Quantitative Conservation of the Gray Wolf (*Canis lupus*): Implications of Monitoring and Modeling the Yellowstone Wolves

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ABSTRACT

The 1995 reintroduction of wolves to the Greater Yellowstone ecosystem had lasting effects on our understanding of reintroduction biology as a whole. However, continued study of a system as complex and intricately interwoven as this should be done with minimal human influence on the ecosystem. The states comprising the tri-state area surrounding Yellowstone National Park—Wyoming, Idaho, and Montana—have recently delisted wolves from the endangered species list. Here, I assess the greater implications in conservation that can be deduced from quantitative analysis of the Yellowstone wolves, and question whether the species is, in fact, stable enough for delisting in this area. I used multiple regressions on population growth as a function of population size to test the claim that the carrying capacity for wolves in Yellowstone is approximately 170 individuals. After finding that the estimate of 170 is much larger than my calculated values of carrying capacity, I move forward to design six distinct models that each enforce a predesignated carrying capacity on 100 different simulated wolf populations over the next 100 years. All of these simulations experienced zero probability of extinction. However, I discuss general trends that may still be extracted from the models, potential flaws in my modeling for this particular system, and a variety of different approaches to designing simulations that may more effectively predict the fate of the Yellowstone wolf population. I offer observations of how population dynamics change with respect to carrying capacities once the carrying capacity has been attained, and address differences between population dynamics in a pre-established population versus and those in a reintroduced population. Overall, I conclude by noting that the fate of the wolves is not certain, and should therefore be monitored and maintained with a more adaptive management strategy.

INTRODUCTION

The gray wolf (*Canis lupus*) is a charismatic species that maintains consistently high levels of public interest (Nie, 2001; Busch, 2007; Bisi & Kurki, 2010). There are culturally engrained anti-wolf sentiments exhibited by many rural communities (Musiani & Paquet, 2004; Chavez et al., 2005), while conservationists tend to emphasize the instrumental importance of protecting such a strong apex predator that is capable of aiding in the maintenance of both natural biodiversity and overall abundances of multiple species (Bump, 2009; Busch, 2007; Creel & Winnie, 2004; Hebblewhite, 2007). Proponents of these latter arguments often note that the gray wolf has proven to be an incredibly important species to the overall structure of riparian (riverbank) ecosystems in Yellowstone National Park due to the trophic effects witnessed upon their reintroduction (Smith & Bangs, 2009; Ripple & Beschta, 2011). However, these claims have also been challenged, with some arguing that their ecological effects may not necessarily be as essential as many claim (Marshall et al., 2013; Allen et al., 2017).

These arguments may have lasting impacts on the ability of the species to withstand the threat of local extirpation, as wolves in the tri-state area surrounding Yellowstone (Wyoming, Montana, and Idaho) have now been removed from the endangered species list in all three states (“Wolves in Idaho”, “Gray Wolf — *Canis lupus*”, and Smith, 2017). While current wolf numbers are not critically low, the regional population may be declining in years to come. A key question is how large and how stable the population is likely to be in the future. Answering this question requires a consideration of both the minimum number of wolves necessary to sustain the total population, as well as an analysis of the maximum number of wolves that could be supported by the ecosystem (henceforth referred to as the carrying capacity). Assessment of the minimum threshold of wolves necessary for a healthy and sustainable population requires consideration of a variety of different influential factors. Beyond developing a general consensus on minimal required numbers for the wolf populations of Yellowstone, one can merely speculate how population size may fluctuate over time. These fluctuations, however, are largely dependent on the park's carrying capacity.

Here I analyze the probability of regional decline in the Yellowstone wolf population. In this work, I consider historical growth rates, negative density dependence (population growth decline due to the carrying capacity), and two different predicted quasi-extinction thresholds. These models provide a reasonably in-depth investigation of population fluctuations in gray wolves and potential future outcomes utilizing population viability analyses, which helps assess whether or not the wolf population of Yellowstone is stable enough for delisting of the species in the tri-state area. In particular, this analysis illustrates the likelihood that Yellowstone's wolves may not survive for as long as predicted, which may in turn have serious implications on several other species of concern in the Greater Yellowstone ecosystem. I emphasize the importance of identifying the most accurate carrying capacity, and move forward to implementing proposed minimum and maximum thresholds for wolf populations into my own population viability analyses. I then compare the results of these analyses to models that Yellowstone may have created in their assessment of wolf population viability, and note any prominent differences. Beyond this, I discuss potential improvements that could be made to acquire further legitimacy in population modeling, and conclude that extensive monitoring of the species should still be a part of Yellowstone's management strategies.

BACKGROUND

On Tuesday, March 21, 1995, a landscape that boasted relatively fearless populations of prey underwent a transformation that would eventually change its topography drastically. The reintroduction of the gray wolf into the Greater Yellowstone National Park not only recreated a long-lost landscape of fear (Laundré et al., 2001) but it also revealed to us the immense influence an apex predator may have on an environment (Ripple & Beschta, 2012; Ripple et al., 2016; Smith & Bangs, 2009). Yellowstone National Park is a place that begs to have wolves (Busch, 2007). The riparian ecosystem is crawling with prey for reintroduced wolves to feed on, which is why the reintroduction program seemed like the best approach to both limiting overcrowded ungulate populations as well as promoting wolf conservation. While the former was certainly accomplished, as evident in the rapid decline of artiodactyl populations (Fortin et al., 2005), there still remains much debate in the realm of wolf restoration.

In 2003, the U.S. Fish and Wildlife Service claimed that its goals for the wolf population's recovery had been met (Busch, 2007). In doing this, the service attempted to downgrade the wolf from endangered to threatened in the regions surrounding the Greater Yellowstone ecosystem (Busch, 2007). Federal courts overturned this idea, however, and the matter has remained a topic of steady debate ever since (Busch, 2007). As of 2016, the wolf population in the Greater Yellowstone region continued to fluctuate—likely a repercussion of food scarcity, interspecific competition, and human-caused mortality. Many other factors also contribute to the immense amount of fluctuation witnessed in the Yellowstone wolf population including stochastic environmental conditions like severe winters and immigration/emigration in and out of the park's boundaries (Coulson, 2011). Another threat to wolf populations, however, is beginning to look like it may be even more prominent in the coming years: death by gunshot. A total of 292 wolves were killed between 1987 and 2004 in the tri-state area as a repercussion of wolf-livestock conflicts (see “Gray Wolf History”). While the park maintains a sanctuary of sorts for wolves, the canines are entirely unaware of the park’s boundaries and often move in and out of the park’s perimeter. This, along with the delisting of wolves by both Montana and Idaho on May 5, 2011 (see “Wolves in Idaho” and “Gray Wolf — *Canis lupus*”) made for an initially concerning atmosphere for the wolf. In addition to this, on April 25, 2017, the wolf was also delisted in Wyoming (Smith, 2017), and may now face additional problematic circumstances. Below, I emphasize the importance of continually monitoring the species, and adaptive management techniques that will assist in preventing local extirpation.

METHODS

Population data for my modeling was collected from Yellowstone’s Annual Wolf Reports from 1995 to 2016 (see “Yellowstone Wolf Reports”) and population growth rates (λ) were calculated for each year as the population in year t+1 (N_{t+1}) over the population in the previous year (N_t) (Fig. 1).

