Summer NDVI
Wolf	0·218				
Conifer forest cover	0·087	0·343			
Broadleaf forest cover	0·133	−0·344	−0·386		
Summer NDVI	−0·084	0·086	0·561	0·036	
Winter precipitation	0·080	0·149	0·418	0·046	0·564

NDVI, normalized difference vegetation index.

Fig. 2. (a) Model-averaged beta coefficients from Cox proportional hazards analysis of factors potentially affecting the 'baseline' (i.e. non-human-related) hazard probability for adult female elk. Light bars show the original analysis with six main effect variables, dark bars show the subsequent analysis that included a *winter* × *wolf* interaction term. (b) Estimated annual adult female elk survival across categories of mean winter precipitation in populations with (black bars) and without (light bars) sympatric 'well-established' wolves; sample size (animal-years) shown above each bar. Error bars in both panels show 95% confidence intervals.

coefficient whose 95% confidence interval did not include zero ($\bar{\beta}$ = 0·134, CI = 0·013: 0·254); it was also in the top 11 (of 64) baseline mortality models, and with very consistent beta coefficient values (Table S3, Supporting information). Although estimated elk survival exhibited a somewhat curvilinear relationship with winter precipitation, when we re-ran the model selection analysis to include a *winter precipitation* quadratic term in all models that contained *winter precipitation*, the quadratic term was not supported ($\bar{\beta}$ = 0·039, CI = −0·015: 0·093).

Due to the high model support for *winter precipitation*, and the additional (although more limited) support for *wolf* in the analysis above (see Table S3, Supporting information and Fig. 2a), we then re-ran the model selection analysis to include a *winter precipitation* × *wolf* interaction term in all models that contained *winter precipitation*. Assessing this interaction was further justified by evidence from other systems showing that wolf-induced mortality on ungulates can be greater in harsh winters (DelGiudice *et al.* 2002). The top model from this analysis included *wolf*, *winter precipitation* and *winter precipitation* × *wolf*; only *winter precipitation* × *wolf* had a model-averaged beta coefficient whose confidence intervals did not include zero ($\bar{\beta}$ = 0·204, CI = 0·049: 0·358; Fig. 2a). In elk populations with well-established wolves, mortality was higher in years with high winter precipitation (Fig. 2b). In populations without wolves, survival was fairly consistent across levels of winter precipitation, although few of the populations without wolves were exposed to the highest levels of precipitation (i.e. >50 cm; Fig. 2b).

CAUSE-SPECIFIC MORTALITY ANALYSIS

Most (67·6%) mortalities that were attributed to a specific cause were related to harvest or carnivores, so the following analyses focus on these factors. This dominance of harvest- and carnivore-induced mortalities was likely to occur because cause-specific mortality captured the
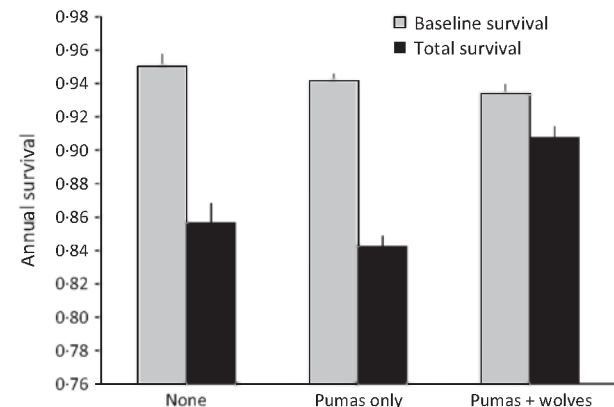

