

Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta

Mark Hebblewhite, Daniel H. Pletscher, and Paul C. Paquet

Abstract: Gray wolves (*Canis lupus*) recolonized the Bow Valley of Banff National Park in the mid-1980s after a 30-year absence. Wolves recolonized one zone of the Bow Valley in 1985 and another in 1991, but human activity excluded wolves from a third zone throughout the study. Elk (*Cervus elaphus*) are the primary prey of wolves in Banff National Park. We studied the effects of wolf predation, snow depth, elk density, and human-caused mortality on the elk population growth rate in the three different wolf recolonization treatments from 1985 to 2000. We constructed a set of generalized linear models of factors affecting population growth, and used Akaike Information Criteria to guide model selection and inference. In the low wolf predation zone, elk population growth was density-dependent and limited by human-caused mortality. In the zone that wolves recolonized in 1991, elk population growth was limited by the combined effects of snow depth and wolf predation after wolf recolonization, in addition to preexisting mortality caused by humans and other predators. Our correlative approach failed to yield insights into population dynamics in the zone where wolves were present throughout the study. However, by comparing zones we demonstrate important differences in ungulate population dynamics in the presence and absence of wolf predation.

Résumé : Après 30 ans d'absence, le loup gris (*Canis lupus*) a effectué un retour dans la vallée de la rivière Bow, dans le Parc national de Banff, au milieu des années 1980. Les loups ont d'abord colonisé une zone de la vallée en 1985, puis une autre en 1991 et l'activité humaine les a exclus d'une troisième zone pour toute la durée de l'étude. Le wapiti (*Cervus elaphus*) est la principale proie des loups dans le parc. Nous avons étudié les effets de la prédation par les loups, de la profondeur de la neige, de la densité des wapitis et de la mortalité due à l'activité humaine sur les taux de croissance des populations de wapitis des trois zones expérimentales de 1985 à 2000. Nous avons construit une série de modèles linéaires généralisés des facteurs qui affectent la croissance des populations, puis nous avons utilisé le critère d'information d'Akaike pour choisir des modèles et guider nos déductions. Dans la zone de faible prédation, la population de wapitis dépend de la densité et est limitée par la mortalité attribuable à l'activité humaine. Dans la zone recolonisée en 1991, les effets combinés de la profondeur de la neige et de la prédation par les loups ont limité la croissance de la population après la recolonisation; ces facteurs se sont ajoutés à la mortalité due à l'activité humaine ou celle d'autres prédateurs qui existait avant le retour des loups. Notre approche corrélatrice n'a pas réussi à jeter de lumière sur la dynamique des populations dans la zone fréquentée par les loups pendant toute la durée de l'étude. Cependant, la comparaison des zones indique des différences importantes dans la dynamique des populations d'ongulés selon que les loups sont présents ou absents.

[Traduit par la Rédaction]

Introduction

Density-dependence and environmental stochasticity are determinants of ungulate population dynamics in areas without major predators (reviewed in Sæther 1997; Gaillard et al. 1998). High ungulate density and severe winters decrease survival (e.g., Clutton-Brock et al. 1987; Singer et al. 1997),

especially when they act concurrently (Portier et al. 1998; Milner et al. 1999). Adult survival is relatively high and constant, whereas juvenile survival varies substantially with weather and density and is less important for population growth (Gaillard et al. 1998).

Which factors affect ungulate population dynamics is less clear when ungulates are sympatric with predators such as gray wolves (*Canis lupus*). Predation by wolves can limit, and perhaps regulate (Sinclair 1989), the growth and size of ungulate populations (Skogland 1991; Dale et al. 1994; Messier 1994; Orians et al. 1997; Hayes and Harestad 2000). Wolf predation increases with snow depth (Nelson and Mech 1986; Huggard 1993a; Post et al. 1999), revealing an interaction effect with weather on ungulate population dynamics. Teasing apart the simultaneous effects of predation and other factors such as food and climate on the population dynamics of northern ungulates is difficult and plagued by experimental difficulties (Boutin 1992; Orians et al. 1997; Minta et al. 1999). Despite this, many researchers conclude that preda-

Received 28 September 2001. Accepted 11 March 2002.
Published on the NRC Research Press Web site at
<http://cjz.nrc.ca> on 9 May 2002.

M. Hebblewhite^{1,2} and D.H. Pletscher. Wildlife Biology Program, School of Forestry, University of Montana, Missoula, MO 59812, U.S.A.

P.C. Paquet. Faculty of Environmental Design, University of Calgary, Calgary, AB T2N 1N4, Canada.

¹Corresponding author (e-mail: mark.hebblewhite@ualberta.ca).

²Present address: Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada.

tion is a strong determinant of ungulate population dynamics (Gasaway et al. 1992; Boertje et al. 1996; Jędrzejewska et al. 1997; Kunkel and Pletscher 1999).

Many studies of factors affecting ungulate population dynamics suffer from two fundamental statistical problems: model-selection uncertainty (Burnham and Anderson 1998; Anderson et al. 2000) and the correlative nature of models (Royama 1992; Boyce and Anderson 1999). Traditional model-selection methods (e.g., stepwise) inadequately address model-selection uncertainty and are often poor at selecting the correct model in complex systems (Burnham and Anderson 1998). Sparse data limit our ability to distinguish among hypotheses in predator-prey research (Marshall and Boutin 1999), yet traditional hypothesis testing allows only single models to be considered (Johnson 1999; Anderson et al. 2000; Guthery et al. 2001). Analysis of complex systems such as ungulate population dynamics may benefit from adopting an information-theoretic approach in which the philosophy of multiple working hypotheses (Chamberlain 1890) is central.

Problems with using correlative approaches in the study of population dynamics are difficult to remedy (Royama 1992, 1996). Experiments are the best way to tease factors apart (Underwood 1997), yet applying classic experimental design to predator-prey systems is difficult (Estes 1996; Minta et al. 1999; Terborgh et al. 1999). The only consistent advice has been to take advantage of natural experiments that provide variation in carnivore and ungulate densities and compare population processes across this range of densities (Sinclair 1991; Boutin 1992; Royama 1992; Orians et al. 1997; Minta et al. 1999; Elkington 2000).

Gray wolves recolonized the Bow Valley of Banff National Park (BNP) during the mid-1980s (Paquet et al. 1996), and elk (*Cervus elaphus*) are the main prey of wolves in BNP (Huggard 1993b). Wolves fully recolonized one area (zone) of the Bow Valley in 1985 and recolonized another midway through 1991, but were excluded from a third zone surrounding the Banff townsite by a high level of human use (Paquet et al. 1996). This provided a serendipitous natural experiment (Sinclair 1991) to evaluate the effects of wolf predation on elk subpopulation growth in three different zones of the Bow Valley. We examined the effects of wolf predation, elk density, human-caused elk mortality, and snow depth (a measure of winter severity) on the elk population growth rate in BNP. We constructed an all-inclusive set of models using these factors to explain population growth rate and fit time-series data from long-term monitoring of elk and wolf population dynamics from 1985 to 2000 to these models. Where wolves were absent, we predicted that elk population growth would be density-dependent and snow depth would interact with elk density to limit elk population growth. Where wolves were present we predicted that wolf predation, and an interaction between predation and snow depth, would limit elk population growth.

