

## Short communication

### Wolf population density: prey biomass limits via intrinsic factors

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Whether gray wolf *Canis lupus* population density is limited intrinsically or extrinsically has occupied researchers for decades. Since 1983, prey biomass, an extrinsic factor, has been accepted as limiting, but that conclusion was recently challenged for unusually high wolf densities which were then said to be limited by behavioral, or intrinsic, factors such as intraspecific strife, dispersal, etc., below prey-biomass constraints. That contention has been disputed, so disagreement remains. This article discusses the models involved, presents revised models that shed new light, and offers evidence that supports the conclusion that at least at densities below 79 wolves 1000 km<sup>-2</sup>, wolf numbers per area are limited by prey biomass. As wolf density increases, behavioral factors limit the density to the number of wolves the prey biomass will support. Extra wolves disperse, and wolf range expands. Thus, while wolf density is self-limiting, the population is not.

Keywords: behavior, *Canis lupus*, density, dispersal, extrinsic limitation, gray wolf, intraspecific strife, intrinsic limitation, population, prey biomass

## Introduction

The gray wolf *Canis lupus* and its management has been controversial for many decades and especially since the animal was listed in the US in 1967 as endangered in the contiguous 48 United States (Mech 1970, Boitani 2003, Fritts et al. 2003). An important wolf-management question is whether wolf-population density is limited by intrinsic or extrinsic factors, an issue that has occupied researchers since Pimlott (1967) proposed intrinsic limitation (Table 1). Intrinsic-limiting factors include territoriality, intraspecific mortality, dispersal, disparate sex ratio, and mate preference, while an obvious extrinsic factor is food, usually expressed as prey biomass (Keith 1983).

Before exploring the question of whether high wolf densities are ultimately restricted by intrinsic or extrinsic factors, it is important to clarify terminology. Classically, the term population 'limitation' has been defined as factors affecting population growth (Watson and Moss 1970, Messier 1991, Fryxell and Sinclair 2000). The term population 'regulation' refers to a 'density-dependent process that reduces the per capita rate of population growth' (Logan 2019, p. 1653). However, not all authors have distinguished

Table 1. History of disparate literature about limitation of wolf populations.

Year	Proposed high wolf density limited by	Reference
1967	Intrinsic	Pimlott (1967)
1970	Intrinsic	Mech (1970)
1975	Extrinsic	Van Ballenberghe et al. (1975)
1981	Extrinsic	Packard and Mech (1980)
1983	Extrinsic	Keith (1983)
1989	Extrinsic	Fuller (1989)
2003	Extrinsic	Fuller et al. (2003)
2011	Intrinsic	Cariappa et al. (2011)
2014	Extrinsic	McRoberts and Mech (2014)
2014	Intrinsic	Cubaynes et al. (2014)
2015	Extrinsic	Mech and Barber-Meyer (2015)
2020	Intrinsic	Smith et al. (2020)

these terms or used them consistently. Herein, I use ‘limit’ or ‘limitation’ in its literal sense, as Smith et al. (2020, p. 92) used it to state ‘Food sets an *upper limit* [italics as in original] but before that limit is reached other factors ....’. In other words, the current article discusses whether high wolf densities are ultimately limited, restricted, or curbed by intrinsic or extrinsic factors. Wolf population regulation is not discussed.

In 25 carnivore species studied, from least weasel *Mustela nivalis* to polar bear *Ursus maritimus*, their population density was determined by prey density (Carbone and Gittleson 2002). Based on criteria that Wolff (1997) considered necessary for intrinsic limitation, wolves would not be qualified. He specified that reproduction must be suppressed in young females by ‘behavioural dominance’ of older females, and he thought it was in wolves, citing, among other articles, Mech (1970) and Packard et al. (1985). However, Mech (1970) gave no such evidence of wolf reproductive suppression, and Packard et al. (1985: p. 36) stated ‘We found no evidence that social interactions suppressed gonadal cycles in wolves that had undergone at least one reproductive cycle’. Smith and Cassidy (2024) argued that because a large number of females in Yellowstone National Park (YNP) did not reproduce, that was evidence of reproductive suppression. However, they considered females at least 2-years old to be sexually mature, whereas many female wolves do not sexually mature for several years (Mech and Seal 1987, Mech et al. 2016, Wikenros et al. 2021). Furthermore, YNP wolf daughters do produce young in approximately 25% of packs (Smith et al. 2020), so are not reproductively suppressed.