Fig. 3. Annual adult female elk survival rates (with SE bars) in populations with different carnivore assemblages. The assemblages are mutually exclusive rather than nested. No populations had wolves without pumas.
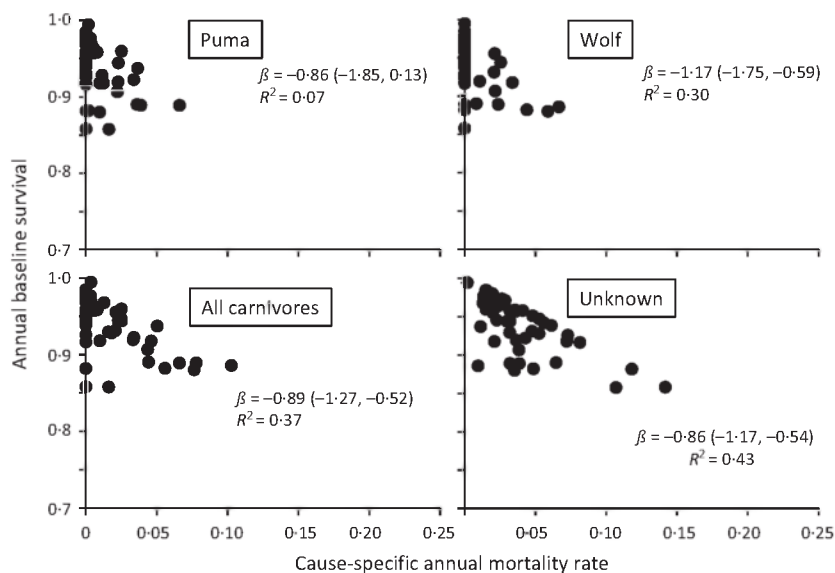
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Fig. 4. Relationships between different causes of mortality and annual 'baseline' (i.e. non-human-related) adult female elk survival. Corrected slope (β) and standard error (in parentheses) shown.

proximate cause of death, not necessarily ultimate factors (such as habitat quality or weather × carnivore interactions) that the proportional hazards analysis could assess. The average baseline survival was 0·947 (95% CI = 0·932: 0·959). Populations with wolves and pumas had average survival only 1·6% lower than populations without either carnivore species (Fig. 3). The confidence intervals for the corrected slope of the relationship between carnivore-induced mortality and annual elk survival included negative one, but not zero (Fig. 4), indicating that increasing rates of mortality from all native carnivore species combined had additive effects on baseline adult female elk mortality. These additive effects may have been due to wolves more than pumas, because wolf-induced mortality was also additive (i.e. confidence intervals included the value negative one but not zero), whereas puma-induced mortality was not additive (i.e. confidence intervals included zero).

Total annual elk survival probabilities were similar in populations with and without pumas (*c.* 0·85) but were higher (0·908) in populations with both pumas and wolves (Fig. 3). Predation on elk increased with the number of sympatric carnivore species; elk living with both pumas and wolves, however, had lower harvest mortality than elk living with only pumas or neither species. Therefore, as the number of well-established native large carnivore species in a particular study area increased, the level of harvest mortality on adult female elk decreased, and total elk mortality remained the same or was even lower (Fig. 3).

Harvest had much stronger effects on total adult female elk survival than did carnivores. The relationship between harvest-induced mortality and annual elk survival was stronger ($R^2 = 0.47$) than the relationship between annual elk survival and mortality induced by any of the native carnivores, either singly or in combination ($R^2 = 0.01$– 0·03; Fig. 5). Moreover, harvest-induced mortality covered

a much greater range of variation (0–25% annual mortality) than other known mortality causes (generally <10% annual mortality). Harvest-induced mortality was partly additive, as the confidence intervals for the corrected slope did not include zero or negative one. Increasing the level of carnivore-induced mortality, either for single carnivore species or all combined, had no effect on total elk survival in the presence of harvest (Fig. 5).

Rates of mortality from harvest were negatively correlated with mortality induced by all carnivores combined ($R = -0.64$, $P < 0.01$), but not mortality from either pumas ($R = -0.23$, $P = 0.33$) or wolves ($R = -0.27$, $P = 0.45$) alone (Fig. 6), suggesting that harvest was reduced in systems with multiple predators. Elk mortality rates from wolves and pumas were negatively correlated ($R = -0.75$, $P = 0.05$, Fig. 6).

As native carnivore species richness increased, harvest appeared to decline (Fig. 7). The peak in daily hazard rate attributable to harvest was strongest in populations with no native large carnivores and became progressively smaller in populations with pumas and then wolves (Fig. 7). Whereas the harvest-induced mortality hazard peaked during the autumn hunting season, the carnivore-induced mortality hazard was higher in late winter and early spring, particularly in populations with both pumas and wolves (Fig. 7).

