

# Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (*Canis lupus*)

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## Summary

**1.** Understanding the population dynamics of top-predators is essential to assess their impact on ecosystems and to guide their management. Key to this understanding is identifying the mechanisms regulating vital rates.

**2.** Determining the influence of density on survival is necessary to understand the extent to which human-caused mortality is compensatory or additive. In wolves (*Canis lupus*), empirical evidence for density-dependent survival is lacking. Dispersal is considered the principal way in which wolves adjust their numbers to prey supply or compensate for human exploitation. However, studies to date have primarily focused on exploited wolf populations, in which density-dependent mechanisms are likely weak due to artificially low wolf densities.

**3.** Using 13 years of data on 280 collared wolves in Yellowstone National Park, we assessed the effect of wolf density, prey abundance and population structure, as well as winter severity, on age-specific survival in two areas (prey-rich vs. prey-poor) of the national park. We further analysed cause-specific mortality and explored the factors driving intraspecific aggression in the prey-rich northern area of the park.

**4.** Overall, survival rates decreased during the study. In northern Yellowstone, density dependence regulated adult survival through an increase in intraspecific aggression, independent of prey availability. In the interior of the park, adult survival was less variable and density-independent, despite reduced prey availability. There was no effect of prey population structure in northern Yellowstone, or of winter severity in either area. Survival was similar among yearlings and adults, but lower for adults older than 6 years.

**5.** Our results indicate that density-dependent intraspecific aggression is a major driver of adult wolf survival in northern Yellowstone, suggesting intrinsic density-dependent mechanisms have the potential to regulate wolf populations at high ungulate densities. When low prey availability or high removal rates maintain wolves at lower densities, limited inter-pack interactions may prevent density-dependent survival, consistent with our findings in the interior of the park.

**Key-words:** Capture–recapture, density dependence, food availability, intraspecific competition, population regulation, top-predator, vital rate

## Introduction

Large carnivores are colonizing areas from which they have been extirpated for several decades, generating conflicts with humans through predation on game and

domestic species (Treves & Karanth 2003; Woodroffe, Thirgood & Rabinowitz 2005). In this context, obtaining accurate estimates of vital rates – survival, reproduction and dispersal – and identifying the sources of variation in these parameters is essential to predict the impact of top-predators on their ecosystem, and to provide adequate management recommendations to address public concerns, while maintaining population viability. In the last

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decade, Gray wolf (*Canis lupus*) conservation status in Europe and the contiguous United States (US) has changed from total protection to partial protection or harvested (European Commission Environment 1992; US Fish & Wildlife Service 2009). The extent to which anthropogenic and natural mortality are compensatory in wolves is currently debated (Adams *et al.* 2008; Creel & Rotella 2010; Murray *et al.* 2010; Gude *et al.* 2012), and the mechanisms that influence wolf vital rates (aside from anthropogenic mortality) remain unclear.

Several authors have argued that the ultimate limit to wolf density is that imposed by food, i.e. prey abundance and their vulnerability to predation (Packard & Mech 1980; Keith 1983; Peterson & Page 1988; Fuller, Mech & Cochrane 2003). Indeed, long-term data from Isle Royale National Park show that wolf population growth depends mainly on the number and age structure of the prey population, although density dependence, winter severity and stochastic events like disease outbreaks also play important roles (Peterson & Page 1988; Peterson *et al.* 1998; Vucetich & Peterson 2004). The influence of winter severity is manifested through changes in prey vulnerability and kill rate, whereas density dependence is likely due to decreasing per capita food availability (Post *et al.* 1999; Vucetich & Peterson 2004). Density-dependent food availability also influences dispersal, which is considered the principle means by which wolves adjust their numbers to food supply and compensate for human-caused mortality (Fuller 1989; Hayes & Harestad 2000; Fuller, Mech & Cochrane 2003; Adams *et al.* 2008).

Other authors have suggested that intraspecific competition related to territoriality may regulate wolf density below that predicted by food availability (Stenlund 1955; Pimlott 1967, 1970). Cariappa *et al.*'s (2011) analysis of 28 wolf populations revealed an asymptotic relationship between wolf and prey densities, suggesting that density-dependent mechanisms unrelated to food impose an upper bound of 69 wolves 1000 km<sup>2</sup>. However, empirical evidence of such mechanisms is lacking.

If wolves are limited solely by food availability, we do not expect density-dependent survival rates at high ungulate densities (i.e. when food is not a limiting factor). On the contrary, if social aggression regulates wolf numbers at high ungulate densities, we expect (i) density-dependent survival rates, (ii) social aggression to be the main cause of mortality and (iii) the occurrence of social aggression to increase with wolf density, independently of food availability. Although the demography of wolves is well-studied (e.g. Fuller 1989; Hayes & Harestad 2000; Fuller, Mech & Cochrane 2003; Vucetich & Peterson 2004; Adams *et al.* 2008; Murray *et al.* 2010; Smith *et al.* 2010), research has yet to demonstrate a negative effect of density on wolf survival or quantify the relationship between wolf social aggression, density and food availability.

Here, we analyse the influence of environmental conditions on the survival of wolves in Yellowstone National Park (YNP) between 1998 and 2010. The gray wolf was

reintroduced to YNP with the release of 41 individuals in 1995 and 1996 (Smith 2005) and minimum numbers within the park have ranged between 72 and 174 wolves since (Smith *et al.* 2013). The northern portion of YNP, also referred to as the Northern Range (NR; 995 km<sup>2</sup>; ~10% of the park), supports a higher density of wolves than do the central and southern portions of the park, known as the Interior (7991 km<sup>2</sup>; 20–99 wolves 1000 km<sup>2</sup> vs. 2–11 wolves 1000 km<sup>2</sup>; Smith & Bangs 2009). Wolves in both areas prey mainly on elk (*Cervus elaphus*) (Smith *et al.* 2004; Metz *et al.* 2012) and although the NR elk herd has decreased from ~16 000 in 1995 to ~6000 elk in 2010, elk densities in the NR (6.1–14.6 elk km<sup>2</sup>) far exceeded prey densities in most other studied wolf-prey systems (reviewed by Fuller, Mech & Cochrane 2003). Low elevations (1500–2000 m) in the NR provide tolerable winter conditions for elk such that elk availability in the area is relatively high all year round (Houston 1982). In the Interior, higher elevations (>2000 m) and higher snowfall push most elk out of the area in winter, leading some wolves to occasionally prey on non-migratory bison (Smith *et al.* 2000; Becker *et al.* 2008), which are three times more difficult to kill than are elk (Smith *et al.* 2000). We treat the NR and the Interior as different study areas to account for their ecological and physiographic differences.

Using 13 years of data on 280 collared YNP wolves, we estimated temporal and spatial variation in age- and sex-dependent survival rates, while accounting for imperfect knowledge of the fate of each individual. In addition, we assessed the effect of wolf density, prey abundance and population structure, as well as winter severity, on variation in age-specific survival rates in the NR and the Interior. We also analysed cause-specific mortality of 155 wolves recovered dead in YNP and explored the factors driving intraspecific aggression in the NR.

## Materials and methods

### WOLF LIFE HISTORY DATA

The study area, wolf reintroduction and field methods used to monitor the wolf population are described in previous publications (see for example Smith 2005), so details are not provided here.

### Survival data, age and sex

Life history data used to estimate survival were obtained through monitoring of 280 radio-collared wolves in YNP between 1998 and 2010. Wolves included in this study were either members of the original reintroduced population or their descendants. In each year after the reintroduction, c. 30–50% of the pups born were captured and radio-marked between November and February, so age and sex were known for each individual (MacNulty *et al.* 2009). As infant mortality in wolves tends to occur in the first 6 month of life (Fuller, Mech & Cochrane 2003) prior to when we radio-collared wolves (9 month of life), we do not report pup

survival. For wolves of 1 year and older, we estimated annual survival rates from the beginning of April in year  $t$  to beginning of April in year  $t + 1$ .

### Wolf density

At least one individual from each pack was marked with a radio-collar, allowing packs to be tracked at least bi-weekly from aircraft. For 30 days in early (mid-November to mid-December) and late (March) winter wolf packs were also intensively monitored from the ground. We used the number of wolves per 1000 km<sup>2</sup> in the NR and the Interior in spring (1st of April) of year  $t$  – before reproduction, including adults and 11-month-old pups from the previous year – and in early winter (31st of December) of the same year – including adults and the surviving pups (8 months old) of the year – to assess the effect of wolf density on annual survival from year  $t$  to  $t + 1$ .