Settling whether intrinsic or extrinsic factors limit wolf density is important not just scientifically (Metz et al. 2020b, Smith et al. 2020) but also for managers. Many wolf advocates believe that wolf populations are self-limited (intrinsic limitation) and thus do not need control (<http://tinyurl.com/ft72b2r2>) by managers (Smith and Cassidy 2024).

## Debate history

The history of debate on this question was most recently updated by Mech and Barber-Meyer (2015), but suffice it to

say here that from Keith (1983) through Fuller et al. (2003), biologists agreed that prey biomass linearly limited wolf densities (Table 1). The more the available biomass of primary prey, the higher the wolf density. Updated support for this contention was based on linear correlation ( $r^2=0.64$ ;  $p=0.001$ ) between primary-prey biomass and wolf density from 32 studies of wolf and prey populations (Fuller et al. 2003).

It is important to understand that the available prey biomass is only an approximation of the vulnerable prey biomass. Generally, the two are necessarily correlated, but the available prey biomass is the standing crop, not the actual amount of biomass that wolves can procure. A classic example is the finding on Isle Royale that wolf population growth rate is highly related not to the standing crop of moose *Alces alces* but to numbers of vulnerable moose, i.e. those at least 9-years old (Vucetich and Peterson 2004). In most wolf populations, only a portion of the main prey population is vulnerable (Mech and Peterson 2003). That might also be why the Denali wolf density during the last eight of the 30 years assessed did not increase with the biomass of a major prey species (Borg and Schirokauer 2022). Since the Fuller et al. (2003) model was published, however, Cariappa et al. (2011) reopened the question by statistically reanalyzing the Fuller et al. (2003) data while deleting four studies from them and proposed that there was better evidence for a curvilinear relationship between prey biomass and wolf density, with an asymptote at 69 wolves 1000 km<sup>-2</sup>. That finding implied that at higher wolf densities, wolves were limited not by food but intrinsically. However, that finding was challenged based on a statistical assessment of the methods used to derive the curvilinear relationships (McRoberts and Mech 2014). Both Cariappa et al. (2011) and McRoberts and Mech (2014) pruned some data from the Fuller et al. (2003) model for various stated reasons. Smith and Cassidy (2024) suggested that such selective use of data points, as well as the probably non-independent data that Fuller et al. (2003) used, weakened the latter model. Nevertheless, all versions of the original Keith (1983) model yielded statistically significant linear relationships between prey density and wolf density.

Smith and Cassidy (2024, p. 4) also criticized the Keith (1983) model as follows: ‘The contribution of Keith (1983) can best be credited for discerning a pattern of wolf density based on prey biomass, not understanding a causal mechanism for wolf population regulation’. This claim fails to recognize that prey biomass fuels wolf density, the closest possible logical link between the two correlated variables, thus strongly supporting a causal relationship. Furthermore, discerning the nature of the relationship between prey biomass and wolf density is precisely what that model and all later versions of it have sought. The actual mechanisms for wolf population limitation have long been agreed on. As Mech and Barber-Meyer (2015, p. 501) put it: ‘It is probably true that one of the main mechanisms involved is intraspecific aggression (Cubaynes et al. 2014) and it is easy to understand how food competition could lead to such aggression. Other social factors discussed in detail by Packard and Mech (1980) presumably operate similarly in conjunction with food availability’.

While the [McRoberts and Mech \(2014\)](#) article was being developed challenging the [Cariappa et al. \(2011\)](#) findings, [Cubaynes et al. \(2014\)](#) were conducting a wolf-mortality study in Yellowstone National Park (YNP). Neither study had the benefit of the other. The YNP group, citing [Cariappa et al. \(2011\)](#) that wolves at higher densities could be limited by intrinsic factors, produced evidence based on wolf-survival data that they believed supported that contention for wolves on YNP's Northern Range (NR). Those findings were then challenged by evidence that prey biomass predicted NR wolf density, supporting the extrinsic explanation ([Mech and Barber-Meyer 2015](#)).

