DENSITY DEPENDENCE OF UNGULATES AND FUNCTIONAL RESPONSES OF WOLVES: EFFECTS ON PREDATOR-PREY RATIOS

David K. Person[1,2,3], R. Terry Bowyer[1], and Victor Van Ballenberghe[4]

[1]Institute of Arctic Biology, and Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK 99775, USA; [2]Alaska Cooperative Fish and Wildlife Research Unit, University of Alaska Fairbanks, Fairbanks, AK 99775, USA; [4]U. S. Forest Service, Pacific Northwest Research Station, 3301 C Street, Suite 200, Anchorage, AK 99503, USA

ABSTRACT: Predator-prey ratios have been used widely to interpret effects of wolf (*Canis lupus*) predation on their ungulate prey. Use of those simple indices may be misleading unless they are interpreted with regard to species composition of available prey, rate of growth of the prey population, proximity of the prey to carrying capacity (K), and the functional response in the rate of predation by wolves to changing density of prey. We incorporate theoretical models for predator-prey dynamics with data from field studies on ungulates and wolves to test for differences between species of ungulates in their ability to support wolves per unit of biomass. We conduct sensitivity analyses of those models, which integrate density-dependent growth of ungulate populations and functional responses of wolves, to evaluate the relative importance of those factors to the relation between ungulate and wolf densities. Finally, we develop a stochastic model that predicts ungulate-wolf ratios at equilibrium, which indicates why interpreting those ratios in the wild, may be problematic. Our models and analysis indicate that some ungulates, such as white-tailed deer (*Odocoileus virginianus*), likely will support a higher density of wolves than will other species with lower intrinsic rates of increase. Thus, we question the use of comparisons of total ungulate biomass and wolf density unless species composition of prey is considered. We hypothesize that growth rates of prey populations, their response to density dependence, and their proximity to K have important influences on the relation between ungulate and wolf density, whereas the functional response exhibited by wolves is relatively unimportant, especially at high density of prey.

Numerous researchers have suggested that relative densities of predators and prey are critical factors influencing predator-prey systems (Arditi and Ginzburg 1989, Berryman 1992, Ginzburg and Akçakaya 1992, Slobodkin 1992), and are especially important to the dynamics between wolves (*Canis lupus*) and their ungulate prey (Mech and Karns 1977, Keith 1983, Van Ballenberghe and Hanley 1984, Ballard et al. 1987, Fuller 1989, Messier 1994, Van Ballenberghe and Ballard 1994, Messier 1995, Seip 1995, Ballard et al. 1997). Reproduction (Boertje and Stephenson 1992), mortality (Fuller 1989), and dispersal (Ballard et al. 1987, Peterson and Page 1988) in wolf packs may be influenced by availability of prey in relation to wolf density. Moreover, stability of ungulate-wolf systems and the potential for wolves to limit prey populations may depend upon the ratio of prey biomass to wolves. That ratio may be particularly

important in systems where multiple predators of ungulates (including humans) exist, and where periodic severe weather may reduce ungulate populations to low levels (Gasaway et al. 1983, 1992; Van Ballenberghe and Ballard 1994; Dale et al. 1995). Hence, some measure of the ratio of the density of ungulate prey or their biomass to wolf density often is used to predict effects of wolf predation on ungulate populations (Gasaway et al. 1983, Keith 1983, Fuller 1989, Gasaway et al. 1992).

Simple linear regressions have been used to predict density of wolves from prey biomass (Keith 1983, Fuller 1989, Gasaway et al. 1992, Messier 1995); the presumption is that density of wolves predicted by prey biomass (total biomass summed for all species of prey available) represented an approximate carrying capacity (K), or equilibrium density for wolves (Gasaway et al. 1992). Alternatively, equilibrium for wolves may be expressed as the ratio of ungulates to wolves. If densities of wolves are greater than predicted, or if ungulate-wolf ratios are less than predicted, then wolves may cause a decline in ungulate populations. Implicit in those models are the assumptions that they are derived with data from wolf and ungulate populations at or near equilibrium, that the density of prey with respect to K has no influence on the number of wolves that could be supported by a particular prey density or biomass, and that all prey biomass is equal in supporting wolves regardless of prey species consumed. Those predator-prey models also ignore effects of seasonal, social, and reproductive behaviors of ungulates that influence their availability to wolves and other predators irrespective of prey density (Bowyer 1984, 1987; Bleich et al. 1997; Bowyer et al. 1998a, 1998b, 1999a). Further, predictive values from those models are compromised by the large confidence intervals associated with estimates of wolf and ungulate density used to compute regression parameters (Ballard et al. 1995).

Use of simple ungulate biomass-wolf density relations or ungulate-wolf ratios, as indices of the potential effects of predation on prey populations, is controversial (Theberge and Gauthier 1985, Theberge 1990, Messier 1994, Eberhardt 1997). Theberge (1990) argued that changes in the functional response of wolves to changes in prey density, prey-switching behavior, and proximity of the prey population to K would complicate interpretation of ungulate-wolf ratios, or any measure of the relation of ungulate biomass to density of wolves. The first 2 factors are related because predation rate per wolf on a particular species of prey may depend upon density of that prey and the simultaneous availability of alternative prey (Dale et al. 1994). Density-dependent changes in the rate of killing by wolves could require a continuous reinterpretation of ungulate-wolf ratios as density of prey varied. Moreover, distinguishing between the types of functional-response curves may require sample sizes that are difficult to obtain in the field (Marshal and Boutin 1999).

Proximity of the ungulate population (U) to K influences the growth rate of the population such that the per capita rate of increase in the absence of predation (r) theoretically approaches 0 as the population nears K (McCullough 1979). If mortality from predation is primarily additive, the fraction of the prey population ($U \times r$) that could be removed by predation without causing a decline in ungulate numbers is reduced as the prey population approaches K. Thus, ungulate density alone, without knowledge of the proximity of the prey population to K, likely would be a poor predictor of the effect of wolf predation on numbers of prey. Further, per capita rate of increase of an ungulate population and shape of the growth curve with respect to K likely is

species specific (McCullough 1987, 1999). Therefore, equilibrium density of wolves supported per unit of ungulate biomass may differ between species of ungulates.

