

ASSESSING THE IMPACT OF WOLVES ON UNGULATE PREY

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Abstract. Simple models may be useful in evaluating definitions of population limitation and regulation, and in considering the impact of wolves (*Canis lupus*) on ungulate prey. Examination of three types of models that have recently been used to assess wolf–ungulate interactions indicates that the “total response” model is inappropriate and that models generating substantial oscillations may not be realistic. Models based on ratio dependence appear to be more useful and are explored further. Because reintroduction of wolves into areas with abundant prey may yield new insights into the controversial issue of population regulation by predators, the available data are used to consider some needs for research on the impact of wolves on Yellowstone elk (*Cervus elaphus*) herds, and for a further assessment of ratio dependence.

Key words: elk–wolf system in Yellowstone National Park; population regulation and density; predator–prey interactions; predator–prey models; ratio-dependence models; ungulates; wolves and ungulate prey; Yellowstone National Park (Wyoming, USA).

INTRODUCTION

An important issue in research on natural populations is that of mechanisms for limitation and regulation of density. Human interference with natural systems has made it especially difficult to determine what regulatory mechanisms may have evolved in populations of large mammals. In particular, ungulate populations may appear to fluctuate quite irregularly at higher population densities, and an important question is whether human interference (e.g., by reducing predator abundance) is responsible. A valuable recent review of current terminology and the evidence for limitation and regulation by predators is that of Van Ballenberghe and Ballard (1994). Dealing with the confusion of terminology may be substantially aided by using simple models. Such models necessarily cannot be accurate in all details, but may provide a consistent view of definitions and terminology. One hypothesis is that, before disruption of the system, wolves may have regulated the abundance of some North American ungulates through predator control. A corollary is that resurgence of wolf populations after predator control was eliminated or greatly reduced brought some moose (*Alces alces*) populations to substantially lower levels than when wolf numbers were severely curtailed. The purpose of this paper is to consider the relevance of recent data on wolf–ungulate systems to various models, and to use the results to further consider the possible impact of wolves on elk in Yellowstone National Park.

In a recent review, Abrams and Ginzburg (2000) discussed the debate about prey dependence and ratio dependence in predator–prey models. They pointed out that a search of articles citing Arditi and Ginzburg (1989), whose paper stimulated much of the recent controversy about ratio dependence, turned up 63 articles published in the last five years. Abrams and Ginzburg reported that only one of these articles gave a direct measurement of a functional response (and considered insects; Reeve 1997) and only one actually measured a numerical response (Fryxell et al. 1999). Data on wolves and their ungulate prey described here appear to provide clear evidence for specific numerical and functional responses.

Given a simple framework for exposition, a hypothesis about ungulate population regulation by wolves may be erected on the basis of recent field data. A difficulty then becomes that of proposing adequate tests of such a hypothesis. Boutin (1992) provided a good review of available information, and proposed three experiments to test four hypotheses previously listed by Van Ballenberghe (1987). As Boutin (1992) noted, apart from some earlier studies where bears and/or wolves were removed, few such experiments have been conducted. These were described and discussed in some detail by the National Research Council (1997). Real-world stakeholders can make such experiments difficult. Environmental activists strongly oppose any efforts to limit wolf populations, while hunters object to leaving predator numbers unchecked. A further major difficulty is that large areas are needed for such experiments, and the prospects for replication and random choice of experimental and control areas are negligibly small. The experience with wolves and moose

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in an isolated system with no hunting (Isle Royale) has shown that extraneous features (parvovirus in wolves and a winter-tick epizootic in moose; Peterson 1999) can exert a strong influence on dynamics of the system so that replications would be essential for a controlled experiment. Hence scientifically based controlled experiments may never be conducted. Consequently, detailed study of wolf introductions may offer the major prospective opportunity for tests of predictions. The recent (1995) reintroduction of wolves to Yellowstone National Park offers one such opportunity, and a model outlined below is used to examine predictions made in planning the reintroduction. This is followed by appraisals of some other models, and further consideration of the available data.

