



An Assessment of Eberhardt's Ratio-Dependent Wolf-Ungulate Model

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Abstract

A growing number of ecological studies suggest ratio-dependence may be common in many predator-prey systems. I assessed Eberhardt's ratio-dependent wolf-ungulate model using 22 years of wolf (*Canis lupus*) and elk (*Cervus elaphus*) survey data, and 28 years of elk hunter harvest data from the northern range of Yellowstone National Park, USA. This model required estimation of eight parameters, of which four were determined from other studies and four were evaluated by statistical model fitting. Modelled trends in wolf and elk abundance were correlated with survey estimates, and modelled trends in wolf predation rates were correlated with empirical estimates. The equilibrium ratio of wolves to elk was 0.0063 and the equilibrium ratio of elk to habitat carrying capacity was 0.680. While this simple model provided a realistic portrait of wolf-elk dynamics in a complex predator-prey system, the performance of the model could be improved by including the sex and age structure of the elk population, a wolf functional response, and temporal variation in wolf and elk demographic rates. This model provides additional support for ratio-dependence in large mammal predator-prey systems.

Keywords: *Canis lupus*, *Cervus elaphus*, ratio-dependence, Wolf-Ungulate model, Yellowstone National Park.

Introduction

Predation by animals is among the most fundamental of all ecological relationships and has been the focus of ecology since its inception (Taylor 1984). Consequently, predator-prey models have been used to inform much of the theory of population, community and conservation biology (Arditi and Ginzburg 2012). Earlier studies focussed on the classic Holling prey-dependent models (Holling 1959, Messier 1994), while more recent studies have examined ratio-dependent and/or predator-dependent models (Skalski and Gillian 2001). Ratio-dependent predation has been documented in invertebrate predator-prey systems (Reeve 1997), as well as large mammal predator-prey systems (Jost *et al.* 2005, Vucetich *et al.* 2011, Hebblewhite 2013).

Eberhardt and his colleagues published a series of five foundational papers where they developed an approach for assessing the impact of wolves on ungulate prey based on ratio-dependence theory (Eberhardt 1997, Eberhardt 1998, Eberhardt and Peterson 1999, Eberhardt 2000 and Eberhardt *et al.* 2003). Their approach was based on constant kill rates and an equilibrium ratio between wolf and ungulates, i.e. the ratio where the number of wolves and their primary prey stabilize. Support for this form of ratio-dependence comes from studies that suggest a relatively constant rate of consumption of moose by wolves in winter, and a linear relationship between ungulate biomass and wolf density (Eberhardt 1997). Eberhardt's ratio-dependent model was based on two difference equations:

$$[1] V_t = V_{t-1} + r_1 V_{t-1} \left[1 - \left(\frac{V_{t-1}}{K} \right)^z \right] - c H_{t-1}$$
$$[2] H_t = H_{t-1} + r_2 H_{t-1} \left(1 - \frac{H_{t-1}}{a V_{t-1}} \right)$$

where V_t denotes ungulate prey numbers at time t , r_1 is the maximal rate of increase for the prey, K is the habitat carrying capacity or asymptotic prey abundance, z is the density exponent that determines the rate of approach to the asymptote, c is the annual killing rate of prey by predators (H_t), r_2 is the maximal rate of increase of wolves and a is the equilibrium ratio of wolves to prey. The equilibrium conditions ($V_t = V_{t-1}$ and $H_t = H_{t-1}$) give the following relationships:

$$[3] V = K \left(1 - \frac{ca}{r_1}\right)^{1/z} \text{ and } H = aV$$

With the inclusion of elk harvesting or hunting by humans, eq. 1 needs to be modified to:

$$[4] V_t = (V_{t-1} - B_{t-1}) + r_1(V_{t-1} - B_{t-1}) \left[1 - \left(\frac{V_{t-1} - B_{t-1}}{K}\right)^z\right] - cH_{t-1}$$

where B_{t-1} is the annual harvest that occurs just after the population survey (Skalski *et al.* 2005).