Study area

BNP, which is 6641 km² in area, is on the eastern slope of the continental divide in the front and main ranges of the Canadian Rocky Mountains (51°15'N, 116°30'W) (Fig. 1) and has extreme mountainous topography (1400–3400 m). The climate is characterized by long, cold winters with in-

frequent warm weather caused by chinook winds, and short, relatively dry summers. Valley bottoms are 2–5 km in width and from 1350 to 1600 m elevation. Vegetation in the study area is divided into montane, subalpine, and alpine ecoregions. The valley bottom montane ecoregion is dominated by closed lodgepole pine (*Pinus contorta*) forests interspersed with riparian Engelmann spruce (*Picea engelmannii*) – willow (*Salix* spp.), aspen (*Populus tremuloides*) – parkland, and dry grasslands. The subalpine and alpine ecoregions comprise Engelmann spruce – subalpine fir (*Abies lasiocarpa*) – lodgepole forests interspersed with willow – shrub meadow riparian communities, subalpine grasslands, and avalanche terrain, giving way to open shrub – forb meadows in the alpine ecoregion. Vegetation is described in more detail by Holland and Coen (1983). Six species of ungulates are available to wolves in BNP: elk, white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*), mule deer (*Odocoileus hemionus*), bighorn sheep (*Ovis canadensis*), and mountain goat (*Oreamnos americanus*). Elk are the most abundant ungulate in BNP and comprise 40–70% of the diet of wolves (Huggard 1993b; Hebblewhite 2000). Mule deer and white-tailed deer occur at low density, while moose, bighorn sheep, and mountain goats are rare and spatially separated from wolves in winter (Holroyd and Van Tighem 1983).

Our study area centered on low-elevation winter elk range in the montane ecoregion of the Bow Valley (Fig. 1) (Woods 1991; McKenzie 2001). Mean winter snowpack depth in the valley bottom was 43 cm at Banff (this study) but increased in side valleys and at higher elevations. Two towns ($\leq 10\ 000$), the national railway (Canadian Pacific Railway) and highway (Trans-Canada Highway, TCH) systems, secondary roads, and human developments (ski resorts, golf courses) fragment the study area (Fig. 1). The Bow Valley is used by more than 5 million visitors per year (Green et al. 1996). See Holland and Coen (1983), Holroyd and Van Tighem (1983), and Huggard (1993a, 1993b) for detailed descriptions of the study area.

Methods

Bow Valley zones

Wolf, human, and elk densities vary throughout the Bow Valley (Green et al. 1996; Paquet et al. 1996; McKenzie 2001; Table 1). We divided the Bow Valley into eastern, central, and western zones, reflecting these differences (Fig. 1). Elk subpopulations in the Bow Valley corresponded to these three zones (Woods 1991; McKenzie 2001). Although individuals occasionally moved between zones, movement was not permanent (McKenzie 2001). High human use of the central zone surrounding the Banff townsite greatly reduced wolf use (Paquet et al. 1996) and predation on elk (Hebblewhite 2000). Highway-caused mortality of elk in the central zone declined after fencing of the TCH was completed in 1990 (Clevenger et al. 2001). Wolf predation on elk was highest in the western zone (Hebblewhite 2000), where elk were also exposed to high railway- and highway-caused mortality (before TCH fencing in 1997). Wolves recolonized the eastern zone in 1992–1993; however, they used only part of this zone because of habitat fragmentation caused by the TCH (Hebblewhite 2000). Elk were exposed to moderate human-caused mortality in the eastern zone.

Fig. 1. Banff National Park study area showing the three analysis zones in the Bow Valley. Elk (*Cervus elaphus*) winter range below 2000 m demarcates the zones. The central zone is dominated by the townsite of Banff, including outlying campgrounds (>800 sites), secondary roads, hotels, and a golf course.

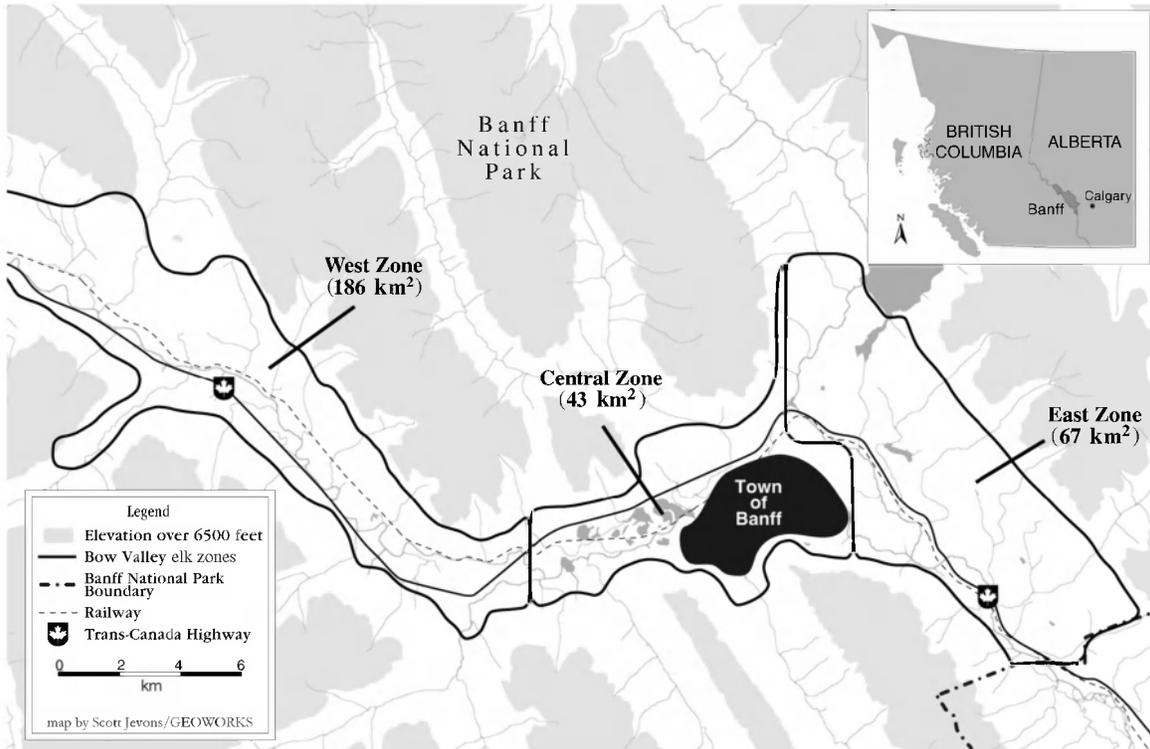


Table 1. Summary of gray wolf (*Canis lupus*) density, wolf predation, and elk (*Cervus elaphus*) mortality patterns in three different zones in the Bow Valley of Banff National Park (BNP), Alberta, from 1986 to 2000 (from Woods 1991; Paquet et al. 1996).

Zone	Wolf density	Wolf predation	Human-caused mortality
Central	Low	Almost none	Low highway mortality after 1990; low railway mortality
Eastern	Medium ^a	Medium ^a	Low highway mortality; high railway mortality
Western	High	High	High highway and railway mortality

^aWolves recolonized this zone midway through the study and then only used areas north of the Trans-Canada Highway.