Discussion

Managing harvested populations under changing ecological conditions requires understanding how diverse factors affect demography and population dynamics. Omitting the effects of harvest, baseline mortality of adult female elk across much of western North America generally increased in years with higher winter precipitation. This increase was particularly evident in populations sympatric with wolves, although populations with wolves also spanned a greater
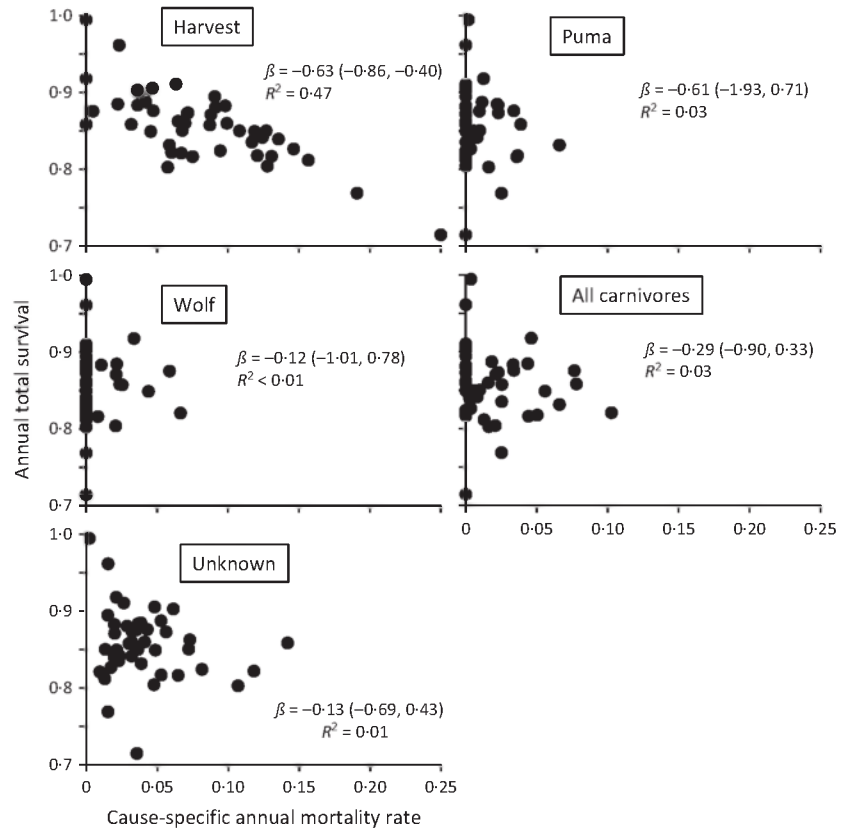
Fig. 5. Relationships between different causes of mortality and annual 'total' (i.e. including human factors) adult female elk survival. Corrected slope (β) and standard error (in parentheses) shown.
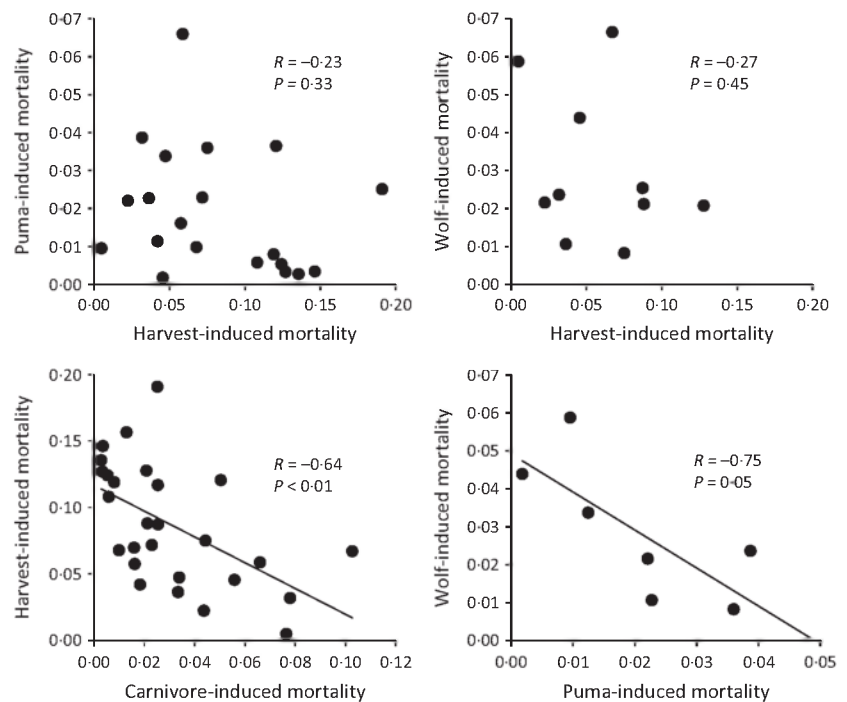

