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Neonatal mortality of elk driven by climate, predator phenology and predator community composition

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Summary

1. Understanding the interaction among predators and between predation and climate is critical to understanding the mechanisms for compensatory mortality. We used data from 1999 radio-marked neonatal elk (*Cervus elaphus*) calves from 12 populations in the north-western United States to test for effects of predation on neonatal survival, and whether predation interacted with climate to render mortality compensatory.

2. Weibull survival models with a random effect for each population were fit as a function of the number of predator species in a community (3–5), seven indices of climatic variability, sex, birth date, birth weight, and all interactions between climate and predators. Cumulative incidence functions (CIF) were used to test whether the effects of individual species of predators were additive or compensatory.

3. Neonatal elk survival to 3 months declined following hotter previous summers and increased with higher May precipitation, especially in areas with wolves and/or grizzly bears. Mortality hazards were significantly lower in systems with only coyotes (*Canis latrans*), cougars (*Puma concolor*) and black bears (*Ursus americanus*) compared to higher mortality hazards experienced with gray wolves (*Canis lupus*) and grizzly bears (*Ursus horribilis*).

4. In systems with wolves and grizzly bears, mortality by cougars decreased, and predation by bears was the dominant cause of neonatal mortality. Only bear predation appeared additive and occurred earlier than other predators, which may render later mortality by other predators compensatory as calves age. Wolf predation was low and most likely a compensatory source of mortality for neonatal elk calves.

5. Functional redundancy and interspecific competition among predators may combine with the effects of climate on vulnerability to predation to drive compensatory mortality of neonatal elk calves. The exception was the evidence for additive bear predation. These results suggest that effects of predation by recovering wolves on neonatal elk survival, a contentious issue for management of elk populations, may be less important than the composition of the predator community. Future studies would benefit by synthesizing overwinter calf and adult-survival data sets, ideally from experimental studies, to test the roles of predation in annual compensatory and additive mortality of elk.

Key-words: compensatory mortality, competing risks, interspecific competition, juvenile survival, Yellowstone National Park

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Introduction

One of the biggest challenges facing animal ecologists is determining whether mortality by predators is additive or compensatory (Boyce, Sinclair & White 1999). Compensatory mortality is defined when an increase in one mortality source causes a decline in another, that is, non-independence between different mortality hazards (Heisey & Patterson 2006). Climate is an important mediating factor because it can interact with both resource availability and the strength of predation (Melis *et al*. 2009). In temperate ungulates, whether predation is additive or compensatory is expected to be mediated by winter severity (Post *et al*. 1999; Hebblewhite 2005). However, the effects of summer climate on forage and female elk body condition may mask climate-predation interactions during winter (Cook *et al*. 2004). Compensatory mortality can also arise because of competition amongst predators (Williams, Nichols & Conroy 2002; Heisey & Patterson 2006) and need not be restricted to the classic definition of compensation that focuses on hunting and overwinter mortality. For example, analyses of wolf (*Canis lupus*) and elk (*Cervus elaphus*) dynamics suggest that wolf predation might be compensatory to mortality from other predators (Vucetich, Smith & Stahler 2005; Garrott, White & Rotella 2009). Testing for compensatory mortality is further complicated by effects of age structure (Coulson, Gaillard & Festa-Bianchet 2005; Wilmers, Post & Hastings 2007).

In general, ungulate population dynamics are determined by the interplay of high and constant adult female survival and high variation in juvenile survival (Gaillard *et al*. 2000; Raithel, Kauffman & Pletscher 2007). Therefore, juvenile survival often determines population trajectories (Gaillard *et al*. 2000; Raithel, Kauffman & Pletscher 2007), although this depends on the manner of environmental variation acting on a population (Coulson, Gaillard & Festa-Bianchet 2005). Because of the vulnerability of juvenile ungulates to density-dependence, climate-induced mortality should be more compensatory with predator caused mortality in juveniles than in adults (Gaillard *et al*. 2000). However, many of the studies included in recent reviews were from populations without ecologically effective densities of large predators. Recent studies have shown that variation in population growth rate, adult and juvenile vital rates, may be lower in ungulate populations with predation, likely because predation interacts with climate to reduce population size and fluctuation (Hebblewhite 2005; Wilmers, Post & Hastings 2007). Thus, the extent to which predation is influenced by climatic variation on juvenile mortality remains unclear.

The expanding recovery of large carnivores in temperate systems emphasizes the importance of understanding mechanisms of compensatory mortality. With increasing cougars (*Puma concolor*), gray wolves (Boitani 2003) and brown bears (*U. arctos*) in Europe and North America (Swenson *et al*. 1995; Pyare *et al*. 2004), ungulate ecologists need to understand additive and compensatory mortality under different predator and climatic conditions. At one extreme, Linnell, Aanes & Andersen (1995) suggested diverse predator communities might render predation additive in mortality of juvenile ungulates. Alternatively, high intraspecific competition and functional redundancy among carnivores in tropical systems suggests mortality could be compensatory (Caro & Stoner 2003). Efforts to unravel these relationships are further complicated by the diversity of predators and ungulates (Linnell, Aanes & Andersen 1995) and that most studies of ungulate mortality are conducted at limited spatial and temporal scales.

Separating compensatory vs. additive mortality is difficult because mortality is often mediated (i.e. confounded) by climatic variability. Experimental or comparative approaches that manipulate body condition or food availability, or predator/harvest levels are therefore needed to critically test the compensatory mortality hypothesis (Bartmann, White & Carpenter 1992; Tveraa *et al*. 2003; White, Zager & Gratson 2010; Sandercock *et al*. 2011). Unfortunately, the difficulty of predator removal and manipulating body condition makes experimental approaches to test predator-caused compensation difficult with free-ranging ungulates. Instead, observational approaches have used temporal variation, for example, in wild boar (*Sus scrofa*) mortality rates from hunting and natural causes to test for additive vs. compensatory mortality using regression (Toigo *et al*. 2008) or state-space modelling (Servanty *et al*. 2010). Ultimately, these approaches are inferentially weaker than experiments (Sandercock *et al*. 2011) and suffer some statistical shortcomings (Schaub & Lebreton 2004), but offer precious insights into the potential for compensatory mortality in important applied settings.