While some efforts were made by Eberhardt and his colleagues to fit these models to actual wolf-ungulate data from North America, much of their work focussed on estimating the equilibrium ratio of wolves to their prey. Initial efforts focussed on wolves and moose (Eberhardt 1997, Eberhardt 1998, Eberhardt and Peterson 1999), while later studies involved wolves and elk in Yellowstone National Park (YNP), USA (Eberhardt *et al.* 2003). However, Eberhardt *et al.* (2003) concluded that “a long-term study of both wolf and elk numbers is essential if the Yellowstone data are to be useful in assessing the impact of wolves on their ungulate prey”. Since then, wolves and elk have continued to be surveyed annually during most years and there may now be sufficient data to determine how well Eberhardt’s model provides a portrait of wolf and elk dynamics in this complex predator-prey system.

The purpose of this study was to assess Eberhardt’s ratio-dependent model based on a time series of elk and wolf survey data from the northern range of YNP. Specifically, I wished to determine if the model could portray

observed changes in elk abundance (1989–90 to 2016–17), wolf abundance (1995–96 to 2016–17) and wolf predation rates (1995–96 to 2010–11). I also used the model to estimate the wolf-elk equilibrium ratio and other equilibrium conditions. Finally, I evaluated hunter harvest levels that would stabilize future elk numbers in the absence of environmental fluctuations.

Material and methods

Study area

YNP is located in the northwest region of the United States within the states of Wyoming, Montana and Idaho (Fig. 1). Northern Yellowstone elk summer within YNP and winter on the northern range. Approximately two-thirds of the northern range lies within the northern portion of YNP and the remainder extends northward (White *et al.* 2012). Wolves were reintroduced into the northern range of YNP in 1995–96. Since then wolf numbers have increased substantially and some wolves in YNP now move outside the park (Smith *et al.* 2016). Elk are the primary prey of wolves on the northern range and comprise > 85% of the wolves’ diet (Metz *et al.* 2012). Hunting occurs when elk migrate out of the park into southern Montana. Although wolves are protected within the park, wolves may be legally shot outside the park boundary (Smith *et al.* 2016).

Data Collections

I used aerial survey counts of elk that were conducted on the northern range by the Northern Yellowstone Wildlife Cooperative Wildlife Working Group from 1989–2017 during December through March (Loveless 2017). Sightability estimates were not available for most years and likely varied under different sighting conditions. Eberhardt *et al.* (2007) concluded that the recorded counts were well below actual population size and adjusted the counts by a “raising factor” of

1.32, which I have also done. I used annual harvest estimates within Hunting Districts 313 and 316 which comprise the Northern Yellowstone Elk Management Unit (Cunningham 2016). Harvests occurred both before and after aerial counts were completed, and both hunting seasons and survey timing varied among years. From 1989–2004, about 70% of the annual harvest occurred during a late hunt in January and February that focussed on antlerless elk, while from 2005–2010 about 32% of the harvest occurred during this late hunt prior to closing in 2011 (Loveless personal communication). Earlier hunts in the autumn focussed primarily on bulls. I estimated the pre-hunt elk population size by adding the harvest during the early season to the adjusted survey count. Taber and Gogan (2002, cited by Eberhardt *et al.* 2007) estimated the habitat carrying capacity for the northern Yellowstone range at $K = 20,000$ – $25,000$ elk and I used the mid-range of these estimates. Eberhardt *et al.* (2003) used $r_1 =$

0.28, which was estimated by Eberhardt *et al.* (1996) as the maximum rate of increase for elk without predators. They did not consider bear predation in their model even though they suggested that bear predation could be a substantial factor affecting calf survival of northern Yellowstone elk. In YNP, Barber-Meyer *et al.* (2008) documented that grizzly (*Ursus arctos*) and black bear (*Ursus americanus*) predation accounted for 58–60% of calf elk deaths, while wolves accounted for 14–17%. Middleton *et al.* (2013) used computer simulations to show that predation by grizzly bears in YNP could result in declining calf recruitment and population growth. Cougars (*Puma concolor*) also occur in YNP and prey on elk (Murphy 1998). Eberhardt *et al.* (2003) noted the uncertainty about the appropriate value of the density exponent for elk and developed models with $z = 2$ and $z = 5$. I considered models with $z = 1$ (logistic), $z = 2$ and $z = 5$.