Wolf monitoring

Wolves were captured and radio-collared by means of modified steel foot-hold traps (toothed and padded No. 4 offset foot-hold traps, Livestock Protection Co., Alpine, Tex., U.S.A.) with trap transmitters (Advanced Telemetry Systems, Isanti, Minn., U.S.A.) in the summer months, or by aerial darting or net-gunning from rotary-wing aircraft during winter. Animal-handling methods were approved by Parks Canada. We studied five wolf packs from 1986 to 2000. The Castle and Spray packs used the western zone and merged to form the Bow Valley pack in 1992–1993, therefore they were treated as one pack for analysis. The Cascade pack formed in 1992–1993 and used the eastern zone. The Fairholme pack, which used the central zone, formed in 1999–2000.

Wolf-pack size and predation

Elk population dynamics within a zone were affected by the total number of elk killed by the total number of wolves in that zone. Mean travelling wolf pack size was determined following Messier (1985). When more than one wolf pack

used a zone, we combined packs to determine the total number of wolves using that zone. We estimated the elk kill rate (number of elk killed per day) per pack in each zone from continuous snow-tracking and radiotelemetry monitoring intervals using a ratio-estimator approach developed by Hebblewhite (2000). If more than one wolf pack used a zone, we added kill rates in that zone. Therefore, we used the total elk kill rate by wolves (number of elk killed per day in each zone) as an independent variable (WOLF) in subsequent analyses to measure the effect of wolf predation on elk population growth. We compared total kill rates among zones using ANOVA.

Post and Stenseth (1998) reasoned that Messier’s (1991) analysis of the effects of predation rate (number of prey killed as a proportion of the prey population) on the moose population growth rate was confounded by a lack of independence between variables (e.g., McCullough 1979, p. 89) because moose population size (N_t) appears in dependent and independent variables. To avoid this problem, Post and Stenseth (1998) used only wolf density in their analysis.

However, we used total kill rate (WOLF) in our analysis, as it is a more informative index than wolf density alone (Taylor 1984) and lacks the spurious correlation problem of predation rate.

We used total elk kill rates estimated for the Spray (1986–1993), Castle (1990–1991), Bow Valley (1994–2000), Cascade (1993–2000), and Fairholme wolf packs (1999–2000) from Hebblewhite (2000). Kill rates were not estimated during the winter of 1992–1993. Although we estimated kill rates for the Castle pack for only 1 year (1990–1991), this pack was active from 1986–1987 to 1991–1992 in the western zone. We assumed that kill rates for the Castle pack were constant during the period when they were active, and added the estimated kill rate for 1990–1991 (0.09 elk/day/pack; Hebblewhite 2000) to the Spray pack's kill rates to obtain the total kill rate in the western zone. We found no difference in model selection with or without this Castle pack adjustment in the western zone (Hebblewhite 2000), therefore we report only the results with the Castle pack adjustment.

Elk population size and population growth rate

Parks Canada estimated elk population size (N_t) using late-winter aerial surveys each year from 1985 to 2000 (Parks Canada, unpublished data). Aerial counts were similar to previous mark–recapture population estimates (Woods 1991). Elk were located below ~2000 m elevation 99% of the time during winter (Hebblewhite 2000). We used this elevation cutoff to delineate zone boundaries using Idrisi16-GIS (Clark Laboratories, Clark University, Worcester, Mass.) and a 1 : 50 000 digital elevation model. Using this cutoff, the eastern zone was 66 km² in area, the central zone 44 km², and the western zone 187 km² (Fig. 1). Winter-range elk density (number of elk/km²; ELK) was calculated using these areas as an independent variable.

We defined the biological year from 1 May to 30 April, following the timing of aerial surveys and approximating the life cycle of elk. We calculated the elk population growth rate, r , using the instantaneous or exponential population growth rate: $r = \ln(N_{t+1}/N_t)$. We used the exponential growth rate (r) instead of relative change in population size ($\lambda = N_{t+1}/N_t$) because taking the natural log of λ reduces statistical dependence between λ and population size (Royama 1992, pp. 6 and 7). This is equivalent to differencing time series to produce the stationarity required for time-series analyses (Royama 1992). Henceforth, we refer to the population growth rate, r , as population growth.

Snow depth

We explored the effects of environmental stochasticity on population growth through snow depth as an index of winter severity. Snow conditions (depth, hardness, density) influence ungulate population growth through their effects on locomotion, foraging, and predation (Telfer and Kelsall 1984; Hobbs 1989; Huggard 1993a). We estimated mean snow depth during each winter by averaging snow depths measured at 15-day intervals between 15 October and 30 April at the base of Banff Mount Norquay ski resort (©Banff Mount Norquay 2000) in the central zone (1700 m elevation). Snow water equivalent (SWE; sensu Turner et al. 1994) is perhaps a more sensitive indicator of winter severity for ungulates such as elk; however, SWE was unavailable for most of the

study. As snow depth and SWE are highly correlated (Goodison et al. 1981), we feel that our analysis of snow depth adequately reflected local climatic conditions.

Previous researchers noted the importance of time-lag effects of snowfall (Post and Stenseth 1998) and cumulative winters' snowfall (snowfall integrated over 1–3 winters) on ungulate growth and survival (Mech et al. 1987; McRoberts et al. 1995; but see Messier 1991, 1995). Hebblewhite (2000), however, failed to find support for the effects of cumulative snowfall for up to 3 years on population growth of elk in BNP. Furthermore, the cross-correlation function (e.g., Post and Stenseth 1998) did not reveal any significant time lags between elk growth rate and snow depth in BNP (Hebblewhite 2000). Therefore, we used mean snow depth (cm) at year = t as an independent variable (SNOW) affecting the population growth rate at year = t to $t + 1$. We included a SNOW \times WOLF interaction in zones with predation (eastern, western) and a SNOW \times ELK term in the central zone to test for interactive effects on population growth.

Human-caused elk mortality

We estimated the number of elk killed by humans on highways and railways in each zone during winter (1 November to 30 April) each year. Accordingly, Parks Canada records (unpublished data) were converted into daily rates (number of elk killed per day) for use as an independent variable (HUMAN). We compared mortality rates among zones using ANOVA. We tested for the overall effect of TCH fencing on the central-zone growth rate by including a dummy variable (FENCE) that indicated whether or not the TCH was fenced (0, not fenced; 1, fenced). Fencing was present in the eastern zone and primarily absent in the western zone during the time series, therefore we did not examine fencing effects in these zones.

Statistical analyses

We tested how elk density (ELK), snow depth (SNOW), winter wolf kill rate (WOLF), winter human-caused kill rate (HUMAN), and TCH fencing (FENCE) affected the elk population growth rate over the 15-year time series. We developed an all-inclusive set of candidate generalized linear models (GLMs) comprising different hypotheses concerning factors affecting the elk population growth (e.g., Appendix C in Orians et al. 1997; for list of candidate models see Hebblewhite 2000). We restricted models to first-order terms and the interactions between (i) snow and wolf predation and (ii) snow and elk density because of the limited length of the time series. GLMs were of the general form

$$[1] \quad r_t = \ln\left(\frac{N_{t+1}}{N_t}\right) = \beta_0 + \beta_1 X_1(t) + \beta_2 X_2(t) + \dots + \beta_m X_m(t) + \varepsilon$$

where $t = 1$ –15 years, r_t is the exponential population growth in year t , β_0 is a constant, $\beta_1 \dots \beta_m$ are coefficients of independent variables $X_1 \dots X_m$, and ε is random error with $\Sigma(\varepsilon) = 0$.