We adopted a comparative approach that exploited temporal and spatial variation in neonatal mortality, climate and predation across 12 elk populations to test two mechanisms for compensatory mortality. First, we tested whether predator mortality was compensatory with climatic variation (compensatory climate–predator mortality hypothesis), and second, whether predator-caused mortality of neonate elk was compensatory amongst predator species (compensatory predator-mortality hypothesis). We analysed survival data of neonatal elk using parametric survival models and estimated cause-specific mortality in a competing risks framework (Heisey & Patterson 2006; Murray & Patterson 2006). Climate itself could mediate predator mortality in two different ways. First, maternal condition could exert the greatest effect on neonate survival through either the amount of female fat reserves in the fall or the severity of winter climate prior to calving. Alternately, neonate mortality could be primarily driven by negative effects of stochastic spring snowfalls or positive effects of precipitation or temperature during the spring and summer of calf birth (Clutton-Brock *et al*. 1987; Unsworth *et al*. 1999; Pettorelli *et al*. 2007). For the predator-mortality hypothesis, if mortality is additive, then predation would be expected to overwhelm climate effects (Linnell, Aanes & Andersen 1995). Thus, predation effects should increase with increasing number of predator species. Alternately, the compensatory predation-mortality hypothesis predicts that as the number of predator species increases,

survival stabilizes; indicating one predator species is replacing another in its effect on neonate survival. We tested whether mortality by each predator was compensatory or additive by regressing the cause-specific mortality rate (accounting for competing risks; Heisey & Patterson 2006) of neonatal elk for each study area against that same area's neonatal survival. A negative linear relationship between cause-specific mortality and survival would suggest additive mortality (Williams, Nichols & Conroy 2002).

Materials and methods

DATA COMPILATION

We synthesized 12 data sets on neonatal elk survival collected across five states in the north-western United States from 1973 to 2007 (Fig. 1, Table 1). We define neonatal survival as the first 93 days of life, approximately 20 May – 31 August (see survival modelling below). We refer readers to the original studies for detailed descriptions of their study areas, which covered wide climatic (Table S1), topographic, vegetative (e.g. coniferous forest, montane, shrub steppe) and predator community gradients in the north-western United States. Oregon contained two study areas, one in the south-west Cascade Mountains (D. Jackson, *unpublished data*) and the other in the Blue Mountains of north-east Oregon (Rearden 2005; B. Johnson, pers. comm.). One study occurred in the Blue Mountains of Washington (Myers *et al.* 1998). Four study areas were located in Idaho: two along the Lochsa/North Fork Clearwater River (Schlegel 1986; White, Zager & Gratson 2010), one along the South Fork Clearwater River (White, Zager & Gratson 2010) and one along the Salmon River (Compton 2009). Two study areas were located in Montana: one in the Garnet Mountains (Raithel 2005; Harris 2007) and another in the Gallatin Valley (Christianson 2008). In Wyoming, two studies were located in Jackson Hole (Smith & Anderson 1998; Smith *et al.* 2006) and one was in Yellowstone National Park (Barber-Meyer, Mech & White 2008).

The original data were collected using comparable field methods to capture and radio-mark neonatal elk. All calves were tagged with either radio ear tags or radiocollars. We estimated age at capture according to Johnson's (1951) criteria and then calculated birth date by subtraction. To standardize predicted birth weight across study areas, we used step-wise model selection to select the best linear regression of capture weight, capture age, sex and study area (e.g. Smith, Robbins & Anderson 1997). Radio-marked calves were monitored from the ground and air (using both fixed-wing aircraft and helicopters). Monitoring intensity was high in May and June with an average of 7·9 observations per week (range 3–14 per week) and then declined through July (average 4·6 observations per week; range 1–14 per week) and August (3·8 observations per week; range 1–7 per week). Mortality signals were investigated usually within 1–2 days; however, some carcasses took longer to reach because of weather and logistics. We censored animals if the radio transmitter detached prematurely or if mortality occurred the same day as capture and mortality was capture related ($n = 16$). Studies used a combination of field-based and laboratory-based (DNA identification of predators, disease profiling) necropsy procedures to investigate cause of mortality. For consistency, we collapsed 19 total mortality causes to five broad categories (cougar, wolf, coyote, ursid and other) that reduced misclassification and resolution inconsistencies across studies (Table S2).

STATISTICAL ANALYSES

Survival modelling

We used Weibull parametric survival models to estimate neonatal survival and test for covariate effects on mortality hazard across all 12 populations (Hosmer, Lemeshow & May 2008). We chose Weibull parametric models because they were more parsimonious than non-parametric models because of the strong exponential decay in neonatal survival (Murray & Patterson 2006). We used shared frailty (Vaida & Xu 2000; Cleves, Gould & Gutierrez 2002; Hosmer, Lemeshow & May 2008), akin to including a random effect, to account for among-group heterogeneity in survival within each of the 12 study

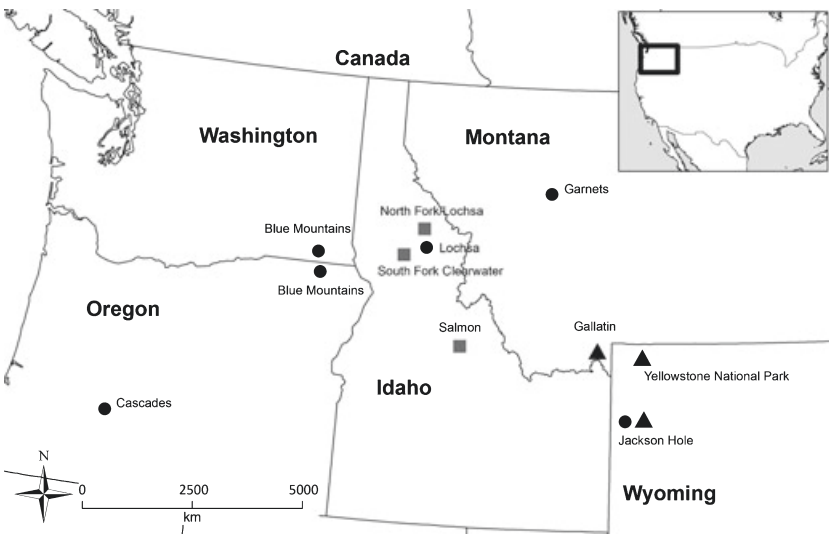

Fig. 1. Location of 12 study areas in the north-western USA, from 1973 to 2007. Black circles indicate study areas with three major predators (cougar, black bears and coyotes); grey squares indicate areas with three major predators prior to 2001 and four major predators (same predators as three-predator system plus wolves) after 2001; and black triangles indicate areas with five predators (same predators as the four-predator system plus grizzly bear). Note that two different studies occurred in Jackson Hole, WY between which additional predator species moved into the area.