MODELS BASED ON RATIO DEPENDENCE

An earlier study (Eberhardt 1997) noted that some of the frequently used differential-equation models may be appropriate for invertebrate populations, but do not seem useful for ungulates and wolves with short annual reproductive seasons. Similarly, actual data on the functional response of wolves to ungulate prey do not support the popular formulations, but instead suggest that assumption of a constant killing rate may be adequate. Consequently, two difference equations were proposed with a time step of one year:

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

$$H_t = H_{t-1} + r_2 H_{t-1} \left(1 - \frac{H_{t-1}}{aV_{t-1}} \right). \quad (2)$$

In these equations, V_t denotes prey numbers at time t , r_1 is the maximal rate of increase for the prey, K is asymptotic prey abundance, z determines the rate of approach to the asymptote ($z \geq 1$), c is the killing rate (per year) of prey by predators (H_t), r_2 is maximal rate of increase of predator numbers, and a is the equilibrium ratio of predators to prey. The equilibrium conditions ($V_t = V_{t-1}$ and $H_t = H_{t-1}$) give the following relationships:

$$V = K \left(1 - \frac{ca}{r_1} \right)^{1/z} \quad H = aV. \quad (3)$$

Efforts to fit these models to actual wolf-ungulate data (Eberhardt 1998) showed the desirability of using a generalized logistic rather than the usual logistic term, due to the fact that a linearly decreasing rate of increase with abundance for prey appears unrealistic in practice (Eberhardt 1977, Fowler 1987).

The ratio-dependence form of Eq. 2 appears to be in accord with extensive field data from the literature (Eberhardt 1998, Eberhardt and Peterson 1999). If wolves and their ungulate prey evolved under such a regime, then it might be supposed that the logistic-like term in Eq. 1 is superfluous, and the prey equation can be reduced to the following:

$$V_t = V_{t-1} + r_1 V_{t-1} - cH_{t-1} \quad (4)$$

with equilibrium conditions

$$ca = r_1 \quad H = aV. \quad (5)$$

The left-hand term of Eq. 5 amounts to an expression for the proportion of the prey population removed by wolves each year:

$$\begin{aligned} ca &= (\text{ungulate kill/wolf/year})(\text{wolves/ungulates}) \\ &= \text{ungulates killed/ungulates present}. \end{aligned} \quad (6)$$

The last ratio is sometimes defined as ‘‘predation rate’’. Consequently, both Eqs. 3 and 4 provide simple expressions for the take of prey by predators. In the absence of predation, the system without ‘‘self-limitation’’ (Eq. 4) will presumably ultimately be limited by resources and weather conditions and thus may fluctuate erratically. However, the difference equations (Eqs. 4 and 2) are unstable and thus not considered in any detail here. The stable system (Eqs. 1 and 2) supposes an asymptotic level (K) and a lower predation rate ($ca < r_1$).

A modification of Eq. 1 is useful for incorporating removals of elk by hunters. It assumes a constant annual kill taken in a short time interval, as is usually the case. The modification is

$$V_t = V_{t-1} + r_1 V_{t-1} \left[1 - \left(\frac{V_{t-1}}{K} \right)^z \right] - B - cH_{t-1} \quad (7)$$

where B denotes the constant annual kill by hunters.

The best available data are those for predation on moose. Winter kill rates per wolf per 100 days are remarkably constant (Eberhardt 2000: Table 1). Unfortunately, rates for the rest of the year are generally not available. Prey density appears to have little effect (Fig. 1) except possibly at the lowest levels. Fig. 1 shows the data used by Eberhardt (2000) with that of Hayes and Harestad (2000) added. More recent data on Isle Royale (Peterson 1999: Figs. 1 and 2) indicate that kills per wolf per 100 days increased significantly when the moose population increased sharply after wolf numbers dropped.