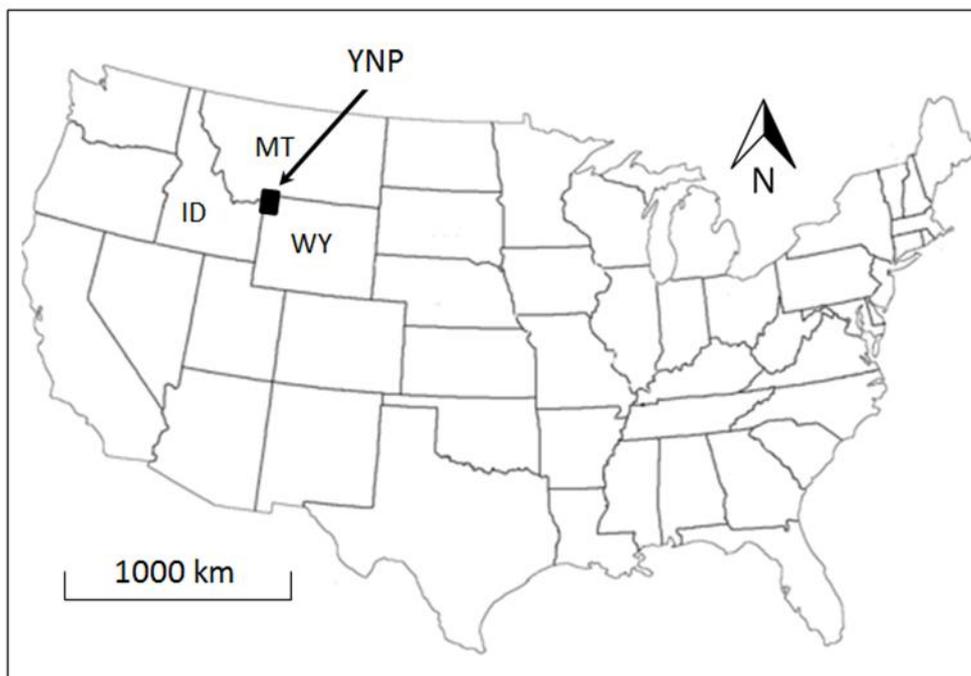


Figure 1. Location of Yellowstone National Park (YNP) within the USA. ID = Idaho, MT = Montana, WY = Wyoming.

I used annual wolf counts from packs occupying the northern Yellowstone range within YNP as reported by Smith *et al.* (2017).

I assumed the maximal rate of increase for wolves was $r_2 = 0.46$ as estimated by Keith (1983) and used by Eberhardt *et al.* (2003). The

average killing rate of ≥ 6 month elk from 1995–2010 on the northern range was 10.5 elk/wolf/year (Peterson *et al.* 2014). As wolves also kill < 6 month old calves, Eberhardt *et al.* (2003) assumed a killing rate of $c = 15$ elk/wolf/year, which I have used as well. The annual predation rate was estimated as ca_t (Eberhardt *et al.* 2003) where c represent kills from early winter in year t to year $t+1$, and a_t is the wolf/elk ratio during early winter in year t .

Modelling Approach

Eberhardt's ratio-dependent model required estimates of eight parameters. Four parameters were determined from other studies (K , z , c , r_2), and four parameters were estimated using statistical model fitting based on maximum likelihood (Haddon 2001, Skalski *et al.* 2005). The parameters estimated by the ratio-dependent model included: (1) the pre-hunt elk population size in 1989–90 ($V_{1989-90}$); (2) the number of wolves in 1995–96 ($H_{1995-96}$); (3) the wolf-elk equilibrium ratio (a); and (4) the maximum potential rate of increase for elk from 1989–90 to 2016–17 (r_1). The estimate r_1 implicitly includes bear and cougar-induced elk mortality as their impact was reflected in the elk survey data, but excludes elk kills by wolves which were explicitly modelled (eq. 2 and 4). Solutions were obtained using the SOLVER tool in Microsoft EXCEL (Microsoft, Redmond, WA). I constructed log-likelihood models for both wolves and elk using