Table 1. Summary of studies conducted on neonate elk in the north-western USA, including study area, citations, years, number of collared and dead calves, number of predator species and three-month survival rates (Kaplan–Meier [KM]) across studies

State	Location	Researcher/Publications	Years	N collared/ mortality	Number of Predators[a]	KM Survival (SE)
OR	SW Cascades	Jackson, *unpubl. data*.	2002–2005	155/29	3	0·75 (0·04)
	NE – Blue Mountains	Johnson, *unpubl. data*., Rearden 2005	2002–2007	444/145	3	0·61 (0·03)
WA	Blue Mountains	Myers *et al*. 1998	1993–1997	50/10	3	0·75 (0·07)
ID	Lochsa	Schlegel 1986	1973–1979	137/57	3	0·44 (0·05)
	Lochsa / North Fork	White, Zager & Gratson 2010	1997–2001, 2004	161/86	3 prior to 2001; 4 after 2001	0·41 (0·04)
	South Fork Clearwater	White, Zager & Gratson 2010	1997–2004	221/96	3 prior to 2001; 4 after 2001	0·49 (0·04)
	Salmon	Compton 2009	2005–2006	112/35	4	0·67 (0·05)
MT	Garnets	Raithel 2005; Raithel, Kauffman & Pletscher 2007; Harris 2007	2002–2006	220/38	3	0·81 (0·03)
	Gallatin	Christianson 2008	2005	29/15	5	0·48 (0·09)
WY	Jackson Hole	Smith *et al*. 2006	1990–1992	165/22	3	0·84 (0·03)
	Jackson Hole	Smith *et al*. 2006	1997–1999	154/42	5	0·70 (0·04)
	Yellowstone National Park	Barber-Meyer, Mech & White 2008	2003–2006	151/96	5	0·31 (0·04)
			Total	1999/671		

[a]Predator composition: 3 = cougar, coyote, and black bear; 4 = cougar, coyote, black bear, and wolf; 5 = cougar, coyote, black bear, wolf, and grizzly bear.

areas. Inferentially, inclusion of shared frailty allows valid population-level inferences across the north-western United States, and we report population-averaged covariate effects here (Cleves, Gould & Gutierrez 2002). For inferences for individual study sites (subject-specific effects), we refer readers to original studies.

We tested our hypotheses about predator community composition (three, four or five predators) and climate using the hazard ratio ($\exp^{\beta x}$) and its significance estimated from parametric Weibull models (Hosmer, Lemeshow & May 2008). As the hazard ratio increases >1, mortality increases and survival decreases. We also estimated survival as a function of the number of predator species using the Kaplan–Meier product limit estimator (Hosmer, Lemeshow & May 2008). We used a left-staggered entry and right censored design with time at risk based on age (Fieberg & DelGiudice 2009) where individual neonate elk entered into the analysis on age at capture and exited at death or censor event (end of study or 94 days); therefore survival is a function of age (days). We graphed the scaled-score residuals and Martingale residuals to test model fit (Hosmer, Lemeshow & May 2008) and removed four extreme outliers (with no effect on results, unpublished data).

We used a comprehensive model selection strategy to select the best Weibull survival model by considering plausible combinations of covariates based on candidate models from each of the original studies for each study area, for a total of 116 potential models. We did not include covariates that were too correlated ($|r| > 0{\cdot}5$) or confounded (Hosmer, Lemeshow & May 2008) in the same model. We selected the top model(s) using Akaike's Information Criteria (Burnham & Anderson 1998). Based on their importance in previous studies (Smith, Robbins & Anderson 1997; Smith *et al*. 2006; Harris 2007; Raithel, Kauffman & Pletscher 2007; Barber-Meyer, Mech & White 2008), we considered the following 'base' covariates as fixed and included them in all subsequent models: sex (male, female), estimated birth weight [sex-specific regression (Smith, Robbins & Anderson 1997)] and estimated birth date (Johnson 1951).

Climate

We considered two main climatic mechanisms for compensatory climate mortality; (i) effects of maternal condition on neonate survival attributed to the previous summer forage availability or previous winter severity; (ii) effects on neonate survival because of precipitation over the spring of birth year. Of course, separating effects of spring climate between maternal effects and direct neonatal effects through forage availability is challenging because of overlapping effects on neonatal condition, but comparing these two climatic effects provides a broad test of potential mechanisms. We used climate data from the Western US Cooperative Observer Program weather station that was in or closest to each study area (Western Regional Climate Center 1986). Summer maternal condition was indexed by the total precipitation (cm), the average daily maximum temperature (°C) of the previous summer (May–August) and their interaction. Winter maternal condition was indexed by the average minimum daily temperature (°C) and winter total snow (cm) in the previous winter (December–May) before calving as well as their interaction. Spring climate effects on neonate elk survival were indexed by the total precipitation (cm) and the average maximum daily temperature (°C) in the current spring (March, April or May, as well as the average of March-April), and their interaction. We also explored whether mean daily temperatures had more explanatory power, but they did not (unpublished data). Finally, we tested for the effect of total snow (cm) in June as a measure of rare, stochastic, weather events on neonates.

Number of predator species

Quantitative data on absolute predator densities were not available for most study areas; therefore, we defined three different predator communities by the number of predator species present (e.g. Linnell, Aanes & Andersen 1995). Study areas with three predator species

included cougar, coyote and black bear (*Ursus americanus*); four-predator systems also had gray wolves, and five-predator systems included grizzly bears (Fig. 1). In the three- and four-predator systems, ''ursid''-caused mortality represented only black bears but in the five-predator system it represented mostly grizzly bear but also some black bear because of the challenge in discriminating mortality caused by the two species (Zager & Beecham 2006; Barber-Meyer, Mech & White 2008). The effect of these predator communities was modelled using categorical covariates for four and five predators in comparison with three. The strongest experimental comparison in our study area for predation was between 1990–1992 (three predators) and 1997–1999 (five predators) when both wolves and grizzly bears became established in Jackson Hole, Wyoming (Smith *et al.* 2006). Therefore, we conducted a restricted analysis on just this study area following similar methods as described above (but without a frailty term), as well as an analysis with all sites excluding Jackson Hole to provide an interpretive check on our global model.