Estimating the equilibrium ratio of wolves per moose has been complicated somewhat by the need to use data on a number of prey species. Eberhardt and Peterson (1999: Fig. 3) expressed the ratio with deer as a common denominator using body-mass equivalents proposed by Keith (1983). For use in the present case, the data have been recalculated as wolves/moose (Fig. 2). The data of Fig. 2 can be used to estimate the equilibrium ratio (a) by solving the fitted regression line for the x intercept (population growth rate $\lambda = 1$; constant wolf population). Data from Eberhardt (1997) provide an estimate of $c = 6.9$ moose killed per wolf per year, and $a = 0.049$ from the relationship of Fig. 2. The product ca is estimated as 0.34. The bootstrapping confidence interval (percentile method of Efron and Tib-

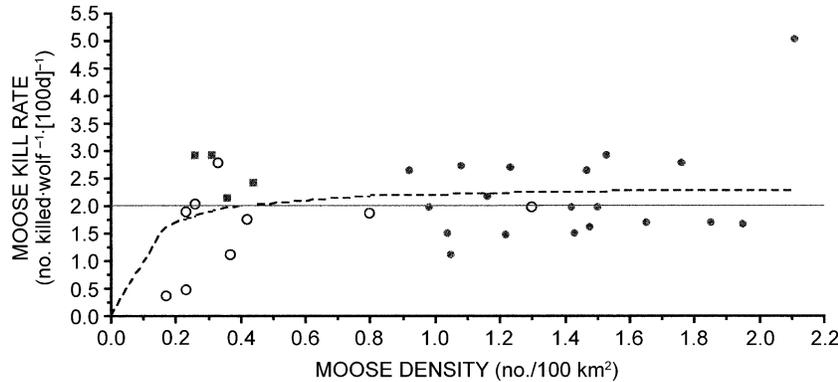


FIG. 1. Data on moose kill rate per wolf per 100 days in winter from Eberhardt (2000) with data from Hayes and Harestad (2000; solid squares) added. Solid circles represent individual-year data from Isle Royale, and open circles show data of Messier (1994: Table 2). The solid (light gray) line shows constant rate used here, while the broken line shows a nonlinear least-squares fit of Holling's (1959) Type II functional-response equation.

shirani 1993) on the product is 0.29–0.45 (95% interval), and the mean of 2000 bootstrap replications is 0.35, indicating little bias in the estimate of ca (Efron and Tibshirani 1993). Bootstrap confidence limits (95%) on the reciprocal of a , or moose per wolf are 16 to 24.

"TOTAL RESPONSE" MODELS

Messier (1994) presented an alternative model based on the notion of a "total response" calculated as the product of the functional response and a presumed "numerical response." He apparently assumed a functional response in accord with the original definition given by Solomon (1949) and widely used by subsequent workers. Solomon's (1949:16) definition of a numerical response is: "an increase in the numbers of the enemy (a numerical influence), due to an increased rate of survival or of reproduction (or both) . . .". This definition is adhered to in the right-hand side of Eq. 2 above, in which the predator growth rate is determined

by prey density. However, Messier (1994: Fig. 4) depicted a "numerical response" by plotting wolf density against moose density. This arrangement can be regarded as a numerical response but it requires the assumption of an instantaneous response by wolves to changes in prey density so that wolves and their ungulate prey are always in equilibrium.

The actual state of affairs appears to be that wolf hunting, trapping, and other "control" activities along with hunting of their ungulate prey usually combine to result in a nonequilibrium state. Consequently, the data used by Messier (1994: Fig. 4) are likely to be from nonequilibrium conditions and thus are not in accord with the presumed numerical response.

The assumed components of the "total response" can be written as follows:

$$\begin{aligned} & (\text{ungulate kill/wolf/year}) \\ & \times (\text{wolves present/ungulates present}) \\ & = \text{total ungulate kill/year/ungulates present} \quad (8) \end{aligned}$$

so that the total response apparently also generates a predation rate as in Eq. 6. However, under nonequilibrium conditions the observed ratio of wolves to prey will be changing over time, so that the apparent predation rate of the total response becomes an artifact of the particular samples obtained, depending on the current status of the individual predator and prey populations with respect to a presumed ultimate equilibrium.