Fig. 6. Relationships between mortality from harvest and native carnivores, and between wolf and puma mortality rates. Linear trendlines shown that are significant at $\alpha = 0.05$. 'Carnivore-induced mortality' indicates the effects of all native carnivores combined.

range of winter precipitation than did populations without wolves. Deep snowpack may hinder winter foraging and also increasing susceptibility to predation (Garrott *et al.* 2003; Creel & Creel 2009). This finding could have impor-tant implications for elk populations across our study region. Winters have become milder in much of western North America (Mote *et al.* 2005); our results suggest that this could increase survival rates of adult female elk,
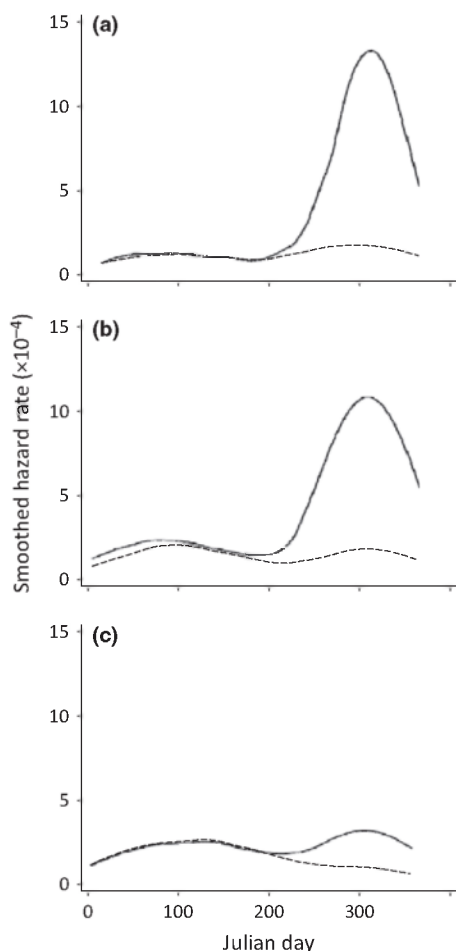
Fig. 7. Smoothed instantaneous hazard rates for daily mortality probability over the course of the year for baseline mortality (i.e. non-human-induced; dashed lines) and total mortality (including human effects; solid lines) in populations with (a) no well-established carnivores, (b) well-established pumas only, (c) well-established pumas and wolves. The carnivore assemblages in panels a–c are mutually exclusive rather than nested; no populations had wolves without pumas.

potentially leading to population increases (also see Creel & Creel 2009). We observed few instances in which malnutrition or winter kill were proximate sources of mortality. Yet, winter precipitation did emerge as a strong ultimate predictor of mortality, probably because harsh winters increased the energy deficits of elk, predisposing them to predation. High precipitation winters generally occurred in populations sympatric with wolves (Fig. 2b), making it difficult to assess potential direct effects of harsh winters on the survival of elk that were not simultaneously exposed to wolf predation.

Although baseline mortality was statistically related to a winter precipitation × wolf interaction, baseline mortality rates were relatively consistent across study populations despite different predator communities, weather patterns and habitat types (Fig. 1). Carnivores (specifically wolves) increased elk mortality in the absence of human influences, but these effects were slight; elk

populations sympatric with wolves had average adult female survival rates only 1·6% lower than populations without wolves.

When we included the effects of humans, however, total adult female elk survival rates differed dramatically among populations (Fig. 1), driven by the effect of harvest (Fig. 5). Harvest was the only factor in our cause-specific mortality analysis to have additive effects on total adult female elk mortality. Survival rates were substantially higher in unharvested populations (Fig. 2). In our elk populations, harvest induced a greater absolute change (across a larger range of variation) in survival than did any other mortality source. This is important because the net impacts on population growth of changing a given vital rate are a function of both the elasticity of the vital rate and the magnitude of change in the rate (Wisdom, Mills & Doak 2000). In elk, adult female survival is the vital rate with the highest elasticity, which reflects the fact that a small change in adult female survival will cause a greater change in the population growth rate than an equivalent change in any other vital rate (Morris & Doak 2002). Because harvest may be designed to remove many prime-age adults with high reproductive value, it should be highly additive relative to carnivore-induced mortality, which is often distributed across different age and sex classes including young or old individuals (Evans *et al.* 2006; Wright *et al.* 2006).