CAUSE-SPECIFIC MORTALITY

To test whether predator mortality was additive or compensatory, we estimated cause-specific mortality using cumulative incidence functions (CIF; Heisey & Patterson 2006). CIFs allow the estimation of cause-specific mortality in the presence of competing mortality risks (Heisey & Patterson 2006). Competing risks occur when an individual is subjected to more than one potential cause of mortality, and the occurrence of one event prevents the occurrence of others. If mortality hazards from different mortality sources are independent, mortality hazard is said to be additive; if there is non-independence between mortality sources, mortality is compensatory (Williams, Nichols & Conroy 2002; Heisey & Patterson 2006). We classified mortality as ursid, cougar, coyote, or wolf, as well as nonpredator caused mortality (disease, starvation, etc); other sources of mortality were rare (Table S2). Given the difficulty of distinguishing scavenging from predator mortality in the case of disease-related mortalities (Smith *et al.* 2006), we may have misclassified some disease-related mortalities as predation, likely underestimating the degree of compensatory mortality.

We tested the compensatory predator-mortality hypothesis among study areas in three ways. First, we examined how cause-specific mortality changed as the number of predator species across areas increased. If mortality was completely additive, we would expect an increase in the risk of mortality as the number of predator species increased. Conversely, if mortality was compensatory, we would expect the risk of mortality to plateau because of the substitution of mortality between different predator species. To test this, first, we compared the hazard ratios (e^{β}) between our three (baseline), four and five predator systems. If there was no difference between our four and five predator systems, for example, then predation by grizzly bears could be considered compensatory to that by the other four predators. We explicitly tested for changes in cause-specific mortality (CIF) of a single predator and other competing risks with increasing number of predators in a system Pepe & Mori (1993). This tests the hypothesis of equality in the CIF of a mortality cause (e.g. cougar predation) with another mortality cause while testing for equality in the remaining competing risks (Pintilie 2006). A significant increase in CIF of ursid predation in the presence of grizzly bears (five predator system) with no change in CIF of the remaining mortality factors would be considered additive. Next, for each predator species, we compared the relationship between cause-specific mortality rate and neonatal elk survival using linear regression (Williams, Nichols & Conroy 2002; Murray *et al.* 2010). If predation by a predator species was additive, then survival should decrease with increasing predator-specific mortality hazard, and the slope (β) for perfectly additive mortality should be $\beta = 1$. If predation was perfectly compensatory, survival should remain constant ($\beta = 0$) with increasing cause-specific mortality. This is a conservative and potentially biased test for additive mortality because of the potential negative sampling covariance between cause-specific mortality hazard from a specific cause and total mortality (Schaub & Lebreton 2004). For example, total mortality will increase if a cause-specific mortality rate increases, to some unknown degree, even if 100% (Schaub & Lebreton 2004). Therefore, this bias would render it more difficult to detect compensatory mortality. Other regression or state-space approaches suffer similar limitations; yet recent studies have used such approaches to gain valuable insight into whether mortality causes are compensatory in the absence of experimental manipulations (Murray *et al.* 2010).

Finally, because the effects of predation and climate can interact on mortality (e.g. Hebblewhite 2005), we considered the interaction between number of predators and both summer and winter climatic variables in Weibull survival models. If predator-mortality increased with climatic severity (drought, winter severity), this is consistent with neonatal mortality also being partially compensatory through the interaction between an ostensibly density-dependent mortality cause, predation, and a density-independent mortality cause, climate. In this sense, in the absence of a predation*climate interaction, neonatal mortality hazard would be lower and calf survival would increase.

Results

We determined the fate of 1999 radio-marked elk calves across the 12 study areas from 1973 to 2007, with the majority of individuals marked from 1990 to 2007. Sample sizes in each study area ranged from 29 (Gallatin, MT) to 444 (Blue Mountains, OR), with an average of 196 (Tables 1, S2). Mean capture date of elk calves was 3 June, study area means ranged from 26 May to 7 June, an overall range from 10 May to 18 July (Table S3). Mean birth date was 31 May, ranging over 1 week from 23 May to 4 June (Table S2); overall birth dates ranged from 8 May to 16 July. Average age at capture was 3 days (range 0–10) (Table S2), and mean capture weight was 21·5 kg and varied from 17·6 to 28·0 kg across study areas. Sex ratio of captured elk calves was 0·9:1 males to females, which varied across study areas from 0·6 to 1·3 and was not significantly different from a 50:50 sex ratio ($\chi^2 = 2{\cdot}28$, df $= 1$, $P = 0{\cdot}131$, see Table S3 for details).

SURVIVAL MODELLING

The Kaplan–Meier 3-month (93 day) survival rate of neonatal elk calves across all 12 studies was 0·61 (SE = 0·01) and ranged from 0·31 (SE = 0·04) to 0·84 (SE = 0·03) (Table 1). Overall Kaplan–Meier summer survival rates varied among study areas with different predator community composition. Average survival was 0·65 (SE = 0·01) with three predators, 0·55 (SE = 0·03) with four, and 0·50 (SE = 0·03) with five (Fig. 2).

The top neonatal elk survival model was a function of the base covariates (sex, birth date and birth weight), predator community composition (three, four or five predators),

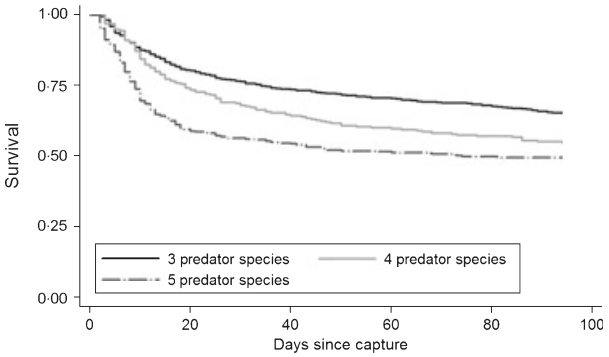

Fig. 2. Kaplan–Meier estimates of neonate elk survival for the first 3 months of life as a function of number of predator species across the north-western USA. Data from 12 studies that occurred between 1973 and 2007.