In devising the total-response model, Holling (1959: 317) warned about the consequences of assuming that model as follows: "The method . . . is an over-simplification, since predator density is portrayed as being directly related to prey density. Animal populations, however, cannot respond *immediately* to changes in prey density, so that there must be a delay of the numerical response" and "the total response obtained when prey or hosts are steadily increasing will be different than when they are steadily decreasing. The

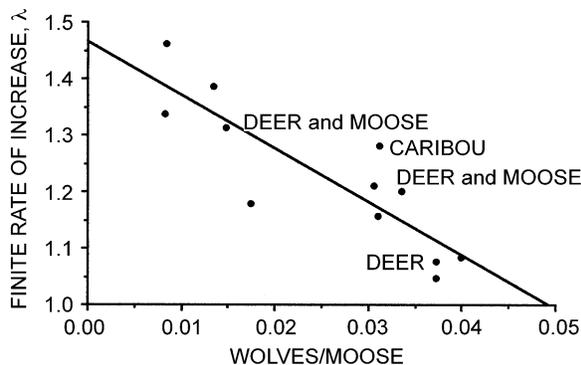
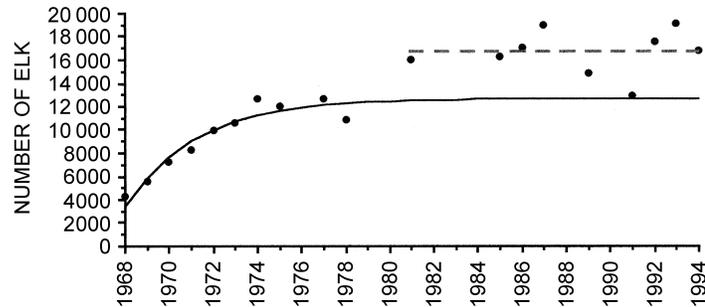


FIG. 2. Relationship of rate of increase (λ) for wolves to ratio of wolves to prey abundance, based on data of Eberhardt and Peterson (1999). Regression line: $y = 1.466 - 9.47x$, $R^2 = 0.74$. Most of the points are from situations where moose were the principal prey. Four points are from cases where deer or caribou were the predominant prey.

FIG. 3. Trend of Yellowstone's northern-herd elk counts. The solid line shows the fit (nonlinear least-squares) of $y = a(1 - \exp(-bt))$ through 1978, and the broken line represents the average of more recent counts.



amount of difference will depend on the magnitude and amount of delay of the numerical response, for the functional response has no element of delay". Eberhardt (1997: Fig. 1) plotted prey density against wolf density and thus implicitly assumed that, on the average, the data represented equilibrium conditions. Further study (Eberhardt 1998, Eberhardt and Peterson 1999) led to the model of Fig. 2 which does not assume equilibrium conditions.

OSCILLATORY MODELS

In a series of publications, Caughley (1976*a, b*, 1977, Caughley and Lawton 1981) popularized a different set of equations for two trophic levels. The equations were proposed by May (1973: Eqs. 4.4) as a predator-prey system. However, Caughley used them to model a vegetation-herbivore system, giving the equations as follows (Caughley 1976*a*: Eqs. 6.6 and 6.7):

$$\frac{dV}{dt} = r_1 V \left(1 - \frac{V}{K} \right) - c_1 H [1 - \exp(-d_1 V)]$$

$$\frac{dH}{dt} = H \{-a + c_2 [1 - \exp(-d_2 V)]\}$$

where V denotes abundance of vegetation and H denotes the herbivore subsisting on this vegetation. Caughley (1976*a*:102) remarked that "Although the example is imaginary it can be thought of, without contradicting current knowledge, as white-tailed deer colonizing a mosaic of grassland and forest." The same parameters were utilized by Caughley (1976*a, b*) and Caughley and Lawton (1981). Some questions about the parameter values used were discussed by Eberhardt (1987*a*:52-53).