The dominance of harvest- and carnivore-induced mortalities in our cause-specific mortality analysis, vs. the influence of winter precipitation in our proportional hazards analysis, reflects the different questions addressed by these analyses. Cause-specific mortality analysis captures the particular factors that killed each marked animal and is a powerful way to assess proximate causes of death. It is complemented by the proportional hazards analysis, which focuses on correlates, such as weather or habitat, which are seldom proximate causes of death despite potentially being ultimate drivers of mortality.

Managers in our study areas used harvest as a tool to manage elk populations via manipulating adult female survival, and this strategy appeared to compensate for carnivore-induced mortality. Indeed, carnivores had no detectable effect on total adult female elk survival when the influence of human harvest was incorporated (Fig. 5). Moreover, the peak in the harvest-induced hazard rate was reduced as native carnivore species richness increased (Fig. 7); this is likely to be because managers implemented more conservative harvest regulations in populations exposed to high rates of carnivore predation to attempt to stabilize population sizes and growth rates as juvenile recruitment declined. Examples of this compensation from specific sites, the northern Yellowstone and Gallatin herds in Montana, are found in Hamlin *et al.* (2009) where, as the level of adult female mortality from wolf predation increased and juvenile elk survival decreased, managers reduced the number of females

harvested. The fact that female harvest levels are reduced in areas with high carnivore-induced mortality means that we cannot directly address the question of whether carnivore recolonization in the presence of unaltered harvest would have additive or compensatory impacts on elk survival.

Despite our large sample size and broad spatial coverage, there were several limitations to our data. First, we were unable to include individual age as a covariate, because the data were not available, but other studies demonstrated that age can affect adult ungulate survival patterns and may interact with climate, predation or habitat quality (e.g. Gaillard *et al*. 2000; Garrott, White & Rotella 2009; Webb *et al*. 2011). Because recruitment tends to decline with increasing population density, the proportion of senescent individuals in unharvested populations can be higher than in harvested populations, potentially leading to lower baseline survival of the 'adult' (including older individuals) age class (Festa-Bianchet, Gaillard & Cote 2003). However, very few of our populations were unharvested (three of 45), so the effects of this bias on overall survival rate estimation, or on the qualitative inference from our data, should have been slight. Second, we relied on indices of carnivore presence (proportional hazards analyses), or measured mortality levels (cause-specific mortality analyses), rather than being able to express either factor as a rate relative to elk population size. Our metrics were thus coarse, and yet still provided insights into the role of carnivores and harvest on elk survival. Finally, our broad-geographical-scale analysis results might differ from those of single-site studies within our study region. For example, at sites, such as the Yellowstone Ecosystem with high carnivore species richness and abundance, carnivores could have an impact on elk survival equal to or greater than hunters (Evans *et al*. 2006), although they typically kill proportionally more individuals with lower reproductive value than adult females (Wright *et al*. 2006; Eberhardt *et al*. 2007; Barber-Meyer, Mech & White 2008).

In our models, we included *population* as a random effect on the intercept but not the model slope. This assumes that the response of elk to candidate variables was the same across all populations. Certain factors can affect ungulate vital rates differently across populations (Ginnett & Young 2000). But we focused our analysis on broad variables that should each have relatively consistent effects across the region, although subtle differences in responses to precipitation across study populations due to variation in soil and vegetation types could not be detected in our analysis.

Our results only assessed a single vital rate for a segment of the population, and thus do not necessarily scale up to population-level trends. For example, while we found little relationship between either puma- or wolf-induced mortality and adult female elk survival (Fig. 3), high-density carnivore populations in some systems may reduce ungulate populations via impacts on other vital rates such as juvenile recruitment (Garrott, White & Rotella 2009; White, Zager & Gratson 2010; Johnson, Coe & Green 2012). Differential yearling survival may also drive variation in population growth among ungulate populations (Nilsen *et al*. 2009). These points have important implications for the management of ungulate populations at local scales. At sites with particularly high carnivore density, the impact of predation on adult female elk survival may differ from the general patterns we assessed across multiple populations and wide spatial scales. Additionally, if carnivore-induced mortality strongly affects other vital rates such as recruitment or yearling survival, adjustment of female harvest alone may not be sufficient to prevent elk population declines. For example, if populations maintain high adult female survival in the face of declining recruitment, this could lead to two outcomes: (i) a gradual declining trend in elk population growth (as opposed to a population crash), because the impacts are largely on <1-year-old individual with low reproductive value and (ii) an increasingly old age structure, which has implications for both productivity of the population and its vulnerability to weather and predation.