### Cause-specific mortality

All radiocollars included a mortality switch that allowed us to determine the time and cause of death when possible (see Murray *et al.* 2010 for details about the protocols). Between 1998 and 2010, we determined cause of death for 155 wolves (not all of them were radio-collared) that died inside YNP. Death was classified as human caused (including incidents with vehicles and four control actions), or natural (intra- or interspecific conflicts, malnutrition, disease or unknown causes of natural mortality) or unknown causes.

### Social aggressions

Intense year-round monitoring and YNP's open environment permitted direct observation of inter-pack aggressive interactions (between two wolf packs or between one wolf pack and an unaffiliated individual). A conflict occurred when one wolf chased and physically displaced another (see Cassidy 2013 for details). We used the total number of aggressive interactions observed each year from 1998 to 2010 as an index of social aggression.

### NORTHERN YELLOWSTONE ELK DATA

We used annual elk counts in winter (absolute and relative to wolf numbers), proportion of calves per 100 females, and proportion of old females (>14 years old) as indices of prey availability in the NR. Of 1800 known-age elk killed by wolves in the NR during 1998–2010, 43% were calves and 18% were old females (Yellowstone Wolf Project, unpublished data). The mean ( $\pm$ SE) age of adult female elk ( $\geq 2$  years old) killed by wolves was  $14.7 \pm 0.17$  years ( $N = 531$  kills), which is similar to previous estimates (Wright *et al.* 2006). Aerial and ground surveys were conducted annually by the Northern Yellowstone Cooperative Wildlife Working Group to estimate elk numbers and calf:cow ratios in the NR during winter. Aerial elk counts are minimum estimates of actual elk numbers because they are uncorrected for imperfect sightability (Eberhardt *et al.* 2007). The survey methods are presented in Taper & Gogan (2002). Because the age distributions for females harvested during the Gardiner Late Hunt were representative of the female elk population, we used Late Hunt harvest data from 1998 to 2009 to calculate the proportion of old female elk in the NR elk herd (Wright *et al.* 2006; Eberhardt

*et al.* 2007). We tested for the effect of elk abundance, proportion of calves and old females measured in winter of year  $t$ , on wolf survival from April of year  $t$  to April in year  $t + 1$ . We only tested for the effect of prey availability on wolf survival in the NR because in winter most elk migrate from the Interior to lower elevation wintering areas in the NR and outside YNP.

### WINTER SEVERITY INDEX

Winter weather can affect wolf populations via increased prey vulnerability and kill rate (Post *et al.* 1999; Vucetich, Smith & Stahler 2005). To explore potential effects of climate on wolf survival, we used maximum annual snow water equivalent (i.e. water content of the snow; hereafter SWE) as an index of winter severity (Vucetich, Smith & Stahler 2005; MacNulty *et al.* 2009). This index was estimated from snow depth, precipitation and temperature at a climatological station in the NR (Mammoth).

### CAPTURE–RECAPTURE SURVIVAL ANALYSIS

We analysed 280 individual capture–recapture (CR) histories to estimate local annual survival probabilities between 1998 and 2010 using multi-state population models (Lebreton *et al.* 2009) implemented in program E-SURGE (Choquet & Nogue 2010). CR methods are useful when the fates of radio-collared individuals are not always known (Devineau *et al.* 2010), which was the case in our study. As detection probability was high, our survival estimates were similar to previous estimates for YNP wolves based on hazard models (MacNulty *et al.* 2009; Smith *et al.* 2010). The CR framework allowed us to analyse survival in the two study areas in a single model including multiple-states and events, allowing movement between areas. We classified wolves as: alive inside the NR of YNP, alive inside the Interior area of YNP, dispersed outside YNP, found dead or missing (unknown fate).

We performed goodness-of-fit tests starting from a general Cormack–Jolly–Seber (CJS) model allowing survival and detection probabilities to vary with time (Lebreton *et al.* 1992) using program U-CARE (Choquet *et al.* 2009). We detected a lack of fit due to 'transience' and 'trap-shyness' effects (Pradel *et al.* 1997). The 'trap-shyness' effect was not significant once we accounted for the presence of transient individuals. To account for the 'transient' effect, we censored individuals that dispersed outside of the park – assuming they were still alive during the year of dispersal – from the likelihood and considered a two age-class structure for survival (Pradel *et al.* 1997). We therefore estimated local survival rates (i.e. inside YNP).

### GENERAL MODEL STRUCTURE

We developed a multi-state CR model (Lebreton *et al.* 2009) to evaluate individual, spatial and temporal variation in survival probability. We considered four states to represent different locations [Northern Range (NR) or Interior (INT)], and status [alive (A), just dead (D), and already dead (†)]. To avoid modelling an additional state for dispersers, we assumed local dispersal events (i.e. the wolf remained inside the park) were instantaneous (wolves cannot remain dispersers for a complete year). Hence, we did not distinguish resident and local disperser survival rates. As dispersers were mostly yearlings and sub-adults an effect of local dispersal on survival should appear as reduced survival for these age classes.

At a given sampling occasion, an individual may be in state NR, INT, D or dead and the following observations may be made: '1' (if detected as a member of a NR pack), '2' (if detected as a member of an Interior pack), '3' (if recovered dead) and '0' (if not detected). We defined the initial state vector  $\Pi$  gathering the initial proportion of individuals in each state, the transition matrix  $\Phi\Psi$  (probability of transition between states conditional on survival in each location) and the event matrix  $\mathbf{B}$  gathering the detection probability  $P$  (detection probability of a collared wolf alive inside YNP) and recovery probability  $r$  (detection probability of a dead wolf inside YNP). Columns of the matrix  $\Pi$  and  $\Phi\Psi$  correspond, respectively, to state NR, INT, D and dead, columns of the matrix  $\mathbf{B}$  correspond to the observations 'non-detected' and 'detected' in state NR, INT or D, respectively, whereas rows of the matrices  $\Phi\Psi$  and  $\mathbf{B}$  correspond, respectively, to state NR, INT, D and dead:

$$\Pi = [\pi_{NR} \quad 1 - \pi_{NR} \quad 0 \quad 0],$$

$$\Phi\Psi = \begin{bmatrix} \Phi_{NR} \times (1 - \Psi_{NR \rightarrow INT}) & \Phi_{NR} \times \Psi_{NR \rightarrow INT} & 1 - \Phi_{NR} & 0 \\ \Phi_{INT} \times \Psi_{INT \rightarrow NR} & \Phi_{INT} \times (1 - \Psi_{INT \rightarrow NR}) & 1 - \Phi_{INT} & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 1 \end{bmatrix},$$

$$\mathbf{B} = \begin{bmatrix} 1 - p & p & 0 & 0 \\ 1 - p & 0 & p & 0 \\ 1 - r & 0 & 0 & r \\ 1 & 0 & 0 & 0 \end{bmatrix}.$$

We compared this general model considering state-dependent survival rates with a combination of sub-models in which survival was set to be equal across study areas.

#### HYPOTHESIS TESTING

We performed model selection step-by-step, first investigating a general structure for the model, then testing for the effects of individual and environmental covariates: (i) we first tested whether survival and detection rates were constant or varied with time [year effect or period effect considering constant survival until 2001 and then annual variation when competition among wolves was apparently higher (Fig. S1, Supporting information)] and between areas (NR and Interior), (ii) we then tested for sex and age effects by first including 8 age classes in this model, corresponding to 1-year old, 2-year old, 3-year old, 4-year old, 5-year old, 6-year old and 7-year old and older and compared with models with alternatively grouped age classes. After identifying the best sex- and age-structure and time-dependent parameters, we assessed the effects of environmental covariates for describing time variation in survival by performing an analysis of deviance (anodev test) and calculated the proportion of variance explained by the covariate using the  $R^2$  statistic (Grosbois *et al.* 2008).

Our models for NR wolf survival included wolf density in April and December (hereafter  $\text{density}_{\text{April}}$  and  $\text{density}_{\text{December}}$  respectively), elk number (elk), proportion of calves per 100 cows (calf:cow), proportion of old elk ( $\text{old}_{\text{elk}}$ ), ratio of elk to wolves ( $\text{elk:wolf}_{\text{December}}$ ) and snow water equivalent (SWE). We considered linear and quadratic effects of these variables, included either as single or additive effects or in interaction with other factors. On the basis of results from the time-dependent model, we also considered a threshold effect of density, with constant

survival below 60 wolves 1000 km<sup>2</sup> and a linear effect of density on survival above this value. Models of Interior wolf survival included  $\text{density}_{\text{April}}$ ,  $\text{density}_{\text{December}}$ , and SWE, but excluded elk-related covariates because few elk inhabit the Interior in winter (November to April).