We examine the influence of growth rates of prey populations, density-dependent response of prey to K, and the functional response of wolves on the relation of ungulate density or biomass to density of wolves. Our purpose is to employ numerical and statistical analyses to compare relative effects of those factors on interpretation of predator-prey ratios. We set forth equations that underpin our analytical framework for interpreting dynamics of wolves and their ungulate prey, so that the mathematical development of ideas as well as constraints and assumptions of those theoretical models can be examined implicitly. We purposely do not consider all conditions necessary for equilibrium. Rather we invoke equilibrium as a benchmark to evaluate effects of density dependence and the functional response on the relative densities of wolves and ungulates. We intentionally ignore the numerical response of wolves to their ungulate prey (Messier 1994, 1995; Seip 1995); this approach is simply a mathematical artifice to allow a clear interpretation of the variables of interest. Thus, our models avoid confounding factors related to time lags in numbers of predators and prey, which are common to dynamics of ungulates and large carnivores (Klein 1968, 1995; Peterson 1977; O'Donoghue et al. 1998; Keeling et al. 2000; Pierce et al. 2000).

We constrained our analyses to conform to the best available data concerning the functional responses of wolves, predation rates, and the growth patterns of ungulate populations. Difference equations have been applied previously to the dynamics of wolf populations (Eberhardt 1998), but no studies have used this approach to evaluate contributions of the functional response of wolves to their ungulate prey, or effects of prey density relative to K on those models. Likewise, effects of different growth rates of large prey species on equilibria of wolf and ungulate dynamics have not been evaluated fully. In addition, we propose a stochastic model that incorporates some of those factors to empirically estimate ungulate-wolf ratios that would result in a stationary prey population and suggest constraints for interpreting ungulate-wolf ratios.

An Analytical Framework

We concentrate on number of wolves at theoretical equilibrium with their ungulate prey to study relations between ungulate density or biomass and density of wolves. First, we construct a series of models that combine the factors of interest in a biologically appropriate fashion. Consider the following simple model of ungulate population growth incorporating an ungulate prey population (U_t) with a fixed per capita rate of increase (r), and a wolf population (P_t) with a constant rate of predation (C):

$$U_{t+1} - U_t = U_t r - CP_t \qquad (1)$$

Mortality from predation is entirely additive in this model and r represents the rate of increase in the absence of wolf predation. The nontrivial solution for equilibrium (i.e., $dU/dt = 0$) in equation (1) is given by:

$$P_t^* = r\frac{U_t}{C} \quad \text{or,} \quad \frac{U_t}{P_t^*} = \frac{C}{r}, \quad (1a)$$

where, P_t^* = equilibrium value for the wolf population. Hence, if U and C are scaled to account for body-size differences between species of ungulates such that U/C is relatively constant, number of wolves supported at equilibrium would be greater for a prey species with a higher rate of population increase (r). Conversely, the ungulate-wolf ratio at equilibrium would be smaller for prey species with higher rates of increase. For example, appropriate average values of

r for moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*) with adequate food and no large predators are estimated to be 0.22 and 0.43, respectively (Keith 1983). Average rates of predation are estimated to be 8.5 moose/wolf/year and 16.6 deer/wolf/year (Keith 1983); therefore, equation (1a) would predict that a population of 100 moose would support about 2.6 wolves at equilibrium and 200 deer (necessary so that U/C remains constant for both species) would support about 5.2 wolves. An adult moose represents about 6 times the biomass of an adult deer (Keith 1983, Fuller 1989); hence, 200 deer are equivalent to only 33% of the biomass represented by 100 moose. When expressed in equivalent units of ungulate biomass (1 unit = 1 deer equivalent), ungulate biomass-wolf ratios are 231:1 for moose and 38:1 for deer. Certainly, relative densities of moose and deer populations and their respective age structures would affect the species-specific biomass available to wolves; nonetheless, equation (1a) indicates that a given biomass of deer should support more wolves than an equivalent biomass of moose.

As most ungulate populations approach K, intraspecific competition for food increases mortality and reduces successful reproduction (Caughley 1977, McCullough 1979). To incorporate density dependence into equation (1), we replace r with $r_{max}[1-(U_t/K)^\theta]$ to produce the following model:

$$U_{t+1} - U_t = U_t r_{max}\left[1 - \left(\frac{U_t}{K}\right)^\theta\right] - CP_t, \quad (2)$$

where,

r_{max} = maximum per capita rate of increase of prey,

K = prey carrying capacity,

θ = parameter controlling the shape of the density-dependent growth curve (i.e., $\theta = 1$ indicates a linear response, $\theta \neq 1$ indicates

curvilinearity).

This model (equation 2) is a modification of the theta-logistic equation (Gilpin and Ayala 1973, Eberhardt 1998). To test the adequacy of this model as an analog for ungulate population growth, we fit it to the curve of population growth of white-tailed deer predicted by the empirically based model described by McCullough (1979) for the George Reserve deer herd in Michigan, USA. Letting $r_{max} = 0.9$ (Lancia et al. 1988) and $\theta = 1.5$, the theta-logistic model matched predictions of the George Reserve model almost exactly ($\chi^2_{12} = 2.07$, $P = 0.999$).

The equilibrium solution for equation (2) is:

$$P_t^* = r_{max}\frac{U_t}{C}\left[1 - \left(\frac{U_t}{K}\right)^\theta\right]$$

or,

$$\frac{U_t}{P_t^*} = \frac{C}{r_{max}[1 - (U_t/K)^\theta]} \quad (2a)$$

Number of predators supported by prey increases as the density of the prey population approaches maximum sustained yield (MSY), and declines after density exceeds MSY and approaches K (Fig. 1; Fowler 1987; McCullough 1987, 1999). Further, if 2 prey species have similar values of r_{max}, but one species exhibits density-dependent recruitment indicative of a higher value of θ, MSY will be shifted closer to K; this parameter is given by the second derivative of the theta-logistic function:

$$\left[\frac{K^\theta}{\theta + 1}\right]^{\frac{1}{\theta}}$$

The species with the higher value of θ will support a greater density of predators at equilibrium (Fig. 1).