Overall, our results help elucidate the relative influence of humans and native carnivores, along with weather and habitat factors, on adult female elk mortality. Variation in carnivore-induced mortality rates had no effect on overall ('total') annual survival rates of adult female elk because managers accounted for increasing carnivore-induced mortality by reducing adult female harvest, thus offsetting the impacts of changing ecological conditions. We caution, however, that carnivores could have stronger influences on juvenile ungulate survival and recruitment than we found on adult survival (Griffin *et al*. 2011); further research is needed to determine whether adjusting human harvest can offset the effects of predation on overall ungulate population dynamics.

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References

Barber-Meyer, S.M., Mech, L.D. & White, P.J. (2008) Elk calf survival and mortality following wolf restoration to Yellowstone National Park. *Wildlife Monographs*, **169**, 1–30.

Biederbeck, H.H., Boulay, M.C. & Jackson, D.H. (2001) Effects of hunting regulations on bull elk survival and age structure. *Wildlife Society Bulletin*, **29**, 1271–1277.

Bischof, R., Mysterud, A. & Swanson, J.E. (2008) Should hunting mortality mimic the patterns of carnivore-caused mortality? *Biology Letters*, **4**, 307–310.

Bonenfant, C., Gaillard, J.M., Coulson, T., Festa-Bianchet, M., Loison, A., Garel, M., Loe, L.E., Blanchard, P., Pettorelli, N., Owen-Smith, N., Du Toit, J. & Duncan, P. (2009) Empirical evidence of density-dependence in populations of large herbivores. *Advances in Ecological Research*, Vol. 41 (ed. H. Caswell), pp. 313–357. Elsevier Academic Press Inc, San Diego, CA.

Boyce, M.S., Knopff, K., Northrup, J., Pitt, J. & Vors, L.S. (2012) Harvest models for changing environments. *Wildlife Conservation in a Changing Climate* (eds J.F. Brodie, E.S. Post & D.F. Doak), pp. 293–306. University of Chicago Press, Chicago, IL.

Burnham, K.P., White, G.C. & Anderson, D.R. (1984) Estimating the effect of hunting on annual survival rates of adult mallards. *Journal of Wildlife Management*, **48**, 350–361.

Cole, E.K., Pope, M.D. & Anthony, R.G. (1997) Effects of road management on movement and survival of Roosevelt elk. *Journal of Wildlife Management*, **61**, 1115–1126.

Cook, J.G., Johnson, B.K., Cook, R.C., Riggs, R.A., Delcurto, T., Bryant, L.D. & Irwin, L.L. (2004) Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. *Wildlife Monographs*, **155**, 1–61.

Creel, S. & Creel, M. (2009) Density dependence and climate effects in Rocky Mountain elk: an application of regression with instrumental variables for population time series with sampling error. *Journal of Animal Ecology*, **78**, 1291–1297.

DelGiudice, G.D., Riggs, M.R., Joly, P. & Pan, W. (2002) Winter severity, survival, and cause-specific mortality of female white-tailed deer in north-central Minnesota. *Journal of Wildlife Management*, **66**, 698–717.

Eberhardt, L.L., White, P.J., Garrott, R.A. & Houston, D.B. (2007) A seventy-year history of trends in Yellowstone's northern elk herd. *Journal of Wildlife Management*, **71**, 594–602.

Evans, S.B., Mech, L.D., White, P.J. & Sargeant, G.A. (2006) Survival of adult female elk in Yellowstone following wolf restoration. *Journal of Wildlife Management*, **70**, 1372–1378.

Festa-Bianchet, M., Gaillard, J.M. & Cote, S.D. (2003) Variable age structure and apparent density dependence in survival of adult ungulates. *Journal of Animal Ecology*, **72**, 640–649.

Fujiwara, M. & Caswell, H. (2002) Estimating population projection matrices from multi-stage mark-recapture data. *Ecology*, **83**, 3257–3265.

Gaillard, J.M., Festa-Bianchet, M. & Yoccoz, N.G. (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology & Evolution*, **13**, 58–63.

Gaillard, J.M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toigo, C. (2000) Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, **31**, 367–393.

Garrott, R.A., White, P.J. & Rotella, J.J. (2009) The Madison Headwaters elk herd: transitioning from bottom-up regulation to top-down limitation. *The Ecology of Large Mammals in Central Yellowstone* (eds R.A. Garrott, P.J. White & F.G.R. Watson), pp. 489–518. Academic Press, Amsterdam.