Standard maximum likelihood procedures were used to obtain parameter estimates (Lebreton *et al.* 1992). Models were ranked using Akaike's information criterion corrected for small sample size (AICc; Sugiura 1978).

#### PATH ANALYSIS

Because wolf density and elk numbers were correlated ( $r = -0.62$ ;  $P$ -value  $< 0.05$ ; Supporting information), we used path analysis (Shipley 2002) to separate their relative effects on survival. This multivariate regression approach allows the evaluation of direct and indirect relationships among a set of correlated variables.

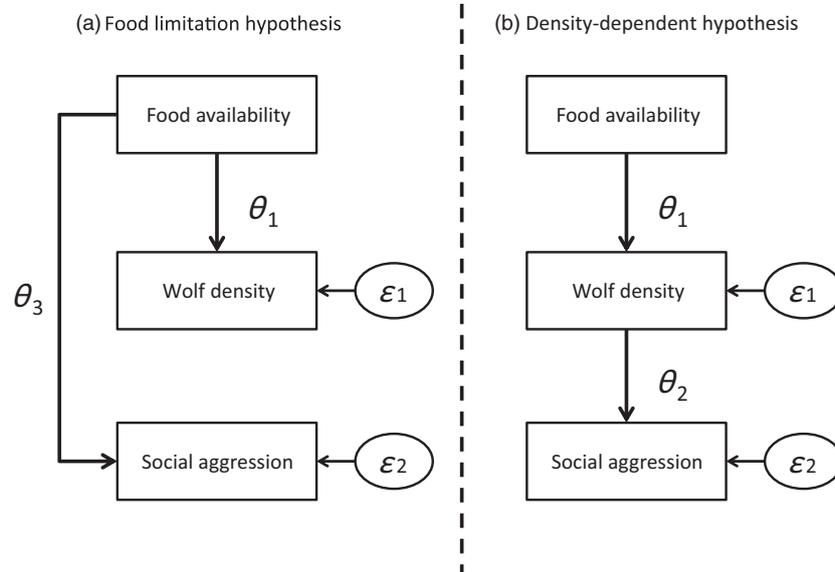
We parameterized two simple models supporting competing hypotheses about the direct and indirect effects of food availability and wolf density on the frequency of intraspecific aggression (identified as the main cause of mortality in the NR, see Results section). We specifically tested whether elk numbers directly influenced social aggression (food limitation hypothesis), vs. density-dependent social aggression independent of elk numbers (density-dependent hypothesis).

Our model consisted of the structural relationships among variables and their hypothesized interdependencies. We constructed the model by specifying a set of pathways describing how variables may affect one another both directly and indirectly (Fig. 1). The set of constraints of conditional independence between two variables not directly related to each other imposed by a given model can then be tested to evaluate the fit of the model using d-separation (Shipley 2009).

Under the food limitation hypothesis (Fig. 1a), social aggression and wolf density should be independent, conditioned on prey availability. Under the density-dependent hypothesis (Fig. 1b), social aggression and prey availability should be independent conditioned on wolf density. If the pattern of conditional independence predicted by the model was not observed in data, the model was not supported and the corresponding biological assumption was rejected (Shipley 2002). Conversely, if a model was supported by data, values of the path coefficients, indicating the strength and direction of the relationships among variables, were estimated using linear regressions on log-transformed data. If the slope of the relationship between two log-transformed variables was  $> 1$ , the relationship on the non-log scale was nonlinear. Analyses were conducted in program *R* (R. Development Core Team 2013).

#### Results

Temporal patterns in NR elk availability and wolf numbers during the study reflect profound ecological changes following wolf reintroduction (Fig. S1, Supporting information). Between 1998 and 2001, both elk abundance and vulnerability (proportion of calves) were high and wolf numbers were low, with an opposite pattern after 2001 suggestive of a more competitive environment for wolves.



**Fig. 1.** Graphical representations of the two competing models. Model (a) assumes a direct effect of food availability on social aggression, independent of wolf density. Model (b) assumes density-dependent social aggression, independent of food availability. Food availability is indicated by elk abundance, wolf density (the number of wolves per 1000 km<sup>2</sup> in April) and social aggression (the number of intraspecific conflicts per year in the Northern Range). The indirect effect of food availability on social aggression is captured by the product of  $\theta_1 \times \theta_2$ , while the direct effect of food on wolf density is captured by  $\theta_1$  and the direct effect of wolf density on social aggression is captured by  $\theta_2$ . The direct effect of food availability on social aggression is captured by  $\theta_3$ . For clarity, intercept parameters were omitted.

#### TEMPORAL AND SPATIAL PATTERNS OF VARIATION IN SURVIVAL AND DETECTION RATES

Among the 280 radio-collared individuals, 95 were found dead, 79 dispersed outside of the park, 37 were still alive at the end of the study and 69 had an unknown fate. Overall in YNP, mean annual survival was high, at about 80%. Results showed considerable year-to-year variation and revealed a general decline since reintroduction (Table 1.1; Fig. 2a). Survival rates dropped after 2001, with lowest annual survival rates recorded in 2005 and 2008 when they dropped below 0.7. Detection probability was very high [0.98 (0.97; 0.99)] and constant during the study (Table 1.1).

To determine whether survival differed between the NR and the Interior, we first added an 'area' effect to a model including only a time effect. These area and time models (Models 4 and 6 in Table 1.1) did not substantially outperform the time only model (Model 5 in Table 1.1), suggesting no clear difference in survival rates between the two areas. Next, we tested for a 'period' effect by distinguishing survival before and after 2001 when competition among wolves apparently changed (Fig. S1, Supporting information). A period  $\times$  area model outperformed all other models (Model 1 in Table 1.1), indicating period-dependent differences in survival between the two areas. Until 2001, survival rates were high and relatively constant in both areas. After 2001, survival decreased in the NR until 2006, while it remained more stable in the Interior (Fig. 2b,c). Survival rates dropped below 0.7 in 2004,

2005, 2008 and 2009 in the NR, while in the Interior survival was  $> 0.7$  for all years except 2005.

#### INDIVIDUAL VARIATION IN SURVIVAL: AGE AND SEX EFFECTS

There were no significant differences in survival rates between yearlings (1 year old) and adults (2–6 years old) (Table 2). Old adults (7 years old and older) had significantly reduced survival ( $\sim 0.63$ ), indicative of senescence. Survival did not differ between males and females: mean estimates with 95% CI were 0.79 (0.75–0.83) for females and 0.80 (0.76–0.84) for males.

The best time and age-structured model included two age classes: 'adults' (1–6 years) and 'old adults' (7+ years old), with temporal variation (year effect) in survival rate for the 'adult' age class only (Model 11 in Table 1.2). A reduced sample size for old adults (only 74 detections of individuals older than six over the whole study period) might explain the absence of time variation in old wolves. We next explored the causes of temporal variation in adult survival in the two areas (Fig. 2b,c) after setting old adult survival constant.

#### ENVIRONMENTAL DRIVERS OF ADULT SURVIVAL IN THE NR AND INTERIOR

We first tested whether wolf density in April (before reproduction) or in December (including pups of the year) affected adult survival in each study area. For NR wolves,