Given that the wolves of Yellowstone experienced extremely high rates of growth immediately following their reintroduction, it’s important that this was considered when establishing how negative density dependence may influence future population dynamics. While numbers were small in these early years, potentially leading to low competition, other aspects of the ecosystem, including naive prey, could have boosted growth rates above what would be expected solely on the basis of a negative density dependent model. In order to establish the prominence of negative density dependence with relation to what some might call this “initial bonanza”, I ran a multiple regression analysis on the relationship between N_t and λ for years 1995-2016 (this model with be henceforth referred to as NDD1995), 1999-2016 (henceforth referred to as NDD1999), and 2002-2016 (henceforth referred to as NDD2002). For each dataset, I fit density-independent, Ricker, and theta-logistic models. Each model fit also returned Akaike information criterion (AIC) values which were then used to identify which regression was best suited for determining the presence and magnitude of negative density dependence. These models also returned estimates of the average intrinsic growth rate as well as residual variance. In the case of a density independent model, there wasn't much more to the regression outputs than this. However, if the model selected for each span of years was indeed density-dependent, then the model also indicated an estimated carrying capacity. The theta-logistic model also returned an estimate of theta, which indicates how curved the line of best fit should be. Then, once the regression had been run and the outputs were noted, I moved on to design my models.

Density-independent growth can be modeled with the following equation:

$$N_{t+1} = N_t e^{r+\varepsilon}$$

In this, N_{t+1} represents the population size at time t+1, N_t represents the population size at time t, e is Euler's number (≈2.71828), r is the intrinsic rate of growth (or log(λ)), and ε is a normally distributed variable with a mean = 0 and variance equal to that estimated for environmental stochasticity. This variable accounts for environmental stochasticity in the projections by adding a randomized ε from this normal distribution. The Ricker equation, however, enforces a carrying capacity on the simulations and can be written as such:

$$N_{t+1} = N_t e^{r\left(1-\frac{N_t}{K}\right)+\varepsilon}$$

This equation is similar to the previous density-independent equation, aside from the introduction of K, the carrying capacity. The theta-logistic regression relies on a slightly more complex version of this equation:

$$N_{t+1} = N_t e^{r\left(1-(\frac{N_t}{K})^{\theta}\right)+\varepsilon}$$

The only difference between this equation and the Ricker equation is the incorporation of θ, which creates the opportunity for a curved regression line on an already-logarithmic set of data.

After creating these initial models that indicate which regression model best fit the data, and therefore which growth equation I might use in my simulations, the simulations were constructed. In order to observe the potential outcomes over the next one-hundred years for the Yellowstone wolf population, I implemented a standard population viability analysis model that simulated 100 distinct populations with r values determined by the regression model and ε values selected stochastically from a normal distribution with standard deviations calculated as the square root of the residual variances output by the regression model.

For each simulation, I determined if any of the individual populations dropped below a proposed biological quasi-extinction threshold. Determining how small to set this quasi-extinction threshold proved difficult as there is no threshold population size or proven reserve design that guarantees long-term (century or more) survival for a gray wolf population (Fritts et al., 1995). However, a similar study on Oregon's wolf populations noted that in simulations with < 6 wolves, the extant population would effectively be extirpated due to inbreeding depression and immigrants from outside sources would be maintaining the Oregon population (Clark, 2015). Thus, my models used two different thresholds for two different clusters of simulations, implementing a threshold of both < 6 wolves and < 11 wolves (the latter threshold reflecting the fact that the threshold of < 6 wolves may be too risky, and 10 wolves may reflect the existence of a remaining single pack which would be subject to negative inbreeding effects). In any simulation, once the population dropped below said threshold it was determined to be biologically-extinct for all remaining time steps. From this, I was able to calculate theoretical extinction probabilities for each analysis as the cumulative proportion of simulations that fell below < 6 and < 11 wolves.

Keeping in mind that my study intends to observe differences between extinction probabilities for models I create based entirely on quantitative metrics and models that Yellowstone officials might have created from pure speculation of a carrying capacity, I then moved forward in an attempt to replicate projection models Yellowstone may have performed in their assessment of wolf population ecology. In doing so, I created three separate models with a carrying capacity of 170 all stemming from the Ricker model. The first projection model (henceforth referred to as K=170(95)) was built using the output numbers from the NDD1995 model, the second (henceforth referred to as K=170(99)) built from the NDD1999 outputs and the third (henceforth referred to as K=170(02)) implementing outputs from NDD2002. For these models, I only altered K, but input the estimated variance and intrinsic growth rates (r) from my model fits. These new projection models were then contrasted with the models I had previously created in order to assess whether or not there is a difference in the trends of simulations with K=170 and the trends of simulations implementing a calculated carrying capacity.

RESULTS AND DISCUSSION

The range of years used to generate model fits had strong effects on the results (Table 1). When I fit models to the observed lambda values from 1995-2016 (Fig. 2), the theta-logistic (AIC=-9.18) outperformed the Ricker (AIC=-5.69) and density-independent (AIC=8.82) models. After limiting the range of years to 1999-2016 (Fig. 3), the Ricker model proved to be the best fit (AIC=-7.13) in contrast with the density independent (AIC=-7.08) and theta-logistic (AIC=-

6.81). Likewise, the model restricted to the years 2002-2016 (Fig. 4) showed highest support for the density-independent model (AIC=-2.92) over the Ricker (AIC=-2.45) and theta-logistic (AIC=-0.30) models. Therefore, we can clearly see there are broad differences between the best fit regressions in relation to the years selected for this model with the earliest years generating almost all the support for strong density dependent effects.

Given that the ultimate goal of performing these regressions is to quantitatively identify a proposed carrying capacity for the Yellowstone wolves, it's interesting to note that none of the regressions resulted in carrying capacities remotely close to Yellowstone's self-reported carrying capacity of around 170 wolves. The NDD1995 model returned a carrying capacity of around 126 individuals, while the NDD1999 model and NDD2002 model returned carrying capacities of 120 and 114 respectively. This leads me to believe the logic behind estimating the carrying capacity to be around 170 is faulty, and likely only derived from a misguided belief that the maximum number of wolves ever witnessed in the park is a reasonable estimate of the park's carrying capacity. This claim was likely proposed from "expert opinion" rather than quantitative analysis, and should be reconsidered in light of recent computational advances that allow us to properly assess carrying capacities.

Another interesting caveat to the regression outputs was evident in the NDD1995 and NDD2002 regressions. The theta-logistic regression returns an intrinsic growth rate (r) value of approximately 58.1. This is particularly problematic when we remember that r is a log-transformed maximum growth rate (λ). This implies that the theta-logistic regression outputs indicate an average λ value of around 15-septillion, which is impossible for not only my study system, but ultimately any mammalian study system. While the maximum value of r, which is estimated to occur at a theoretical population size of ~zero, may often be higher than is biologically realistic, the estimated lambda value for a population size of 10 from the theta logistic model is around 158, which is still unrealistically high. Therefore, rather than constructing a simulation based on the theta-logistic outputs, I instead moved to create a simulation based on the Ricker outputs for the NDD1995 model. The NDD2002 outputs were also ignored for the density-independent model, as I am striving to replicate nature as effectively as possible, and therefore must consider negative density dependence as a constraining influence on my system. Hence, the NDD2002 model was also based on the Ricker outputs of the regression rather than the density-independent outputs.

Projection models performed from these regressions and their proposed carrying capacities resulted in no simulations experiencing regional extinction based on my proposed extinction thresholds. However, the projection models still returned rather interesting results that still suggest considerable risk for the future of this population. The first of these is evident in the tendency for the designed simulations with a carrying capacity of 170 to increase at unrealistically fast rates. Using the population size at the year 2016 (108) as a starting value, simulations with a carrying capacity of 170 tended to increase by nearly 50% in the first five years (Fig. 5). This immediate leap to higher projected population sizes may not be surprising in certain organisms that have reproductive strategies which could achieve this rate of increase. However, given that the average pack size was approximately 9.8 wolves in 2016 (Fig. 6), and packs typically possess a single breeding pair (Mech, 1990), we can hypothesize that around 10 litters might be produced in the most optimistic of circumstances. With an average litter size of 4.4 pups, and an average of only 3.2 of these offspring surviving to December (“YS 24-1 Yellowstone Wolf Facts”, 2016), we might actually be able to witness this sudden increase in population, but demographic analysis (i.e. matrix modeling) would likely be required to truly assess the plausibility of this occurrence. Likewise, this immediate spike would be highly unlike the trends in population numbers actually observed for the Yellowstone wolves (Fig. 1). All this implies that the proposed carrying capacity of ~170 wolves is simply unrealistic.