Five years later, the YNP group further explained and developed their support for intrinsic limitation, without considering either [Cariappa et al. \(2011\)](#) or [McRoberts and Mech \(2014\)](#). Their article wound down by concluding that 'Food sets the *upper limit* [sic], but before this limit is reached, other factors, particularly higher mortality due to intraspecific strife, reduce population density' ([Smith et al. 2020](#), p. 91). It then cited [Mech and Barber-Meyer \(2015\)](#) as follows: 'Of course, after these findings were published, another point was added to the linear relationship – one from Yellowstone ([Mech and Barber-Meyer 2015](#)) which counters density-dependent [intrinsic] regulation. The debate continues!' (note that in this quote, [Smith et al. \[2020\]](#) are using 'regulation' where I would have used 'limitation').

Meanwhile, [Wallach et al. \(2015\)](#), based partly on the findings of [Cariappa et al. \(2011\)](#) and [Cubaynes et al. \(2014\)](#), used life-history traits of various carnivores to propose that those above a certain size, including wolves, tended to self-regulate (intrinsic limitation). Those authors did not cite the [McRoberts and Mech \(2014\)](#) rebut to [Cariappa et al. \(2011\)](#).

It is important to note that, contrary to [Smith and Cassidy \(2024\)](#), both schools who favor intrinsic limitation of wolf density at high densities and those who contend that food ultimately limits all wolf densities agree that the mechanisms by which that limitation operates are intrinsic ([Mech and Barber-Meyer 2015](#)). The difference is that the extrinsic school contends that intrinsic factors adjust the wolf density to what its food supply (an extrinsic factor) can support. The intrinsic school believes that intrinsic factors adjust wolf density to below what its food availability can support ([Smith et al. 2020](#)). For example, the extrinsic-limitation position holds that as wolf density reaches food-availability limitation, competition increases, so wolves might disperse at higher rates or at earlier ages ([Fuller 1989](#), [Hayes and Harestad 2000](#), [Fuller et al. 2003](#), [Adams et al. 2008](#)).

[Mech and Barber-Meyer \(2015\)](#) discussed several reasons why the [Cubaynes et al. \(2014\)](#) results might have led erroneously to a conclusion that the YNP Northern-Range wolf density was intrinsically limited. [Smith et al. \(2020\)](#) did not challenge those reasons nor have other workers, and some of the same authors ([Metz et al. 2020b](#), p. 177) wrote that '... at higher numbers of prey, it is unclear whether wolf abundance continues to grow or levels off due to intraspecific strife ...,' citing both [Cariappa et al. \(2011\)](#) and [McRoberts and Mech \(2014\)](#).

[Metz et al. \(2020b](#), p. 178) did expect that '... elk abundance was a primary driver of wolf abundance'. They tested that hypothesis by examining the relationship between annual elk biomass and wolf density on YNP's NR and found at higher wolf densities 'equivocal statistical support' that density was both directly related to elk biomass ([Fuller et al. 2003](#), [Mech and Barber-Meyer 2015](#)) and that it was limited intrinsically ([Cubaynes et al. 2014](#)).

A new contention in this controversy is that population density is not the 'correct measure of a wolf numeric response to prey' ([Smith and Cassidy 2024](#), p. 3). However, no support for what is 'correct' was given other than citation to an article that used population growth rate in a study. That article did not discuss what response variable is 'correct' to use; it merely used that variable in a study of Eurasian lynx *Lynx lynx* and roe deer *Capreolus capreolus*. In any study of predator response to prey, there are several possible numeric variables that could be investigated besides predator density or growth rate, such as predator reproductive rate, mortality rates and causes, sex ratio, longevity, and others. I know of no 'correct' study variable.

Thus, the contradictory contentions for whether high wolf densities are limited extrinsically or intrinsically have not yet been resolved, leaving this important question still open. Among the proponents of intrinsic wolf density at higher wolf densities, there does seem to be agreement that low to intermediate wolf densities are determined by prey availability ([Cubaynes et al. 2014](#), [Smith et al. 2020](#)).

## Resolving the issue

The present article overviews the scientific controversy; explores new analyses; challenges the above quote that, at high wolf densities, food sets the upper limit but intrinsic factors determine wolf density below that limit; and presents information that proposes to resolve the question.