Although different parameter values were used in Caughley (1977), the general shape of the curves appear similar in all four examples (Caughley 1976*a, b*, 1977, Caughley and Lawton 1981). However, if the equations are to be taken as a model of a deer-vegetation system, the time scale needs to be reconsidered. Caughley (1977:130) described the basis for calculating the curves as follows: "The population has been grown in a programmable desk calculator by estimating growth rates twenty times per year and adding on the appropriate increment each time. For this exercise the

constants representing yearly rates. . . are divided by the number of iterations per year." This amounts to approximating the differential equations as difference equations:

$$V_{t+1} = V_t - r_1 V_t \left(1 - \frac{V_t}{K} \right) - c_1 H_t [1 - \exp(-d_1 V_t)]$$

$$H_{t+1} = H_t \{1 - a_2 + c_2 [1 - \exp(-d_2 V_t)]\}.$$

Using the constants listed by Caughley produces curves essentially the same as those in the various illustrations (e.g., Caughley 1977: Fig. 9.6). The difficulty is that deer reproduce only once annually, not 20 times. This means that much more pronounced oscillations are generated, and a much longer time (roughly 600 years) will be required to reach an equilibrium than suggested in the figures used by Caughley (e.g., Caughley 1977: Fig. 9.6).

A model with similarly complex functional and numerical responses has been used (Boyce 1995, 1996) to supply predictions for wolf and ungulate populations in Yellowstone National Park. This model also generated dramatic oscillations (Boyce 1996: Figs. 1 and 2). The number of wolves predicted in the Yellowstone area ranges in amplitude from lows of about 25 to highs of roughly 150 wolves with a periodicity of ~10 years. Less regular, but nonetheless dramatic cycles were postulated for elk. For the northern Yellowstone herd, amplitude of the predicted fluctuations in elk numbers ranges over 10 000 or more individuals and periodicity is also ~10 years. It was proposed (Boyce 1996:123) that "predation by wolves should dampen the substantial fluctuations that park ungulates undergo due to variations in climate. . ." and "variation in winter severity causes substantial population fluctuations in all ungulates in the Greater Yellowstone Ecosystem" (Boyce 1996:129). Boyce (1995:206) stated that the model "predicts that wolf predation will enforce a reduction in the variance in population size for ungulates" but that "there are still very substantial fluctuations in ungulate numbers, due largely to perturbations caused by severe winters of heavy snowfall and low temperatures."

Actual counts of the northern herd do not support the assumption of such dramatic weather-induced fluctuations in elk numbers. The major influence in past

abundance has been substantial removals of elk made in an effort to reduce the presumed impact of elk on range conditions. Data on counts made since the 1930s show a continuing decline until cessation of the major removals in the late 1960s, which was then followed by a dramatic increase (Eberhardt 1987b: Fig. 3, right panel). More recent counts (Fig. 3) show continued high numbers of elk in the northern herd. Data on actual counts and estimates from population reconstructions and "sightability" corrections were reported by Singer et al. (1997: Table 1) through 1991–1992. Lemke et al. (1998) gave counts through 1996–1997. Several low counts (1976–1977, 1988–1989, 1990–1991) were attributed to poor census conditions (Singer et al. 1997, Lemke et al. 1998), and are not included in Fig. 3. The recent estimates do not indicate extreme weather-induced fluctuations in elk numbers on the northern Yellowstone range, but sizable losses in 1988–1989 were recorded (Singer et al. 1989) and the winter of 1996–1997 was also rather severe. Taper and Gogan (2002: 106) reported a "short-lived increase in the elk population growth rate following the 1988 drought and fires." Singer et al. (1997:21) stated that "We found no effect of winter severity during the 21-year period when elk populations were mostly below ecological carrying capacity. . ." but suggested some effects at recent, higher numbers of elk. Lemke et al. (1998:4) reported that "In the late 1970's, the estimated elk winter range included about 100 000 ha. . ." and that "Based on current winter elk distribution, elk occupy a winter range of 152 663 ha. . ." This large increase in winter range has very likely substantially increased carrying capacity and thus the size of the herd. Consequently Fig. 3 shows a curve fitted to counts through 1978 that suggests an asymptotic elk population size of about 12 500, but later counts (1980–1994) average about 16 500 elk (shown by a dashed line in Fig. 3). Eberhardt (1987b) and Singer et al. (1997) both estimated carrying capacity herd for the northern herd of 12 000 elk for the earlier data. Counts of ~19 000 in 1987–1988 and 1993–1994 suggest that carrying capacity of the expanded winter range of the northern herd may well approach or exceed 20 000 elk. Coughenour and Singer (1996) reported an "ecological carrying capacity" of about 22 000 elk, while the National Research Council (2002) reported a carrying capacity of 20 000 to 22 000 elk.