We used maximum-likelihood estimation (Type III) (PROC GENMOD in SAS 8.0; SAS Institute Inc. 1998) to estimate GLMs for elk population growth within each zone. For each model, Akaike Information Criteria (AICs) were calculated

from the general formula $AIC = -2(\log \text{likelihood}) + 2K$, where K is the number of parameters. We corrected AIC for small sample size using AIC_c (Burnham and Anderson 1998). We then used ΔAIC_c to select the best approximating model(s) within a zone, using an approximate cutoff of $\Delta AIC_c = 4$ to describe the top model set (Burnham and Anderson 1998; Anderson et al. 2000). We used the sum of Akaike weights (ω_i) for each variable to rank them by importance (Burnham and Anderson 1998, p. 141) when model-selection uncertainty arose in the top model set, following suggestions for presenting information-theoretic results in ecological research (Anderson et al. 2001).

In the eastern zone we also partitioned the time series into before (8 years) and after (7 years) wolf recolonization periods. Within these partitioned samples, we used Pearson's correlations to examine relationships between individual variables and population growth. For parametric tests (ANOVA, regression, Pearson's correlations) we transformed variables when necessary to meet parametric assumptions and report significance at $\alpha = 0.05$ and confidence intervals and effect size where appropriate.

Autocorrelation, time lags, and detecting density dependence

Autocorrelation, time lags, and the problem of detecting density dependence can affect regression analyses of population dynamics (Royama 1992; Post and Stenseth 1998). We examined autocorrelation functions (ACFs) of independent variables to test for autocorrelation (Royama 1992, p. 112). To test for time lags between independent variables and population growth, we used cross correlation function analysis. Testing for density dependence by regressing N_t against population growth, $r_t = \ln(N_{t+1}/N_t)$, may negatively bias density coefficients because of lack of independence (Royama 1992). However, the methods reviewed by Elkington (2000) to remedy the problem of detecting density dependence in time series were of limited utility in our study because of our relatively short time series (15 years). Following advice from Elkington (2000) we made use of natural experiments to overcome statistical problems in the detection of density dependence and did not correct for autocorrelation unless important differences existed among zones. Furthermore, we did not correct elk density parameter estimates in growth-rate models because time-series length, and therefore bias, were equal between zones.

Model validation

We decomposed GLMs for each zone into difference equations representing linear models of elk abundance (N_t) following Merrill and Boyce (1991) as a limited form of model validation (Boyce 2000). We used observed values for individual variables (Table 2) in the models to compare model predictions to observations, using the starting value for the elk population at $t = 1$. This is equivalent to rewriting GLMs (eq. 1) as a form of the logistic growth equation (Merrill and Boyce 1991), where the GLM becomes

$$[2] \quad N_{t+1} = N(t)e^{[\beta_0 + \beta_1 X_1(t) + \dots + \beta_m X_m(t)]}$$

where N_t is elk population size at time t , $t = 1-15$ years, and $\beta_{1...m}$ is the coefficient of independent variable $X_{1...m}$. We regressed predicted N_t and observed N_t for each model in the

top model set in each zone (analysis of explained variation in logistic regression; Mittleböck and Schemper 1996) as a preliminary measure of the explanatory power of our modeling approach. We present model-validation results for the model with the highest R^2 in each zone.

Results

After beginning at similar elk densities in 1985, densities declined in the eastern and western zones and increased in the central zone (Table 2). Elk density in all three zones was autocorrelated (ACF: eastern zone, $r = 0.57$, $P = 0.04$; central zone, $r = 0.45$, $P = 0.02$; western zone, $r = 0.68$, $P = 0.06$) with density at a time lag of $t - 1$. However, the degree and strength of autocorrelation were relatively similar between zones, therefore we did not adjust SEs of parameter estimate for our comparative approach across zones.

Wolf kill rates were highest in the western zone (0.17 elk/day/pack), intermediate in the eastern zone (0.12 elk/day/pack), and lowest in the central zone (0.06 elk/day/pack; ANOVA, $F_{[2,21]} = 8.51$, $P = 0.006$; Table 2). Wolf kill rates varied considerably within zones (CVs from 67 to 82%; Table 2) but were least variable in the western zone, where wolves resided continuously throughout the study. Human-caused mortality was highest in the western zone (0.08 elk/day) followed by the eastern zone (0.06 elk/day) and central zone (0.05 elk/day) (ANOVA, $F_{[2,24]} = 3.24$, $P = 0.07$). Human-caused mortality in the western zone was higher than in the central zone ($P = 0.002$) but not in the eastern zone ($P = 0.14$). Human-caused mortality rates in the eastern and central zones were similar ($P = 0.30$, post-hoc Bonferroni multiple comparisons). We found no autocorrelation between wolf or human kill rates and no time-lag effects on population growth in any zone.

Central zone: low wolf use

The top model, ELK + FENCE ($\omega_i = 0.41$), was three times more likely than the second model, ELK + HUMAN + FENCE ($\omega_i = 0.13$, $\Delta AIC_c = 2.4$; Table 3), to be the best approximating model, given the data (Table 3; the ratio $\omega_{\text{ELK+FENCE}}/\omega_{\text{ELK+HUMAN+FENCE}}$ is the likelihood of model ELK + FENCE being the better approximating model; Burnham and Anderson 1998, p. 126). In the top model, elk density was negatively related to population growth and TCH fencing was positively related to growth rate (Table 3). Across all four top models, the effects of elk density were strongly negative (Table 3). The negative effect of snow depth and human-caused mortality in the second and fourth models was consistent with expectations (Table 3). Poor estimates, however, indicated that the evidence was insufficient to support their effect.

Eastern zone: wolf recolonization in 1991

The top population-growth model, $r = \text{SNOW}$, was only one and a half times as likely as the second model, WOLF + SNOW, to be the best approximating model (Table 3). Summing the Akaike weights ($\Sigma \omega_i$) for parameters included in the top model set (0–4 ΔAIC_c) provides a method for evaluating variable importance (Burnham and Anderson 1998, p. 141). Summing the Akaike weights across the top four models ranked variables in the following order: SNOW ($\omega_i = 0.87$),

Table 2. Data for the elk population in the Bow Valley, BNP, from 1985 to 2001.