The functional response in rates of predation by wolves on ungulate prey has been
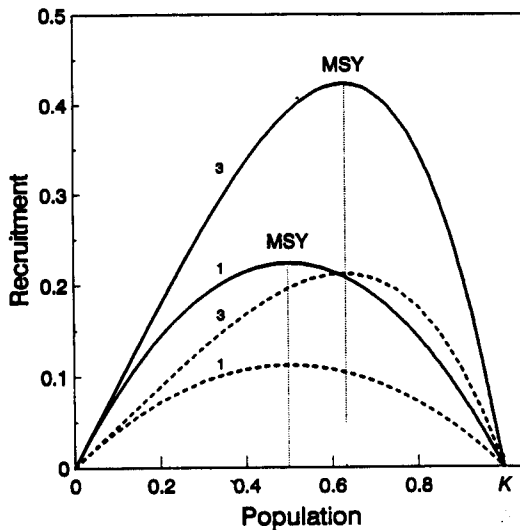
Fig. 1. Ungulate recruitment versus population density based on a theta-logistic model of population growth. Graph shows examples in which r_{max} was assigned the values 0.45 (dotted lines) and 0.9 (solid lines). Numbers next to the curves represent the values assigned to θ. Carrying capacity (K) was set at 100 animals. The curves clearly show how maximum sustained yield (MSY) shifts toward K as θ increases. Recruitment represents the maximum number of animals that can be removed by predators without causing a decline in the prey population.

considered an important factor in ungulate-wolf dynamics (Theberge and Gauthier 1985, Theberge 1990, Dale et al. 1994, Messier 1994, Van Ballenberghe and Ballard 1994). Both type II and type III functional responses (Holling 1965) have been hypothesized for wolves (Dale et al. 1994, Messier 1994). Nevertheless, empirical evidence from ungulate-wolf studies indicates that the functional response may be type II, with predation rates reaching an asymptote at very low densities of prey (Dale et al. 1994, Messier 1994, Hayes 1995). For our purposes, whether a functional response is type II or III is irrelevant because differences in the effects of either type on the density of wolves is likely to be important only when the density of prey is very low.

For simplicity, we only consider a type II functional response and include it in equation (2) to derive the following model:

$$U_{t+1} - U_t = U_t r_{max}\left[1 - \left(\frac{U_t}{K}\right)^{\theta}\right] - P_t \frac{CU_t}{(D+U_t)}, \quad (3)$$

where, D is density (or number) of ungulates at which predation rate C is halved, and the quantity $CU_t/(D+U_t)$ is the functional response of predation rate to changes in the density or number of prey. This form of the type II functional response is mathematically equivalent to the Michaelis-Menten function described by Real (1977). The nontrivial equilibrium solution of equation (3) is given by:

$$P_t^* = \frac{(D+U_t)r_{max}}{C}\left[1 - \left(\frac{U_t}{K}\right)^{\theta}\right]$$

or,

$$\frac{U_t}{P_t^*} = \frac{C}{\left(\frac{D}{U_t}+1\right)r_{max}\left[1 - \left(\frac{U_t}{K}\right)^{\theta}\right]} \quad (3a)$$

Equation (3a) shows clearly that a half-saturation constant $D > 0$ could increase the equilibrium density of wolves. Nonetheless, as the ratio of D to U becomes smaller, influence of the functional response on the equilibrium density of wolves decreases, indicating that if D is small with respect to K, the functional response may have little effect on the predator-prey system, unless prey density is a small fraction of K.

Equations (1a), (2a), and (3a) combine the principal elements affecting the relation between wolf and ungulate density that we wish to examine, namely rates of increase of prey populations, their response to density dependence, and the functional response of wolf predation to changes in prey density. Thus, we have derived an analytical framework that mathematically translates the conceptual notions of ungulate-wolf,

predator-prey dynamics (which likely are relevant for most predator-prey systems involving large terrestrial mammals), enabling us to address the following questions:

1. With respect to predictions made by equation (1a), data from studies in which biomass available to wolves is estimated for individual species of prey and compared with estimates of wolf density, should show species-specific differences in the density of wolves supported by a given unit of biomass. Those trends should be consistent with our hypothesis that ungulate species with higher rates of population increase such as deer would support more wolves per unit of biomass than populations with lower rates of increase such as moose and caribou (*Rangifer tarandus*).

2. How sensitive is the number of wolves at equilibrium to effects of density dependence on growth rates of prey populations and their proximity to K? Would this sensitivity seriously confound the interpretation of ungulate-wolf ratios or other indices of ungulate density (or biomass) versus wolf density used to assess effects of predation on prey populations?

3. How sensitive is the number of wolves supported at equilibrium to the functional response, and would this sensitivity confuse interpretation of ungulate-wolf ratios or other indices of ungulate density (or biomass) versus wolf density?

A Stochastic Model of Ungulate-wolf Equilibrium

Superficial interpretation of relative wolf and ungulate densities to determine population trajectories of wolves and their prey potentially is misleading unless factors that we have discussed previously are considered. Herein we describe a stochastic model that predicts the number of wolves that could be supported by a particular density of prey without causing a decline in prey numbers.

As shown in equation (1a), theoretical equilibrium is reached when wolf predation removes a number of ungulates equal to the annual recruitment ($U \times r$), provided predation is primarily a source of additive mortality (Mech and Karns 1977, Keith 1983, Hayes 1995). Ungulates are pulse breeders, so population growth may be expressed in the discrete form:

$$U_{t+1} = U_t + U_t r,$$

where, t represents 1 year and U_t is the preparturient ungulate population in the absence of predation. The finite rate of increase, λ, is given by:

$$\lambda = \frac{U_{t+1}}{U_t} = \frac{U_t + U_t r}{U_t} = 1 + r.$$

Described in this manner, λ encompasses reproduction, emigration, immigration, and all forms of compensatory mortality. Substituting λ for r in equation (1a) yields:

$$P_t^* = \frac{U_t}{C}(\lambda - 1) \text{ or } \frac{U_t}{P_t^*} = \frac{C}{(\lambda - 1)}. \quad (4)$$

The theoretical number of ungulates per wolf required for equilibrium in our model can be computed by equation (4). If other additive sources of mortality exist, such as other predators or human hunters, the fraction of the ungulate population that can be removed by wolves that will result in a stationary ungulate population is reduced, and the model can be modified in the following way:

$$P_t^* = \frac{U_t}{C}(\lambda - 1)(1 - H)$$

or,

$$\frac{U_t}{P_t^*} = \frac{C}{(\lambda - 1)(1 - H)}, \quad (5)$$

where, H is the fraction of annual recruitment removed by other predators or hunting by humans. This is the model, or equilibrium function, proposed by Keith (1983) to estimate ungulate-wolf ratios necessary to maintain a stationary population of prey.