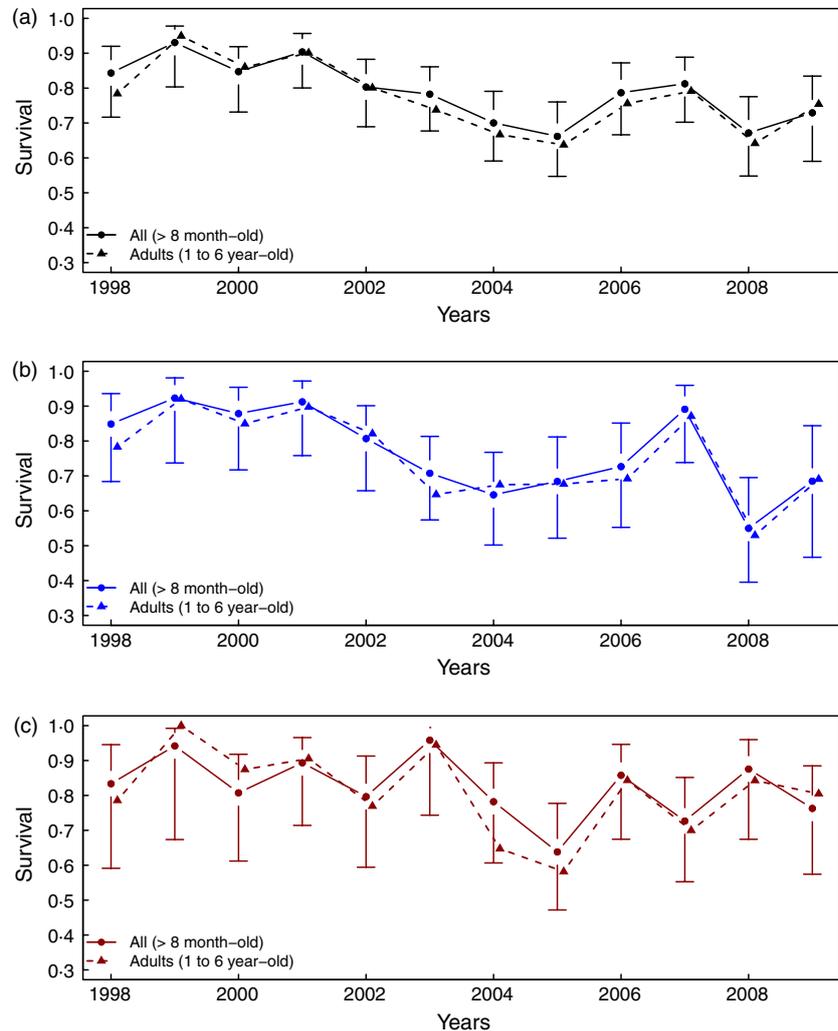
**Table 1.** Model selection results. For each model (Models 1–38), the number of parameters (#Par.), deviance (DEV), AICc and number of units of AICc difference from the best model in each section ( $\Delta$ AICc) are provided. In section 1, ‘time’ denotes a year effect, ‘period’ assumes constancy until 2001 and a year effect for the following years, ‘area’ defines estimates for wolves inhabiting the Northern Range (NR) and Interior of YNP, ‘ $\Phi$ ’ represents survival, ‘p’ detection probability, ‘i’ denotes constancy. In section 2, ‘AD(1–2)’ denotes an age-class grouping of 1 and 2-year-old wolves, ‘AD(1–6)’ denotes an age-class grouping of 1 to 6-year-old wolves, and ‘AD(7+)’ denotes an age-class grouping of wolves older than 6 years of age. In section 3, ‘density’ is an effect of wolf density (number of wolves 1000 km<sup>-2</sup>) in the NR or Interior in April (before reproduction) or in December (including pups of the year), ‘calf:cow’ an effect of the ratio of the number of calves per 100 elk cows, ‘elk’ an effect of the number of elk in the NR, ‘old<sub>elk</sub>’ the proportion of female elk > 14 years old in the NR, ‘elk:wolf’ an effect of the ratio of prey over predators calculated in the NR in April or in December, and ‘swe’ represents an effect of winter severity measured by snow water equivalent. In each section, the best model is in bold

Model structure	#Par.	DEV	AICc	$\Delta$ AICc	Model	
<b>(1) Temporal and spatial effects</b>						
$\Phi_{\text{period}} \times \text{area } P_i$	<b>21</b>	<b>1287.15</b>	<b>1330.15</b>	<b>0.00</b>	<b>1</b>	
$\Phi_{\text{period}} + \text{area } P_i$	14	1306.23	1334.68	4.53	2	
$\Phi_{\text{period}} P_i$	13	1309.27	1335.66	5.51	3	
$\Phi_{\text{time}} + \text{area } P_i$	17	1303.60	1338.27	8.12	4	
$\Phi_{\text{time}} P_i$	16	1306.61	1339.20	9.04	5	
$\Phi_{\text{time}} \times \text{area } P_i$	28	1283.79	1341.57	11.42	6	
$\Phi_a P_i$	6	1334.32	1346.41	16.26	7	
$\Phi_i P_i$	5	1336.85	1346.92	16.76	8	
$\Phi_{\text{time}} P_{\text{time}}$	26	1296.44	1349.98	19.82	9	
$\Phi_i P_{\text{time}}$	16	1326.28	1358.87	28.72	10	
<b>(2) Age and sex effects</b>						
<b>AD(1–6).time; AD(7+)</b>	<b>18</b>	<b>1264.01</b>	<b>1300.76</b>	<b>0.00</b>	<b>11</b>	
AD(1–2); AD(3–6) $\times$ time; AD(7+)	19	1269.01	1307.82	7.06	12	
AD(1–6); AD (7+)	7	1294.50	1308.62	7.87	13	
[AD(1–6) + AD(7+)] $\times$ time	19	1269.88	1308.69	7.94	14	
AD(1–2); AD(3–6); AD(7+)	8	1293.05	1309.36	8.60	15	
[AD(1–2) + AD(3–6)] $\times$ time; AD(7+)	20	1268.73	1309.61	8.86	16	
AD(1–6) + sex; AD (7+)	8	1294.48	1310.64	9.88	17	
AD(1–2) $\times$ time; AD(3–6); AD(7+)	19	1271.87	1310.68	9.93	18	
[AD(1–2) + AD(3–6)].time; AD(7+) $\times$ time	30	1251.39	1313.21	12.46	19	
AD(1–2); AD(3–6).time; AD(7+) $\times$ time	29	1254.40	1314.10	13.35	20	
AD(1–2).i; AD(3–6); AD(7+) $\times$ time	18	1278.46	1315.20	14.45	21	
AD(1–2).time; AD(3–6); AD (7+) $\times$ time	29	1257.29	1317.00	16.24	22	
<b>(3) Environmental covariates</b>						
Northern Range						
<b>density<sub>April</sub></b>	<b>i</b>	<b>9</b>	<b>1277.88</b>	<b>1296.07</b>	<b>0.00</b>	<b>23</b>
density <sub>April</sub> + elk	i	10	1275.94	1296.18	0.11	24
elk	i	9	1281.10	1299.30	3.23	25
elk:wolf <sub>December</sub>	i	9	1284.78	1302.98	6.91	26
density <sub>April</sub> (threshold effect)	i	9	1285.07	1303.26	7.19	27
i	density <sub>April</sub>	9	1286.42	1304.62	8.54	28
time	i	19	1266.51	1305.34	9.27	29
i	density <sub>December</sub>	9	1287.68	1305.87	9.80	30
old <sub>elk</sub>	i	10	1286.60	1306.83	10.76	31
time	time	30	1245.39	1307.43	11.36	32
i	i	8	1291.99	1308.14	12.07	33
swe	i	9	1290.35	1308.54	12.47	34
i	time	19	1270.86	1309.69	13.62	35
i	swe	9	1291.61	1309.80	13.73	36
density <sub>December</sub>	i	9	1291.68	1309.86	13.79	37
calf:cow	i	9	1291.96	1310.16	14.09	38

the best model included a linear effect of density in April on adult survival (Model 23 in Table 1.3) that revealed density dependence (Fig. 3). Variation in wolf density explained about 55% of year-to-year variation in adult survival rates (anodev test:  $F_{1,10} = 12.42$ ;  $P$ -value = 0.005). A threshold effect of density on survival, with reduced survival expected only above 60 wolves per 1000 km<sup>2</sup>, was also considered but it received less support (Model 27 in Table 1.3). Wolf density in December had

no significant effect on adult survival (Model 37 in Table 1.3; anodev test:  $F_{1,10} = 0.12$ ;  $P$ -value = 0.73), suggesting that the number of mature wolves in the population (>11 month old) was the most important aspect of density affecting adult survival.

In contrast, we found no evidence of density dependence among Interior wolves (Model 28 in Table 1.3; anodev test:  $F_{1,10} = 3.58$ ;  $P$ -value > 0.05). Adult survival rates appeared more stable in the Interior than in the NR, as a



**Fig. 2.** Annual survival rates from 1998 to 2009 for all radio-collared individuals (plain line, mean with 95% confidence intervals are provided) and adults only (dotted line, dots represent mean estimate) across Yellowstone National Park (a), in the Northern Range (b) and in the Interior (c).