Year	Central zone					Eastern zone				Western zone			
	Mean snow depth (cm)	r_t	No. of elk/km ²	No. of elk killed per day by:		r_t	No. of elk/km ²	No. of elk killed per day by:		r_t	No. of elk/km ²	No. of elk killed per day by:	
				humans	wolves			humans	wolves			humans	wolves
1985–1986	39.00	0.40	5.20	0.12	—	0.53	2.08	0.06	0.00	-0.21	2.20	0.149	—
1986–1987	45.51	-0.19	7.79	0.07	0.13	-0.22	3.55	0.08	0.00	0.10	1.78	0.199	0.47 ^a
1987–1988	30.18	0.29	6.46	0.01	0.02	0.37	2.86	0.06	0.00	-0.24	1.96	0.061	0.41 ^a
1988–1989	45.83	0.04	8.60	0.01	0.10	-0.21	4.15	0.06	0.00	-0.28	1.54	0.094	0.19 ^a
1989–1990	39.54	-0.04	8.97	0.03	0.04	-0.06	3.37	0.06	0.00	0.33	1.17	0.099	0.34 ^a
1990–1991	80.39	0.10	8.65	0.09	0.11	-0.40	3.16	0.09	0.00	-0.52	1.62	0.238	0.28 ^a
1991–1992	32.64	-0.05	9.60	0.01	0.01	0.27	2.11	0.10	0.00	-0.46	0.96	0.061	0.28 ^a
1992–1993	32.89	0.31	9.09	0.01	—	0.04	2.75	0.07	0.00	-0.25	0.61	0.028	—
1993–1994	46.84	-0.15	12.42	0.01	0.07	0.01	2.87	0.05	0.16	-0.20	0.47	0.066	0.27
1994–1995	45.79	0.08	10.70	0.06	0.02	-0.11	2.90	0.04	0.12	0.32	0.39	0.017	0.08
1995–1996	62.92	-0.08	11.59	0.04	0.01	-0.66	2.60	0.10	0.28	-0.70	0.53	0.055	0.13
1996–1997	67.24	-0.01	10.68	0.08	0.10	-0.22	1.35	0.03	0.25	-0.20	0.26	0.022	0.04
1997–1998	30.96	-0.16	10.61	0.07	0.10	0.27	1.08	0.07	0.03	0.22	0.21	0.039	0.03
1998–1999	46.08	0.19	9.04	0.06	0.02	-0.28	1.41	0.03	0.07	0.32	0.27	0.061	0.16
1999–2000	33.28	0.00	10.89	0.04	0.21	0.03	1.06	0.05	0.04	-0.01	0.37	0.039	0.04
2000–2001	—	na	10.89	—	—	na	1.09	—	—	na	0.36	—	—
Mean	45.27	0.05	9.35	0.05	0.06	-0.04	2.49	0.06	0.12	-0.12	0.96	0.08	0.17
CV	32.29	—	20.50	73.77	82.40	—	37.90	34.57	82.9	—	—	79.87	67.2

Note: See the text for descriptions of variables. The mean snowpack depth was set equal across zones. na, not applicable.

^aKill rates in the western zone were adjusted using data from the Castle wolf pack.

Table 3. Top GLM model set according to Bow Valley zone for elk population growth, with model deviance, model structure and corresponding ΔAIC_c and Akaike weight (ω_i ; Burnham and Anderson 1998), BNP, 1985–2000.

Model structure	Deviance	ΔAIC_c	ω_i	β_0	SE	β_1	SE	β_2	SE	β_3	SE
Central-zone models: low wolf use											
1. $\beta_0 + \beta_1(\text{ELK}) + \beta_2(\text{FENCE})$	0.175	0	0.41	0.89	0.174	-0.106	0.023	0.23	0.09	—	
2. $\beta_0 + \beta_1(\text{HUMAN}) + \beta_2(\text{ELK}) + \beta_3(\text{FENCE})$	0.157	2.40	0.13	1.03	0.19	-1.14	0.87	-0.118	0.02	0.267	0.09
3. $\beta_0 + \beta_1(\text{ELK})$	0.255	2.44	0.12	0.632	0.173	-0.062	0.018			—	
4. $\beta_0 + \beta_1(\text{SNOW}) + \beta_2(\text{ELK}) + \beta_3(\text{FENCE})$	0.172	3.60	0.07	0.924	0.19	-0.001	0.02	-0.106	0.02	0.238	0.09
Eastern-zone models: wolf recolonization in 1991											
1. $\beta_0 + \beta_1(\text{SNOW})$	0.609	0	0.37	0.68	0.175	-0.016	0.004	—		—	
2. $\beta_0 + \beta_1(\text{SNOW}) + \beta_2(\text{WOLF})$	0.573	0.63	0.27	0.63	0.177	-0.014	0.004	-0.62	0.25	—	
3. $\beta_0 + \beta_1(\text{SNOW}) + \beta_2(\text{WOLF} \times \text{SNOW})$	0.577	2.38	0.12	0.619	0.183	-0.014	0.004	-0.009	0.010	—	
4. $\beta_0 + \beta_1(\text{SNOW}) + \beta_2(\text{ELK})$	0.586	2.60	0.11	0.767	0.206	-0.016	0.004	-0.044	0.05	—	
Western-zone models: wolf recolonization in 1985											
1. $\beta_0 + \epsilon$	1.459	0	0.21	-0.120	0.081	—		—		—	
2. $\beta_0 + \beta_1(\text{SNOW})$	1.229	0.11	0.20	0.278	0.25	-0.01*	0.005	—		—	
3. $\beta_0 + \beta_1(\text{ELK})$	1.364	1.68	0.09	-0.007	0.135	-0.12	0.116	—		—	
4. $\beta_0 + \beta_1(\text{SNOW}) + \beta_2(\text{ELK})$	1.127	2.00	0.08	0.40	0.026	-0.01*	0.005	0.12	0.105	—	
5. $\beta_0 + \beta_1(\text{HUMAN})$	1.406	2.13	0.07	-0.043	0.13	-0.95	1.25	—		—	

Note: Maximum-likelihood estimates (type III) for coefficients in the models are presented with standard errors; coefficients shown in boldface type have likelihood-ratio χ^2 probabilities <0.05 and those with an asterisk have likelihood-ratio χ^2 probabilities <0.10. Coefficients are reported in the same order as in the model, i.e., for β_i , $i = 1$ if the model only has one parameter.

WOLF ($\Sigma\omega_i = 0.37$), WOLF \times SNOW ($\Sigma\omega_i = 0.12$), and ELK ($\Sigma\omega_i = 0.11$). SNOW had a strong and consistent negative effect on elk population growth, as did predation by wolves (Table 3). Although the models SNOW, SNOW \times WOLF, and SNOW + ELK were included in the top model set, parameter estimates for ELK and SNOW \times WOLF had 95% confidence intervals overlapping zero (Table 3) and were estimated with broad SEs.

In the two partitioned time series (before and after wolf recolonization), elk density was negatively correlated with elk population growth before wolf recolonization (Pearson's $r = -0.77$, $P = 0.03$, $n = 8$) but not afterwards ($P = 0.42$, $n = 7$). Wolf predation was negatively related to elk growth rates after recolonization ($r = -0.74$, $P = 0.05$). Snow depth was negatively related to elk growth rates after wolf recolonization ($r = -0.78$, $P = 0.04$) but not before ($P = 0.14$). Finally, human-caused mortality was unrelated to elk growth rates before ($P = 0.39$) or after wolf recolonization ($P = 0.19$).

Western zone: high wolf density

Elk population growth in the western zone was best fit by a constant rate of decline ($Y = \text{INTERCEPT}$; Table 3). Model selection was uncertain (low ω_i values for all models) and all models had high deviance and poor fit (Table 3). SNOW was the best predictor ($\Sigma\omega_i = 0.28$), followed by ELK ($\Sigma\omega_i = 0.17$) and HUMAN ($\Sigma\omega_i = 0.07$). However, all variables had low Akaike weights (Table 3).

Model validation

In the central zone, the top-ranked model, ELK + FENCE, matched observed elk populations more closely ($R^2 = 0.71$, $P = 0.05$) than other models. In the eastern zone, the second-

ranked model, WOLF + SNOW, matched observed elk population trends more closely than other models in the top set ($R^2 = 0.77$, $P = 0.03$). In the western zone, the top-ranked model, INTERCEPT, matched observed population size similarly ($R^2 = 0.85$, $P = 0.04$).