$$\ln(L) = -\frac{n}{2}(\ln(2\pi) + 2\ln(\hat{\sigma}) + 1)$$

where $\ln(L)$ is the log-likelihood, n is the number of elk or wolf surveys and $\hat{\sigma}$ is the standard deviation of the residuals between the observed and modelled abundance (Haddon 2001). Combining the likelihoods for wolves and elk provided the total likelihood to be maximized, i.e. $\ln(L) = \ln(L_H) + \ln(L_V)$. Following Haddon (2001) I constructed both uncorrected and first-order biased-corrected 2.5 and 97.5 percentile confidence intervals for the estimated parameters by resampling the residuals from the optimum fit to generate 5000 bootstrap samples of observed wolf and elk

numbers. Bootstrapping was performed using Visual Basic for Applications in EXCEL. The model was refitted and the parameters re-estimated for each bootstrap sample. As confidence intervals obtained by bootstrapping are only approximate and likely to be underestimates, I adopted the widest values as providing the best estimates as suggested by Haddon (2001). I used model selection based on information theory (Burnham and Anderson 1998) to select among the competing models with different density exponents (i.e. $z = 1, 2$ and 5) using the Akaike's Information Criterion adjusted for small sample sizes (AIC_c)

$$AIC_c = -2(\ln(L)) + 2k + \frac{2k(k+1)}{(n-k-1)}$$

where k is the number of parameters estimated and n is the sample size. I also calculated the difference between the model with the lowest AIC_c and a particular model (ΔAIC_c), and the relative model likelihood (w_i) to determine the best-fitting model.

Previous modelling approaches for wolves and elk in YNP include Vucetich *et al.* (2005) and Varley and Boyce (2006). Both of these studies emphasized the importance of annual variations in snowfall and precipitation as factors affecting this predator-prey system.

Results

The statistical fit of the model to the survey and harvest data was substantially improved with $z = 5$ ($AIC_c = -151.6$, $\Delta AIC_c = 0.0$, $w_i = 1.0$), compared to $z = 2$ ($AIC_c = -133.2$, $\Delta AIC_c = 17.9$, $w_i = 0.0$) or $z = 1$ ($AIC_c = -133.2$, $\Delta AIC_c = 31.5$, $w_i = 0.0$). The optimum parameter estimates for the best model ($z = 5$) were $V_{1989-90} = 23,932$ (95% CI = 21,036–26,228), $H_{1995-96} = 16$ (95% CI = 14–17), $a = 0.0063$ (95% CI = 0.0055–0.0069) and $r_1 = 0.111$ (95% CI = 0.104–0.117).

The modelled estimates of elk and wolf abundance were correlated with the survey estimates (elk: $r = 0.931$, $df = 20$, $P < 0.001$, Fig. 2; wolf: $r = 0.849$, $df = 20$, $P < 0.001$, Fig. 3). Wolf predation rates increased sharply during the first 10 years reaching 11% in 2004–

05 and were correlated with maximum estimates of the wolf predation rate on recruited (>6 months old) elk reported by Peterson *et al.* (2014) from 1995–96 to 2010–11 ($r = 0.880$, $df = 14$, $P < 0.001$, Fig. 4). The equilibrium ratio (a) was 0.0063 (158 elk/wolf), and the equilibrium predation rate (ca) was 0.095 (95% CI = 0.083, 0.102). Equilibrium conditions were $H = 96$ (95% CI = 88, 102) and $V = 15,296$ (95% CI = 13,736, 16,291) which suggests that wolves, in the absence of hunting, may reduce and maintain the northern Yellowstone elk herd at 68% of habitat carrying capacity ($V/K = 0.680$, 95% CI = 0.610, 0.724). With wolf predation and hunting, elk numbers were reduced to about 25% of habitat carrying capacity ($V_{2016-17}/K = 0.253$, 95% CI = 0.177, 0.327). An annual harvest of 78 elk from 2017–18 to 2038–39 was projected to stabilize the population at 5400 animals (Fig. 5). This harvest level was much lower than the average harvest from 2012–13 to 2016–17 ($\bar{x} = 286$, $SD = 149$). However, the model assumed all sex/age classes were harvested in proportion to their abundance, whereas current harvests on northern Yellowstone elk were primarily bulls.