Garrott, R.A., Eberhardt, L.L., White, P.J. & Rotella, J. (2003) Climate-induced variation in vital rates of an unharvested large-herbivore population. *Canadian Journal of Zoology*, **81**, 33–45.

Ginnett, T.F. & Young, E.L.B. (2000) Stochastic recruitment in white-tailed deer along an environmental gradient. *Journal of Wildlife Management*, **64**, 713–720.

Griffin, K.A., Hebblewhite, M., Robinson, H.S., Zager, P., Barber-Meyer, S.M., Christianson, D., Creel, S., Harris, N.C., Hurley, M.A., Jackson, D.H., Johnson, B.K., Mech, L.D., Myers, W.L., Raithel, J.D., Schlegel, M., Smith, B.L., White, C.G. & White, P.J. (2011) Neonatal mortality of elk driven by climate, predator phenology and predator community composition. *Journal of Animal Ecology*, **80**, 1246–1247.

Hamlin, K.L., Garrott, R.A., White, P.J. & Cunningham, J.A. (2009) Contrasting wolf-ungulate interactions in the Greater Yellowstone Ecosystem. *The Ecology of Large Mammals in Central Yellowstone* (eds R.A. Garrott, P.J. White & F.G.R. Watson), pp. 541–578. Academic Press, Amsterdam.

Hebblewhite, M. (2005) Predation by wolves interacts with the North Pacific Oscillation (NPO) on a western North American elk population. *Journal of Animal Ecology*, **74**, 226–233.

Heisey, D.M. & Patterson, B.R. (2006) A review of methods to estimate cause-specific mortality in presence of competing risks. *Journal of Wildlife Management*, **70**, 1544–1555.

Hidalgo, M., Rouyer, T., Molinero, J.C., Massuti, E., Moranta, J., Guijarro, B. & Stenseth, N.C. (2011) Synergistic effects of fishing-induced demographic changes and climate variation on fish population dynamics. *Marine Ecology-Progress Series*, **426**, 1–12.

Hosmer, D.W., Lemeshow, S. & May, S. (2008) *Applied Survival Analysis: Regression Modeling of Time-to-event Data*. John Wiley & Sons, Hoboken, NJ.

Johnson, B.K., Coe, P.K. & Green, R.L. (2012) Abiotic, bottom-up, and top-down influences on recruitment of Rocky Mountain elk in Oregon: a retrospective analysis. *Journal of Wildlife Management*, **77**, 1.

Kauffman, M.J., Brodie, J.F. & Jules, E.S. (2010) Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. *Ecology*, **91**, 2742–2755.

Manfredo, M.J., Fix, P.J., Teel, T.L., Smeltzer, J. & Kahn, R. (2004) Assessing demand for big-game hunting opportunities: applying the multiple-satisfaction concept. *Wildlife Society Bulletin*, **32**, 1147–1155.

McCorquodale, S.M., Wiseman, R. & Marcum, L. (2003) Survival and harvest vulnerability of elk in the Cascade range of Washington. *Journal of Wildlife Management*, **67**, 248–257.

Melis, C., Jedrzejewska, B., Apollonio, M., Barton, K.A., Jedrzejewski, W., Linnell, J.D.C., Kojola, I., Kusak, J., Adamic, M., Ciuti, S., Delehan, I., Dykyy, I., Krapinec, K., Mattioli, L., Sagaydak, A., Samchuk, N., Schmidt, K., Shkvyrya, M., Sidorovick, V.E., Zawadzka, B. & Zhyla, S. (2009) Predation has a greater impact in less productive environments: variation in roe deer, *Capreolus capreolus*, population density across Europe. *Global Ecology and Biogeography*, **18**, 724–734.

Minns, C.K. & Moore, J.E. (1992) Predicting the impact of climate change on the spatial pattern of fresh-water fish yield capability in eastern Canadian lakes. *Climatic Change*, **22**, 327–346.

Morris, W.F. & Doak, D.F. (2002) *Quantitative Conservation Biology*. Sinauer Associates, Sunderland, MA.

Mote, P.W., Hamlet, A.F., Clark, M.P. & Lettenmaier, D.P. (2005) Declining mountain snowpack in western north America. *Bulletin of the American Meteorological Society*, **86**, 39–49.

Murray, D.L., Smith, D.W., Bangs, E.E., Mack, C., Oakleaf, J.K., Fontaine, J., Boyd, D., Jiminez, M., Niemeyer, C., Meier, T.J., Stahler, D., Holyan, J. & Asher, V.J. (2010) Death from anthropogenic causes is partially compensatory in recovering wolf populations. *Biological Conservation*, **143**, 2514–2524.