Discussion

The limiting effect of wolf predation and mean snow depth on elk population growth, and the regulatory effect of elk density on elk population growth in the absence of wolves, are consistent with the findings of researchers studying northern ungulates elsewhere (Messier 1991; Gasaway et al. 1992; Orians et al. 1997; Singer et al. 1997; Sæther 1997; Gaillard et al. 1998; Taper and Gogan 2002). Without predation by wolves, elk numbers in the central zone increased during the early part of the study, whereas elk numbers in zones with wolf predation decreased. Fencing of the TCH in 1991 reduced human-caused mortality in the central zone (Clevenger et al. 2001), thereby increasing population growth rates and densities. Population growth rates subsequently declined as density increased in the central zone and was regulated around a carrying capacity (K) of approximately 10 elk/km² (Hebblewhite 2000). The causes of regulation were not investigated, but most likely include competition for food or the occurrence of density-dependent disease through a high prevalence of giant liver flukes (*Fascioloides magna*; Pybus 1990).

Like the central-zone GLM analysis, correlation analysis indicated that the elk population growth rate in the eastern zone was density-dependent in the 8 years prior to wolf recolonization, and regulated around a carrying capacity of ~3.0 elk/km² (Hebblewhite 2000). Differences in carrying

capacity between the eastern and central zones may be related to higher food quality in the central zone associated with human developments (McKenzie 2001) and predation by predators other than wolves in the eastern zone before wolf recolonization. In the 7 years after wolf recolonization of the eastern zone, predation by wolves and snow depth limited elk population growth. The two best population-growth models in the GLM analysis suggested that snow depth and wolf predation limited elk population growth in this zone. Snow depth did not affect elk population growth until after wolves recolonized this zone.

Elk population dynamics in the western zone (high wolf density) were difficult to interpret. A constant rate of decline and no relationship between wolf kill rate and elk growth rate seemed to be counter to results from the eastern zone. This may be due to the pitfalls of correlative studies in predator-prey research (Royama 1996; Boyce and Anderson 1999). Boyce and Anderson (1999) demonstrated that obtaining insights into population dynamics using regression analyses of time series depends on the variation in explanatory variables. In the western zone we observed little variation in elk population growth (Table 2) or wolf kill rate over the time series, rendering the results from this zone uninformative compared with those from the central and eastern zones. In these zones, large differences occurred during the time series: TCH fencing in the central zone and wolf recolonization in the eastern zone. We agree with others (Royama 1996; Boyce and Anderson 1999; Minta et al. 1999) that key-factor-type regression analyses on population growth have limited use without an experimental approach. Western-zone analyses would have been more informative had elk populations been monitored before wolf recolonization.

Comparison of the eastern and central zones provided a clearer test of the limiting role of wolf predation and approximated an experimental design using before- and after-control impact (BACI; Minta et al. 1999). Predation by wolves was low in the central zone (control) throughout the study, whereas wolves recolonized (impact) the eastern zone (treatment) midway through the study. Support for the limiting effect of wolf predation comes from the comparison of density dependence and the effects of snow across zones. After wolves recolonized the eastern zone, density dependence was not observed. Wolf predation appeared to limit elk to densities that would regulate growth rates, as in other northern ungulates (e.g., Gasaway et al. 1992; Jędrzejewska et al. 1997). Our limited model validation generally supported the model-selection results, with the top- or second-ranked model explaining the most variation in observed elk time series. Future validation should be conducted in BNP.

Comparison of the effects of snow across zones suggests that snow depth decreased population growth only in combination with wolf recolonization. The lack of a strong SNOW \times WOLF interaction in the eastern zone may be an artifact of the temporal scale of the time-series analysis. Huggard (1993a) found that kill rates increased with snow depth within a particular winter. Using mean snow depths and wolf predation rates for each year in time-series analysis masks this important within-year snow-predation interaction. Therefore, we suggest that the main effects of snow depth on elk are realized jointly with wolf predation through this within-winter interaction in BNP.

Furthermore, the effects of snow were not manifested without predation in the central zone or before wolf recolonization in the eastern zone. This could have arisen because starving elk follow a risk-sensitive foraging strategy (Sinclair and Arcese 1995), feeding on more abundant vegetation (e.g., Nietvelt 2000) in riskier habitats at the periphery of the central zone in winters with deep snow. McKenzie (2001) reported that all central-zone elk mortality occurred in this peripheral zone. Therefore, on a regional scale, predation by wolves on starving elk may be partially compensatory. Alternatively, snow removal and compaction in the central zone by humans may have reduced some of the costs associated with deep snow. Future research should examine risk-sensitive foraging in elk.

Inferences from our study would have been strengthened if we had detailed measures of survival of elk calves and adults. McKenzie (2001) showed differential survival of elk in the central and western zone from 1997 to 1999, with an annual mean survival rate of 0.89 and 0.61, respectively. McKenzie (2001) noted that 50% of all mortality (8 of 16 total mortalities) was caused by wolf predation compared with 12.5% (2 mortalities) by cougars (*Felis concolor*), and all predation-related mortality occurred outside the central zone. These survival rates lend further support to our analysis of population growth, and suggest that wolf predation was the mechanism for differences between zones. However, without detailed survival data we were unable to infer how snow depth, wolf predation, or elk density affects demographic processes. In addition, we were unable to address summer wolf predation rates. Although winter and summer predation rates are certainly correlated (because of pack size), the effect of increased predation on ungulate calves by wolves in summer (e.g., Mech et al. 1995) could affect our conclusions. The elk population growth rate is also affected by vegetation quality during summer (Merrill and Boyce 1991).

Furthermore, we did not document mortality caused by other predators such as cougars and bears (*Ursus* spp.). Attributing changes in population dynamics of elk solely to predation by wolves ignores the effects of predation by other predators (including humans). Therefore, we suggest that the addition of predation from the recolonization by wolves to existing mortality sources (including cougar and bear predation) limited elk populations in conjunction with snow depth to below a density at which they were regulated by other density-dependent factors. However, we did not address whether or not wolf predation was density-dependent, and our time-series analysis only applies to the range of elk densities and kill rates that we observed. It appears that elk populations in the western zone were beginning to stabilize near the end of the study, suggesting the potential for density-dependent regulation of elk by wolves. The positive relationship between elk group size and elk density, combined with increased encounters and kills in larger herds, might provide a mechanism for such density-dependent predation (Hebblewhite and Pletscher 2002). Future research should test if wolf predation is density-dependent by examining the functional and numeric responses of wolves to elk density.

We interpret the reduced elk numbers in the eastern zone as being the result of direct lethal effects of predation and snow depth. However, some elk in this zone appeared to adopt an antipredator strategy to minimize predation risk by moving for short periods of time to the central (wolf-free)

zone or south of the fenced TCH, which wolves did not cross (M. Hebblewhite, personal observation). Therefore, our analysis could include both the direct lethal effects of predation and the indirect effects. Nevertheless, the consequences of direct and indirect effects could manifest themselves similarly at other trophic levels (Schmitz 1998). Elk in the western zone, however, did not appear (or were unable) to respond to wolf recolonization by moving to the lower predation central zone (McKenzie 2001), which suggests that they would have been more susceptible to the direct effects of wolf predation.

In the analysis of complex ecological systems such as ungulate population dynamics, using an information-theoretic approach to guide data-based model selection and inference offers several advantages. Considering alternative models, especially with high model-selection uncertainty, allowed us to gain a deeper understanding of factors affecting elk population dynamics. Adopting a single model for inference (i.e., using stepwise model selection) may have caused us to overlook the effects of wolf predation and snow depth in comparing across zones. Model-selection uncertainty is not a weakness of this approach, because this uncertainty measures our confidence in the models (Burnham and Anderson 1998). Adopting such an approach may have preempted debate about the population dynamics of moose on Île Royale (i.e., Mech et al. 1987; Messier 1991; Hebblewhite 2000).