previous summer average maximum temperature, May precipitation, and the interaction between May precipitation and four predators (Table 2). The second ranked model was a function of base covariates, number of predator species, May precipitation and previous summer maximum temperature, and the interaction between May precipitation and both four and five predators (ΔAIC = 1·7). Despite some model selection uncertainty, because there was sufficient weight and similarities between the top two models, we focus our results on these (Table 2) and report hazard ratios for both in Table 3. Including frailty improved model fit over the fixed-effect survival model (LRT of $\theta = 0$ in equation 1, $\chi^2 = 139{\cdot}5$, $P < 0{\cdot}00005$; also, ΔAIC of the top-ranked model without frailty = 85; note both tests are potentially optimistic, Cleves, Gould & Gutierrez 2002). Variance in survival among study areas was significant ($\theta = 0{\cdot}351$, SE = 0·148), confirming substantial within-study-area correlation in survival. Expressed as a proportion of the total variance in our Kaplan–Meier survival rate, our survival model explained 40·1% of the variation in survival across all study areas (Vaida & Xu 2000; Cleves, Gould & Gutierrez 2002). We emphasize our inferences from the top shared-

Table 2. Top ten Weibull neonatal elk survival models showing number of parameters (*k*), deviance (Dev), change in AIC compared to the best-ranked model (Δ AIC), and Akaike model weights (*w*) across the north-western United States. The base model included sex (male, female, unknown), birth date, and birth weight, as well as two Weibull survival parameters, and a random effect term (seven base parameters). Climatic coefficients are previous summer mean maximum temperature (PSt), May precipitation (Mp), mean May minimum temperature (MMt), June snow (Js), total snow (TSnow) and mean winter minimum temperature (WMt). Number of predator species was Pred 4 and Pred 5, respectively; covariate interactions are indicated by*

Model rank	Model	*k*	Dev	Δ AIC	*w*
1	PSt + Mp + Pred 4 + Pred5 + Mp*Pred4	11	−1837·6	0·0	0·659
2	PSt + Mp + Pred 4 + Pred5 + Mp*Pred4 + Mp*Pred5	12	−1837·4	1·7	0·287
3	PSt + Mp + Pred4 + Pred5 + Mp*Pred4 + Mp*Pred5 + PSt*Pred4 + PSt*Pred5	14	−1837·1	5·1	0·050
4	WMt + PSt + MMt + Mp + Js	11	−1844·0	12·8	0·001
5	WMt + PSt + MMt + Mp	10	−1845·4	13·7	0·001
6	PSt + MMt + Mp + Pred5	10	−1845·6	14·1	0·001
7	WMt + PSt + MMt + Mp + Js + Pred5	12	−1843·4	14·1	0·001
8	WMt + PSt + MMt + Mp + Js + TSnow	12	−1843·8	14·4	< 0·001
9	WMt + PSt + MMt + Mp + Js + Pred4	12	−1843·8	14·5	< 0·001
10	WMt + PSt + MMt + Mp + Pred5	11	−1844·8	14·5	< 0·001

Table 3. Mortality hazard ratios for the top two Weibull survival models for neonate elk survival in the north-western United States, 1973–2007. See Table 2 for descriptions of the two top models. As the risk of mortality hazard increases, survival decreases such that a hazard ratio > 1·0 means lower survival. The reference category for sex is male and for number of predator species is three predators

	No. 1 Model			No. 2 Model		
Covariate	Hazard Ratio	*P*	95%CI	Hazard Ratio	*P*	95%CI
Female	1. 09 (0·087)	0·30	(0·93 – 1·27)	1·09 (0·087)	0·30	(0·93 – 1·27)
Birth weight	0·98 (0·011)	0·06	(0·96 – 1·00)	0·98 (0·011)	0·05	(0·96 – 1·00)
Birth date	1·00 (0·007)	0·730	(0·98 – 1·01)	1·00 (0·007)	0·74	(0·98 – 1·01)
Prev. summer max temp	1·11 (0·033)	< 0·0001	(1·05 – 1·18)	1·11 (0·033)	< 0·0001	(1·05 – 1·18)
May precip.	1·01 (0·015)	0·43	(0·98 – 1·04)	1·01 (0·015)	0·38	(0·98 – 1·04)
4 Predators	2·98 (0·858)	< 0·0001	(1·69 – 5·24)	3·01 (0·869)	< 0·0001	(1·71 – 5·30)
5 Predators	2·39 (1·009)	0·04	(1·04 – 5·47)	3·12 (1·929)	0·07	(0·93 – 10·48)
May precip*4 predators	0·90 (0·022)	< 0·0001	(0·86 – 0·95)	0·90 (0·022)	< 0·0001	(0·86 – 0·95)
May precip*5 predators	–			0·95 (0·078)	0·56	(0·81 – 1·12)

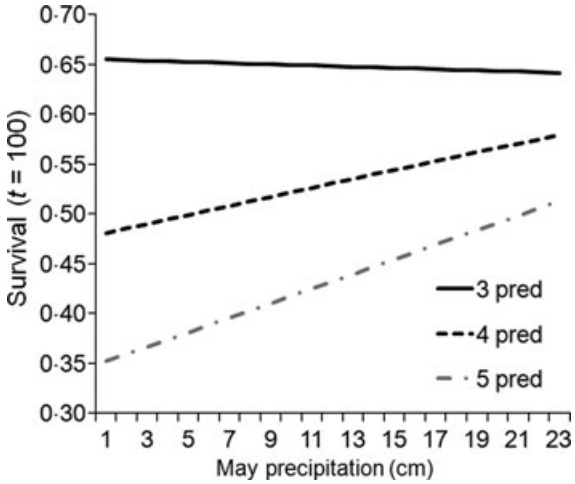

Fig. 3. Neonatal elk survival at day 100 as a function of May precipitation (cm) under different number of predator species across the north-western United States, 1973–2007.

frailty model should be interpreted as the population-averaged effects across all 12 study areas representing the average elk calf survival experience, adjusting for covariates, and not the expectation within any specific study area.