Behavior of the equilibrium function (Keith 1983) can be understood by letting $U/P^* = N$ and taking first-order partial derivatives with respect to input variables:

$$\frac{\partial N}{\partial C} = \frac{1}{(\lambda-1)(1-H)}, \text{ for } \lambda > 1 \text{ and } H < 1 \text{ (5a)}$$

$$\frac{\partial N}{\partial \lambda} = \frac{-C}{(\lambda-1)^2(1-H)}, \text{ for } \lambda > 1 \text{ and } H < 1 \text{(5b)}$$

$$\frac{\partial N}{\partial H} = \frac{C}{(\lambda-1)(1-H)^2}, \text{ for } \lambda > 1 \text{ and } H < 1 \text{(5c)}$$

Predation rate C is a constant; therefore, change in N for a particular predation rate is solely a function of λ and H (equation [5a]). Although predation rates may vary with changes in prey density, we will show in our analysis of equation (3a) that under most circumstances, the functional response of predation by wolves can be ignored. Equations (5b) and (5c) indicate that changes in N with respect to λ or H are nonlinear, dependent on the instantaneous values of λ and H, and likely dominate behavior of the model. Clearly, as λ and $H \rightarrow 1$, $N \rightarrow \infty$ in a rapidly increasing fashion.

Predicted ratios of ungulates to wolves at equilibrium (N) that are lower than ratios observed in the wild imply that prey populations will increase regardless of predation by wolves. In contrast, if predicted ratios at equilibrium are greater than observed ratios of ungulates to wolves, prey populations likely will decline as a result of predation. Ungulate-wolf ratios observed in the wild that are equal to equilibrium ratios predicted by the model would indicate

potential for stability in the predator-prey system. Nevertheless, time lags in the numerical response of wolves to changes in prey density and stochastic events such as severe winters must be considered before stability can be assumed.

Our model is useful for understanding multiple-prey systems because prey selection by wolves would be reflected in the predation rate observed for each species involved. This procedure is an advantage over simple comparisons of total biomass of prey to wolf density, which do not compensate for prey selectivity by wolves. Our model, however, does not deal with numerical responses of wolves to changing density of prey. For instance, Seip (1992) hypothesized that wolves did not decline with a decreasing population of caribou because a larger population of moose sustained those canids. That outcome may reflect wolves sometimes selecting caribou as prey in preference to moose (Dale et al. 1994). Barten et al. (2001) reported substantial effects of large mammalian carnivores on the ecology and behavior of a small population of caribou in a system where moose density also was low. Further, Gasaway et al. (1992) noted that moose were held at low density while caribou populations varied. The forgoing examples, however, are unlikely to alter the general conclusions of our model—those results are for extremely low-density populations of ungulates where prey switching by wolves, and potential changes in the type of their functional response, are relatively unimportant.

Unfortunately, the equilibrium function is deterministic, and input variables are assumed to be measured without error. This assumption poses no real problem when the function is used as a theoretical device, but is a serious limitation if the equation is applied empirically. Estimates of λ and H must be precise; error in estimation of λ, particularly when the ungulate population

nears K, may result in equilibrium ratios very different from ratios that would be predicted if the true value of λ were known. Effects on sensitivity of the model to values of λ and H near 1, combined with sampling errors associated with input variables, may result in predicted ratios of equilibrium that are possibly misleading or even meaningless.

The equilibrium function would be more useful for interpreting data from the field if outcomes were probabilistic, reflecting error in the variable inputs and accommodating the potential sensitivity of the model to levels of input variables. That result can be achieved by incorporating input variables that are random samples rather than discrete values. In most instances where predation rate (C), λ, and mortality caused by other predators (H) are estimated empirically, those estimates will be sample means and their standard deviations. Assuming the sample was extracted from a population exhibiting a specific statistical distribution, a random sample from the probability density functions (pdf) of each variable can be substituted for the discrete values used as input in the equilibrium function. The model retains the same general form as equation (5):

$$N' = \frac{C'_{(a,b)}}{(\lambda'_{(a,b)} - 1)(1 - H'_{(a,b)})} , \quad (6)$$

where,

$N'_{(a,b)} = [N_1, N_2, N_3, ... N_n]$, vector of solutions for equilibrium ratios,

$C'_{(a,b)} = [C_1, C_2, C_3, ..., C_n]$, a random sample from the pdf of C with parameters a and b representing upper and lower limits of a range as in a uniform distribution, or a mean and SD as in a normal distribution,

$\lambda'_{(a,b)} = [\lambda_1, \lambda_2, \lambda_3, ..., \lambda_n]$, a random sample from the pdf of λ with parameters a and b as defined for C', and

$H'_{(a,b)} = [H_1, H_2, H_3, ..., H_n]$, a random sam-

ple from the pdf of H with parameters a and b as defined for C'.

Equation (6) is a natural extension of the original model described by Keith (1983), and is appropriate for any potential sampling distribution. Assuming that each parameter is an independent random variable, the variance of N' can be approximated by:

$$Var(N') = Var(C') \left[\frac{\partial N}{\partial C} \right]^2 + Var(\lambda') \left[\frac{\partial N}{\partial \lambda} \right]^2 + Var(H') \left[\frac{\partial N}{\partial H} \right]^2$$

(Seber 1982). Substituting equations (5a-c) into the equation for $Var(N')$ yields:

$$Var(N') = Var(C') \left[\frac{1}{(\lambda-1)(1-H)} \right]^2 + Var(\lambda') \left[\frac{-C}{(\lambda-1)^2(1-H)} \right]^2$$
$$+ Var(H') \left[\frac{C}{(\lambda-1)(1-H)^2} \right]^2 . \quad (7)$$

We conduct a series of simulations of equation (6) to describe the behavior of the model and to illustrate its limitations and application to data from the field.

METHODS

We analyzed data relating ungulate biomass to density of wolves (Fuller 1989) to test for species-specific differences in number of wolves supported by a particular biomass of ungulate prey. Following the method of Fuller (1989), prey biomass was converted to equivalent units such that one unit of biomass equaled 1 deer (Table 1). Biomass units representing individual species were as follows: 1 bison (*Bison bison*) = 8 units, 1 moose = 6 units, 1 elk (*Cervus elaphus*) = 3 units, 1 caribou = 2 units, and 1 mountain sheep (*Ovis* sp.), 1 mountain goat (*Oreamnos americanus*), or 1 deer (*Odocoileus* sp.) = 1 unit. We regressed biomass units by species against wolf density and used F tests of the differences between the error sum of squares for full and reduced models to test for differences between regression coefficients (Neter et al. 1985).

