

Yellowstone wolf (*Canis lupus*) density predicted by elk (*Cervus elaphus*) biomass

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Abstract: The Northern Range (NR) of Yellowstone National Park (YNP) hosts a higher prey biomass density in the form of elk (*Cervus elaphus* L., 1758) than any other system of gray wolves (*Canis lupus* L., 1758) and prey reported. Therefore, it is important to determine whether that wolf–prey system fits a long-standing model relating wolf density to prey biomass. Using data from 2005 to 2012 after elk population fluctuations dampened 10 years subsequent to wolf reintroduction, we found that NR prey biomass predicted wolf density. This finding and the trajectory of the regression extend the validity of the model to prey densities 19% higher than previous data and suggest that the model would apply to wolf–prey systems of even higher prey biomass.

Key words: gray wolf, *Canis lupus*, elk, *Cervus elaphus*, Yellowstone, population regulation, prey biomass, biomass index, intraspecific mortality.

Résumé : Le domaine nord (Northern Range; NR) du parc national de Yellowstone (YNP) contient une biomasse de proies de plus grande densité, représentée par les wapitis (*Cervus elaphus* L., 1758), que tout autre système de loups gris (*Canis lupus* L., 1758) et proies connu. Il importe donc de déterminer si le système loups–proies concorde avec un modèle établi de longue date qui relie la densité des loups à la biomasse des proies. En nous servant de données de 2005 à 2012 après l'atténuation sur une période de 10 ans des fluctuations de la population de wapitis à la suite de la réintroduction des loups, nous avons constaté que la biomasse des proies du NR prédisait la densité des loups. Cette constatation et la trajectoire de la régression élargissent la validité du modèle à des densités de proies de 19 % supérieures aux données antérieures et donnent à penser que le modèle s'appliquerait à des systèmes loups–proies de biomasse de proies encore plus grande. [Traduit par la Rédaction]

Mots-clés : loup gris, *Canis lupus*, wapiti, *Cervus elaphus*, Yellowstone, contrôle de la population, biomasse de proies, indice de biomasse, mortalité intraspécifique.

Introduction

The question as to whether wolf (*Canis lupus* L., 1758) numbers are determined by food supply or social factors has been debated since 1967 (summarized in Cariappa et al. 2011; Cubaynes et al. 2014; McRoberts and Mech 2014). For many years, the issue seemed settled, as Keith's (1983) meta-analysis showing a significant relationship between wolf density and prey biomass was continually updated with new data and became stronger (Fuller 1989; Fuller et al. 2003). (Unfortunately, Wolff (1997) seemed unaware of this literature when Wolff published "Population regulation in mammals: an evolutionary perspective".)

Recently, Cariappa et al. (2011) presented a more-refined analysis of the data used by Fuller et al. (2003) which suggested that at higher prey densities, wolf numbers might be self-regulated rather than determined by prey biomass. McRoberts and Mech (2014) challenged the Cariappa et al. (2011) statistical methodology and found that parsimoniously even at high prey densities there was no significant evidence that the relationship between wolf density and prey biomass would be any different from the Fuller et al. (2003) model. However, concurrently, Cubaynes et al. (2014) concluded that more variation in adult wolf survival in the Northern Range (NR) of Yellowstone National Park (YNP) was explained by wolf density than by the abundance of the wolf's main prey there, the elk (*Cervus elaphus* L., 1758). During the years Cubaynes et al. (2014) studied (1998–2010), the NR hosted a higher density of

wolves and prey than any of the other systems included in the Fuller et al. (2003) model. Cubaynes et al. (2014: 1344) reported that their findings suggested that "...intrinsic density-dependent mechanisms have the potential to regulate wolf populations at higher ungulate densities". While not disputing that intraspecific aggression can be an important proximate factor in wolf population regulation, McRoberts and Mech (2014) concluded that such a mechanism would not in itself regulate wolf populations.

The Cubaynes et al. (2014) findings, however, do raise the question of why variation in their adult wolf survival was better explained by wolf density than by prey biomass if prey biomass ultimately determines wolf populations. Is Yellowstone wolf density ultimately determined by intraspecific strife instead of prey biomass? If so, this conclusion would represent the only known exception to the Keith (1983), Fuller (1989), and Fuller et al. (2003) model based on 32 wolf–prey systems. Thus, a closer examination of wolf density and prey biomass in the NR is required. We hypothesized that, like in all other wolf–prey populations studied except for those recolonizing or heavily hunted (Cariappa et al. 2011) (summarized by Fuller et al. 2003), Yellowstone wolf density would be predicted by prey biomass even though that biomass is higher than any previous wolf–prey biomass studied.