**Table 2.** Age-specific annual survival rates in Yellowstone wolves, 1998–2010. Estimates are obtained from a model considering age-dependent survival rates and constant detection probability

Parameter	Mean estimates with 95% CI
Yearling	0.79 [0.72; 0.84]
Adult age 2	0.76 [0.69; 0.83]
Adult age 3	0.79 [0.71; 0.86]
Adult age 4	0.80 [0.70; 0.88]
Adult age 5	0.78 [0.66; 0.87]
Adult age 6	0.85 [0.71; 0.92]
Old adults age 7+	0.63 [0.52; 0.74]

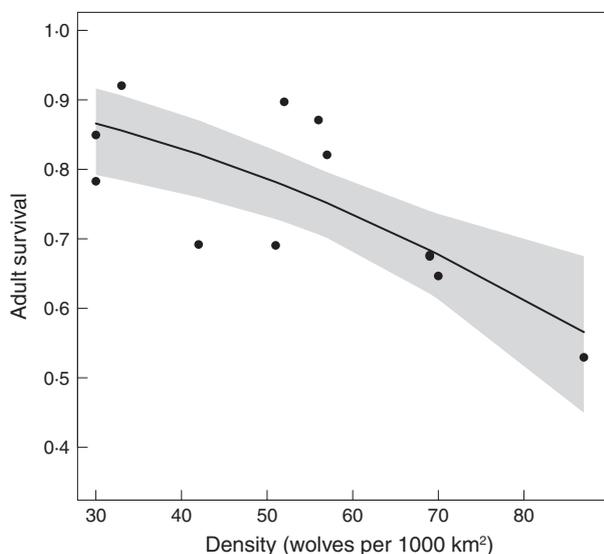
model with constant survival over the whole period fitted the data better than did a model with annual changes in survival rates (Models 33 and 35 in Table 1.3).

Although a model of NR wolf survival including only an effect of elk numbers (elk) was not the best-supported model (Model 25 in Table 1.3;  $\Delta\text{AICc} = 3.23$ ), variation in elk numbers explained about 43% of variance in adult survival rates in the NR (anodev test:  $F_{1,10} = 7.46$ ;  $P$ -value = 0.02). In contrast, indices of prey vulnerability (represented by calf:cow and proportion of old elk), ratio

of elk to wolves ( $\text{elk:wolf}_{\text{December}}$ ) and winter severity (SWE) did not affect adult survival rates (Models 26, 31, 34, 36 and 38 in Table 1.3). In addition, when included as additive effects in models that also included density, or in interactions with wolf density or elk abundance, these variables did not explain additional variation in survival (results not shown). After controlling for the effect of wolf density, variation in elk numbers (Model 24 in Table 1.3) did not improve model fit in terms of AICc and did not explain significant additional deviance compared to a model with wolf density only, suggesting that elk numbers did not have an additional effect on survival unrelated to density.

#### PROXIMATE CAUSES OF MORTALITY

Among 155 individuals found dead in YNP, intraspecific aggression was the most frequent cause of mortality (~37%) followed by unknown natural causes (~27%). Less than 5% of deaths were from malnutrition (Table 3). The proportion of deaths due to intraspecific aggression was high in the NR (~41%), and the number of wolf-caused mortalities increased with wolf density ( $r = 0.74$ ;



**Fig. 3.** Annual survival rates of adult wolves in the Northern Range as a function of wolf density in April. The intercept and slope were obtained from a model in which adult survival was modelled as a function of wolf density in April (Model 23), the zone filled with grey represent 95% confidence. Points represent mean survival estimates obtained from a model in which survival was time-dependent (Model 29).

**Table 3.** Cause-specific mortality of 155 wolves found dead inside the park between 1998 and 2010. The main cause of mortality in each area is in bold

	Northern Range		Interior		YNP	
	No.	%	No.	%	No.	%
Human-caused mortality						
Control action	1	0.95	1	2.01	2	1.29
Vehicle collision	4	3.81	9	18.00	13	8.39
Other (anthropogenic)	2	1.90	0	0	2	1.29
Natural mortality						
Disease	4	3.81	0	0	4	2.58
Interspecific	8	7.62	4	8.00	12	7.74
Intraspecific	43	<b>40.95</b>	15	30.00	58	<b>37.42</b>
Malnutrition	4	3.81	1	2.00	5	3.23
Other (natural)	1	0.95	3	6.00	4	2.58
Unknown (natural)	29	27.62	12	<b>24.00</b>	41	26.45
Unknown mortality						
Unknown	9	8.57	5	10.00	14	9.03
Total	105	100	50	100	155	100

$P$ -value = 0.004, Fig. S2a, Supporting information). In addition, the number of intraspecific aggressive interactions was strongly positively correlated with the number of wolf-caused mortality events recorded in the NR each year ( $r = 0.70$ ,  $P$ -value = 0.009, Fig. S2b, Supporting information). These results suggest that intraspecific aggression was the proximate cause of density-dependent survival in the NR. In contrast, the proportion of wolf-caused mortalities was lower in the Interior (~30%) and

inter-annual variation was uncorrelated with wolf density ( $r = 0.20$ ;  $P$ -value = 0.53).

#### RELATIONSHIPS BETWEEN WOLF DENSITY, ELK ABUNDANCE AND SOCIAL AGGRESSION IN THE NR

We used elk abundance as a proxy for food availability in the path analysis, wolf density in April, and the number of intraspecific conflicts as an index of social aggression in the NR (Appendix S2, Supporting information). Between 1998 and 2010, 321 cases of intraspecific aggression were observed in the NR. The model hypothesizing a direct effect of prey availability on social aggression (food limitation hypothesis; Fig. 1a) was not supported by the data ( $P$ -value = 0.01). We consequently rejected the hypothesis that social aggression increased in response to decreasing elk numbers independently of wolf density.

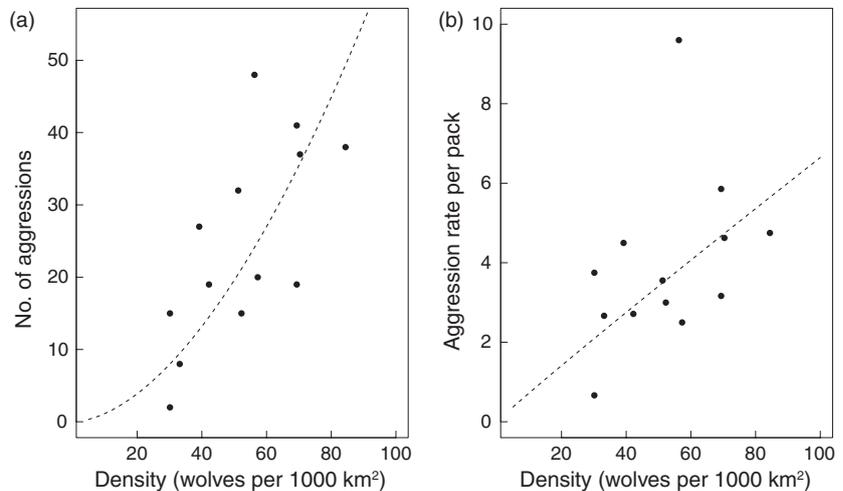
In contrast, the model hypothesizing a direct effect of wolf density on social aggression and an indirect effect of food availability via its effect on wolf density (density dependence hypothesis; Fig. 1b) was well supported by the data ( $P$ -value = 0.53). Estimates of the path coefficients confirmed that wolf density was not limited by elk numbers in the NR ( $\theta_1 = -0.40 < 0$ ,  $SD = 0.27$ ), and that social aggression increased with wolf density ( $\theta_2 = 1.77 > 1$ ,  $SD = 0.53$ , Fig. 4a). The average value estimated for  $\theta_2$  was  $>1$ , suggesting that the rate of aggression per wolf increased with wolf density. However, the non-linearity was not statistically significant [95% CI for  $\theta_2$ : (0.61–2.93)], possibly due to a small sample size. As conflicts usually occur between packs rather than individuals, we accounted for the number of packs in the population to quantify changes in the rate of aggression per pack (calculated as the number of intraspecific aggressions/number of packs) as wolf density increased. We first verified that the rate of aggression per pack was not correlated with the number of packs ( $r = 0.17$ ,  $P$ -value = 0.56), which ensured that the effect of wolf density on the rate of aggression per pack did not reflect the correlation existing between wolf density and the number of packs ( $r = 0.67$ ,  $P$ -value = 0.01). The rate of aggression per pack markedly increased with wolf density (Fig. 4b), supporting a density-dependent increase in the rate of intraspecific aggression.

In addition, when considering a model with an additive effect of wolf density and elk abundance on the number of conflicts ( $\log(\text{aggression}) = \beta_1 \times \log(\text{density}_{\text{April}}) + \beta_2 \times \log(\text{elk})$ ), only the effect of wolf density was significant ( $\beta_1 = 1.40$ ,  $SD = 0.53$ ,  $P$ -value  $< 0.02$ ;  $\beta_2 = -0.86$ ,  $SD = 0.53$ ,  $P$ -value = 0.13). Together, these results indicate a density-dependent increase in social aggression, independent of food availability.