Table 1. Estimated ungulate biomass and wolf densities during winter in various areas of North America, adapted from Fuller (1989)[1]. Prey biomass is expressed as deer equivalents per 1,000 km^2 and wolf density is expressed as wolves per 1,000 km^2.

Location	Prey species	Biomass	Wolves	References
North-central Canada	caribou	11,000	37	Parker 1973
Isle Royale, Michigan	moose	10,570	40	Peterson and Page 1988
Isle Royale, Michigan	moose	9,696	43	Peterson 1977
Northeast Minnesota	deer	5,100	42	Van Ballenberghe et al. 1975
	moose	4,200		
Southwest Manitoba	elk	3,600	26	Carbyn 1982, 1983
	moose	4,800		
	deer	340		
Northeast Minnesota	deer	3,500	40	Mech et al 1971, Peek et al.
	moose	3,600		1976, Nelson and Mech 1986b
East-central Ontario	deer	5,769	38	Pimlott et al. 1969
	moose	1,014		
Southern Quebec	deer	3,000	28	Potvin 1988
	moose	3,600[2]		
North-central Minnesota	deer	6,160	39	Fuller 1989
	moose	120		
North-central Minnesota	deer	6,000	28	Berg and Kuehn 1980
Northeast Minnesota	deer	3,475	23	Stenlund 1955
Kenai Peninsula, Alaska	moose	4,800	14	Peterson et al. 1984
	caribou	26		
East-central Ontario	deer	3,098	36	Pimlott et al. 1969
	moose	924		
Northeast Minnesota	deer	600	25	Mech 1986, Nelson and
	moose	3,300		Mech 1986a, 1986b
Jasper Park, Alberta	deer	80	8	Carbyn 1974
	moose	480		
	caribou	80		
	other[3]	2,170		
Denali Park, Alaska	moose	984	6	Haber 1977
	caribou	540		
	other[3]	478		
South-central Ontario	moose	1,776	12	Bergerud et al. 1983
	caribou		26	
Southwest Quebec	moose	1,800	11	Messier and Crête 1985
Interior Alaska	moose	1,110	8	Gasaway et al. 1983
Northeast Alberta	moose	1,350	6	Fuller and Keith 1980
	caribou		34	
Northern Alberta	other[3]	1,224	8	Oosenbrug and Carbyn 1982
West-central Yukon	moose	372	7	Sumanik 1987
	caribou	20		
	other[3]	681		
Denali Park, Alaska	moose	564	3	Singer and Dalle-Molle 1985
	caribou		212	
	other[3]		86	

[1] Table excludes data reported by Fuller (1989) for wolf populations that were heavily exploited (Davis 1978, Ballard et al. 1987) or that were newly protected (Fritts and Mech 1981).

[2] The biomass value for moose was incorrectly reported by Fuller (1989).

[3] Other species include bison, elk, sheep, and mountain goats.

Moose constituted > 50% of the total biomass in 12 of 23 instances described by Fuller (1989). We regressed total biomass against wolf density for those instances to produce a model that was primarily a function of availability of moose biomass. We then used the model to predict wolf density from total biomass reported for all instances presented by Fuller (1989), and calculated residuals by subtracting wolf density predicted by the model from observed densities of wolves. We used analysis of variance and Dunnet's t test (with data used to derive the model as the control group) to examine species-specific differences among residuals. We used the chi-square method of Sokal and Rohlf (1981) for combining probabilities for species of ungulates.

We conducted sensitivity analyses of equation (3a) to determine relative effects of number of wolves supported at equilibrium on the functional response, proximity of the prey population to K, and shape of the curve representing the density-dependent response of r to increasing prey density (i.e., how far MSY was shifted towards K). Those conditions were represented by parameters D, U, and θ, respectively. We used a factorial design in which D, U, and θ were each a random sample from a uniform distribution, and values of predation rate (C), r_{max} and K were fixed. We performed 2 sets of 6 groups of Monte Carlo simulations of equation (3a). Each group consisted of 1,000 recalculations of the equilibrium number of wolves (P^*), including random permutations of D, U, and θ. In the first group, the half-saturation parameter (D) was bounded by 0 and K. In groups 2, 3, 4, and 5, the upper bound of D was set at $K/2$, $K/4$, $K/8$, and $K/16$, respectively. In the last group, D was set to 0, thereby eliminating the functional response from the model. Reducing the upper bound of D constrained the functional response within each group, which resulted in progressively steeper slopes for the functional-response curve.

The first set of 6 simulations used values for C and r_{max} of 9 and 0.45, respectively, which were similar to the range of values reported for moose (Keith 1983, Cederlund and Sand 1991, Bowyer et al. 1999b). Ungulate density (U) was limited to the interval between 0 and maximum sustained yield (MSY), because the effect of increasing ungulate density on density of wolves at equilibrium should be positive over that range. In the second set of simulations, U was constrained between MSY and K—a range over which the effect of increasing ungulate density on wolf numbers at equilibrium would be negative. We set K at 1; therefore, ungulate density (U) and D were expressed as fractions of K. The shape parameter for the curve of population growth of ungulate prey (θ) was bounded by the interval [1,3]. A value of 1 produced a standard logistic growth curve with MSY equal to $K/2$. A value of 3 shifted the recruitment curve to the right such that MSY was at approximately 63% of K. The population growth curves produced by the range of values used for θ are appropriate for ungulates (McCullough 1987, 1999).

Using multiple regression, we regressed the values of P^* against the values of D, U, and θ for each group within a set, and compared the standardized regression coefficients as a measure of the influence of each parameter. Because parameter values were randomized, correlations between parameters were not significant, and standardized coefficients for each parameter were directly comparable (Neter et al. 1985).