Materials and methods

Study area

Gray wolves were reintroduced to Yellowstone in 1995 and 1996, and their numbers immediately began increasing (Smith 2005).

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Table 1. Wolf (*Canis lupus*) and elk (*Cervus elaphus*) numbers (Peterson et al. 2014) and density in the Northern Range (NR), Yellowstone National Park (YNP).^a

Year	Wolf abundance (NR inside YNP) ^b	No. of wolves/1000 km ²	Elk abundance ^{c,d}	No. of elk/km ²
1998	42	42.21	17 838	11.66
1999	35	35.18	16 888	11.04
2000	65	65.33	15 638	10.22
2001	70	70.35	13 938	9.11
2002	78	78.39	12 838	8.39
2003	98	98.49	11 138	7.28
2004	84	84.42	12 861	8.41
2005	54	54.27	8 849	5.78
2006	75	75.38	9 241	6.04
2007	94	94.47	8 570	5.60
2008	57	57.29	9 675	6.32
2009	40	40.20	8 012	5.24
2010	38	38.19	6 118	4.00
2011	38	38.19	5 496	3.59
2012	34	34.17	5 168	3.38

^aFor 2005–2012, mean wolf density is 54 wolves/1000 km² and biomass index (BMI) = 4.99 elk/km² × 3 = 14.98. BMI was multiplied by a factor of 3 because one elk equals three white-tailed deer (*Odocoileus virginianus*) “relative biomass equivalents” as per Fuller (1989) and Fuller et al. (2003).

^bNR area inside Yellowstone National Park is 995 km².

^cIn the full 1530 km² of NR.

^dFrom 2003 through 2008, White et al. (2012) listed these values 1 year later, i.e., for 2004 through 2009. Thus, we also transposed the elk densities accordingly. The mean was 5.62, so the BMI (mean density × 3) = 16.86. Substituting that BMI for the 14.98 in the regression based on the data from Table 2 predicted a wolf density of 58 wolves/1000 km² and yielded $r^2 = 0.81$ ($P < 0.0001$).

Although wolves colonized the entire park, their greatest concentration was in the northern part of the park on 995 km² of the 1530 km² NR (Cubaynes et al. 2014). There they preyed primarily on elk (Smith et al. 2004), which numbered >17 000 (Table 1). As wolves increased on the Yellowstone NR, elk decreased, although the role of wolves in the elk decline is not agreed upon (Vucetich et al. 2005; White and Garrott 2005; Varley and Boyce 2006). By 2003, wolf numbers peaked, and by 2005, elk numbers began to stabilize (Table 1). Adult wolf mortality was due primarily to intra-specific strife (Cubaynes et al. 2014) and pup mortality was due to disease (Almberg et al. 2009, 2010, 2012).

A test of whether prey biomass on the NR determines wolf density must include a period when wolf and prey numbers had persisted long enough to have reached some kind of equilibrium (Cariappa et al. 2011). Examination of Fig. S1c in Cubaynes et al. (2014) suggests that a reasonable starting point for such an analysis would be 2005 because extreme fluctuations in elk numbers began dampening then (Table 1). Thus, we generated mean wolf density and mean prey biomass index (BMI; number of elk/km² × 3 because one elk equals three white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) “relative biomass equivalents” as per Fuller et al. 2003) from the NR wolf and elk numbers for 2005–2012 (the last data available) from Peterson et al. (2014). The elk-density data applied to the entire 1530 km² NR, but because they are densities (number/area), they apply as well to the 995 km² area where the wolf-density data were from (Table 1).

We used these data to test how well they fit in the Keith (1983), Fuller (1989), and Fuller et al. (2003) model minus the six data points that Cariappa et al. (2011) and McRoberts and Mech (2014) concluded should be deleted (Table 2). We employed a weighted regression (weight = 1/BMI_i, where BMI is the mean prey BMI as per Fuller 1989; Fuller et al. 2003) to account for the heteroscedasticity (McRoberts and Mech 2014). Keith (1983), Fuller (1989), and Fuller et al. (2003) all used an intercept in their regressions, reflecting the fact that the prey-density data used included only primary prey, for example, not American beavers (*Castor canadensis* Kuhl,

Table 2. Prey biomass and wolf (*Canis lupus*) density data used for Fig. 1 from Fuller et al. (2003: Table 6.2) minus four data points that Cariappa et al. (2011) and McRoberts and Mech (2014) concluded should be deleted, and two more that McRoberts and Mech (2014) deleted, but including the Yellowstone Northern Range data from this study.