## Discussion

Intraspecific killing occurs in many taxa, including insects, birds, fish and mammals (Polis 1981), and is a

**Fig. 4.** Number of intraspecific aggressive interactions as a function of wolf density in April, obtained from the path analysis (a), and rate of aggression per pack calculated as the ratio of the number of intraspecific aggressions over the number of packs as a function of wolf density in April (b) in the Northern Range from 1995 to 2010. Points are observed values and dashed lines are predictions from the corresponding log-linear model.



density-dependent regulator of population size in some fish and invertebrate species (e.g. walleye, Forney 1974; desert scorpions, Polis 1980). In large carnivores, however, the scarcity of long-term demographic data has limited attempts to address its consequence for population dynamics (but see Pusey & Packer 2008). In wolves, intraspecific killing is a known cause of mortality, but was previously thought to have little influence on population dynamics because it occurs infrequently in most populations, and is not necessarily density-dependent (e.g. Mech & Boitani 2003; Adams *et al.* 2008).

Our results indicate that in the prey-rich NR of YNP, intraspecific aggression regulated adult wolf survival in a density-dependent manner, independently of prey availability. The effect of density explained ~55% of temporal variation in adult survival rates during the study, and was best captured by an effect of wolf density in April (before young of the year are born) rather than in December (including 8-month-old pups), which is consistent with pups being less influential than adults in inter-pack conflicts (Cassidy 2013). In contrast, neither the ratio of elk to wolves nor the relative abundance of vulnerable elk (calves, old females) affected survival. Models considering additive and interaction effects of these three variables were also considered (results not shown) but received less support than a model with a single effect of elk abundance. Although the effect of elk abundance on adult survival was statistically significant, it received less support in terms of AICc than a model including only wolf density, and explained a lower proportion of the deviance. Winter severity (SWE), previously shown to affect wolves via its impact on the amount of vulnerable prey available (Post *et al.* 1999; Vucetich & Peterson 2004), did not affect survival either. These results suggest that prey availability had little, if any, direct influence on adult wolf survival in the NR during our study period.

Effects of winter severity and prey availability may not be perfectly captured by the indices used in our analyses. In particular, elk counts were uncorrected for sightability. We are confident that the decline in elk numbers is real

given documented decreases in adult (Evans *et al.* 2006) and juvenile survival (Barber-Meyer, Mech & White 2008), climate, hunting and predation (Vucetich, Smith & Stahler 2005). A study of elk habitat use in northern Yellowstone also revealed that 'compared to the pre-wolf period, elk selected for more open habitats after wolf reintroduction' apparently because they 'rely on other behavioural anti-predator strategies, such as grouping, in winter' (Mao *et al.* 2005), which is when elk are counted. Together, these results suggest that the observed decline in elk numbers is not due to decreased sightability of elk since wolf reintroduction. We also acknowledge that other factors not included in this analysis potentially influenced wolf survival. Disease could be an additional driver of adult survival in YNP, acting either additively or in interaction with the effect of density, via potential effects on energetics and nutritional health of infected individuals (Almberg *et al.* 2010, 2012). Current work is exploring the effects of infection by canine distemper and sarcoptic mange, which were not included in this analysis. In the NR, three canine distemper outbreaks likely affected the population growth rate by reducing pup survival (Almberg *et al.* 2012; Stahler *et al.* 2013), but seemed to have less impact on adult survival as <3% of death events were attributed to disease during our study.

Several other lines of evidence suggest that competition for food was not the primary mechanism generating density-dependent survival rates in the NR. First, food was superabundant: the average ( $\pm$ SE) annual elk density in the NR during the study ( $9.3 \pm 0.86$  elk km<sup>2</sup>) was 1.11 to >100 times greater than prey densities in 25 other North American wolf-prey systems (including deer, moose, caribou, sheep, goat and multi-prey systems; Fuller, Mech & Cochrane 2003). Despite decreasing elk numbers, elk to wolf ratios remained high compared to other wolf-prey systems, with 161 elk per wolf on average (range = 67–415 elk:wolf). Second, results of the path analysis indicated that prey availability had little influence on the occurrence of intraspecific aggression, which was the primary cause of mortality. The path model describing an

effect of elk abundance on intraspecific aggression was not supported by the data, confirming that the effect of elk abundance on survival was likely an artefact of the correlation between elk abundance and wolf density. Finally, survival rates decreased after 2001, when all suitable territories were occupied on the NR (Smith, Peterson & Houston 2003). While wolf territory size decreases with increasing ungulate density (Fuller, Mech & Cochrane 2003), a lower limit has been shown to exist, suggesting a minimum exclusive territory size required for successful reproduction (Jędrzejewski *et al.* 2007). In the NR, wolves even shifted their territories away from the best hunting grounds as the degree of overlap between pack territories increased with wolf density (Kauffman *et al.* 2007). Together, these results suggest that space rather than food was the limiting resource for NR wolves. Increased levels of intraspecific killing due to competition for space is likely the primary cause of density-dependent survival in NR wolves, as previously observed in territorial species including mice, scorpions, damselfly and pike (Fox 1975; Polis 1981 and references therein). Hence, whereas several authors have concluded that the only natural limits to wolf density are those ultimately imposed by food (Keith 1983; Fuller, Mech & Cochrane 2003), our findings provide empirical support for the hypothesis that intrinsic density-dependent mechanisms might regulate wolf populations at high ungulate densities (Pimlott 1967, 1970; Cariappa *et al.* 2011).

Our results suggest that intraspecific aggression can be an important mechanism of population regulation in territorial carnivores, although it has received little attention compared to other regulatory mechanisms including social dominance, food availability, dispersal and inhibitive breeding of subordinates (Fuller, Mech & Cochrane 2003). Variation in adult survival rates in the NR was substantial for a non-hunted population (0.55–0.92), and likely to affect the population growth rate, as population decline is expected when natural mortality rates are >30% (Fuller 1989). Adult survival was predicted to drop below 0.7 above 65 wolves 1000 km<sup>2</sup>, a finding that is consistent with Cariappa *et al.*'s (2011) results suggesting that density-dependent regulatory mechanisms impose an upper limit of 69 wolves 1000 km<sup>2</sup>, although further work is needed to quantify the contribution of variation in survival rates to population growth. A hypothesis put forward by Polis (1981) is that intraspecific killing might be a mechanism that reduces population size before acute resource shortage causes severe physiological stress. Since mortality is direct and immediate, intraspecific aggression has a strong potential to limit population growth rate, and could facilitate a rapid numerical response if the decline of the northern Yellowstone elk herd continues. In contrast to other natural causes of mortality (e.g. starvation and disease) which primarily affect younger individuals, older adults (often breeders) are more aggressive during inter-pack conflicts, and therefore put themselves at higher risk (Cassidy 2013). In this study, age-specific survival rates declined after age

6, consistent with previous findings for this population (MacNulty *et al.* 2009), but with no age effect for younger wolves (1–6 years). This pattern could result from higher mortality risk during interpack conflicts for older individuals, that are often dominant, or lower survival of dispersing and young wolves may only occur in harvested wolf populations (Pletscher *et al.* 1997). As breeder loss can induce pack dissolution, competitive disadvantage, breeding failure and reduced survival of other pack members (Brainerd *et al.* 2008; Cassidy 2013), such effects are likely to be less compensatory than starvation or disease-induced mortality. Moreover, smaller packs have reduced hunting success of elk (MacNulty *et al.* 2012) and members of smaller packs (<5 individuals) experience an increased risk of mortality during inter-pack conflicts (Smith *et al.* 2010; Cassidy 2013). We therefore expect the effect of density on individual survival to weaken as an individual's pack size increases, and even more so with decreasing prey availability. This could ultimately reduce the prevalence, tenure, and success of smaller packs. In the long term, decreasing prey availability could also lead to decreased pup survival (Fuller, Mech & Cochrane 2003) and increased dispersal rates of yearlings (Hayes & Harestad 2000); ultimately reducing wolf density and thereby decreasing the strength of density dependence mechanisms acting on survival.