Covariate effects in terms of hazard ratios (HR) from the top two models are reported in Table 3. No significant effect of sex on survival was found in either model ($P = 0{\cdot}30$), nor was birth date related to hazard ($P = 0{\cdot}73$). Survival increased with increasing birth weight, as expected (i.e., increasing weight decreased mortality hazard, Table 3). Survival decreased in the top model as the number of predator species increased from three (reference case) to include wolves (HR = 2·98, $P < 0{\cdot}0001$) and wolves and grizzly bears (HR = 2·39, $P = 0{\cdot}04$). There was no difference in hazard ratios between wolves and wolves and grizzlies ($P = 0{\cdot}35$), supporting our interpretation of increasing compensatory mortality as the number of predators increased. When adult females experienced hot summers, survival of calves the following summer decreased (HR = 1·11, $P < 0{\cdot}0001$) over and above the effect of birth weight, which was also in the model. Increasing May precipitation had no main effect on survival by itself (HR = 1·01, $P = 0{\cdot}43$), only through its interaction with predation (Table 3). In both top models, increasing May precipitation increased survival of calves (Fig. 3); however, the interaction was only significant in areas with four predators (HR = 0·90, $P < 0{\cdot}0001$). Analysis of the restricted Jackson Hole data before (1990 – 1992) and after (1997 – 1999) grizzly bear and wolf recovery showed the same two top models and hazard ratios (Table S4), as did the analysis excluding Jackson Hole data from the overall data (M. Hebblewhite., unpubl. data), confirming our interpretation of the overall models.

CAUSE-SPECIFIC MORTALITY

We detected 671 mortalities across the 1999 marked calves, 70% of which occurred within the first 30 days (median age of death = 14 days). Average cause-specific mortality rates were 0·15 (SE = 0·01) for ursids, 0·11 (SE = 0·01) for cougars, 0·02 (SE < 0·01) for coyotes, 0·01(SE < 0·01) for wolves, 0·04 (SE = 0·01) for nonpredators and 0·06 (SE = 0·01) for all other mortalities (Table S5). In predator communities with wolves (four predators), cougar-caused mortality declined from 0·14 (SE = 0·01) to 0·07 (SE = 0·02) (Pepe-Mori test of the hypothesis that cougar mortality did not change with additional predators, $P < 0{\cdot}001$), and ursid predation marginally increased (Pepe-Mori test $P \leq 0{\cdot}08$) from 0·11 (SE = 0·01) to 0·16 (SE = 0·02). See Table S6 for full details of tests. Including wolves in the system added only a small amount of wolf-caused mortality, 0·04 (SE = 0·01), with essentially no change in coyote predation ($P = 0{\cdot}17$) (Figs 4 and 5). With both wolves and grizzly bears, cougar predation declined to negligible levels ($P < 0{\cdot}001$) to <0·01 (SE < 0·01), ursid predation significantly increased ($P < 0{\cdot}001$) almost doubling to 0·30 (SE = 0·03) while coyote predation remained similar ($P = 0{\cdot}18$) from 0·03 (SE = 0·01) to 0·04 (SE = 0·01). Wolf predation changed in systems with grizzly bears, despite similar hazards ($P = 0{\cdot}08$; four predators, wolf mortality rate = 0·04, SE = 0·01 vs. five predators = 0·04, SE = 0·01) (Figs 4 and 5), because the timing of wolf-caused mortality shifted. Without grizzly bears, wolf predation occurred later, but peaked earlier with grizzly bears (Figs 4 and 5). Timing of bear mortality, however, always peaked early from day 0 to 30 and was the most important overall source of neonatal mortality (Fig. 5). Across systems, the timing of coyote and cougar mortality during the early 0–30 days did not change either (Fig. 5). We found no relationship between nonpredator caused mortality rates and overall survival (Table S2, S5).

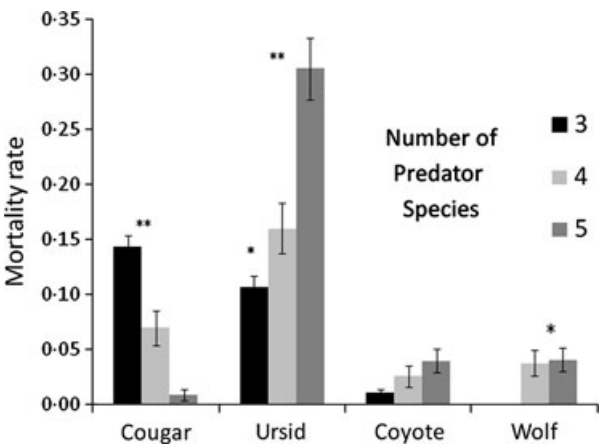

Fig. 4. Cause-specific mortality (3 months) for neonate elk by number of predator species for major predators using cumulative incidence function analysis. "Ursid" in the three and four-predator system represents only black bear but in the five-predator system "ursid" represents both black and grizzly bear. Bars represent 95% confidence intervals. Significant differences for a predator species between mortality hazard in different predator communities are marked with an *($P = 0{\cdot}05$) or **($P = 0{\cdot}01$) using Pepe & Mori (1993) tests.

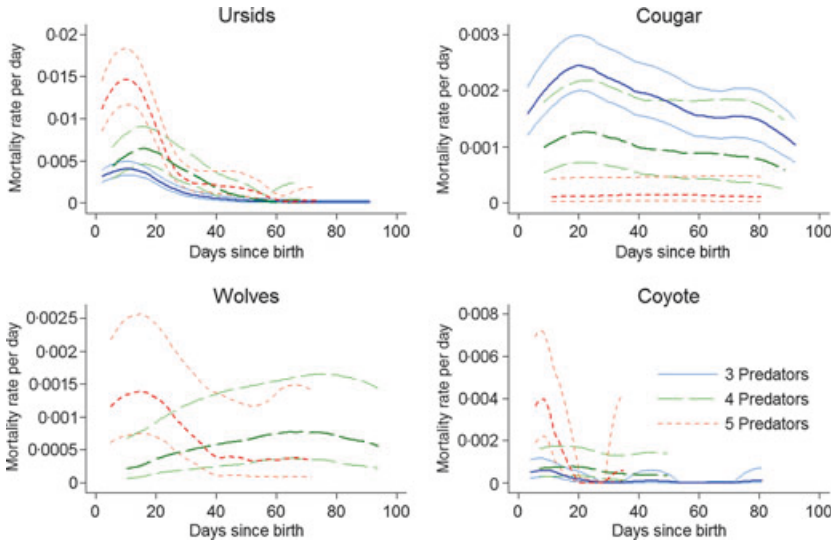

Fig. 5. Instantaneous smoothed hazard functions (relative probability of mortality) showing timing of mortality on neonatal-elk calves since capture across the north-western United States by each of the 4 main predator species as a function of changing predator community composition (three predators; black bears, coyotes, cougars; four predators including wolves, and five predators including grizzly bears). We calculated smoothed hazards using the unconditional (population averaged) Epanechnikov kernel smoothing at the mean covariate value for all continuous covariates for females. Hazards are graphed with 95% confidence intervals. Note the different magnitude of the *Y*-axis especially between Ursid and all other mortality.