Furthermore, the five-number summaries (consisting of minimum, first quartile, median, third quartile, and maximum simulations) of each set of simulations raise doubts about the applicability of my mathematical modeling to real-world scenarios. The NDD1995 model seems to have a similar magnitude of population increase as it does decrease (Fig. 7). However, the NDD1999 model begins to show a slight preference for positive growth over negative growth (Fig. 8) and the NDD2002 model illustrates this trend even more-so (Fig. 9). Models implementing the carrying capacity of 170 also show this trend. This gives the impression that the range of years in consideration may have an effect on the projection models produced, and therefore raises questions about the validity of the modelling approach for this study system. It is likely that the tendency for later models to be skewed towards positive growth is a repercussion of the carrying capacity not being enforced as strictly as it would be in a real ecosystem (as opposed to my purely theoretical projection models). When we look at the maximum trends, it’s notable that the maximum simulation from each model reaches far above their respective proposed carrying capacities—in some cases reaching nearly double the proposed carrying capacity. Since we are assuming a normally distributed array of projections, however, we might expect to see such a trend in order to maintain average population projections that are not heavily influenced by the extremely low simulations. This is to say that the higher end of the simulation extremes is necessary to balance out the lower end of the simulation extremes. Another way of understanding these results is that the estimated environmental stochasticity in annual growth rates is estimated to be quite high (Table 1), resulting in dynamics that sometimes lead to rapid growth even when at the long term carrying capacity.

Nevertheless, it’s not the maximum or minimum simulations that incite a questioning of the validity of such simulations. Rather, an observation of the third quartile results seems to illustrate the necessity for questioning the relevance of this modeling approach. Third quartile results are significantly higher than the proposed carrying capacities in all six models, which implies the carrying capacity is not being enforced strong enough on the most successful 25% of simulations. This may be evidence of unrealistic modeling because it seems highly unlikely that a population of any organisms has anywhere near a 25% chance of being relatively unaffected by the carrying capacity of their ecosystem.

Another interesting remark concerning the wolf population of Yellowstone is something I noticed in observing the historical wolf numbers as they stopped fluctuating with such great magnitude. Although the immediate success of the wolf populations is clearly evident in their rapid initial growth, the past eight years of data show population sizes ranging from a maximum of 108 in 2016 to a minimum of 83 in 2012. These past eight years all seem to possess population sizes that show analogous patterns of fluctuation to the projection models I created, wherein they centralize around some value (~95-96 wolves). For the models I had created, these central values fluctuated around the carrying capacities. Therefore, if we continue to see similar patterns of population fluctuation ranging from approximately 83-108 wolves, it would be reasonable to conclude that the true carrying capacity of the Yellowstone wolves lies within that range, rather than any of my calculated values, or the Yellowstone estimate of ~170 individuals.

Finally, it’s pivotal in the realm of quantitative conservation that we seek to replicate nature as effectively as possible. That said, identifying the true carrying capacity of

Yellowstone’s wolves requires a strong consideration of the range of years that is applicable to perform the calculation of carrying capacity. After observing the differences between calculated carrying capacities in my models, I moved forward to perform the same regression on every range of years from 1995-2016 to 2013-2016. Resulting carrying capacities were then contrasted with the year ranges implemented (Fig. 10) and results indicate that there is a strong relationship between the proposed carrying capacity and the year range designated as appropriate for the calculation ($F=108.1$, $R^2=0.8561$, $p=8.747E-9$). This implies that the range of years chosen for a calculation of the carrying capacity has immense effects on not only the carrying capacity predicted, but also on the results of the projection models created based off of this carrying capacity.

CONCLUSIONS

In conclusion, I have investigated carrying capacities for the Yellowstone wolves, and have modeled this population’s potential fate using the Ricker equation in six separate instances. When the carrying capacity of the wolves was proposed to be 170 there was no risk of regional extinction, and the populations were projected to thrive with no foreseeable problems. Lower carrying capacities integrated into the simulations returned similar results, as the populations seemed to simply stabilize around their respective carrying capacities with no risk of local extinction. Therefore, I moved on to question whether or not my methodology of calculating extinction risk may have something to do with this zero-risk outcome. I presented many reasons why my models may not be as realistic as we might hope for population modeling. I believe more complex methods of modeling will return results that are representative of what we might expect to see naturally.

Additional studies that may further our understanding of population dynamics in the Yellowstone wolves might include demographic analysis that considers the life history of the species to understand if there is an observable relationship between demographics of the Yellowstone wolves and their population dynamics. To this line of thought, it’s important to note that wolves are an interesting species in the realm of density dependence, as they may be subject to both positive *and* negative density dependence. Negative density dependence is likely enforced when prey is less abundant, and positive density dependence is likely enforced when population numbers and pack sizes are low enough that an introduction of more individuals to the pack confers a greater advantage in hunting. Therefore, there may be some threshold effect for both negative and positive density dependence wherein both of these concepts are evident at some level, but this is largely dependent on the demographic makeup of not only the wolf population in general, but also at the pack-level.

Likewise, directly accounting for environmental stochasticity as it relates to the wolf population may also help us to better predict the fate of this population. While we can’t effectively determine exactly how the climate will vary over the next 100 years, we can most certainly infer whether or not there is a relationship between some climatic variable (such as snowpack or average annual winter precipitation) and the birth, death, and growth rates of the population (henceforth referred to as vital rates). This understanding of the relationship between abiotic pressures and wolf vital rates would be pivotal to narrowing down the total extent of detail that future projection models should be seeking to attain, which would assist in guiding wolf population biologists tremendously.

Additionally, something important to note about this study system in particular as it relates to other studies of population viability is that this study focuses on a reintroduced species.

One mistake in the realm of population biology for reintroduced species might maintain that the carrying capacity of a particular organism is near-constant. However, in observation of the Yellowstone wolves' population dynamics, it's relatively safe to say that this is not the case. The number of wolves that may have been capable of thriving in the Yellowstone ecosystem in 1995 is almost definitely not the same number of wolves that could potentially exist there currently. Rather, the carrying capacity likely changed from 1995 to present, especially considering prey-reduction was so prominent in the formative years. This is why I proposed calculating different carrying capacities considering different ranges of years, and why it seems reasonable that limiting the range to more recent years produces an overall lower projected carrying capacity. Thus, in order for us to effectively pinpoint the true carrying capacity of the Yellowstone wolves after the initial bonanza they experienced, we should continue to monitor them closely for several more years, while attempting to have as little human-caused effect on any of their vital rates.

This leads me to a potential problem with developing our understanding of reintroduction biology as it relates to carrying capacities. There is a great necessity for us to refrain from influencing the population dynamics of the wolves in any significant way if we wish to understand how a reintroduced apex carnivore naturally impacts the ecosystem in which they are reintroduced to. It's pivotal that we do our best to cease actions that may influence the population, and therefore introduce an unnecessary confounding variable into the system before we get the chance to make any observations. The wolves of Yellowstone seemed like they may have been stabilizing near an average of 97 wolves over the years of 2009 (96 wolves), 2010 (97), and 2011 (98). However, when the wolf was delisted in Idaho and Montana in 2011, there was a slight decrease in the wolf population size in 2012 to 83 individuals. Whether the delisting contributed to this decrease in population is difficult to assess, as only 6 of the 15 wolf mortalities were wolves shot during the hunting season. However, a loss of one individual wolf may have negative effects on the pack's overall ability to hunt, which in turn may result in more casualties than the original singular mortality. If the reported wolf population for 2017 shows a substantial drop in population size after Wyoming's delisting of the wolf in 2017, we may have reason to believe our influence on the species via hunting is disrupting our ability to draw more invariable conclusions about reintroduction biology. Of course, we should keep in mind that correlation does not imply causation. Nevertheless, it is equally important to recognize that human influences on populations, regardless of species, may confound our ability to draw conclusions of ecological principles.