Comparatively low wolf densities might explain the lack of density-dependent survival rates in other systems. Indeed, winter wolf densities reported in the literature rarely exceeded 40 wolves 1000 km<sup>2</sup>, whereas it averaged 65 wolves 1000 km<sup>2</sup> in the NR, peaking at 98 wolves 1000 km<sup>2</sup>, which is the highest density ever reported for a North American wolf population (Fuller, Mech & Cochrane 2003). For some populations, high harvest rates can potentially suppress wolf numbers below levels determined by food availability (Ballard, Whitman & Gardner 1987), thus decreasing the strength of density dependence. However, wolf survival may remain density-independent even when moderate anthropogenic mortality does not limit wolf numbers (Adams *et al.* 2008; Murray *et al.* 2010). As wolves can target a large variety of prey species cross their geographical distribution (Fuller, Mech & Cochrane 2003), differences in prey availability and usage might also explain differences between the NR and other systems. In the Interior of YNP, wolf survival was density-independent and intraspecific killing was less frequent than in the NR (30% vs. 41%) despite no human-caused mortality and reduced availability of a preferred prey species (elk, Smith *et al.* 2004; Metz *et al.* 2012). These results suggest that different mechanisms could govern wolf population dynamics under different environmental conditions (Cariappa *et al.* 2011). When food is limiting, variation in population growth rate should be driven to a greater extent by year-to-year variation in recruitment (including pup survival and dispersal rates), than by variation in adult survival (Gaillard & Yoccoz 2003; Patterson & Murray 2008). These predictions are largely supported by empirical evidence from North American populations showing

that annual variation in population growth rate was mainly explained by decreased pup survival during winter and increased dispersal rates in response to a decrease in food availability, while survival rates (aside from anthropogenic mortality) showed little variation and appeared density-independent (Fuller 1989; Bergerud & Elliott 1998; Hayes & Harestad 2000; Fuller, Mech & Cochrane 2003; Adams *et al.* 2008). Hence, reduced recruitment rates could maintain low wolf densities in populations subsisting on low density prey, while density-dependent survival rates may only occur when prey density is high and human-caused mortality is low as in the NR.

Wolves living primarily in YNP that occasionally leave the park now face increased risk of human mortality due to hunting adjacent to the park. Under density-dependent conditions, theory predicts that populations should compensate for low to moderate levels of anthropogenic mortality through decreases in natural mortality and/or increases in recruitment to buffer effects on population growth rate (e.g. Lebreton 2005). The debate about the compensatory nature of anthropogenic mortality is ongoing, with some studies suggesting fully to partly compensatory effects (Murray *et al.* 2010), and others suggesting additive or even super-additive effects (Creel & Rotella 2010). If compensation can occur, empirical evidence suggests that dispersal is likely the primary mechanism through which wolves can compensate for human exploitation, whereas responses in natural mortality seem to have little or no role in offsetting harvests (Bergerud & Elliott 1998; Hayes & Harestad 2000; Adams *et al.* 2008; Gude *et al.* 2012). However, little is known about changes in natural mortality in response to anthropogenic mortality within the same population. Our finding of density-dependent survival rates in the NR offers one of the necessary conditions for compensation through decreased natural mortality, but the potential for compensation will mainly depend on the rate and selectivity of these two sources of mortality, which still have to be investigated. For example, depending on the age and status (breeder or non-breeder, resident or disperser) of individuals dying from intraspecific killing and anthropogenic causes, both sources of mortality could be compensatory or not (Lebreton 2005). Moreover, harvesting can have additional effects on population dynamics by destabilizing social structure (Brainerd *et al.* 2008). Given the importance of this issue from a conservation and management point of view, future work should aim to assess the potential of anthropogenic and natural sources of mortality to interact, by monitoring changes in age-specific vital rates, pack composition and the dynamics of inter-pack conflicts in response to increased risk of anthropogenic mortality due to hunting adjacent to the park.

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## Data accessibility

Data available from the Dryad Digital Repository: <http://doi.org/10.5061/dryad.f32n1> (Cubaynes *et al.* 2014).

## References

- Adams, L.G., Stephenson, R.O., Dale, B.W., Ahgook, R.T. & Demma, D.J. (2008) Population dynamics and harvest characteristics of wolves in the central Brooks Range, Alaska. *Wildlife Monographs*, **170**, 1–25.
- Almberg, E.S., Cross, P.C. & Smith, D.W. (2010) Persistence of canine distemper virus in the Greater Yellowstone Ecosystem's carnivore community. *Ecological Applications*, **20**, 2058–2074.
- Almberg, E.S., Cross, P.C., Dobson, A.P., Smith, D.W. & Hudson, P.J. (2012) Parasite invasion following host reintroduction: a case study of Yellowstone's wolves. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**, 2840–2851.
- Ballard, W.B., Whitman, J.S. & Gardner, C.L. (1987) Ecology of an exploited wolf population in south-central Alaska. *Wildlife monographs*, **98**, 3–54.
- 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.
- Becker, M.S., Garrott, R.A., White, P.J., Gower, C.N., Bergman, E.J. & Jaffe, R. (2008) Chapter 16 Wolf prey selection in an elk-bison system: choice or circumstance? *Terrestrial Ecology*, (eds R.A. Garrott, P.J. White & F.G.R. Watson), pp. 305–337. Elsevier, New York.
- Bergerud, A. & Elliott, J. (1998) Wolf predation in a multiple-ungulate system in northern British Columbia. *Canadian Journal of Zoology*, **76**, 1551–1569.
- Brainerd, S.M., Andr n, H., Bangs, E.E., Bradley, E.H., Fontaine, J.A., Hall, W. *et al.* (2008) The effects of breeder loss on wolves. *The Journal of Wildlife Management*, **72**, 89–98.
- Cariappa, C., Oakleaf, J.K., Ballard, W.B. & Breck, S.W. (2011) A reappraisal of the evidence for regulation of wolf populations. *The Journal of Wildlife Management*, **75**, 726–730.
- Cassidy, K. (Quimby) (2013) Group composition effects on inter-pack aggressive interactions of Yellowstone gray wolves. Master thesis, University of Minnesota, Saint Paul, Minnesota.
- Choquet, R. & Nogue, E. (2010) E-SURGE 1.7 user's manual. CEFE, Montpellier.
- Choquet, R., Lebreton, J.D., Gimenez, O., Reboulet, A.M. & Pradel, R. (2009) U-CARE: utilities for performing goodness of fit tests and manipulating CApture–REcapture data. *Ecography*, **32**, 1071–1074.
- Creel, S. & Rotella, J.J. (2010) Meta-analysis of relationships between human off-take, total mortality and population dynamics of gray wolves (*Canis lupus*). *PLoS ONE*, **5**, e12918.
- Cubaynes, S., MacNulty, D., Stahler, D., Quimby, K., Smith, D. & Coulson, T. (2014) Data from: Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (*Canis lupus*). *Dryad Digital Repository*, doi:10.5061/dryad.f32n1.
- Devineau, O., Shenk, T.M., White, G.C., Doherty, P.F. Jr, Lukacs, P.M. & Kahn, R.H. (2010) Evaluating the *Canada lynx* reintroduction programme in Colorado: patterns in mortality. *Journal of Applied Ecology*, **47**, 524–531.
- Eberhardt, L.L., White, P.J., Garrott, R.A. & Houston, D.B. (2007) A seventy-year history of trends in the Yellowstone's Northern Elk Herd. *Journal of Wildlife Management*, **71**, 594–602.
- European Commission Environment. (1992) Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. European Commission Environment, Brussels, Belgium.