Gaillard et al. (1998) suggested that constant and high adult survival rates and variable juvenile recruitment characterize northern ungulate population dynamics. Their review included populations with and without major predators in sensitivity analyses of ungulate population growth. Although we report population growth and not age-specific survival of elk in BNP, we show that ungulate population processes differ in the presence and absence of wolves, and wolf predation appears to reduce interactions of density and environmental stochasticity on ungulate population dynamics. Therefore, with wolf predation we may expect juvenile and (or) adult survival to vary less with environmental factors, which could alter the results of sensitivity analyses. Northern ungulates evolved with predators such as wolves, and combining results across studies may mask important differences between ungulate population dynamics in the presence and absence of predation.

Acknowledgements

Parks Canada, the Central Rockies Wolf Project, John/Paul and Associates, Alberta Human Resources and Employment, Human Resources Development Canada, the Canadian Pacific Foundation, Shell Environment Fund, Paquet Wildlife Fund, and World Wildlife Fund-U.S.A., and World Wildlife Fund-Canada funded this research throughout its ~15-year duration. The BNP Warden Service and numerous research assistants helped to collect field data. We thank John Thornton of Banff Mount Norquay Ski Resort for snow-depth data. We thank P. Biro and M.S. Lindberg for advice on statistical modelling. L.S. Mills, K. Foresman, and two anonymous reviewers provided useful comments on the manuscript. We thank S. Jevons for producing Fig. 1. The L. Pengelly and G. Bright memorial scholarships, School of Forestry, and the J. Paquet Wildlife Fund supported M. Hebblewhite while at the University of Montana.

References

- Anderson, D.R., Burnham, K.P., and Thompson, W.L. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *J. Wildl. Manag.* **64**: 912–923.
- Anderson, D.R., Link, W.A., Johnson, D.H., and Burnham, K.P. 2001. Suggestions for presenting the results of data analyses. *J. Wildl. Manag.* **65**: 373–378.
- Boertje, R.D., Valkenburg, P., McNay, and M.E. 1996. Increases in moose, caribou, and wolves following wolf control in Alaska. *J. Wildl. Manag.* **60**: 474–489.
- Boutin, S. 1992. Predation and moose population dynamics: a critique. *J. Wildl. Manag.* **56**: 116–127.
- Boyce, M.S. 2000. Modeling predator–prey dynamics. *In* Research techniques in animal ecology: controversies and consequences. Edited by L. Boitani and T.K. Fuller. Columbia University Press, New York. pp. 253–287.
- Boyce, M.S., and Anderson, E.M. 1999. Evaluating the role of carnivores in the Greater Yellowstone Ecosystem. *In* Carnivores in ecosystems: the Yellowstone experience. Edited by T.K. Clark, A.P. Curlee, S.C. Minta, and P.M. Kareiva. Yale University Press, New Haven, Conn. pp. 265–284.
- Burnham, K.P., and Anderson, D.R. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.
- Chamberlain, T.C. 1890. The method of multiple working hypotheses. *Science* (Washington, D.C.), **15**: 93.
- Clevenger, A.P., Chruszcz, B., and Gunson, K. 2001. Highway mitigation fencing reduces wildlife–vehicle collisions. *Wildl. Soc. Bull.* **29**: 646–653.
- Clutton-Brock, T.H., Major, M., Albon, S.D., and Guinness, F. 1987. Early development and population dynamics in red deer. I. Density-dependent effects on juvenile survival. *J. Anim. Ecol.* **56**: 53–67.
- Dale, B.W., Adams, L.G., Bowyer, R.T. 1994. Functional response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. *J. Anim. Ecol.* **63**: 644–652.
- Elkington, J.S. 2000. Detecting stability and causes of change in population density. *In* Research techniques in animal ecology: controversies and consequences. Edited by L. Boitani and T.K. Fuller. Columbia University Press, New York. pp. 191–209.
- Estes, J.A. 1996. Predators and ecosystem management. *Wildl. Soc. Bull.* **34**: 390–396.
- Gaillard, J.-M., Festa-Bianchet, M., and Yoccoz, N.G. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends Ecol. Evol.* **13**: 58–63.
- Gasaway, W.C., Boertje, R.D., Grangaard, D.V., Kellyhouse, D.G., Stephenson, R.O., and Larsen, D.G. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. *Wildl. Monogr.* No. 120. pp. 1–59.
- Goodison, B.E., Ferguson, H.L., and McKay, G.A. 1981. Measurement and data analysis. *In* Handbook of snow: principles, processes, management and use. Edited by D.M. Gray and D.M. Male. Pergamon Press, New York. pp. 191–274.
- Green, J.C., Pacas, C., Comwell, L., and Bayley, S. 1996. Ecological Outlooks Project: a cumulative effects assessment and futures outlook of the Banff Bow Valley. Prepared for the Banff Bow Valley Study, Department of Canadian Heritage, Ottawa, Ont.
- Guthery, F.S., Lusk, J.J., and Peterson, M.J. 2001. The fall of the null hypothesis: liabilities and opportunities. *J. Wildl. Manag.* **65**: 379–384.
- Hayes, R.D., and Harestad, A.S. 2000. Wolf functional response and regulation of moose in the Yukon. *Can. J. Zool.* **78**: 60–66.