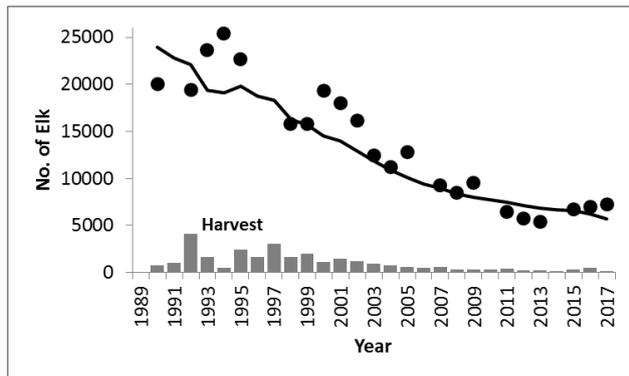


Figure 2. Adjusted survey counts (dots), hunter harvest (bars), and model estimates (line) for abundance of the northern Yellowstone elk herd. Initial elk population (solid line) = 23,932; c (elk kills/wolf/year) = 15, a (equilibrium ratio of wolves to elk) = 0.0063, K (carrying capacity) = 22,500; r_1 (maximum rate of increase) = 0.111; z (density dependent exponent) = 5. The year 1990 refers to 1989–90.

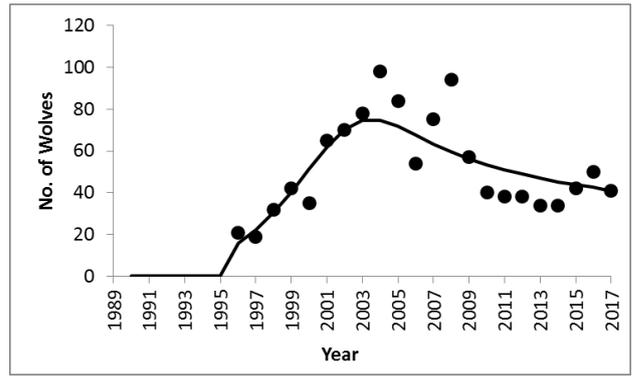


Figure 3. Survey counts (dots) and model estimates (line) for the abundance of northern Yellowstone wolves. Initial wolf population = 16 in 1995-96; c (kill/wolf/year) = 15; r_2 (maximum rate of increase) = 0.46. The year 1996 refers to 1995–96.

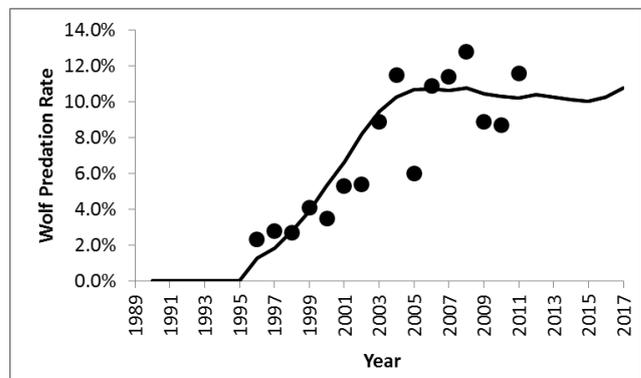


Figure 4. Modelled predation rates (line) by wolves on northern Yellowstone elk from 1995–96 to 2016–17 and empirical maximum estimates of predation rates for > 6 month elk (dots) from 1995–96 to 2010–11. The year 1990 refers to 1989–90.