Another important aspect of population modeling that may confound our ability to draw legitimate conclusions is clear in the lack of a standard for what range of years should be used in the calculation of carrying capacities. This standard, however, would likely vary from species to species, and therefore remains difficult to estimate universally. I propose that a reintroduced species should be monitored extensively after reintroduction, and in the case of a reintroduction event similar to Yellowstone's wolves, the drastic initial increase and subsequent decrease of population numbers should be ignored in estimating the carrying capacity, due to the tendency for regressions on these years to predict carrying capacities that are significantly higher than realistic. Of course, this drastic increase is not always a phenomenon that is evident in reintroduced species, and therefore would likely only remain applicable for species that experience such a shift in population size. However, for study systems that mimic this pattern of population growth, it is clear that carrying capacities calculated from a consideration of all years the species has inhabited the new landscape are unrealistically optimistic.

Looking forward, it may be the case that the wolves of Yellowstone are not in any danger at all. Perhaps the decline in population from estimates of around 170 individuals to our current estimates of around 100 individuals were inevitable considering the stark decline in ungulate populations that followed the reintroduction event. Yet, it would be a shame for the reintroduction project if the populations continued to decline in coming years, regardless of whether this decline was caused by human-influence or simply via natural processes. Therefore, I contend that continued monitoring of the Yellowstone wolves is necessary not only for developing our understanding of population dynamics in a reintroduction system, but also in order to ensure that the wolf population of Yellowstone maintains an adequate population size to persist for years to come.

FIGURES AND TABLES

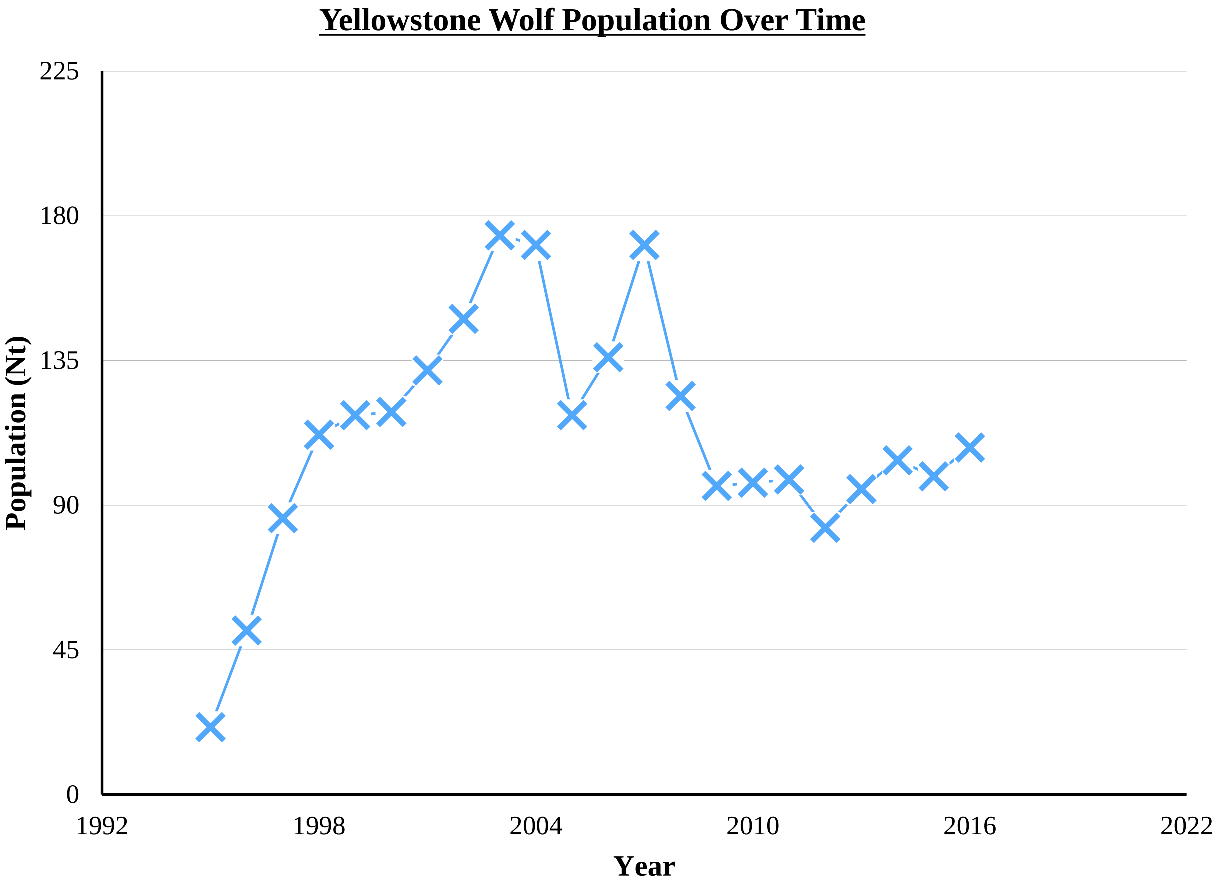


Figure 1: Data collected from Yellowstone Wolf Reports consisted of population estimates for the years 1995-2016.

Year	Model	r (intrinsic growth rate)	K (carrying capacity)	Theta	Residual Variance	AIC
1995	D-I	0.07798137	0	0	0.07137091	8.824923
	Ricker	0.69094728	126.3023	0	0.031381	-5.685425
	Theta-Logistic	58.10307691	121.5959	0.008417581	0.02293369	-9.182699
1999	D-I	-0.00520923	0	0	0.02901151	-7.080014
	Ricker	0.294464896	120.3996	0	0.02426204	-7.130258
	Theta-Logistic	0.04228651	150.5666	13.27012	0.02013702	-6.81108
2002	D-I	-0.02250579	0	0	0.03304683	-2.916428
	Ricker	0.28618011	113.5025	0	0.02697321	-2.4504789
	Theta-Logistic	0.03250403	147.3991	12.89964	0.02356066	-0.2997553

Table 1: Outputs from the multiple regression indicating the best-suited model, carrying capacity, intrinsic growth rate, residual variance, and theta for each range of years