WOLF NUMBERS, RATES OF INCREASE AND PREDATION RATES

Prior to the reintroduction, predictions of the number of wolves in the Yellowstone system were 50 to 170 wolves (Boyce 1995:204) and 90 to 140 wolves (Boyce 1996:130). Wolves were released in 1995 and 1996. By 2001 there were estimated to be ~220 wolves with a population growth rate of $\lambda = 1.26$ (95% confidence limits 1.16–1.38) over the last five years (1997–2001). Boyce (1996:128) used $\lambda = 1.80$, while the maximum

reported by Keith (1983) was $\lambda = 1.46$. Other estimates of λ for wolves appear in Fig. 2. The maximum rate of increase for elk in the northern herd was given by Boyce (1995: Table 1) as $r_0 = 0.28$. This is the value estimated by Eberhardt et al. (1996) as a maximum likely rate for elk. Houston (1982) estimated adult female survival rates of ~0.99 for the northern herd during its period of rapid increase. His data suggest that first-year survival was about 0.67 then. Singer et al. (1997: Table 2) reported variable annual survival rates for radiocollared elk calves, with a maximum of 0.62 and a minimum of 0.14. In a continuing study of the small Madison-Firehole herd in Yellowstone National Park, adult female survival was estimated to be 0.97 from radiotelemetry studies, and first-year survival was highly variable and strongly correlated with winter snowpack (R. A. Garrott, *personal communication*). However, this is the only nonmigratory elk herd in Yellowstone National Park, and depends substantially on thermal features for winter range.

Detailed data for assessing Eqs. 1 and 2 for Yellowstone elk are not yet available. Carbyn (1983) reported about 14 elk taken per wolf per year. This agrees with consumption rates for moose (2 elk = 1 moose from Keith [1983]) inasmuch as the average of about 7 moose per wolf per year (Eberhardt 1997) translates to 14 elk per year on a biomass basis. Data on wolf kills in Yellowstone have been obtained from two surveys each year, one from 15 November to 14 December, and the other for the month of March. Early winter killing rates were 0.046 elk/wolf/d, while the March rate was 0.076 elk/wolf/d. Using Carbyn's estimate or that translated from moose data would give an average daily consumption rate for elk of $14/365 = 0.038$, appreciably lower than the rates observed thus far in Yellowstone. What is needed is a way to estimate the constant, a , from data on elk. To use the method of Fig. 2 evidently calls for a number of independent data points for elk. Work has begun on wolves and elk in two additional herds (Gallatin and Lower Madison, R. A. Garrott, *personal communication*). Thus there potentially will be data on four sites (data for four years have been collected on the Madison-Firehole site) for comparison with Fig. 2, assuming the necessary data can be collected. This will require annual data on wolf and elk population sizes, and killing rates (c).

