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Note

A Reappraisal of the Evidence for Regulation of Wolf Populations

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ABSTRACT The dogma that gray wolf (*Canis lupus*) population densities in naturally occurring systems are limited almost solely by available ungulate biomass is based upon studies that fit straight line linear regressions (Type 1 numerical response) to data collected at 32 sites across North America. We fit Type 1, 2, and 3 response functions to the data using linear and nonlinear regression as appropriate and found that the evidence supported wolf population regulation by density-dependence as much as limitation by prey availability. When we excluded 4 of 32 points from the original data set because those points represented exploited or expanding wolf populations the data suggested that wolf populations are self regulated rather than limited by prey biomass by at least a 3:1 margin. In establishing goals for sustainable wolf population levels, managers of wolf reintroductions and species recovery efforts should account for the possibility that some regulatory mechanism plays an important role in wolf population dynamics. © 2011 The Wildlife Society.

KEY WORDS numerical response, prey limitation regulation, Type 1, Type 2, Type 3, wolves.

Understanding whether predator populations are prey limited or regulated is critical for conserving and managing large carnivores throughout world. Such an understanding is impossible without the concept of a numerical response function—a description of the changes in predator population density as a function of changes in prey density (Solomon 1949, Holling 1959). For wolves (*Canis lupus*), which have been the focus of global restoration efforts, the generally accepted dogma is that population density in naturally occurring systems is limited almost solely by available ungulate biomass (Keith 1983, Fuller 1989, Fuller et al. 2003). The idea that predator populations may be limited solely by available prey has long been questioned however, by biologists studying other large carnivore species. Hornocker (1969, 1970) and Seidensticker et al. (1973) reported that increases in ungulate populations did not lead to increases in the population of mountain lions (*Puma concolor*) that preyed upon the ungulates. Yet, wolf biologists have overlooked the possibility that wolf populations, too, might not increase in response to increases in prey populations.

The prey limitation doctrine regarding wolf populations is predicated upon a few studies that fit straight line linear regressions (Type 1 numerical response) to data such that changes in wolf density (WD) are explained by changes in an ungulate biomass index (UBI; Keith 1983, Fuller 1989, Fuller et al. 2003). A linear relationship between these variables suggests that WD will continue to increase without

limit as long as the UBI increases. It is theoretically possible however, for the numerical response function to take on other shapes as well (e.g., a Type 2 response function, which is a monotonically increasing function with a monotonically decreasing slope and an asymptote, or a Type 3 response function, which is a sigmoid function with an asymptote; Messier 1995). The Type 2 and Type 3 response functions both suggest that there is an upper limit that WD will not exceed regardless of increases in UBI and that density dependent limitation or regulation will become more intense as WD approaches the upper limit. Fitting a Type 1 function to data does not constitute evidence per se that a Type 1 function is the most appropriate model to describe how WD responds to changes in the UBI. We thus explored the extent to which the evidence supports each of the 3 theoretically possible numerical response functions in order to determine whether wolf populations are prey limited or regulated.

METHODS

The most recent attempt to fit a Type 1 numerical response function to data relied upon data gathered by different investigators at 32 study sites in North America (Fuller et al. 2003). All the study sites were in northern part of the United States and Canada. The recently reintroduced wolves in the northern Rockies and the southwest were not included because these populations are still growing. The data set used by Fuller et al. (2003) reflected average WD and average UBI over several years at the 32 sites. The use of an index to measure prey availability was justified because wolves are known to prey on several species of ungulates (Mech 1970, Fuller et al. 2003).

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The scientific literature points to the theoretical possibility of 3 models to describe the numerical response of predators: a Type 1, a Type 2, or a Type 3 numerical response function (Holling 1959, Messier 1995). Specifically, the functions all describe how WD responds to changes in UBI. The Type 1 numerical response function is a straight line ($WD = K_0 \times UBI$; K_0 is a constant). A Type 2 response is a monotonically increasing function with a monotonically decreasing slope and an asymptote ($WD = [K_1 \times UBI]/[K_2 + UBI]$; K_1 and K_2 are constants). A Type 3 response is a sigmoid function with an asymptote as well ($WD = [K_3 \times UBI^2]/[K_4 + UBI^2]$; K_3 and K_4 are constants). Although any exponent >1 will produce a sigmoid shape in the response curve (Marshall and Boutin 1999), we chose an exponent of 2 because that value is typically used to describe a Type 3 response (Gotelli 2001).