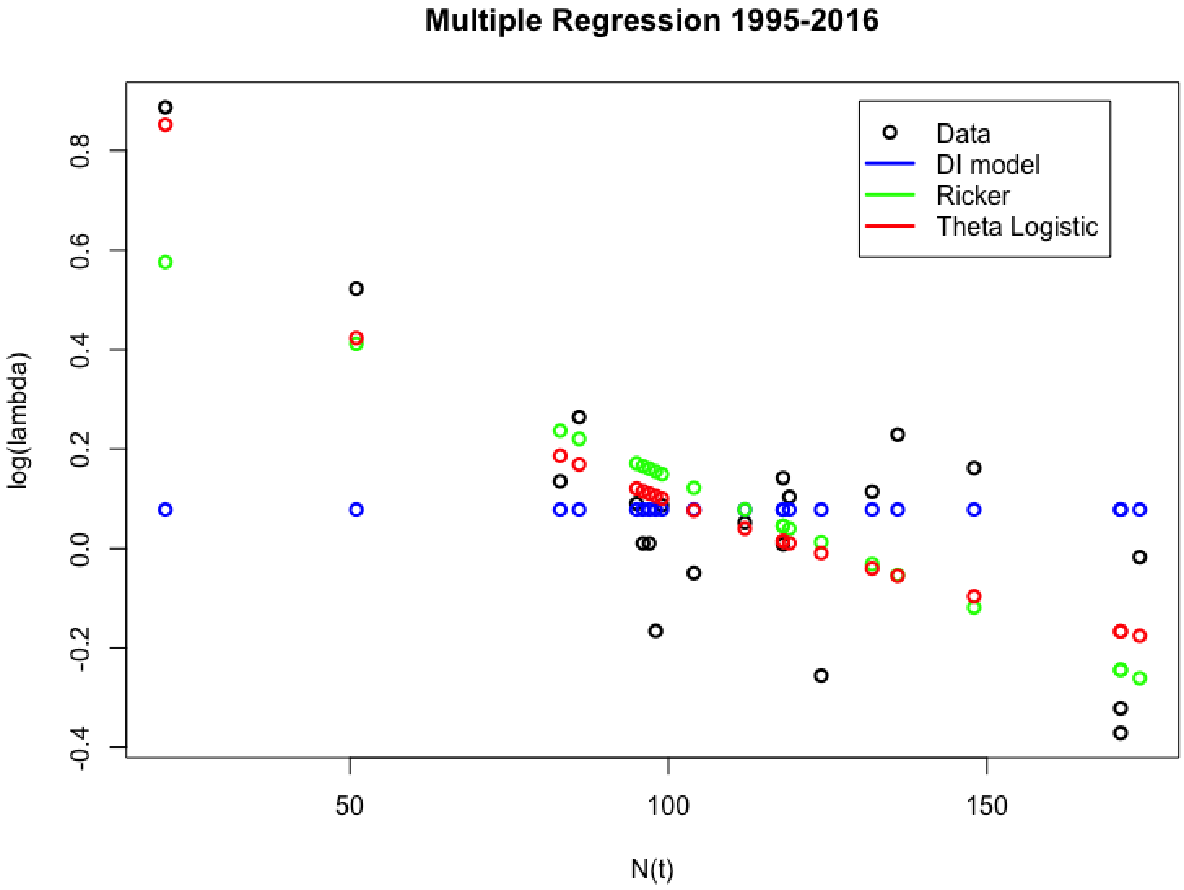


Figure 2: Multiple regression performed for years 1995-2016. The Theta-logistic model was best suited for this regression.

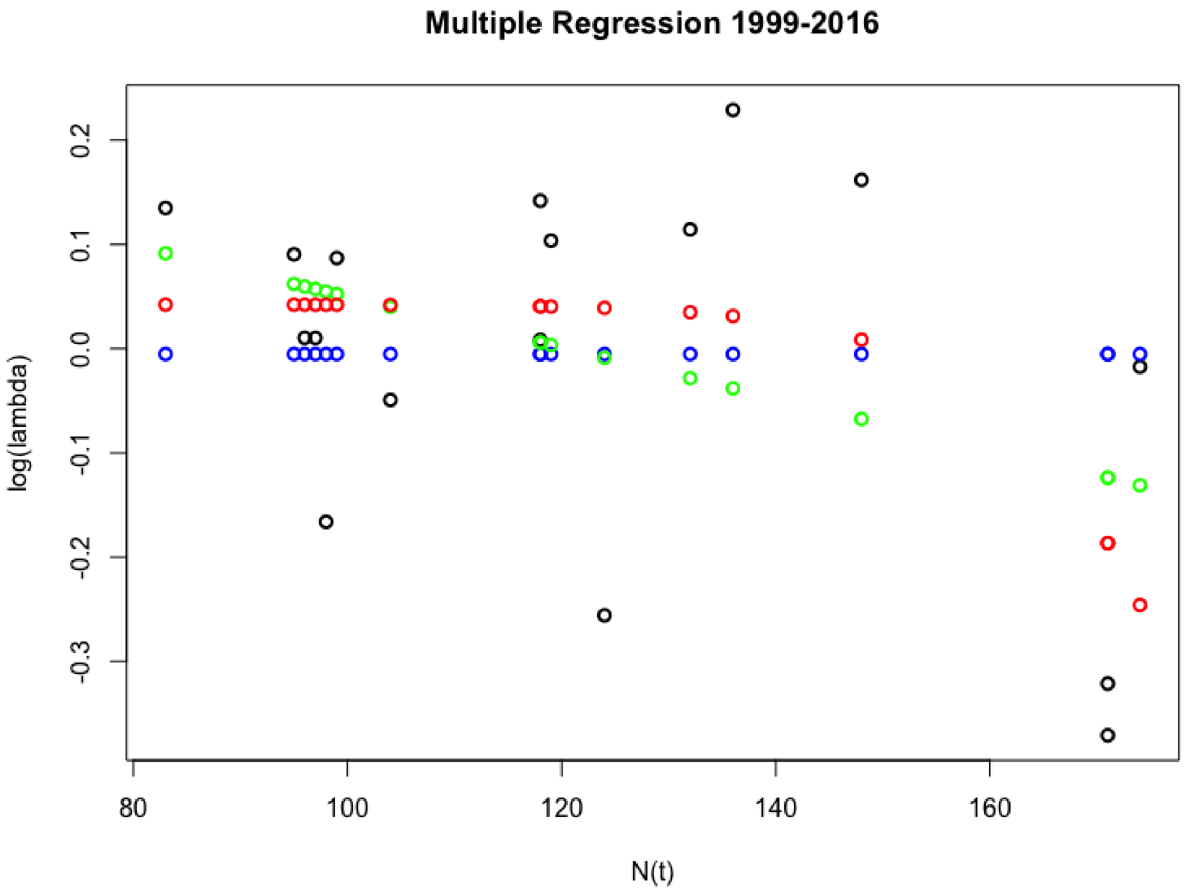


Figure 3: Multiple regression performed for years 1999-2016. The Ricker model was best suited for this regression.