Prey biomass index	No. of wolves/1000 km ²	Location
0.865	3	Denali Park, Alaska, USA
1.3	5	Northwestern Alaska, USA
2.002	6	Denali Park, Alaska, USA
1.531	6	Denali Park, Alaska, USA
1.114	6	Northeastern Alberta, Canada
2.24	7	Northern Alaska, USA
1.143	7	West-central Yukon, Canada
1.38	8	Southwestern Quebec, Canada
1.224	8	Northern Alberta, Canada
2.73	8	Jasper Park, Alberta, Canada
1.56	9	Interior Alaska, USA
6.17	10	North-central Minnesota, USA
1.789	12	Puksakwa Park, Ontario, Canada
2.2	14	Southwestern Quebec, Canada
4.826	14	Kenai Peninsula, Alaska, USA
7.2	18	Northern Wisconsin, USA
5.791	23	Northeastern Minnesota, USA
7.2	24	Northwestern Alberta, Canada
8.74	26	Southwestern Manitoba, Canada
6.6	28	Southern Quebec, Canada
4.572	28	Northeastern Minnesota, USA
9.15	33	Voyageurs Park, Minnesota, USA
6.645	38	East-central Ontario, Canada
6.28	39	North-central Minnesota, USA
9.9	42	Northeastern Minnesota, USA
12.576	44	Isle Royale, Michigan, USA
14.98	54	This study

1820), hares (genus *Lepus* L., 1758), and other small prey, so we also used an intercept. (Cariappa et al. 2011) challenging the Fuller et al. (2003) model, and thus McRoberts and Mech (2014) challenging Cariappa et al. (2011), did not use intercepts.)

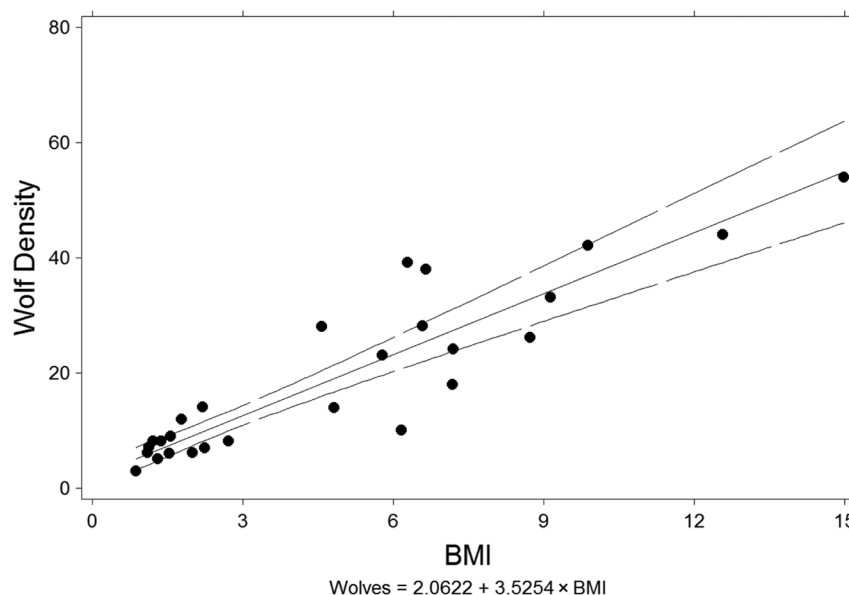
Some of the NR wolf packs range outside the park at times; the wolf-pack density outside the park is lower, but the wolf-density data in the park, based on intensive aerial radio-tracking and observation, are quite accurate. The BMI data (based on aerial elk counts) may be less accurate. As per Peterson et al. (2014), the elk data are from Eberhardt et al. (2007) for 1998–2004 and White et al. (2012) for 2005–2009. Estimates for 2010–2012 used the methods of White et al. (2012), multiplying the number of elk aurally observed by 1.32 to account for those not observed.

Since 2008, half or more of the elk typically migrated out of the park during winter (P.J. White, personal communication). Because some of the elk migrate out of the 995 km² part of the NR inside the park for part of the year, a reviewer suggested that we should also analyze the data accordingly. That reviewer supplied a range of wolf numbers (18–34) for the 535 km² of the NR outside the park, admitting that those numbers were not as accurate as those for wolves in the park. Thus, we added the midrange of the reviewer’s data (26) for the 535 km² to the mean of the wolf data for the 995 km² of the NR inside the park and used the resulting density for the full 1530 km² of the NR in our analysis. We also performed weighted regressions assuming that the mean NR BMI data were lower and higher by 20%.