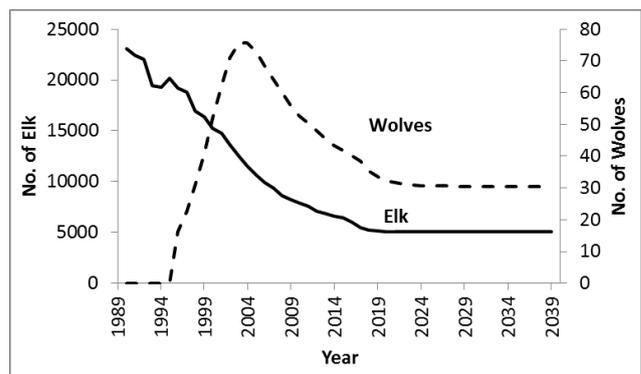


Figure 5. Modelled trends in elk (solid line) and wolf numbers (dashed line) on the northern range from 1989–90 to 2038–39 with parameters as in Figures 2 and 3, and future annual elk harvests (2017–18 to 2038–39) held constant at 78. The year 1990 refers to 1989–90.

Discussion

Eberhardt's wolf-ungulate model provided a reliable portrait of wolf-elk interactions on the northern range of YNP from 1995–96 to 2016–17. The model portrayed changes in wolf and elk abundance, and trends in predation rates as determined from empirical studies (Peterson *et al.* 2014, Loveless 2017, Smith *et al.* 2017). The equilibrium ratio of $a = 0.0063$ was at the lower range of 0.01–0.02 estimated by Eberhardt *et al.* (2003, 2007).

The ratio-dependent model, however, was too simple to reflect the full range of complex wolf-elk interactions that are known to occur on the northern range. While I accounted for the impact of bears and cougars by estimating the maximal rate of increase for elk with these predators present, the model could have been improved with estimates of their abundance and kill rates. A second shortcoming of the model was the lack of a wolf functional response. Hebblewhite (2013) found evidence that wolf predation on elk in Banff National Park was described by a Type II ratio-dependent functional response. Becker (2008) also found strong support for a Type II ratio-dependent functional response for the wolf-elk system in the Madison headwaters area of YNP, and recent studies have documented a wolf functional response and declining predation rates on the northern range (M. Metz personal communication). A third limitation of the model was that wolf estimates were only available for the northern range within YNP. Wolves also exist on the northern range outside the park, although at much lower densities than within the park (Smith *et al.* 2016). Another weakness of the model was the lack of consideration for other factors such as weather (e.g. winter snow depth and summer precipitation), fire, and disease that are known to affect elk and wolves in this system (Vucetich *et al.* 2005, Barber-Meyer *et al.* 2008, Peterson *et al.* 2014, Smith *et al.* 2016). Finally, the model lacked a population sex and age structure for elk and was unable to account for the effect of switching from an either-sex to

bull-only hunting, as currently occurs on northern Yellowstone elk. Studies on northern Yellowstone elk have shown that wolves tend to prey on calves and older adult cows while hunting removes more prime age animals, which has varying effects on elk population dynamics (Wright *et al.* 2006, Eberhardt *et al.* 2007). Because of the influence of selective harvesting on the population growth rate (Caughley 1977) and the complexity of wolf-elk dynamics in YNP (Peterson *et al.* 2014), future projections of elk numbers and the impact of hunting were considered to be unreliable. Vucetich *et al.* (2005) and Peterson *et al.* (2014) identified other challenges with understanding northern Yellowstone elk dynamics after wolf reintroduction, and a full assessment of these impacts would require a much more detailed modelling approach than used here. As noted by Eberhardt and Peterson (1999) their model “clearly needs to be elaborated in order to encompass the age structure of the prey population, and in other ways, before reliable estimates of the actual impact of wolves on northern Yellowstone elk are feasible.”

Conclusion

Eberhardt's wolf-ungulate model provided a reliable portrait of wolf-elk interactions on the northern range of YNP from 1995–96 to 2016–17. The model also provided additional support for radio-dependence in large mammal predator-prey systems. Improvements to the model could be made by including the sex and age structure in the elk population, a wolf functional response in kill rates, and temporal variation in demographic rates.

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