We simulated our stochastic model of ungulate-wolf equilibria (equation [6]) 1,000 times as means of sampling distributions for each input variable using values reported by Fuller (1989) for white-tailed deer and wolves in Minnesota. We represented λ' as a normal distribution with $\bar{\lambda} = 1.21$ (Fuller 1989). Fuller (1989) did not report a

variance about that value of λ; therefore, we arbitrarily assigned a SD = 0.03. Consequently, 95% of the values in a random sample from the distribution of λ' were between 1.15 and 1.27 (± 5% of the mean, or 2 SD). In addition, we represented C' as a normal distribution with $\overline{C}$ = 19 and SD = 0.5, resulting in 95% of the values in a random sample from C' occurring within 5% of the mean. Similar to Fuller (1989), we let $H = 0$. Without changing the distributions of C' and H', we repeated simulations of the model with λ' represented by a normal distribution with $\overline{\lambda}$ = 1.1 and SD = 0.03. We generated a sampling distribution for each variable in the model by multiplying random normal deviates by the SD of each input variable.

RESULTS
Factors Affecting the Relation Between Wolf and Ungulate Density

Multiple-regression analysis of data presented by Fuller (1989; Table 1), in which wolf density was regressed against ungulate biomass by species, showed significant differences in the regression coefficients for deer and moose (Table 2). The equation for moose density (x) alone also predicted Y, the density of wolves ($Y = 6.93 + 0.0037x$; $r^2 = 0.73$, P < 0.001). Consistent with predictions from equation (1a), the coefficient for deer was larger than that for moose (Table 2). The coefficient for moose was larger but not statistically different than that for caribou (Table 2). We included all other species of prey in one category because sample sizes were too small to include them individually. The coefficient for other species was not different from zero, probably because of small sample sizes even after combining those species into 1 category.

We regressed total biomass against wolf density for those studies in which moose composed > 50% of the available biomass.

Based on results from our multiple regression analysis, we only grouped residuals for instances in which deer or caribou were present. We defined "present" as including those instances not used in the regression model in which deer or caribou constituted > 10% of the available biomass. Of necessity, we stabilized the variance of residuals to conform to the assumption of equality of variances among groups. Therefore, we used a square-root transformation of wolf density and recalculated the regression model and residuals. The mean for the residual group in which deer were present ($\overline{X}$ = 0.875, n = 6) was larger than the mean for those data (representing moose) used to derive the model ($\overline{X}$ = 0.095, n = 12, P = 0.013; Fig. 2). The mean for the residual group representing caribou ($\overline{X}$ = -0.746, n = 2) was less than the mean for the control group representing moose, although not statistically different ($P = 0.095$; Fig. 2). The joint probability for both species, however, was significant (χ^2_4 = 13.39, $P < 0.05$).

In all simulations of equation (3a), coefficients for D, U, and θ were different from zero ($P \geq 0.05$). In the first set of simulations (U bounded by 0 and MSY), average number of wolves predicted at equilibrium ($\overline{p}^*$) declined from 0.034 to 0.013 as the upper bound of parameter D was reduced from 100% of K to 6.2% of K (K/16; Table 3). Similarly, in the second set of simulations (U bounded by MSY and K), $\overline{p}^*$ declined from 0.022 to 0.013 as the upper bound of D was reduced from K to K/16. In the absence of a functional response ($D = 0$), average number of wolves at equilibrium was 0.012 for the first set and 0.013 for the second set of simulations.

For U < MSY, the standardized regression coefficients for D indicated that the functional response had the most influence on number of wolves at equilibrium when the upper bound of D was > K/4. When D was constrained to values $\leq K$/4, however,

Table 2. Results from multiple regression of ungulate biomass[1] versus wolf density with tests of coefficients. Data are from Fuller (1989)[2].

Species	Coefficient (β)	SE	t	P
Constant	3.93	2.07	1.90	0.074
Deer	0.0051	0.001	9.71	0.000
Moose	0.0036	0.000	8.74	0.000
Caribou	0.0030	0.001	5.81	0.000
Other[3]	0.0010	0.001	0.76	0.459

Model:

$$\#\text{Wolves}/1000\,\text{km}^2 = 3.93 + 0.0051(\text{Biomass}_{deer}) + 0.0036(\text{Biomass}_{moose}) +$$
$$0.003(\text{Biomass}_{caribou}) + 0.001(\text{Biomass}_{other}) + \varepsilon$$

$F = 37.4, P < 0.0001, \text{Adjusted } R^2 = 0.87, n = 23$

Tests of Coefficients:

$H_0 : \beta_{deer} = \beta_{moose}$ $H_0 : \beta_{moose} = \beta_{caribou}$

$H_a : \beta_{deer} \neq \beta_{moose}$ $H_a : \beta_{moose} \neq \beta_{caribou}$

$F_{1,18} = 7.10, P = 0.02$ $F_{1,18} = 1.01, P = 0.35$

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[1] Ungulate biomass is represented as deer equivalents per 1,000 km² such that 1 moose = 6 deer, 1 elk = 3 deer, 1 caribou = 2 deer, 1 bison = 8 deer, and 1 sheep or goat = 1 deer (Fuller 1989).

[2] Data presented in Fuller (1989) for a heavily exploited wolf population (Davis 1978, Ballard et al. 1987) and for a newly protected wolf population (Fritts and Mech 1981) were excluded.

[3] Includes bison, mountain sheep, and mountain goats.

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density of prey (U) was more influential than the functional response (Table 3). Indeed, when D was held below $K/4$, effect of the functional response on P^* was overwhelmed by the combined influence of θ and U. Our model simulations indicated that the functional response had little influence on the equilibrium density of wolves if D was $\leq K/8$ (12.5% of K). The functional response also had an unimportant effect on number of wolves when ungulate density was > MSY, unless the upper bound for D was K.

Ungulate density (U) was the dominant factor affecting P^* when the upper bound for D was < $K/4$ and U was constrained below MSY. Beyond MSY, ungulate density was still the most influential factor with a strong negative effect on P^*. The effect of θ on P^* was small when U was < MSY and remained relatively constant despite

changes in the influence of D and U (Table 3). Beyond MSY, the influence of θ increased because that parameter determined how rapidly the growth rate of the prey population decayed to 0 as the population density of prey approached K.

Simulations of the Stochastic Equilibrium Model

One thousand simulations ($\bar{\lambda} = 1.21$) incorporating random combinations of each input variable resulted in a mean equilibrium ratio of 92 deer per wolf (CV = 15.6%), with 95% of the predicted values occurring between 70 and 130 deer per wolf (Table 4). Repeating the simulations with $\bar{\lambda} = 1.10$ yielded a mean equilibrium ratio of 219 deer per wolf (CV = 75.6%), with 95% of the predicted values occurring between 120 and 370 deer per wolf (Table 4).