DISCUSSION

A set of prospective models has been outlined above. It appears that the total-response model is unlikely to be useful in wolf-ungulate systems because it assumes that wolf numbers are always in equilibrium with those of their prey. Models of the type proposed by Caughley (1976a, b, 1997, Caughley and Lawton 1981) yield dramatic oscillations due to the form of the functional and numerical response functions (further details as to the behavior of such models have been furnished by May [1973, 1981]). Boyce (1995, 1996) apparently used

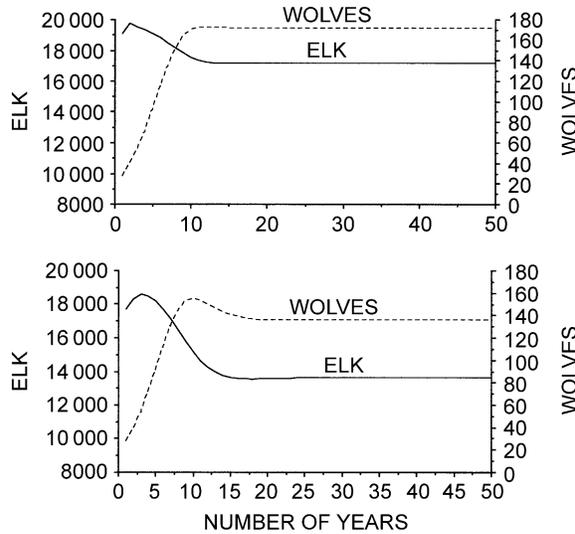


FIG. 4. Examples of curves generated from Eqs. 1 and 2. Initial elk population (solid line) = 16 500 individuals; initial wolf population (broken line) = 20 individuals; c (the killing rate per year of prey by predators) = 15; a (the equilibrium ratio of predators to prey) = 0.01, K (asymptotic prey abundance) = 20 000. Upper panel, $z = 5$; lower panel, $z = 2$. Maximum rate of increase for elk $r_1 = 0.28$; maximum rate of increase for wolves $r_2 = 0.46$.

similar forms for functional and numerical responses, but claimed that the dramatic fluctuations in his model outputs were due to effects of inclement weather on elk numbers. The data do not support such claims. In contrast, the models of Eqs. 1 and 2 predict a steady approach to the equilibrium state after an initial fluctuation if the initial ratio of prey to predator is high, as it was in Yellowstone.

The difference equations considered here are readily implemented on spreadsheets and can thus be examined by any interested reader, using parameter values suggested above. Eq. 4 is very sensitive to initial conditions, and thus does not appear to be useful. Inasmuch as the predation rate (Eq. 6) obviously cannot exceed rate of increase of the prey (r_1) for any protracted period, it does not seem reasonable to consider initial conditions (numbers of prey and predators) other than those where $H < aV$ (so that $ca < r_1$). Results are also sensitive to the value of z (the rate of approach to the asymptote). Examples (Fig. 4) of the curves generated from Eqs. 1 and 2 suggest the range of patterns to be expected. Wolves may “overshoot” and then settle down to an equilibrium within ~10 years. Without direct estimates of the critical parameter (a), such curves cannot be claimed to represent reality. However, they do illustrate the general pattern. One consideration is that it should be expected that 10 or more years of observation may be required to ascertain whether the populations will oscillate as indicated by the results of Boyce (1995, 1996) or will approach an equilibrium as predicted by the ratio-dependence model. A second is-

sue is uncertainty about the appropriate value of z . Eberhardt (1997, 1998) used $z = 5$ (Fig. 4: upper panel), but it may be preferable to use the more conservative value of $z = 2$, which gives lower equilibrium values and a somewhat more pronounced initial fluctuation (Fig. 4: lower panel). A long-term study of both wolf and elk numbers is thus essential if the Yellowstone data are to be useful in assessing the impact of wolves on their ungulate prey.