Wolves may derive nutrition from non-ungulate sources such as lagomorphs (Ballard et al. 1987, Mech 2007) and salmonids (Adams et al. 2010). However, these non-ungulate sources of nutrition are only supplemental. We are not aware of any studies that show that wolves can persist on solely non-ungulate sources of nutrition for several years. The points in the data set of Fuller et al. (2003) were averages of wolf and ungulate prey densities at individual sites over several years with a food index that included all potential ungulate sources of food as the independent variable. In this context, a non-zero intercept would imply that wolf populations may persist for several years solely on nutrition derived from non-ungulate sources. Therefore, we eliminated the possibility that the fitted functions described above could have a non-zero ordinate intercept because wolf populations could not persist for prolonged periods at densities above zero without of ungulates. Accordingly, none of the functional forms we described above contain an intercept term.

The Type 1 response supports the hypothesis that wolf populations are limited solely by prey abundance. The Type 2 and Type 3 response functions, individually and cumulatively, support the hypothesis that wolf populations are regulated or limited in a density-dependent fashion. Neither of these functions suggests the mechanism by which such regulation occurs. Although there is no strong biological justification for the sigmoid portion of the Type 3 response function, we analyzed it because it is mentioned in the literature.

We fit the 3 functional forms to the 32 point data set using linear regression methods for the Type 1 function and non-linear regression methods for the Type 2 and Type 3 functions. We used Akaike's Information Criterion (AIC_C) adjusted for small sample size to determine the most

parsimonious model and to calculate evidence ratios in favor of both hypotheses (prey limitation and regulation) by comparing the Type 1 model to the Type 2 and Type 3 models cumulatively and by comparing the Type 1 model to the Type 2 model only (Burnham and Anderson 2002). However, the 32 data points included 4 sites (northwestern Minnesota, southcentral Alaska, eastcentral Yukon, and southern Yukon) in which wolves recently arrived and were expanding or were being hunted (Fuller et al. 2003). We excluded these 4 points from the data set because exploited and expanding wolf populations would not have achieved the highest WD possible given some level of the UBI (Fuller et al. 2003). We again fit the 3 numerical response functions to the new 28-point data set. We recalculated evidence ratios in favor of the prey limitation and regulation hypotheses and the most parsimonious model using AIC_C as the criterion. We estimated the asymptotes of the Type 2 and Type 3 numerical response functions (K_1 and K_3 , respectively) using the 28-point data set and model averaged the asymptotes using methods described by Burnham and Anderson (2002). We conducted linear and nonlinear regressions and estimated all parameters using the R 2.10.0 statistical package (R Version 2.7, www.r-project.org, accessed 9 Nov 2009).

RESULTS

With the full data set, the Type 1, Type 2, and Type 3 models received 49.0%, 45.0%, and 6.0% of support, respectively (Table 1). Cumulative support for the prey limitation hypothesis and regulation hypothesis was 49.0% and 51.0%, respectively, when the regulation hypothesis was supported by the Type 2 and Type 3 models. Support for the prey limitation hypothesis and regulation hypothesis was 52.0% and 48.0%, respectively, when the regulation hypothesis was supported by only the Type 2 model and we excluded the Type 3 model from the candidate set (Table 2). We did not estimate the value of the asymptotes for the full 32-point data set.

After omitting 4 points from the data, the Type 1, Type 2, and Type 3 models received 22.2%, 57.2%, and 20.6% model support, respectively (Table 3). Thus, the prey limitation and regulation hypotheses received 22.2% and 77.8% cumulative support, respectively, when the regulation hypothesis was supported by the Type 2 and Type 3 models. Support for the prey limitation hypothesis and regulation hypothesis was 28.0% and 72.0%, respectively, when the regulation hypothesis was supported by only the Type 2 model and the Type 3 model was excluded from the candidate set (Table 4). The Type 2 and Type 3 model asymptotes occurred at 81.5 (SE = 35.6) wolves per 1,000 km² and 35.2 (SE = 3.9)

Table 1. Model support for numerical response functions (with full data) for 32 North American wolf populations during 1945–1994 (data from Fuller et al. 2003) using Akaike's Information Criterion adjusted for small sample size (AIC_C).

Model	Log likelihood	Sample size	Parameters estimated	AIC_C	Delta AIC_C	Wt
Type 1	-111.09	32	1	224.32	0	0.49
Type 2	-110.04	32	2	224.49	0.17	0.45
Type 3	-112.05	32	2	228.52	4.20	0.06

Table 2. Model support for Type 1 and Type 2 numerical response functions (with full data and Type 3 model excluded) for 32 North American wolf populations during 1945–1994 (data from Fuller et al. 2003) using Akaike’s Information Criterion adjusted for small sample size (AIC_C).