Comparing the relationship between CIF mortality rate and neonatal survival among study areas revealed that only ursid predation appeared additive (Fig. 6, linear $\beta = -1{\cdot}01$, $P < 0{\cdot}001$, $R^2 = 0{\cdot}76$, $n = 12$ studies), showing that survival decreased linearly with increasing ursid predation. For all other predators, cause-specific mortality was not significantly related to survival, and coefficients were all between 0 and 1, supporting the partially compensatory hypothesis, although among-study area sample sizes were low for some tests. For example, there was no additive relationship between neonatal survival and coyote ($\beta = 0{\cdot}74$, $P = 0{\cdot}79$, $R^2 = 0{\cdot}01$, $n = 12$), cougar ($\beta = -0{\cdot}16$, $P = 0{\cdot}81$, $R^2 = 0{\cdot}01$, $n = 12$) or wolf predation ($\beta = -0{\cdot}74$, $P = 0{\cdot}71$, $R^2 = 0{\cdot}04, n = 6$).

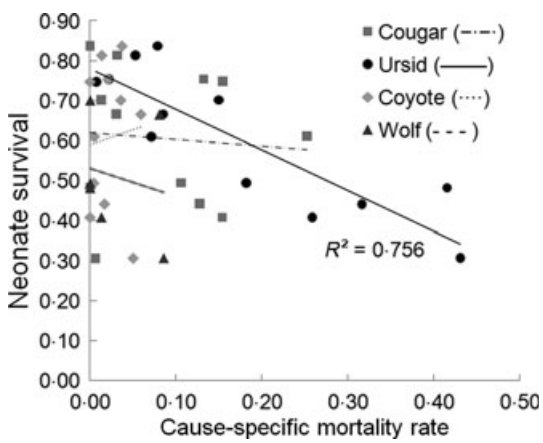

Fig. 6. Neonate elk survival by cause-specific mortality by the major predators across the north-western United States. Linear regressions are displayed for all species; however, only one category, ursids, was significant ($P \leq 0{\cdot}001$), confirming that only ursid mortality was additive (see text for details).

Discussion

Survival patterns of approximately 2000 neonatal elk in the north-western United States were consistent with the compensatory-mortality hypothesis via two important mechanisms. The compensatory-mortality hypothesis predicts that as the number of predator species increase, neonatal survival will stabilize, indicating that one predator is replacing another in its effect on neonate survival. As the number of predator species increased, neonates survival declined, and bears and cougars were the dominant predators of neonates. Based on hazard ratios, survival declined most between three and four predator communities, but not as much with the addition of a major calf predator, grizzly bears. Analysis of competing risks suggested that this was because of interspecific compensation between cougars with increasing ursids, especially grizzly bears, but that unlike other predators, bear predation was additive with other causes of predation. Predation by ursids on neonates was consistent with additive mortality compared to other predators whose mortality was at least partially compensatory, emphasizing the key role of ursids in setting the stage for neonate survival. We also found evidence for climatic-predation interaction that may lead to compensatory predation mortality. Increased precipitation during May likely increased forage quality for ungulates, reducing mortality in systems with four or five predators. Therefore, given the evidence for compensatory mortality from the interaction of climate and predation, interspecific competition amongst predators, and evidence

for compensatory mortality by all predators except bears, the effect of neonatal predation on population dynamics may be weaker than expected if all predation was additive.

Our results supported the effects of spring/summer temperature and precipitation on neonate survival more so than effects of winter severity, consistent with the important role of summer forage on ungulates (McArt *et al*. 2009; Parker, Barboza & Gillingham 2009). We found a negative effect of hotter previous summers on neonate survival 1 year later over and above the effects of cooler and wetter summers on calf birth weight. These effects may have been driven by long-term drought conditions experienced in many study areas in the 1990s (e.g. in Yellowstone National Park; Vucetich, Smith & Stahler 2005). However, effects of spring climate were less certain (Table 2), perhaps because of variation in the mechanisms of spring climate downscaling across our 12 study areas (Pettorelli *et al*. 2005). For example, many studies report a positive effect of spring climate on neonate survival (Albon, Clutton-Brock & Guiness 1987; Raithel 2005; Harris 2007), but Smith *et al*. (2006) reported mean April temperatures, and others found March or May climate patterns drove neonate survival. Across all 12 areas, we found that calf survival increased with increasing May precipitation, but interestingly, only in the presence of four or five predators. May precipitation could influence calf survival through effects on summer forage quality and quantity on both lactation and forage intake by the calf (Cook *et al*. 2004). May precipitation patterns could also drive spring forage phenology, and hence, neonatal survival (Pettorelli *et al*. 2005, 2007). Alternately, because the effects of precipitation were only apparent in systems with increased predation, May precipitation could influence spatial distribution of forage that indirectly affects vulnerability to predation (Hegel *et al*. 2010). The obvious next step to tease apart these competing mechanisms is analyses that combine spatial measures of forage quality/quantity (such as NDVI, Pettorelli *et al*. 2005), climate and predation. Regardless, our results emphasize the potential for climate-mediated compensatory mortality occurring during spring and summer in addition to classic winter starvation-mediated mortality (Singer *et al*. 1997).

The survival rates we observed in our study are consistent with positive population growth of elk only under certain ecological conditions. Given that annual elk calf survival explains $\sim$ 73% of the variation in population growth rate (Raithel, Kauffman & Pletscher 2007) and a mean adult female survival rate reported by Raithel, Kauffman & Pletscher (2007) of 0·873 (which included our study areas), our observed calf survival rates could be consistent with growing (three predator systems), stable (four predators) and declining elk populations (five predators). This simple approach emphasizes the importance of understanding both adult and annual calf survival, not just neonatal survival, to assess impact of predators. Consistent with this coarse interpretation, however, recent experimental predator reductions in Idaho (White, Zager & Gratson 2010) also show that reducing bear densities increased neonate calf survival, consistent with our finding of bear predation being a dominant cause of additive mortality for neonates. Moreover, our restricted analysis of the Jackson Hole area following recovery by wolves and grizzly bears represents pseudo-experimental evidence for strong effects of grizzly bears, but not wolves, on calf survival (supporting information table S4). However, recent experimental manipulations of winter food (Bishop *et al*. 2009) and densities of two of four main predators (Hurley *et al*. 2011) of another ungulate, mule deer (*Odocoileus hemionus*), suggest that the effects of food availability on juvenile survival were stronger than effects of predator removal. Thus, mortality caused by climate–predator interactions and competition among predators may make efforts to increase population growth rate of elk through predator control challenging.