Predictions from the system of Eqs. 1 and 2 amount to the proposal that wolves may take a high yield of moose, and achieve an equilibrium ratio of about 1 wolf to 20 moose. Using $z = 5$, $ca = 0.34$, as estimated above (see *Models based on ratio dependence*), and $0.35 \leq r_1 \leq 0.38$ (Eberhardt 1997) gives a range of ratios of equilibrium moose numbers (V) to carrying-capacity level (K) of $0.49 \leq V/K \leq 0.64$. The substantial variability associated with the data of Fig. 2, plus the uncertainty as to whether “self-limitation” (the “generalized logistic”) of Eq. 2) holds, and whether $z = 5$, all contribute to limit the utility of this result. However, the data of Gasaway et al. (1992: Fig. 13) suggest that wolf and bear predation may reduce moose populations substantially. Extending the results to Yellowstone elk is as yet an uncertain proposition, but it does seem important, on the basis of the extensive experience with moose, to consider the prospect of a more substantial reduction than the 5–20% (Boyce 1995:203) or 10–25% (Boyce 1996:129) predicted previously. A major issue is that many elk migrate to winter ranges outside the Park, where conflicts with human interests may limit wolf density. Data on wolves and elk from the Yellowstone system should be followed closely as the wolf population grows in order to determine whether the new data support the linear model of Fig. 2. If so, then an estimate of the equilibrium ratio (a) specific to elk may be established and used with kill rate (c) data to forecast the likely elk removal rate.

A weakness in such a prediction is the impact of wolf territory size and the movement of wolves outside Yellowstone National Park. Walters et al. (1981: Fig. 7) summarized data that showed pack territory size

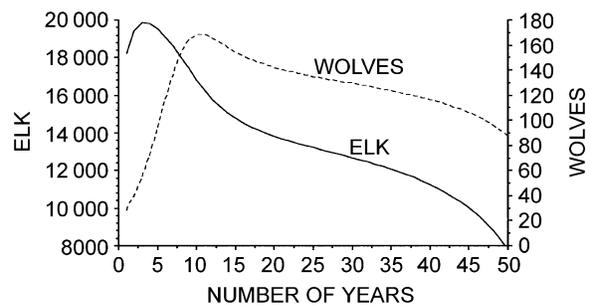


FIG. 5. Trend of elk and wolf populations using Eqs. 2 and 7 with parameters and format as in Fig. 4, with $z = 5$, and B (the constant annual kill by hunter) = 1500. See *Discussion* for further details.

contracts slowly at high prey density, which can be taken to suggest that the Yellowstone wolf population might be limited by territoriality. However, it seems likely that much larger packs may be formed where prey are very abundant, as in Yellowstone, so this limitation is also somewhat uncertain. Another very important consideration is the impact of the present harvests of the northern elk herd outside of the Park, which have averaged about 1350 elk per year (T. Lemke [Montana Department of Fish, Wildlife and Parks], *personal communication*) over the last five years (through 2001–2002). Data on the Nelchina caribou (*Rangifer tarandus*) herd (Eberhardt and Pitcher 1992) illustrate the danger of a constant removal by hunters in the presence of an increasing wolf population. That herd dropped from about 80 000 in the 1960s to <10 000 in 1972 due to the combined impact of wolves, hunters, and some inclement winter weather.

A possible impact of annual hunter harvests can be illustrated by using Eq. 7 instead of Eq. 1 but continuing to use Eq. 2, and the parameters used for Fig. 4 (with $z = 5$), along with B (the constant annual kill by hunters) = 1500. This yields a continuing decrease in both elk and wolf populations (Fig. 5). Due to the several uncertainties about parameter values, and the oversimplification represented by the models, such a result should not be regarded as a reliable prediction, but it illustrates the need for close and continued monitoring of elk numbers and harvests (both by humans and by wolves). It also emphasizes that the ratio-dependence model predicts that wolf numbers will “track” elk herd size. Hence harvests by hunters may “drive” the elk–wolf system. We anticipate that the Montana Department of Fish, Wildlife and Parks will adaptively manage the harvest of elk based on close and continued monitoring of elk numbers and harvests. Thus actual trends in elk and wolf populations can be expected to differ from the extreme result suggested in Fig. 5.

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