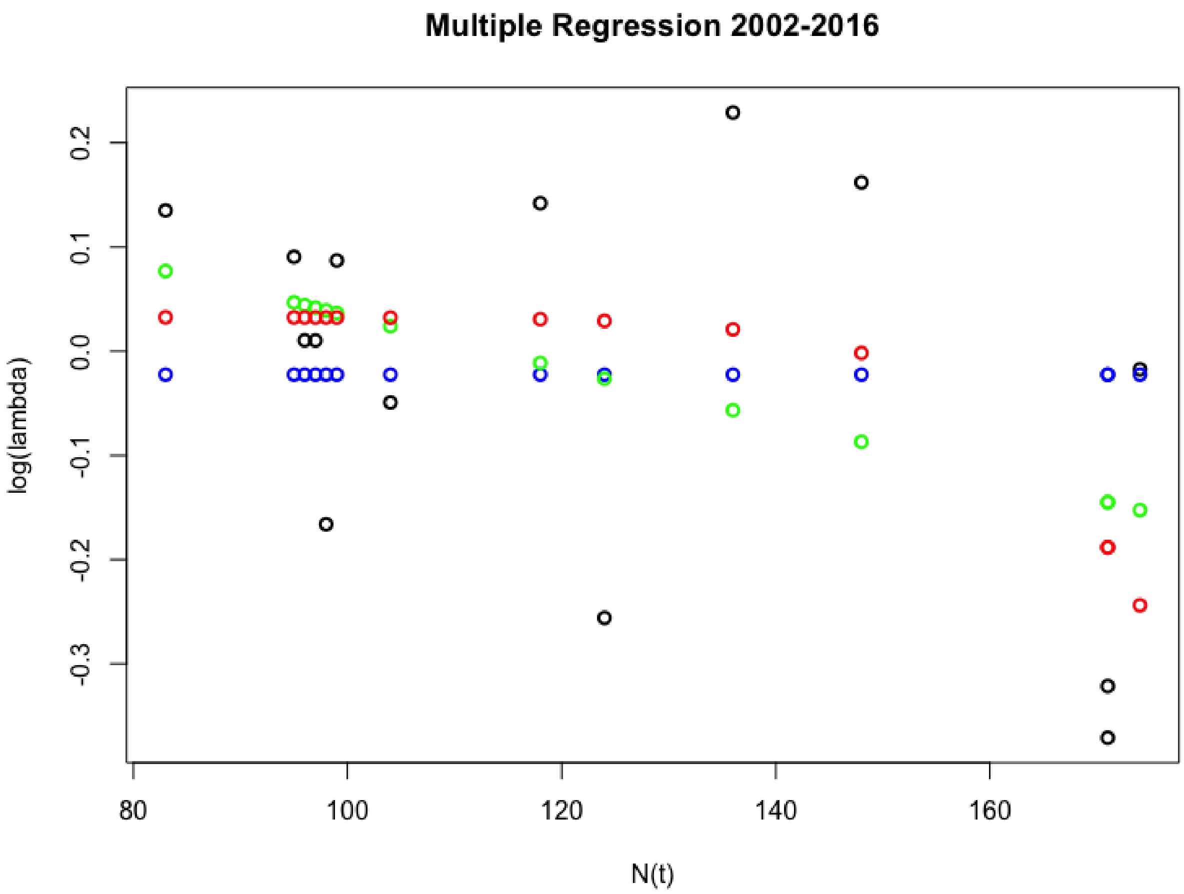
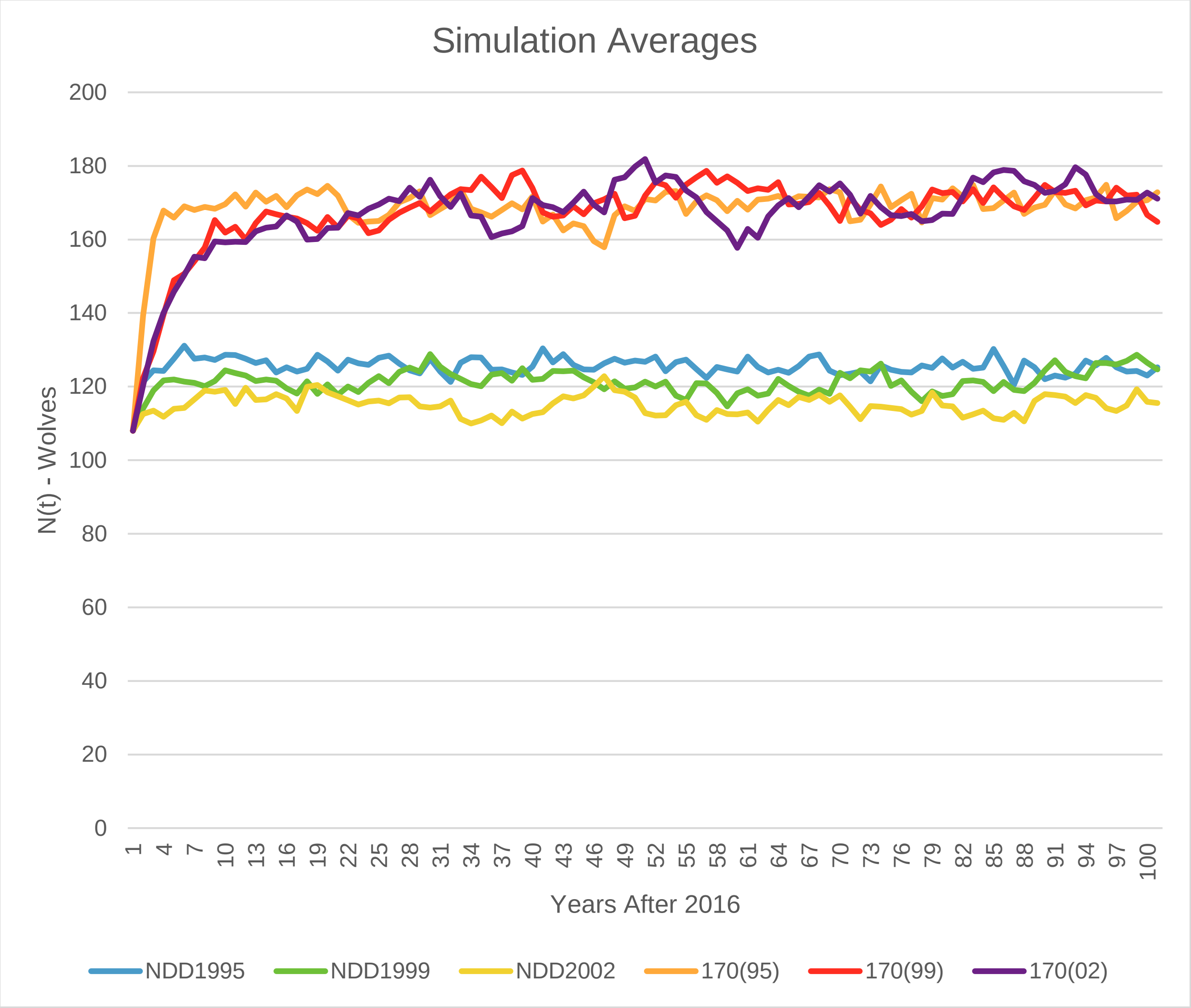


Figure 4: Multiple regression performed for years 2002-2016. The density-independent model was best suited for this regression.



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2 **Figure 5:** Average trends from each modelling approach.

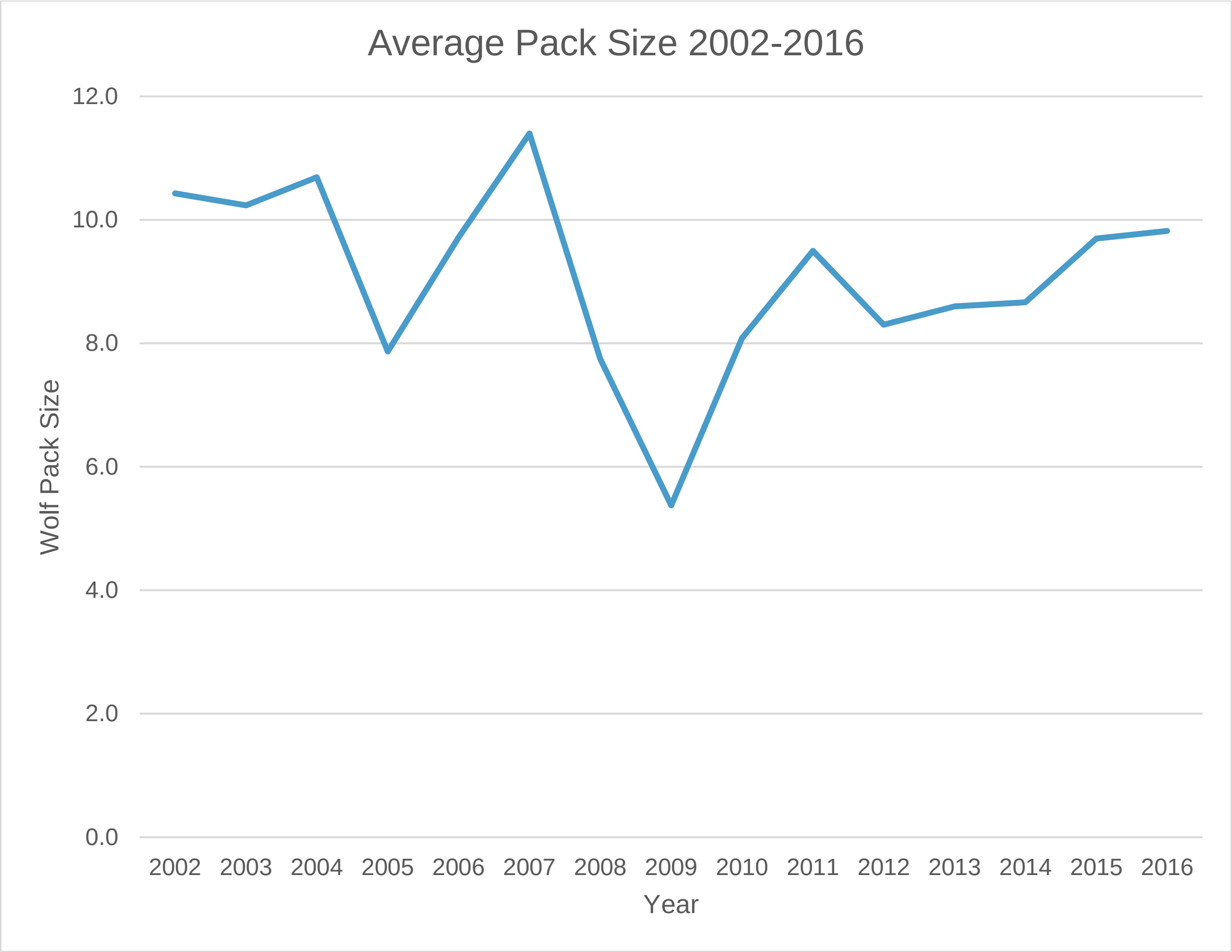

Figure 6: Average pack size from 2002-2016. Data for 1995-2001 was not available in the Yellowstone Wolf Reports.