Results and discussion

The mean wolf density on the 995 km² of the Yellowstone NR inside the park was 54 wolves/1000 km² and the mean prey BMI was 14.98 (Table 1). The Fuller et al. (2003) model predicted a wolf density of 55 wolves/1000 km² based on the BMI of 14.98 (Table 1).

Fig. 1. Relationship between Yellowstone National Park Northern Range (NR) wolf (*Canis lupus*) density and biomass index (BMI) based on wolf and elk (*Cervus elaphus*) populations during 2005–2012 (Table 1) in relation to data from Fuller et al. (2003) with deletions by Cariappa et al. (2011) and McRoberts and Mech (2014). Weighted regression: $r^2 = 0.81$ ($P < 0.0001$). The Yellowstone NR point is the highest point in the graph. The broken lines represent 95% confidence intervals.



Thus, these data fit the Fuller et al. (2003) BMI model well (Fig. 1), increasing the r^2 from 0.79 to 0.81 ($P < 0.0001$). Even assuming the BMI data were higher or lower by as much as 20%, r^2 still was 0.80–0.81 ($P < 0.0001$). Using the wolf density on the full 1530 km² of the NR inside and outside the park (52 wolves/1000 km²) in the analysis also yielded an r^2 of 0.81 ($P < 0.0001$).

The question remains as to why the variations in Yellowstone NR adult wolf survival were better explained by wolf density rather than by prey biomass (Cubaynes et al. 2014). Two important aspects of the Cubaynes et al. (2014) study are key. First, the study demonstrated that adult wolf survival, not wolf numbers, was density dependent. Wolf-population regulation, however, is the net result of both adult and pup survivals, along with dispersal and pup production (Mech et al. 1998; Adams et al. 2008). Second, the period of the Cubaynes et al. (2014) study (starting in 1998, which was 3 years after reintroduction of wolves to the ecosystem) included several years during which the wolf population was still establishing itself and during which there was a surfeit of elk, the wolf's primary prey there (Smith et al. 2004). For at least several years of the study, there was not enough time for wolf and elk numbers to reach any kind of equilibrium. For example, the Yellowstone NR elk numbers during the Cubaynes et al. (2014) study dropped from an estimated 17 838 to 8 012 from 1998 to 2004 (Table 1). Wolf density in the 995 km² park part of the NR also fluctuated between 35 wolves/1000 km² and 98 wolves/1000 km². This instability itself might explain why elk biomass did not explain more variability in adult wolf survival, although it did explain 43% of the variance, compared with 55% explained by wolf density (Cubaynes et al. 2014). It is notable that from about 2005 when the elk population started stabilizing (Table 1), the mean wolf density was very close to that which the Fuller et al. (2003) model predicted. Before that period (1998–2004), the model using the mean BMI of 28.33 predicted a wolf density of 102 wolves/1000 km², 4 wolves more than the 2003 wolf density, the highest density the wolves reached (Table 1).

Thus, although more variation in adult wolf survival from 1998 to 2010 in the Yellowstone NR was explained by wolf density in the Cubaynes et al. (2014) study, the best evidence is that ultimately the wolf population in the Yellowstone NR, as in other wolf-prey systems studied (Fig. 1), is determined by prey biomass. It is prob-

ably true that one of the main mechanisms involved is intra-specific 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.

These findings not only support the hypothesis that the Yellowstone NR wolf density is ultimately determined by prey biomass, but they also extend the model of Keith (1983), Fuller (1989), and Fuller et al. (2003) to higher prey biomass, as Cariappa et al. (2011) stated should be attempted. The updated regression suggests that the model would apply to wolf-prey systems of even higher biomass. Known winter wolf densities in some systems greatly exceed even the Yellowstone NR wolf density (McRoberts and Mech 2014), implying that in those systems prey biomass would be correspondingly higher. In view of our findings, future research on those systems (and a re-analysis following Cubaynes et al. (2014) but of NR data only—excluding the interior—from 2005 to 2012) would be valuable to determine whether the model continues to apply there.