A complication to addressing this issue lies in the fact that when [Mech and Barber-Meyer \(2015\)](#) assessed the question, they chose a period during the YNP NR wolf population trajectory that they felt was relatively stable after peaking at 98, 2005–2012 ([Table 2](#), 3). Another logical alternative approach would have tested the same period that [Cubaynes et al. \(2014\)](#) had studied in concluding that their evidence based on adult wolf mortality supported intrinsic limitation, 1998–2010.

Thus, I tested that 1998–2010 period, using mean, annual, elk biomass ([Table 2](#)) with the model that [Mech and Barber-Meyer \(2015\)](#) used ( $y = 3.6997x + 0.1562$ ). The biomass index of 22.8 predicted a density of 71–101 wolves 1000 km<sup>-2</sup> (95% confidence intervals). However, the actual mean, annual wolf density for that period was only 64 ([Table 3](#)). This finding, that the actual density was less than the linear models predicted, supported the [Cubaynes et al. \(2014\)](#) intrinsic-limitation conclusion. That result directly conflicted with the conclusion by [Mech and Barber-Meyer \(2015\)](#).

More importantly, the [Cubaynes et al. \(2014\)](#) and [Mech and Barber-Meyer \(2015\)](#) analyses, which both covered six

Table 2. Wolf and elk counts on Yellowstone National Park Northern Range. Data provided by Yellowstone Center for Resources, US National Park Service. Wolf numbers approximate density (wolves 1000 km<sup>-2</sup>) because the Northern Range includes 995 km<sup>2</sup> (Cubaynes et al. 2014).

Year	Wolves	Elk
1995	21	16 274
1996	19	15 368
1997	32	14 304
1998	42	13 303
1999	35	12 349
2000	65	11 513
2001	70	10 559
2002	78	8916
2003	98	7659
2004	84	6623
2005	54	5789
2006	75	5428
2007	94	4870
2008	57	4638
2009	40	3754
2010	38	3349
2011	38	2740
2012	34	2389
2013	34	2287
2014	42	2179
2015	50	2119
2016	41	1982
2017	33	2104
2018	39	1998
2019	55	1887
2020	79	1844
2021	55	1787
2022	60	1727
2023	69	–

of the same years, yielded opposing results. This outcome demonstrated that the difference between support for these two long-competing explanations depended on the specific period of the YNP NR wolf population chosen. That disqualifies selecting certain periods in the wolf-population history to test these hypotheses.

Therefore, I tested the entire YNP NR wolf population after establishment in 2003, that is from 2003 to 2022, with the above Mech and Barber-Meyer (2015) model. The resulting mean annual elk biomass index, 10.1 per km<sup>2</sup>, predicted

Table 3. Results of estimating mean Yellowstone National Park Northern Range (YNP NR) wolf density from elk density (number/1000 km<sup>-2</sup> from Table 2 using the Fuller et al. (2003) model minus the six data points that Cariappa et al. (2011) and McRoberts and Mech (2014) removed, and which Mech and Barber-Meyer (2015) used.

Years	Actual mean annual density (Table 2)		Estimated mean annual wolf density	Study years based on
	Wolves	Elk		
2005–2012	54	4990	55	Mech and Barber-Meyer (2015)
1998–2010	64	7597	79	Cubaynes et al. (2014)
2003–2022	55	3358	37	This study

a mean annual wolf density of 31–44 wolves 1000 km<sup>-2</sup> (95% confidence limits) while the actual average was 55. However, bison *Bison bison* comprised at least 25% of the biomass the wolves acquired (Metz et al. 2020a). Assuming that, and occasional other prey adding 25–35% to the available biomass (Smith and Cassidy 2024), that would predict a wolf density of approximately 53. That finding supported the prey-biomass model of wolf limitation at high wolf densities.

The question does arise, however, as to what constitutes the highest wolf density at which prey biomass limits it and beyond which intrinsic limitation supposedly takes over. Cariappa et al. (2011) felt that their analysis suggested 69 wolves 1000 km<sup>-2</sup> would be the upper limit for prey-biomass limitation. However, because their analysis was demonstrated to be flawed (McRoberts and Mech 2014), that number is a questionable candidate.