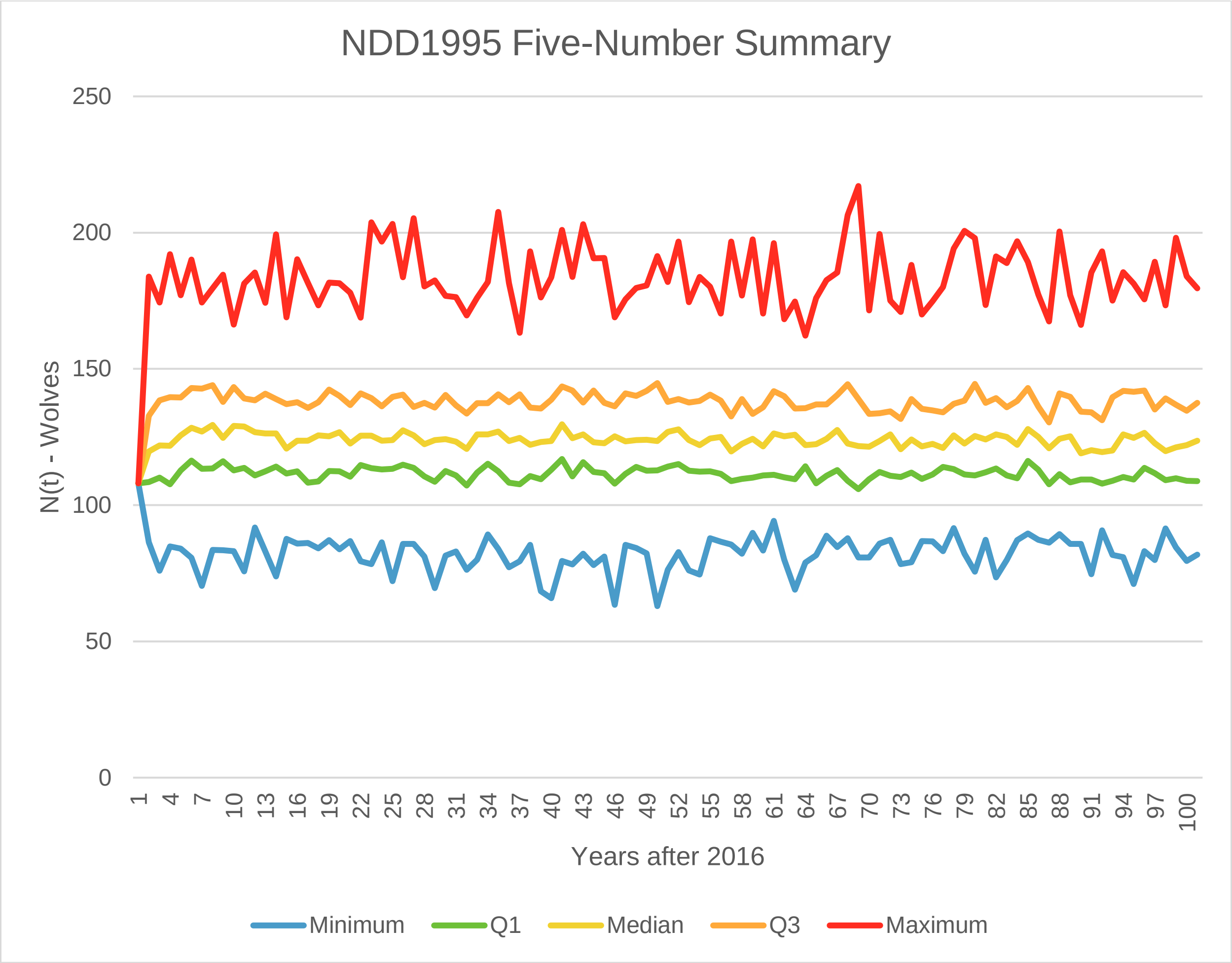

Figure 7: Five-number summary produced for each year of simulations in the model NDD1995.

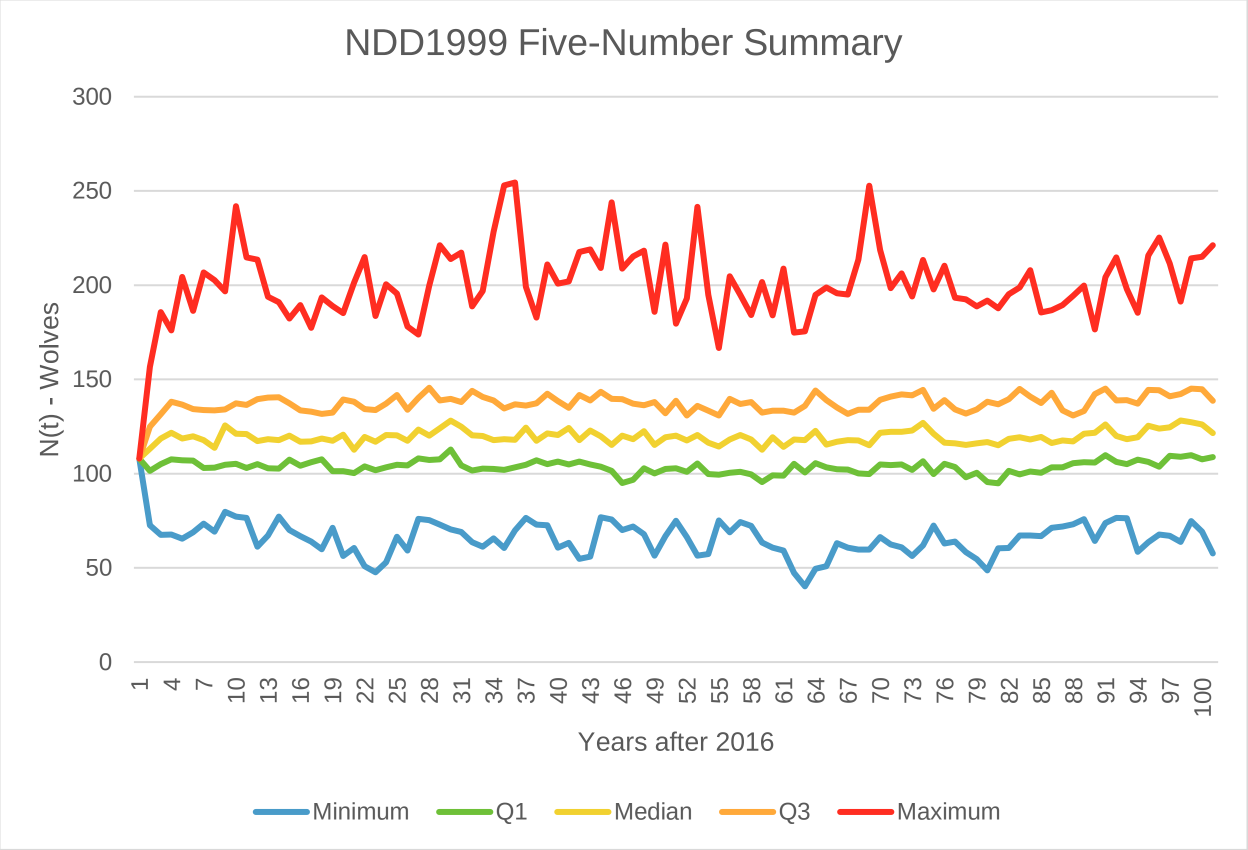

Figure 8: Five-number summary produced for each year of simulations in the model NDD1999.