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References

- Adams, L.G., Stephenson, R.O., Dale, B.W., Ahgook, R.T., and Demma, D.J. 2008. Population dynamics and harvest characteristics of wolves in the central Brooks Range, Alaska. *Wildl. Monogr.* 170: 1–25. doi:10.2193/2008-012.
- Almberg, E.S., Mech, L.D., Smith, D.W., Sheldon, J.W., and Crabtree, R.L. 2009. A serological survey of infectious disease in Yellowstone National Park's canid community. *PloS ONE*, 4(9): e7042. doi:10.1371/journal.pone.0007042. PMID: 19756151.
- Almberg, E.S., Cross, P.C., and Smith, D.W. 2010. Persistence of canine distemper virus in the Greater Yellowstone Ecosystem's carnivore community. *Ecol. Appl.* 20: 2058–2074. doi:10.1890/09-1225.1. PMID:21049890.
- Almberg, E.S., Cross, P.C., Dobson, A.P., Smith, D.W., and Hudson, P.J. 2012. Parasite invasion following host reintroduction: a case study of Yellowstone's wolves. *Philos. Trans. R. Soc. B Biol. Sci.* 367: 2840–2851. doi:10.1098/rstb.2011.0369.
- Cariappa, C.A., Oakleaf, J.K., Ballard, W.B., and Breck, S.W. 2011. A reappraisal of the evidence for regulation of wolf populations. *J. Wildl. Manage.* 75: 726–730. doi:10.1002/jwmg.74.

- Cubaynes, S., MacNulty, D.R., Stahler, D.R., Quimby, K.A., Smith, D.W., and Coulson, T. 2014. Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (*Canis lupus*). *J. Anim. Ecol.* **83**: 1344–1356. doi:10.1111/1365-2656.12238.
- Eberhardt, L.L., White, P.J., Garrott, R.A., and Houston, D.B. 2007. A seventy-year history of trends in Yellowstone's elk herd. *J. Wildl. Manage.* **71**: 594–602. doi:10.2193/2005-770.
- Fuller, T.K. 1989. Population dynamics of wolves in north-central Minnesota. *Wildl. Monogr.* No. 105.
- Fuller, T.K., Mech, L.D., and Fitts-Cochran, J. 2003. Wolf population dynamics. In *Wolves: behavior, ecology, and conservation*. Edited by L.D. Mech and L. Boitani. University of Chicago Press, Chicago, Ill. pp. 161–191.
- Keith, L.B. 1983. Population dynamics of wolves. In *Wolves in Canada and Alaska: their status, biology, and management*. Edited by L.N. Carbyn. *Can. Wildl. Serv. Rep. Ser. No. 45*. Canadian Wildlife Service, Edmonton, Alta. pp. 66–77.
- McRoberts, R.E., and Mech, L.D. 2014. Wolf population regulation revisited—again. *J. Wildl. Manage.* **78**: 963–967. doi:10.1002/jwmg.744.
- Mech, L.D., Adams, L.G., Meier, T.J., Burch, J.W., and Dale, B.W. 1998. The wolves of Denali. University of Minnesota Press, Minneapolis.
- Packard, J.M., and Mech, L.D. 1980. Population regulations in wolves. In *Biosocial mechanisms of population regulation*. Edited by M.N. Cohen, R.S. Malpass, and H.G. Klein. Yale University Press, New Haven, Conn. pp. 135–150.
- Peterson, R.O., Vucetich, J.A., Bump, J.M., and Smith, D.W. 2014. Trophic cascades in a multicausal world: Isle Royale and Yellowstone. *Annu. Rev. Ecol. Evol. Syst.* **45**: 325–345. doi:10.1146/annurev-ecolsys-120213-091634.
- Smith, D.W. 2005. Ten years of Yellowstone wolves, 1995–2015. *Yellowstone Science*, **13**: 7–33.
- Smith, D.W., Drummer, T.D., Murphy, K.M., Guernsey, D.S., and Evans, S.B. 2004. Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995–2000. *J. Wildl. Manage.* **68**: 153–166. doi:10.2193/0022-541X(2004)068[0153:WPSAEO]2.0.CO;2.
- Varley, N., and Boyce, M.S. 2006. Adaptive management for reintroductions: updating a wolf recovery model for Yellowstone National Park. *Ecol. Model.* **193**: 315–339. doi:10.1016/j.ecolmodel.2005.09.001.
- Vucetich, J.A., Smith, D.W., and Stahler, D.R. 2005. Influence of harvest, climate and wolf predation on Yellowstone elk, 1961–2004. *Oikos*, **111**: 259–270. doi:10.1111/j.0030-1299.2005.14180.x.
- White, P.J., and Garrott, R.A. 2005. Yellowstone's ungulates after wolves—expectations, realizations, and predictions. *Biol. Conserv.* **125**: 141–152. doi:10.1016/j.biocon.2005.01.048.
- White, P.J., Proffitt, K.M., and Lemke, T.O. 2012. Changes in elk distribution and group sizes after wolf restoration. *Am. Midl. Nat.* **167**: 174–187. doi:10.1674/0003-0031-167.1.174.
- Wolff, J.O. 1997. Population regulation in mammals: an evolutionary perspective. *J. Anim. Ecol.* **66**: 1–13. doi:10.2307/5959.