The Cubaynes et al. (2014) results suggested that 65 was the upper limit. It is true that 65 wolves 1000 km<sup>-2</sup> is higher than most reported population densities (Fuller et al. 2003). Still, wolf densities within individual pack territories (as distinct from densities within wolf populations) in winter have reached up to 182 per 1000 km<sup>2</sup> (Mech and Tracy 2004) and other pack densities of more than 100 per 1000 km<sup>2</sup> are known (McRoberts and Mech 2014). However, their consideration during these deliberations is questionable because one of the primary intrinsic factors proposed to limit densities is intraspecific strife, which rarely occurs within packs.

Evidence refuting whether intrinsic factors limit high wolf densities, then, would be restricted to population (not pack) densities higher than 65 per 1000 km<sup>2</sup> that persist for more than a year. If wolf density is limited intrinsically below food limitation, that implies a species-wide, behaviorally determined, saturated density. That is, such limitation should characterize wolf populations everywhere at any time regardless of external factors such as amount of available food.

Some of those populations have existed, even with YNP NR wolves. From 2001 to 2007, the annual wolf density averaged 79 (Table 2). True, the density then dropped for several years, but seven years at such high densities should be long enough for intrinsic factors to affect the population. Such a period should satisfy the contention that wolf density response to prey biomass is not instantaneous (Smith and Cassidy 2024). Notably, the YNP elk population dropped from a mean annual herd size of 7121 during the high-wolf-density period to 3048 during the next seven years (2008–2014), when the wolf density averaged 40 (Table 2). That is further evidence of food-limited wolf density.

Similarly, the Isle Royale wolf population exceeded a density of 65 per 1000 km<sup>2</sup>, from 1975 to 1980 when its density was 77 per 1000 km<sup>2</sup> (calculated from Peterson and Page 1988). ‘Known mortality during the decline took the form of starvation and intraspecific killing, direct and indirect manifestations of reduced food supply’, as Peterson and Page (1988, p. 89) explained.

Given that the two above examples refute the intrinsic-limitation contention, proponents of that view could propose, then, that that process operates at wolf densities



exceeding 79, not 65 or 69. That could be the case, but the high densities for individual packs cited above make that possibility seem unlikely. Part of the reason that Cubaynes et al. (2014, p. 1353) felt that ‘... space rather than food was the limiting resource for NR wolves’ was that they believed that wolf packs could not tolerate breeding territories smaller than approximately 80–100 km<sup>2</sup>, citing Jędrzejewski et al. (2007). However, wolf packs can tolerate breeding territories as small as 23 km<sup>2</sup> (Mech and Tracy 2004, McRoberts and Mech 2014). Thus, territory size is highly compressible, so neither does it seem to be limiting. In any case, evidence to date is that up to at least 79 wolves 1000 km<sup>-2</sup> there are no intrinsic factors that are limiting below food supply.

One final factor that suggests that the evidence for intrinsic limitation may be suspect involves the specific period of the YNP NR wolf population that was used in the Cubaynes et al. (2014) study. During the first five of the 13 years of the study, 1998–2002, the reintroduced wolves were still establishing themselves, so their population was still increasing (Table 2). Concurrently, the NR elk population was still near its pre-wolf-reintroduction high that it has not come close to reaching since, and it had hardly experienced the effects of wolf predation (Table 2). Thus, the NR wolf–elk relationship was totally different during the Cubaynes et al. (2014) study (parabolic) than after wolves established a population in 2003 (positive linear) (Fig. 1).

This critical difference (Fig. 1) almost certainly was the reason that the Cubaynes et al. (2014) modeling showed that the variable that better explained adult wolf-mortality rate was wolf density (intrinsic limitation) rather than elk numbers (extrinsic limitation). Notably, the delta Akaike information criterion (AIC) between the two variables, wolf density or prey numbers, was 3.23, and the amount of variation explained by the two models was not overwhelming (50 versus 43%). The Cubaynes et al. (2014) finding might be valid, but it would only apply to the unique period when wolves are reestablishing a population amid a surfeit of prey, not to most extant wolf populations.