Nilsen, E.B., Gaillard, J.M., Andersen, R., Odden, J., Delorme, D., van Laere, G. & Linnell, J.D.C. (2009) A slow life in hell or a fast life in heaven: demographic analyses of contrasting roe deer populations. *Journal of Animal Ecology*, **78**, 585–594.

Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.-M., Tucker, C.J. & Stenseth, N.C. (2005) Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology and Evolution*, **20**, 503–510.

Pfister, C.A. (1998) Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. *Proceedings of the National Academy of Sciences of the United States of America*, **95**, 213–218.

Riggs, R.A., Tiedemann, A.R., Cook, J.G., Ballard, T.M., Edgerton, P.J., Vavra, M., Krueger, W.C., Hall, F.C., Bryant, L.D., Irwin, L.L. & DelCurto, T. (2000) Modification of Mixed-conifer Forest by Ruminant Herbivores in the Blue Mountains Ecological Province. Research Paper PNW-RP-527. Pacific Northwest Research Station, US Department of Agriculture, Forest Service, Portland, OR.

Salo, P., Banks, P.B., Dickman, C.R. & Korpimaki, E. (2010) Predator manipulation experiments: impacts on populations of terrestrial vertebrate prey. *Ecological Monographs*, **80**, 531–546.

Schaub, M. & Lebreton, J.-D. (2004) Testing the additive versus the compensatory hypothesis of mortality from ring recovery data using a random effects model. *Animal Biodiversity and Conservation*, **27**, 73–85.

Seber, G.A. (1982) *The Estimation of Animal Abundance and Related Parameters*, 2nd edn. Chapman, London and Macmillan, New York.

Toigo, C., Gaillard, J.M., Festa-Bianchet, M., Largo, E., Michallet, J. & Maillard, D. (2007) Sex- and age-specific survival of the highly dimorphic alpine Ibex: evidence for a conservative life-history. *Journal of Animal Ecology*, **76**, 679–686.

Toïgo, C., Servanty, S., Gaillard, J.M., Brandt, S. & Baubet, E. (2008) Disentangling natural from hunting mortality in an intensively hunted wild boar population. *Journal of Wildlife Management*, **72**, 1532–1539.

Vucetich, J.A., Smith, D.W. & Stahler, D.R. (2005) Influence of harvest, climate and wolf predation on Yellowstone elk, 1961–2004. *Oikos*, **111**, 259–270.

Webb, S.L., Dzialak, M.R., Wondzell, J.J., Harju, S.M., Hayden-Wing, L.D. & Winstead, J.B. (2011) Survival and cause-specific mortality of female Rocky Mountain elk exposed to human activity. *Population Ecology*, **53**, 483–493.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R. & Swetnam, T.W. (2006) Warming and earlier spring increase western U.S. forest wildlife activity. *Science*, **313**, 940–943.

White, C.G., Zager, P. & Gratson, M.W. (2010) Influence of predator harvest, biological factors, and landscape on elk calf survival in Idaho. *Journal of Wildlife Management*, **74**, 355–369.

Williams, B.K., Nichols, J.D. & Conroy, M.J. (2002) *Analysis and Management of Animal Populations*. Academic Press, San Franciso, CA.

Wisdom, M.J., Mills, L.S. & Doak, D.F. (2000) Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. *Ecology*, **81**, 628–641.

Wright, G.J., Peterson, R.O., Smith, D.W. & Lemke, T.O. (2006) Selection of northern Yellowstone elk by gray wolves and hunters. *Journal of Wildlife Management*, **70**, 1070–1078.

Supporting Information

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

Table S1. Attributes of the study populations by name, game management unit (GMU), or hunting district (HD).

Table S2. Number of mortalities ascribed to different causes in the studies contributing to our analysis.

Table S3. Cox proportional hazards models from 'baseline' survival analysis showing parameter coefficients for study year, carnivore presence/absence, proportion cover by conifer and broadleaf forest, summer NDVI ('summer'), and winter precipitation ('winter').

Table S4. Cox proportional hazards models from 'baseline' survival analysis showing parameter coefficients for study year, carnivore presence/absence, proportion cover by conifer and broadleaf forest, summer NDVI ('summer'), winter precipitation ('winter'), and the winter precipitation × wolf interaction ('winter*wolf').