Model	Log likelihood	Sample size	Parameters estimated	AIC_C	Delta AIC_C	Wt
Type 1	−111.09	32	1	224.32	0	0.52
Type 2	−110.04	32	2	224.49	0.17	0.48

Table 3. Model support for numerical response functions for 28 (with 4 expanding and exploited wolf populations excluded) North American wolf populations during 1945–1994 (data from Fuller et al. 2003) using Akaike’s Information Criterion adjusted for small sample size (AIC_C).

Model	Log likelihood	Sample size	Parameters estimated	AIC_C	Delta AIC_C	Wt
Type 1	−97.33	28	1	196.82	1.90	0.22
Type 2	−95.22	28	2	194.92	0	0.57
Type 3	−96.24	28	2	196.96	2.04	0.21

Table 4. Model support for numerical response functions for 28 (with 4 expanding and exploited wolf populations excluded) North American wolf populations during 1945–1994 with Type 3 model excluded (data from Fuller et al. 2003) using Akaike’s Information Criterion adjusted for small sample size (AIC_C).

Model	Log likelihood	Sample size	Parameters estimated	AIC_C	Delta AIC_C	Wt
Type 1	−97.33	28	1	196.82	1.90	0.28
Type 2	−95.22	28	2	194.92	0	0.72

Table 5. Model averaged estimate of asymptote of Type 2 and Type 3 numerical response functions for 28 (with 4 expanding and exploited wolf populations excluded) North American wolf populations during 1945–1994 (data from Fuller et al. 2003).

Model	Asymptote	Wt	Relative wt	Estimate
Type 2	81.54	0.57	0.74	69.28
Type 3	35.23	0.21	0.26	

wolves per 1,000 km². The model averaged value of the asymptotes was 69.3 wolves per 1,000 km² (Table 5, Fig. 1).

DISCUSSION

Our reanalysis of the data collected by Fuller et al. (2003) suggests that the evidence in favor of density-dependent regulation outweighs the evidence in favor of prey limitation

by at least a 3:1 margin. Our analysis reopens a debate begun by researchers who have speculated that wolf populations may be held in check, in a density-dependent manner, by intraspecific competition (Murie 1944, Stenlund 1955, Mech 1970, Pimlott 1970, Van Ballenberghe et al. 1975). Pimlott (1970) furthermore claimed that regulatory mechanisms held wolf populations at an upper threshold of approximately 40 wolves per 1,000 km². More recently,

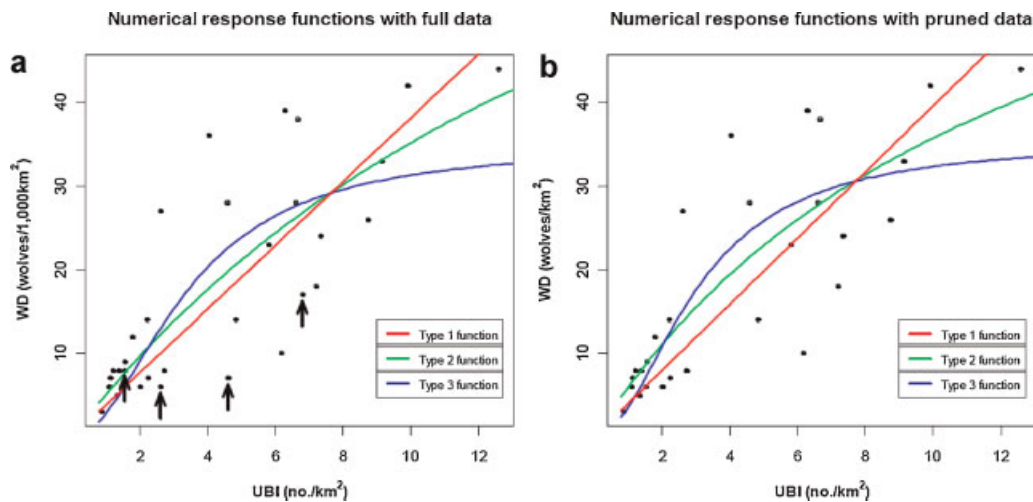


Figure 1. Linear and nonlinear regression lines for Type 1, Type 2, and Type 3 numerical response functions for North American wolf populations, 1945–1994. (a) full 32 data points from Fuller et al. (2003). Parameter estimates were $K_0 = 3.81$, $K_1 = 104.56$, $K_2 = 19.77$, $K_3 = 34.87$, $K_4 = 11.58$. (b) Twenty-eight data points after removing 4 populations designated by Fuller et al. (2003) as expanding or exploited. Parameter estimates were $K_0 = 3.95$, $K_1 = 81.54$, $K_2 = 12.85$, $K_3 = 35.23$, $K_4 = 9.14$. Black arrows indicate the 4 points we removed from the initial data set.

researchers have suggested there are no intrinsic limits on wolf populations except those imposed by availability of vulnerable prey biomass (Packard and Mech 1980, Keith 1983, Fuller et al. 2003). We did not attempt to incorporate data from additional sites because we wanted the theoretically possible models to confront the existing data set. By so doing, we sought to determine whether the confidence reposed in the prey limitation hypothesis by recent researchers, on the basis of the existing data set, was warranted.