- Hebblewhite, M. 2000. Wolf and elk predator-prey dynamics in Banff National Park. M.S. thesis, University of Montana, Missoula.
- Hebblewhite, M., and Pletscher, D.H. 2002. Effects of elk group size on predation by wolves. *Can. J. Zool.* **80**: 800–809.
- Hobbs, N.T. 1989. Linking energy balance to survival in mule deer: development and test of a simulation model. *Wildl. Monogr.* No. 101. pp. 1–39.
- Holland, W.D., and Coen, G.M. 1983. Ecological (biophysical) land classification of Banff and Jasper National Parks. Vol. 1. Summary. Alberta Institute of Pedology, Edmonton.
- Holroyd, G.L., and Van Tighem, K.J. 1983. Ecological (biophysical) land classification of Banff and Jasper National Parks. Vol. 3. The wildlife inventory. Canadian Wildlife Service, Edmonton, Alta.
- Huggard, D.J. 1993a. Effect of snow depth on predation and scavenging by gray wolves. *J. Wildl. Manag.* **57**: 382–388.
- Huggard, D.J. 1993b. Prey selectivity of wolves in Banff National Park. I. Prey species. *Can. J. Zool.* **71**: 130–139.
- Jędrzejewska, B., Jędrzejewski, W., Bunevich, A.N., Milkowski, L., and Krasinski, Z. 1997. Factors shaping population densities and increase rates of ungulates in Bialowieza Primeval Forest (Poland and Belarus) in the 19th and 20th centuries. *Acta Theriol.* **42**: 399–451.
- Johnson, D.H. 1999. The insignificance of statistical significance testing. *J. Wildl. Manag.* **63**: 763–772.
- Kunkel, K.E., and Pletscher, D.H. 1999. Species-specific population dynamics of cervids in a multipredator system. *J. Wildl. Manag.* **63**: 1082–1093.
- Marshall, J.P., and Boutin, S. 1999. Power analysis of wolf-moose functional responses. *J. Wildl. Manag.* **63**: 396–402.
- McCullough, D.R. 1979. The George Reserve deer herd: population ecology of a *K*-selection species. University of Michigan Press, Ann Arbor.
- McKenzie, J. 2001. The selective advantage of urban habitat use by elk in Banff National Park. M.Sc. thesis, University of Guelph, Ont.
- McRoberts, R.E., Mech, L.D., and Peterson, R.O. 1995. The cumulative effect of consecutive winters' snow depth on moose and deer populations: a defense. *J. Anim. Ecol.* **64**: 131–135.
- Mech, L.D., McRoberts, R.E., and Peterson, R.O. 1987. Relationship of deer and moose populations to previous winters' snow. *J. Anim. Ecol.* **56**: 615–627.
- Mech, L.D., Meier, T.J., Burch, J.W., and Adams, L.G. 1995. Patterns of prey selection by wolves in Denali National Park, Alaska. *In Ecology and conservation of wolves in a changing world.* Edited by L.N. Carbyn, S.H. Fritts, and D.R. Seip. Canadian Circumpolar Institute, Edmonton, Alta. pp. 231–243.
- Merrill, E.H., and Boyce, M.S. 1991. Summer range and elk population dynamics in Yellowstone National Park. *In The Greater Yellowstone ecosystem: redefining America's wilderness heritage.* Edited by R.B. Keiter and M.S. Boyce. Yale University Press, New Haven, Conn. pp. 263–73.
- Messier, F. 1985. Social organization, spatial distribution, and population density of wolves in relation to moose density. *Can. J. Zool.* **63**: 1068–1077.
- Messier, F. 1991. The significance of limiting and regulating factors on the demography of moose and white-tailed deer. *J. Anim. Ecol.* **60**: 377–393.
- Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. *Ecology*, **75**: 478–488.
- Messier, F. 1995. Is there evidence for a cumulative effect of snow depth on moose and deer populations? *J. Anim. Ecol.* **64**: 136–140.
- Milner, J.M., Elston, D.A., and Albon, S.D. 1999. Estimating the contributions of population density and climatic fluctuations to interannual variation in survival of Soay sheep. *J. Anim. Ecol.* **68**: 1235–1247.
- Minta, S.C., Kareiva, P.M., and Curlee, A.P. 1999. Carnivore research and conservation: learning from history and theory. *In Carnivores in ecosystems: the Yellowstone experience.* Edited by T.K. Clark, A.P. Curlee, S.C. Minta, and P.M. Kareiva. Yale University press, New Haven, Conn. pp. 323–404.
- Mittleböck, M., and Schemper, M. 1996. Explained variation for logistic regression. *Stat. Med.* **15**: 1987–1997.
- Nelson, M.E., and Mech, L.D. 1986. Relationship between snow depth and gray wolf predation on white-tailed deer. *J. Wildl. Manag.* **50**: 471–474.
- Nietvelt, C.N. 2000. Effects of herbivory by elk on riparian willow community ecology in Banff National Park. M.Sc. thesis, University of Alberta, Edmonton.
- Orians, G., Cochran, P.A., Duffield, J.W., Fuller, T.K., Gutierrez, R.J., Henemann, W.M., James, F.C., Kereiva, P., Kellert, S.R., Klein, D., McLellan, B.N., Olson, P.D., and Yaska, G. 1997. Wolves, bears, and their prey in Alaska. National Academy Press, Washington, D.C.
- Paquet, P.C., Wierzchowski, J., and Callaghan, C. 1996. Summary report on the effects of human activity on gray wolves in the Bow River Valley, Banff National Park. *In Ecological Outlooks Project: a cumulative effects assessment and futures outlook of the Banff Bow Valley.* Edited by J.C. Green, C. Pacas, L. Cornwell, and S. Bayley. Prepared for the Banff Bow Valley Study, Department of Canadian Heritage, Ottawa, Ont. p. 74.
- Portier, C., Festa-Bianchet, M., Gaillard, J.-M., Jorgenson, J.T., and Yoccoz, N.G. 1998. Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*). *J. Zool. (Lond.)*, **245**: 271–278.
- Post, E., and Stenseth, N.C. 1998. Large scale climatic fluctuations and population dynamics of moose and white-tailed deer. *J. Anim. Ecol.* **67**: 537–543.
- Post, E., Peterson, R.O., Stenseth, N.C., and McLaren, B.E. 1999. Ecosystem consequences of wolf behavioral response to climate. *Nature (Lond.)*, **401**: 905–907.
- Pybus, M.G. 1990. Survey of hepatic and pulmonary parasites of wild cervids in Alberta, Canada. *J. Wildl. Dis.* **26**: 453–459.
- Royama, T. 1992. Analytical population dynamics. Chapman and Hall, New York.
- Royama, T. 1996. A fundamental problem in key factor analysis. *Ecology*, **77**: 87–93.
- SAS Institute Inc. 1998. SAS user's guide, ed. 8. SAS Institute Inc., Cary, N.C.
- Schmitz, O.J. 1998. Direct and indirect effects of predation and predation risk in old-field interaction webs. *Am. Nat.* **151**: 327–342.
- Sinclair, A.R.E. 1989. Population regulation of animals. *In Ecological concepts.* Edited by J.M. Cherrett. Blackwell Scientific Publications, Oxford. pp. 197–241.
- Sinclair, A.R.E. 1991. Science and the practice of wildlife management. *J. Wildl. Manag.* **55**: 767–773.
- Sinclair, A.R.E., and Arcese, P. 1995. Population consequences of predation-sensitive foraging: the Serengeti wildebeest. *Ecology*, **76**: 882–891.
- Singer, F.J., Harting, A., Symonds, K.K., and Coughenour, M.B. 1997. Density dependence, compensation and environmental effects on elk calf mortality in Yellowstone National Park. *J. Wildl. Manag.* **61**: 12–25.
- Skogland, T. 1991. What are the effects of predators on large ungulate populations? *Oikos*, **61**: 401–411.
- Sæther, B.-E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends Ecol. Evol.* **12**: 143–149.

- Taper, M.L., and Gogan, P.J. 2002. The northern Yellowstone elk: density dependence and climatic conditions. *J. Wildl. Manag.* **66**: 106–122.
- Taylor, R.J. 1984. *Predation*. Chapman and Hall, New York.
- Telfer, E.S., and Kelsall, J.P. 1984. Adaptation of some large North American mammals for survival in snow. *Ecology*, **65**: 1828–1834.
- Terborgh, J., Estes, J.A., Paquet, P., Ralls, K., Boyd-Heger, D., Miller, B.J., and Noss, R.F. 1999. The role of top carnivores in regulating terrestrial ecosystems. *In* *Continental conservation: scientific foundations of regional reserve networks*. Edited by M.E. Soulé and J. Terborgh. The Wildlands Project, Island Press, Washington, D.C. pp. 39–64.
- Turner, M.G., Wu, Y., Wallace, L.L., Romme, W.H., and Brenkert, A. 1994. Simulating winter interactions among ungulates, vegetation, and fire in northern Yellowstone Park. *Ecol. Appl.* **4**: 472–496.
- Underwood, A.J. 1997. *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge University Press, Cambridge.
- Woods, J.G. 1991. *Ecology of a partially migratory elk population*. Ph.D. dissertation, University of British Columbia, Vancouver.