The coefficient of variation for N' when

Table 3. Results of multiple regression of parameters D, U, and θ versus wolf numbers at equilibrium P^*, as predicted by Monte Carlo simulations of equation (3a).

| Distribution	Standardized coefficients			$\overline{P}*$
	D	θ	U	
$r_{max}=0.45, C=9, U=\mathrm{Uniform}(0,\mathrm{MSY}), \theta=\mathrm{Uniform}(1,3), K=1.0$				
$D=\mathrm{Uniform}(0,K)$	0.922	0.185	0.247	0.034
$D=\mathrm{Uniform}(0,K/2)$	0.753	0.210	0.546	0.023
$D=\mathrm{Uniform}(0,K/4)$	0.484	0.212	0.794	0.017
$D=\mathrm{Uniform}(0,K/8)$	0.259	0.196	0.898	0.015
$D=\mathrm{Uniform}(0,K/16)$	0.131	0.179	0.932	0.013
$D=0$	——	0.157	0.949	0.012
$r_{max}=0.45, C=9, U=\mathrm{Uniform}(\mathrm{MSY},K), \theta=\mathrm{Uniform}(1,3), K=1.0$				
$D=\mathrm{Uniform}(0,K)$	0.407	0.406	-0.810	0.022
$D=\mathrm{Uniform}(0,K/2)$	0.283	0.455	-0.852	0.017
$D=\mathrm{Uniform}(0,K/4)$	0.171	0.485	-0.873	0.015
$D=\mathrm{Uniform}(0,K/8)$	0.099	0.493	-0.874	0.014
$D=\mathrm{Uniform}(0,K/16)$	0.055	0.503	-0.869	0.013
$D=0$	——	0.510	-0.875	0.013
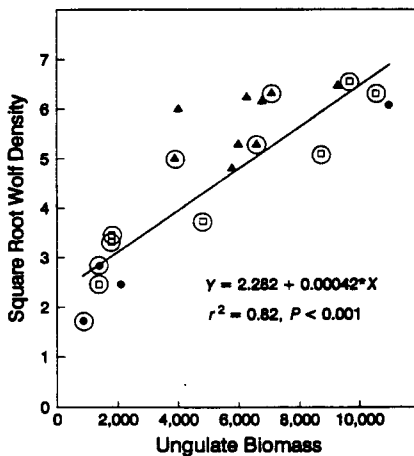
Fig. 2. Plot showing the square root of density for wolves versus total ungulate biomass available (1 unit of biomass = 1 deer equivalent); data are from Fuller (1989). The regression line was computed with data from areas in which moose constituted > 50% of the total biomass available to wolves (data points surrounded by large circles; $n = 12$). Data also are shown from areas in which deer (triangles; $n = 9$) and caribou (dots; $n = 4$) were present ($\geq$ 10% of total biomass), and from areas where both those species were absent (squares; $n = 7$).

$\overline{\lambda}$ = 1.10 exceeded the CV for the simulations with $\overline{\lambda}$ = 1.21 by a factor of nearly 5, even though input variables retained the same precision. This outcome reflects the influence of λ on the model as it approaches 1. In the deterministic form (equation [5]), the equilibrium function predicts ratios of 90 deer per wolf (Fuller 1989) and 190 deer per wolf for $\overline{\lambda}$ = 1.21 and 1.10, respectively. In the stochastic form (equation [6]), an appropriate probability that a stationary ungulate population would occur can be selected, and the corresponding number of ungulates per wolf can be determined from a table of cumulative probabilities (Table 4). For example, approximately 90% of the simulations predict equilibrium ratios < 110 deer per wolf when $\overline{\lambda}$ = 1.21. Therefore, given the distribution of input variables, there would be a high probability that wolves would not cause a decline in deer numbers if a ratio $\geq$ 110 deer per wolf was observed, and no other additive mortality occurred. The difference between this

Table 4. Frequency and cumulative percent of equilibrium ratios predicted by simulations of the equilibrium function (Keith 1983) with stochastic inputs for predation rate, finite rate of increase in prey, and fraction of prey recruitment removed by hunting (equation [6]).

N'	$\overline{\lambda} = 1.10$		$\overline{\lambda} = 1.21$	
Deer:wolf	Freq.	Cum.%	Freq.	Cum.%
60 - 79	0	0.000	24	0.024
80 - 99	0	0.000	451	0.475
100-119	14	0.014	417	0.892
120-139	49	0.063	87	0.979
140-159	146	0.209	19	0.998
160-179	145	0.354	1	0.999
180-199	140	0.494	1	1.000
200-219	122	0.616		
220-239	100	0.716		
240-259	75	0.791		
260-279	54	0.845		
280-299	28	0.873		
300-319	24	0.897		
320-339	30	0.927		
340-359	13	0.940		
360-379	13	0.953		
380-399	8	0.961		
400-419	3	0.964		
420-439	8	0.972		
440-459	4	0.976		
460-479	3	0.979		
480-499	2	0.981		

ratio and the deterministic result of 90 deer per wolf indicates the level of conservatism that should be applied to the equilibrium ratio as a consequence of uncertainty surrounding the input variables. Conservatism is magnified as $\lambda \rightarrow 1$ (or as $H \rightarrow 1$), such that the 90% probability that wolves would not cause a decline in deer numbers when λ averaged 1.10 corresponds to a ratio ≈ 320 deer per wolf rather than 190 deer per wolf predicted by the deterministic model.

DISCUSSION

Results of our analysis of data presented by Fuller (1989) indicated that significant differences existed between ungulate species in their ability to support wolves. That deer supported more wolves per unit of biomass than either moose or caribou was consistent with high rates of population increase for deer. Evidence indicating a difference between caribou and moose was inconclusive, probably because of small sample sizes. The influence of caribou numbers on wolf density was difficult to evaluate adequately because some herds are migratory and may not be available to wolves in a particular area for more than a few months (Dale et al. 1994). Nonetheless, we believe our results are sufficient to question the validity of simple comparisons of total ungulate biomass available and wolf density when multiple species of prey are involved.