Using a more rigorous methodology, we also updated Pimlott's (1970) estimate of an upper bound on WD, from his estimate of 40 wolves per 1,000 km² to our model averaged asymptote of 69 wolves per 1,000 km². Our estimate is more consistent with reports of temporary wolf densities as high as 92 wolves per 1,000 km² on Isle Royale (Peterson and Page 1988) and 69 wolves per 1,000 km² in north-central Minnesota (Fuller 1989). We did not report a standard error on our estimate of the upper bound for 2 reasons: 1) the points in the data set collected by Fuller et al. (2003) were averages of wolf and prey densities at individual sites over several years, and hence mask some variability, and 2) data appeared to exhibit heteroskedasticity. Both these conditions would lead to a severe underestimation of the standard error.

The regulation versus prey limitation discussion, as well as questions regarding the mechanism by which regulation occurs, can be found in the literature regarding other large carnivores (Hornocker 1970, Schaller 1972, Macdonald 1983, Pierce et al. 2000). Land-tenure systems, territoriality, and social strife have all been suggested as the potential mechanisms by which regulation occurs. Intraspecific strife and territoriality are endemic to wolves and may set upper limits on WD (Murie 1944, Marhenke 1971, Mech 1994). Fatal intraspecific attacks are known to occur even when WD is low and food is plentiful (Fritts and Mech 1981, Wydeven et al. 1995). Wydeven et al. (1995) and Jedrzejewski et al. (2007) found that territory size in wolves was inversely related to prey abundance. Jedrzejewski et al. (2007) also concluded that when ungulate abundance was high and prey abundance was increasing, wolf territory size asymptotically approached a lower limit. A lower limit on territory size may lead to an upper asymptote for WD when UBI increases. Data of Fuller et al. (2003) and our results are consistent with all these mechanisms but cannot exclude any of them as potential explanations for regulation in wolf populations.

Using hypothesis testing to distinguish between the different shapes of functional response functions has proven to be problematic, especially when sample size is limited and systems under investigation are highly variable (Hassell et al. 1977, Livdahl and Stiven 1983, Marshal and Boutin 1999). Marshal and Boutin (1999) found in simulations that sample sizes >300 were required to distinguish between a Type 2 and Type 3 function with a power of 0.80. This difficulty in distinguishing between different shapes can be expected to carry over to tests of numerical response functions as well because theoretical numerical response functions of predators take on the same shape as the theoretical functional response functions. Moreover, the problem of sample size is even more

intractable with numerical response functions because each additional data point would require a new wolf-prey system to be studied. With such severe constraints on data collection, model selection and evidence ratios within the AIC framework offer a tenable method to help understand how WD responds to changes in the UBI. Future efforts that would help strengthen our understanding of this relationship include 1) data from more systems, particularly those with higher densities of ungulate biomass, 2) incorporating mechanistic features (e.g., territory size, social strife) into a wolf population model, and 3) experimental manipulation of systems.

Management Implications

It is likely an intrinsic regulatory mechanism (e.g., social strife, territoriality, or some other mechanism) that leads to the limitation of wolf populations in a density-dependent fashion at high ungulate densities. At ungulate biomass indices <8, wolf populations are likely limited by ungulate availability, as previously posited (Fig. 1). The prey limitation dogma has led managers to believe that food availability is the only relevant limiting factor affecting wolves. Our analysis shows that intraspecific strife, territoriality, or some other regulatory mechanism is relevant and likely plays an important role in wolf population dynamics. Managers of wolf reintroductions and species recovery efforts should account for this possibility in establishing goals for sustainable wolf population levels. Based on our results, calculating the UBI for a particular area and estimating wolf population based on the linear regression model (Fuller et al. 2003) would result in an overestimate of wolf populations at ungulate biomass indices >8. That wolf populations may be regulated by intrinsic mechanisms is important when wolf managers determine how big of an area to select for individual reintroductions. Finally, the shape of the numerical response function for wolves may also have important implications for managers of ungulate species. If wolf populations respond to increases in prey density in a Type 2 manner and the functional response (kill rate) has also leveled off at high prey densities, total predation (kill rate × no. of wolves) will remain relatively constant and the predation rate will be clearly depensatory.

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