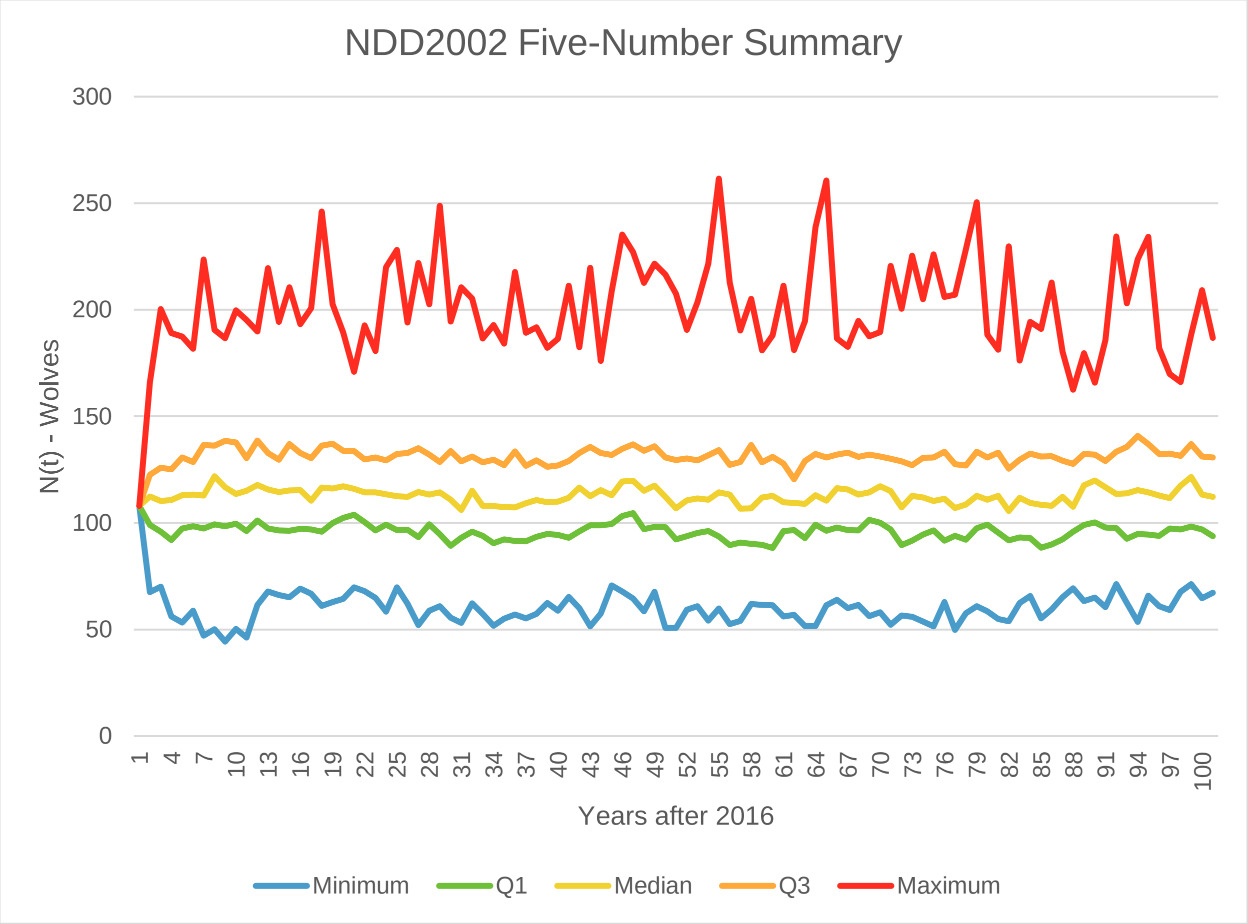

Figure 9: Five-number summary produced for each year of simulations in the model NDD2002.

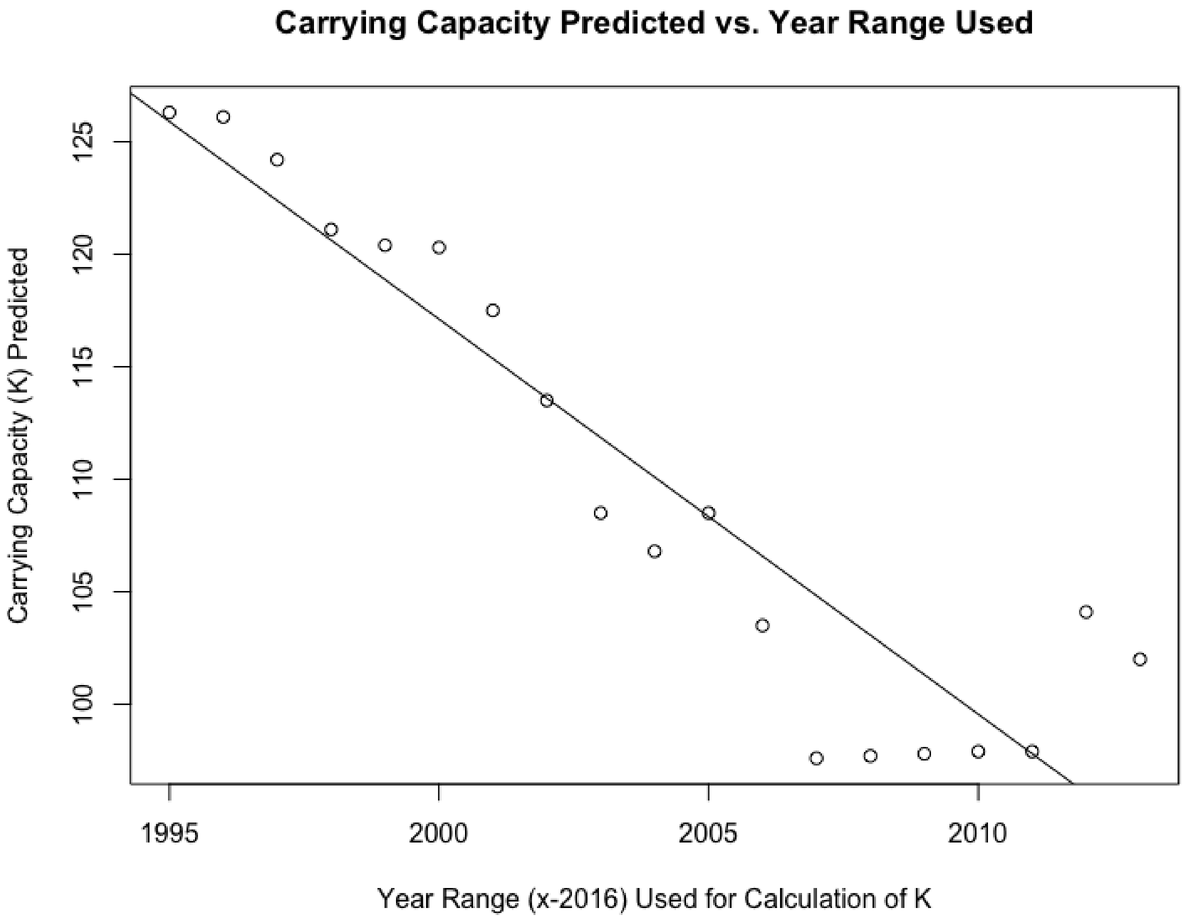

Figure 10: Carrying capacities as predicted by the Ricker regression model in relation to the range of years that were considered for the regression (F=108.1, R^2=0.8561, p=8.747E-9).

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