Our results emphasize the strongly additive and 'preemptive' role of early predation by ursids on neonates and emphasizes that the phenology of predation may dictate juvenile survival patterns. This echoes recent studies that emphasize the critical importance of bear predation to neonatal calf survival (Linnell, Aanes & Andersen 1995; Gustine *et al*. 2006; Zager & Beecham 2006; Barber-Meyer, Mech & White 2008). Across our 12 study areas, we found 0·01 to 0·44 probability of mortality as a result of predation by black and/or grizzly bears, which additively explained approximately 50% of the variance in neonatal survival. Furthermore, when grizzly bears were in a system, mortality from ursids doubled. Additive bear mortality may be a result of 'predation phenology' in the timing of the pulse of ursid mortality on neonates. Bear predation peaked within the first 2 weeks of a neonate's life during the critical 'hiding' period when female elk hide their calves (Fig. 5). Following the hiding period, elk cow–calf pairs form large groups and bear predation declines to almost zero. In contrast, mortality by other predators occurred throughout the summer, after the pulse of bear predation (Fig. 5). Thus, in a competing risks framework, earlier bear predation out-competed later predators. Bear predation may be additive because bears become specialist predators during early calving before body condition can start to mediate vulnerability to predation (White, Zager & Gratson 2010). Alternately, increased bear predation could simply be attributed to spatial overlap. For example, ungulate avoidance of low-elevation valley bottoms during calving effectively reduces predation by canids (Hebblewhite & Merrill 2007), but perhaps not by bears which often select the same forage as ungulates during calving (Nielsen *et al*. 2003).

Functional redundancy among the predator community may have been an important compensatory mechanism suggested by the decelerating mortality hazard with the addition of wolves and wolves and grizzlies. Declining cougar predation in the presence of wolves and grizzly bears is suggestive of interspecific competition. Wolves are known to be effective competitors with cougars and coyotes through interference and exploitative competition (Kortello, Hurd & Murray 2007; Berger, Gese & Berger 2008; Hebblewhite & Smith 2009). Similarly, grizzly bears can be an important natural cause of mortality for black bears (Hebblewhite, Percy & Serrouya 2003), and wolves and grizzly bears also compete

both directly and indirectly (Hebblewhite & Smith 2009). Puzzlingly, however, calf survival was lower in systems that contained wolves (four or five predator systems), despite the fact that these systems had low wolf mortality rates. These results might be consistent with the hypothesis that wolves affect calf recruitment through indirect risk effects (Creel *et al*. 2007). Thus, the addition of new carnivore species to already diverse predator communities may not affect neonatal survival additively, but mortality could also manifest through indirect effects.

Our study suffers some of the inferential weaknesses of observational studies, regardless of the large number of calves, as we only had 12 populations to compare across, and would be strengthened if more of our studies were experimental manipulations. Thus, some caution is warranted. For example, we were unable to measure predator densities to explicitly test the effects of predator density on neonatal survival. Our results could therefore be because of other uncontrolled differences among study areas that were correlated with the number of predator species such as predator density, habitat fragmentation or human harvest. For example, there was an east–west gradient in bear to cougar predation that may reflect regional trends in carnivore abundance, not the predator community per se. Moreover, as previously mentioned, our tests for additive or compensatory mortality were biased towards detecting additive mortality (Schaub & Lebreton 2004) and limited by low sample sizes of systems for some predators, such as wolves ($n = 6$), for example. However, we believe our results warrant consideration for several reasons. First, our survival estimates and estimates of risk factors matched the results of previous analyses within individual study areas well. The restricted analysis with the before-after comparison in Jackson Hole corroborated our pooled model results almost exactly (Table S4), and our data included the predator manipulation study in Idaho conducted by White, Zager & Gratson (2010). Our survival model also predicted 'out-of-sample' survival well in Yellowstone National Park under drought conditions before wolves' recolonized (Singer *et al*. (1997) calf survival estimate of 0·646 [SE = 0·132], compared to that predicted by model 1 of 0·585 [SE = 0·06]). Second, our shared-frailty Weibull survival modelling framework addressed unobserved, shared heterogeneity among populations that was unrelated to the measured covariates, including predator density. Shared-frailty models could explain 41% of observed variation in survival across studies, and while this is quite high for an ecological study, it certainly leaves a substantial degree of variation that could be attributed to unmeasured variables. These results should aid management of elk populations across a gradient of predator communities across the north-western United States and allow basic predictions of neonate survival for the first 3 months under different ecological conditions. We encourage future studies to examine elk calf survival in areas with known or experimentally manipulated predator densities. Finally, because overwinter calf survival was not addressed in this study, there may be important compensation between additive summer bear mortality and winter causes of mortality, especially because wolf mortality increases during mid to late winter with increasing snow depth (Smith *et al*. 2004).

Future studies should also examine whether primary productivity will buffer survival against predation and climate. We did not incorporate spatial measures of primary productivity (e.g. NDVI) here, although such analyses are the obvious next step. Regardless, based on recent studies, we can make future predictions. In one of the most compelling recent meta-analyses, Melis *et al*. (2009) showed predation and primary productivity interacted in roe deer (*Capreolus capreolus*) across 79 populations in continental Europe spanning a wide latitudinal gradient. At a low primary productivity (northern latitudes), predation had a dramatic effect on roe deer, reducing densities almost 50%. Yet at high primary productivity, no difference between roe deer densities with and without predation was found. Therefore, we predict that predation will be largely compensatory where primary productivity is high and mostly additive where primary productivity is low.

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Supporting Information

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

Table S1. Summary climate statistics for all 12 elk calf survival study areas.

Table S2. Cause of mortality as originally categorized by researchers compared to mortality codes used in our analyses.

Table S3. Summary statistics for all study areas.

Table S4. Hazard ratios for the top neonatal elk survival model using only data from Jackson Hole.

Table S5. Neonatal elk survival and cause-specific mortality to 100 days of life by study area and major predators.

Table S6. Result of Pepe-Mori tests of equality in cause-specific mortality between areas with differing numbers of predators.

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