## Conclusion

The total above considerations, then, weigh heavily towards the prey-biomass model remaining the most valid for explaining wolf densities of any size. In any discussion about that model, it is important to understand that it is based only on primary prey as the food variable, and almost all wolf populations also rely on secondary prey to widely varying extents (Smith and Cassidy 2024). In YNP’s NR wolf population, for example, probably the reason the prey-biomass model underpredicts that elk biomass would support an average annual wolf density of 39 wolves per 1000 km<sup>2</sup> when the actual density was 55 (above) was because wolves also fed on bison (Metz et al. 2020a, Smith and Cassidy 2024). Wolves fed on bison as well as elk during the period when Mech and Barber-Meyer (2015) tested their model, but bison constituted an annual average of only approximately

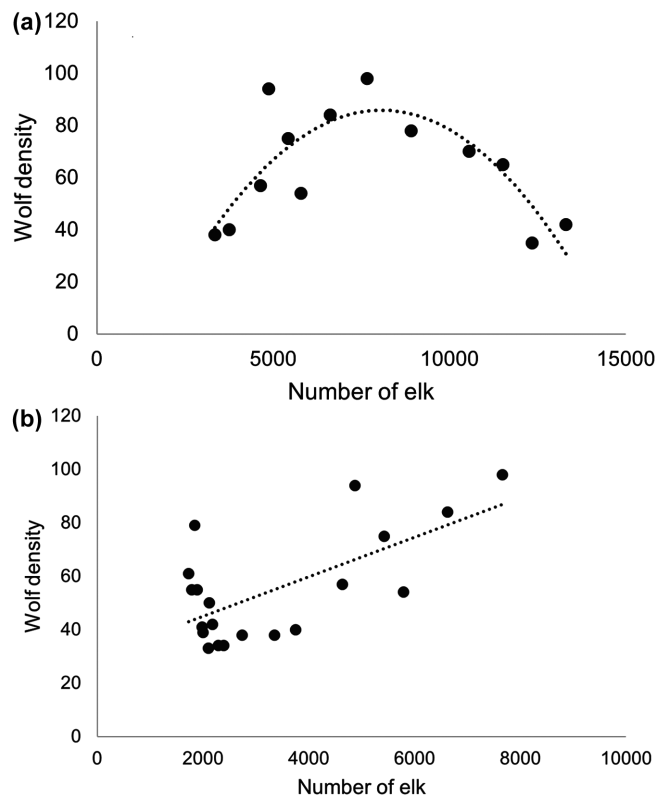


Figure 1. Yellowstone National Park Northern Range wolf–elk relationship (a) during Cubaynes et al. (2014) study, 1998–2010, (b) during 2003–2022. Data from Table 2.

10% of their diet during the years of that study (calculated from Metz et al. 2020a). Because the Mech and Barber-Meyer (2015) findings held even with a biomass index up to 20% more than the primary biomass the authors used, their results were still valid, contrary to the concern of Smith and Cassidy (2024).

Because of these considerations as well as error, the relationship between estimates of wolf density from prey biomass are only approximations. Nevertheless, the relationship between prey biomass and wolf density appears strong at all wolf densities measured, thus evincing that food supply, an extrinsic factor, is the ultimate limit on wolf density. The study of wolf-population growth rate (i.e. population regulation) (Smith and Cassidy 2024) is a welcome new approach to investigating wolf response to prey, but it does not settle the long controversy over whether high wolf density is limited by intrinsic or extrinsic factors.

## Management implications

Most often when agencies or the public refer to wolf populations they are not referring to densities (number per area) but rather to the number of wolves in a specific geographic region. Each state or country, for example, regularly publicizes changes in the number of wolves in its legal jurisdiction. Although wolf densities are limited by prey biomass, one of the mechanisms limiting them is dispersal, which then via

contiguous or distant recolonization of new areas expands the population. The most noticeable and publicized wolf population increases are those occurring via dispersal and population expansion, not wolf density.

Contentions that wolf populations are self-limiting can be considered valid only if they refer to local wolf densities, as explained above. The distinction between density and population, however, is one that might not be clear to the lay public. As long as enough prey exists outside of local extant wolf populations, regional wolf numbers continue to expand into new areas (Mech 2017, Ausband and Mech 2023). Therefore, in that respect, ever-expanding regional wolf populations are neither self-limiting nor self-regulating. Therefore, the only way of limiting regional wolf populations without actual control would be to eliminate prey biomass.

It is important for managers to remain ever aware of this distinction.

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### Data availability statement

This article contains no original data.

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