Our results indicated that under most conditions, the equilibrium density of wolves was a function of the density-dependent growth rate of the prey population with the functional response having only a minor influence. Indeed, empirical data indicated that parameter D is likely a small fraction of K, well below $K/8$. For example, combining data from a number of studies on wolf predation in which moose were the primary prey, Messier (1994, 1995) estimated D to be 0.46 moose/km^2. He also suggested that 2 moose/km^2 represented an average K for the studies surveyed; therefore D was about 23% of K. Nonlinear regression analysis presented by Messier (1994, 1995) is extremely sensitive to individual data points and his estimate of D is strongly influenced by one extreme value reported from studies of wolves on Isle Royale, Michigan. Elimination of that point as an outlier changes the regression parameters substantially with D estimated at 0.29 moose/km^2 or 14.5% of K. Hayes (1995) repeated Messier's analysis,

but included data from his own study on rates of predation on moose in the Yukon, Canada, and estimated D at only 0.07 moose/km² or 3.5% of K. Dale et al. (1994) described a functional response for wolves preying on caribou that indicated a half-saturation constant equal to about 0.026 caribou/km² or about 1.1% of the maximum density of caribou observed in their study. Viewed in conjunction with our model simulations, those data indicate that the functional response may be relatively unimportant to the dynamics between wolves and their ungulate prey except when prey populations are at low densities.

We believe that the influence of the functional response often would be difficult to discern from background noise created by error in the measurement of predation rates, measurement rates of prey population increase, and estimates of prey and wolf density (Fig. 3). Data presented by Fuller (1989) undoubtedly contained noise created by errors associated with the estimates of wolf and prey density, the likelihood that populations were not at equilibria, and other site-specific factors. Wolves also may exhibit strong prey selection regardless of the availability of alternative prey (Potvin 1988; Dale et al. 1994, 1995; Forbes and Theberge 1995). Indeed, Marshal and Boutin (1999) cautioned that distinguishing between type II and III functional responses could be problematical because of low statistical power resulting from small sample size. In contrast, proximity of the prey population to K and response of rate of increase of the population to density-dependent factors likely has a profound influence on the number of wolves supported at equilibrium.

Management Implications

Although some wolf-ungulate ratios have been too variable to be predictive (Ballard et al. 1995), biologists have used them as a
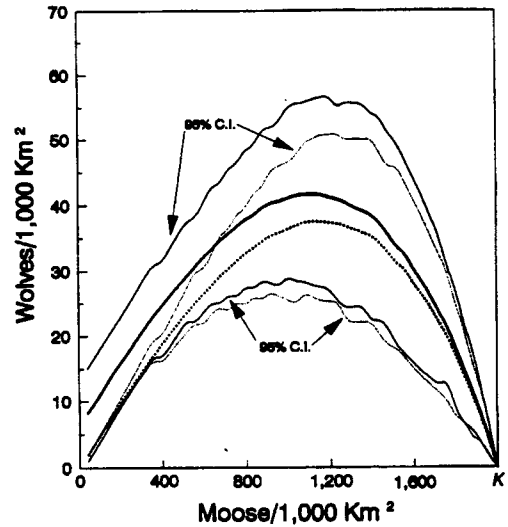

Fig. 3. Results of simulations of equation 3a showing wolf density versus moose density for D bounded by $[0,K/8]$ (solid lines) and $D = 0$ (thus eliminating the functional response from the model—dotted lines). Other model parameters are as shown in Table 3, except that K is set at 2,000 moose and output is scaled to represent numbers/1,000 km². The confidence intervals represent variation in wolf density because of variation in D and θ. Note that results for simulations in which $D = 0$ are almost completely encompassed by the confidence intervals associated with the simulations incorporating a functional response. Effects of the functional response on the number of wolves supported by a particular density of ungulates observed in the wild probably would be indistinguishable from other sources of variation, except at extremely low densities of prey.

benchmark to judge general relationships between wolves and their prey. We believe the wide confidence intervals from our simulations indicate caution should be employed in even a general interpretation of such ratios.

Our model incorporated the finite rate of increase of an ungulate population, and thereby accounted for density-dependent effects on growth rate of the prey population by default; however, the model purposely did not consider the numerical re-

sponse of wolves to their ungulate prey. Likewise, densities of ungulates and wolves measured in the field often are point estimates in time, and the population trajectory of wolves before or after the measurement period usually is not considered when determining whether predation may cause a decline in ungulate numbers. Clearly, the numerical response of wolves is important to the stability of the predator-prey system, and likely would produce additional variability in predator-prey ratios. This likely outcome requires further conservatism in applying wolf-ungulate ratios to manage large carnivores and their ungulate prey.

We also caution that equilibrium ratios will increase rapidly as the prey population exceeds the point at which MSY is achieved. Consequently, confidence intervals surrounding predicted equilibrium ratios would become very large even if λ was estimated with high precision. Mortality from predation likely would become increasingly compensatory as prey populations exceeded MSY and approached K (McCullough 1979); thus, the assumption that mortality from predation was additive would be violated. At what point the transition of predation from additive to compensatory mortality would seriously affect the interpretation of ungulate-wolf ratios is unknown and warrants further study.

Some biologists may object to our reliance on the measure of K as a guide for interpreting effects of functional responses and density-dependent growth rates of prey populations on ungulate-wolf ratios. Carrying capacity often is viewed as a Chimera; an abstraction rather than a practical concept. Nevertheless, estimates of the potential density of ungulates that an area can support have been used by biologists seeking to assess the effects of predation by wolves on ungulate populations (Gasaway et al. 1992). We suggest that these estimates be used as approximate measures of

K. We also advocate incorporating measures of animal and range condition to help calibrate the position of the population with respect to K. Without some index to K, comparisons of rates of increase between populations are not valid (Bowyer et al. 1999b).

The functional response in rates of predation by wolves to changes in ungulate density has been the focus of numerous studies (Theberge 1990, Dale et al. 1994, Messier 1994, Van Ballenberghe and Ballard 1994, Hayes 1995, Messier 1995, Seip 1995; Marshal and Boutin 1999). Our analyses indicate that rate of increase of ungulate populations is much more important than the functional response as a determinant of wolf density. We suggest that the limited resources available for conducting research on ungulate-wolf systems be concentrated on understanding the growth of prey populations with respect to habitat quality in relation to the predation behavior of wolves.

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