- 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.
- Fish and Wildlife Service, Interior, (2009) Endangered and Threatened Wildlife and Plants; Final Rule Designating the Northern Rocky Mountain Population of Gray Wolf as a Distinct Population Segment and Removing This Distinct Population Segment From the Federal List of Endangered and Threatened Wildlife.
- Forney, J.L. (1974) Interactions between yellow perch abundance, walleye predation, and survival of alternate prey in Oneida Lake, New York. *Transactions of the American Fisheries Society*, **103**, 15–24.
- Fox, L.R. (1975) Cannibalism in natural populations. *Annual Review of Ecology and Systematics*, **6**, 87–106.
- Fuller, T.K. (1989) Population dynamics of wolves in north-central Minnesota. *Wildlife Monographs*, **105**, 3–41.
- Fuller, T.K., Mech, L.D. & Cochrane, J.F. (2003) Wolf population dynamics. *Wolves: Behavior, Ecology, and Conservation*, (eds D.L. Mech & L. Boitani), pp. 161–191. University of Chicago Press, Chicago.
- Gaillard, J.-M. & Yoccoz, N.G. (2003) Temporal variation in survival of mammals: a case of environmental canalization? *Ecology*, **84**, 3294–3306.
- Grosbois, V., Gimenez, O., Gaillard, J.M., Pradel, R., Barbraud, C., Clobert, J. *et al.* (2008) Assessing the impact of climate variation on survival in vertebrate populations. *Biological Reviews*, **83**, 357–399.
- Gude, J.A., Mitchell, M.S., Russell, R.E., Sime, C.A., Bangs, E.E., Mech, L.D. *et al.* (2012) Wolf population dynamics in the US Northern Rocky Mountains are affected by recruitment and human-caused mortality. *The Journal of Wildlife Management*, **76**, 108–118.
- Hayes, R.A. & Harestad, A.S. (2000) Demography of a recovering wolf population in the Yukon. *Canadian Journal of Zoology*, **78**, 36–48.
- Houston, D.B. (1982) *The Northern Yellowstone Elk: Ecology and Management*. Macmillan, New York.
- Jędrzejewski, W., Schmidt, K., Theuerkauf, J., Jędrzejewska, B. & Kowalczyk, R. (2007) Territory size of wolves *Canis lupus*: linking local (Biaowieża Primeval Forest, Poland) and Holarctic-scale patterns. *Ecography*, **30**, 66–76.
- Kauffman, M.J., Varley, N., Smith, D.W., Stahler, D.R., MacNulty, D.R. & Boyce, M.S. (2007) Landscape heterogeneity shapes predation in a newly restored predator–prey system. *Ecology letters*, **10**, 690–700.
- Keith, L.B. (1983) Population dynamics of wolves. *Wolves in Canada and Alaska: Their Status, Biology, and Management*, (eds L.N. Carbyn), pp. 66–77. Canadian Wildlife Service Report Series, Ottawa.
- Lebreton, J.D. (2005) Dynamical and statistical models for exploited populations. *Australian & New Zealand Journal of Statistics*, **47**, 49–63.
- Lebreton, J.-D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological monographs*, **62**, 67–118.
- Lebreton, J.D., Nichols, J.D., Barker, R.J., Pradel, R. & Spendelov, J.A. (2009) Modeling individual animal histories with multistate capture–recapture models. *Advances in ecological research*, **41**, 87–173.
- MacNulty, D.R., Smith, D.W., Vucetich, J.A., Mech, L.D., Stahler, D.R. & Packer, C. (2009) Predatory senescence in ageing wolves. *Ecology letters*, **12**, 1347–1356.
- MacNulty, D.R., Smith, D.W., Mech, L.D., Vucetich, J.A. & Packer, C. (2012) Nonlinear effects of group size on the success of wolves hunting elk. *Behavioral Ecology*, **23**, 75–82.
- Mao, J.S., Boyce, M.S., Smith, D.W., Singer, F.J., Vales, D.J., Vore, J.M. *et al.* (2005) Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. *Journal of Wildlife Management*, **69**, 1691–1707.
- Mech, L.D. & Boitani, L. (2003) *Wolf: Behavior, Ecology, and Conservation*. University of Chicago Press, Chicago, Illinois, USA.
- Metz, M.C., Smith, D.W., Vucetich, J.A., Stahler, D.R. & Peterson, R.O. (2012) Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. *Journal of Animal Ecology*, **81**, 553–563.
- Murray, D.L., Smith, D.W., Bangs, E.E., Mack, C., Oakleaf, J.K., Fontaine, J. *et al.* (2010) Death from anthropogenic causes is partially compensatory in recovering wolf populations. *Biological Conservation*, **143**, 2514–2524.
- Packard, J.M. & Mech, L.D. (1980) Population regulation in wolves. *Bio-social Mechanisms of Population Regulation*, (eds M.N. Cohen, R.S. Malpas & H.G. Klein), pp. 135–150. Yale University Press, New Haven, Connecticut.
- Patterson, B.R. & Murray, D.L. (2008) Flawed population viability analysis can result in misleading population assessment: a case study for wolves in Algonquin park, Canada. *Biological Conservation*, **141**, 669–680.
- Peterson, R.O. & Page, R.E. (1988) The rise and fall of Isle Royale wolves, 1975–1986. *Journal of Mammalogy*, **69**, 89–99.
- Peterson, R.O., Thomas, N.J., Thurber, J.M., Vucetich, J.A. & Waite, T.A. (1998) Population limitation and the wolves of Isle Royale. *Journal of Mammalogy*, **79**, 828–841.
- Pimlott, D.H. (1967) Wolf predation and ungulate populations. *American Zoologist*, **7**, 267–278.
- Pimlott, D.H. (1970) Predation and productivity of game populations in North America. *Transactions of the International Congress of Game Biologists*, **9**, 63–72.
- Pletscher, D.H., Ream, R.R., Boyd, D.K., Fairchild, M.W. & Kunkel, K.E. (1997) Population dynamics of a recolonizing wolf population. *The Journal of Wildlife Management*, **61**, 459–465.
- Polis, G.A. (1980) The effect of cannibalism on the demography and activity of a natural population of desert scorpions. *Behavioral Ecology and Sociobiology*, **7**, 25–35.
- Polis, G.A. (1981) The evolution and dynamics of intraspecific predation. *Annual Review of Ecology and Systematics*, **12**, 225–251.
- Post, E., Peterson, R.O., Stenseth, N.C. & McLaren, B.E. (1999) Ecosystem consequences of wolf behavioural response to climate. *Nature*, **401**, 905–907.
- Pradel, R., Hines, J.E., Lebreton, J.-D. & Nichols, J.D. (1997) Capture–recapture survival models taking account of transients. *Biometrics*, **53**, 60–72.
- Pusey, A.E. & Packer, C. (2008) Chapter 12 Infanticide in lions: consequences and counterstrategies. *Infanticide and Parental Care*, (eds S. Parmigiani & F.S. vom Saal), pp. 277–300. Harwood Academic Publishers, Chur.
- R. Development Core Team (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Shipley, B. (2002) *Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference*. Cambridge University Press.
- Shipley, B. (2009) Confirmatory path analysis in a generalized multilevel context. *Ecology*, **90**, 363–368.
- Smith, D. (2005) Ten years of Yellowstone wolves. *Yellowstone Science*, **13**, 7–33.
- Smith, D.W. & Bangs, E.E. (2009) Reintroduction of wolves to Yellowstone National Park: history, values, and ecosystem restoration. In: *Reintroduction of Top-order Predators*, (eds M.W. Hayward & M. Somers), pp. 92–125. Wiley-Blackwell, Oxford.
- Smith, D.W., Peterson, R.O. & Houston, D.B. (2003) Yellowstone after wolves. *BioScience*, **53**, 330–340.
- Smith, D.W., Mech, L.D., Meagher, M., Clark, W.E., Jaffe, R., Phillips, M.K. *et al.* (2000) Wolf–bison interactions in Yellowstone National Park. *Journal of Mammalogy*, **81**, 1128–1135.
- Smith, D.W., Drummer, T.D., Murphy, K.M., Guernsey, D.S. & Evans, S.B. (2004) Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995–2000. *Journal of Wildlife Management*, **68**, 153–166.
- Smith, D.W., Bangs, E.E., Oakleaf, J.K., Mack, C., Fontaine, J., Boyd, D. *et al.* (2010) Survival of colonizing wolves in the northern Rocky Mountains of the United States, 1982–2004. *The Journal of Wildlife Management*, **74**, 620–634.
- Smith, D.W., Stahler, D.R., Stahler, E., Metz, M., Quimby, K., McIntyre, R. *et al.* (2013). Yellowstone Wolf Project: Annual Report, 2012. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming, YCR-2013-02
- Stahler, D.R., MacNulty, D.R., Wayne, R.K., vonHoldt, B. & Smith, D.W. (2013) The adaptive value of morphological, behavioural and life-history traits in reproductive female wolves. *Journal of Animal Ecology*, **82**, 222–234.
- Stenlund, M.H. (1955) *A Field Study of the Timber Wolf (Canis Lupus) on the Superior National Forest, Minnesota*. Minnesota Department of Conservation, St. Paul, USA.
- Sugiura, N. (1978) Further analysts of the data by akaike's information criterion and the finite corrections: further analysts of the data by akaike's. *Communications in Statistics-Theory and Methods*, **7**, 13–26.
- Taper, M.L. & Gogan, P.J. (2002) The northern Yellowstone elk: density dependence and climatic conditions. *The Journal of Wildlife Management*, **66**, 106–122.
- Treves, A. & Karanth, K.U. (2003) Human–carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology*, **17**, 1491–1499.

- Vucetich, J.A. & Peterson, R.O. (2004) The influence of prey consumption and demographic stochasticity on population growth rate of Isle Royale wolves *Canis lupus*. *Oikos*, **107**, 309–320.
- 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.
- Woodroffe, R., Thirgood, S. & Rabinowitz, A. (2005) *People and Wildlife, Conflict or Co-existence?*. Cambridge University Press, Cambridge.
- 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.

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## Supporting Information

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

**Fig. S1.** Wolf population size in April (a), and in December (b) in the Northern Range (NR) and the interior range (INT), and total population size in Yellowstone National Park (YNP) from 1998 to 2009.

**Fig. S2.** Number of wolf-caused mortalities as a function of wolf density in April, expressed in number of wolves per 1000 km<sup>2</sup> (a), and as a function of the number of intraspecific aggressive interactions (b) in the NR between 1995 and 2012.

**Appendix S1.** Annual changes in wolf and elk populations and index of winter severity.

**Appendix S2.** Cause-specific mortality data.