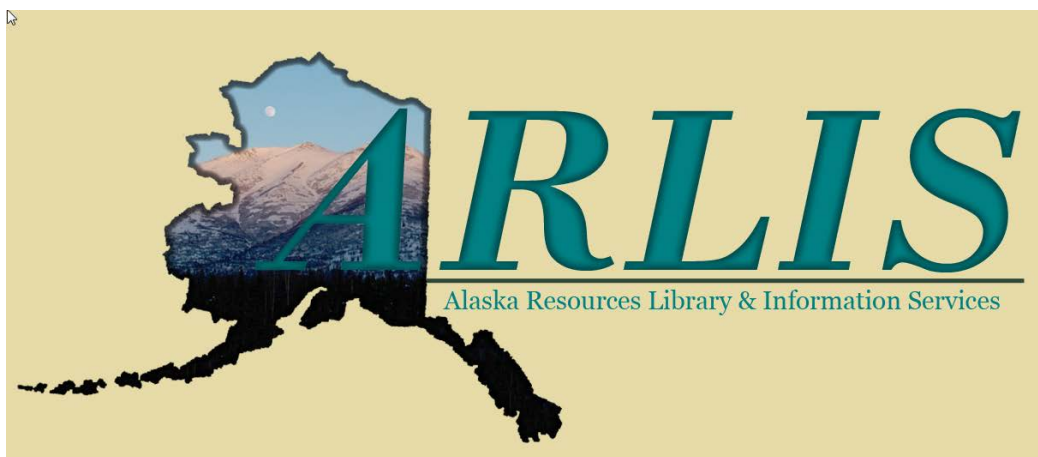


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Commentary

Wolf Population Regulation Revisited—Again

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ABSTRACT The long-accepted conclusion that wolf density is regulated by nutrition was recently challenged, and the conclusion was reached that, at greater levels of prey biomass, social factors such as intraspecific strife and territoriality tend to regulate wolf density. We reanalyzed the data used in that study for 2 reasons: 1) we disputed the use of 2 data points, and 2) because of recognized heteroscedasticity, we used weighted-regression analysis instead of the unweighted regressions used in the original study. We concluded that the data do not support the hypothesis that wolf densities are regulated by social factors. Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS biomass, *Canis lupus*, numerical response, population regulation, predation, prey biomass, wolf.

Ever since Pimlott (1967) proposed that wolf (*Canis lupus*) populations are regulated by social factors, researchers have examined that thesis. Early studies tended to accept the possibility (Mech 1970, Pimlott 1970, Wolfe and Allen 1973, Van Ballenberghe et al. 1975), but eventually workers started to question it. Packard and Mech (1980) discussed the role of vulnerable-prey biomass in regulating wolf populations and concluded that food supply was more important than previously recognized. Vulnerable-prey biomass is a valid concept but is dynamic and rarely measurable (Fuller et al. 2003). However prey biomass itself has been used as a proxy for vulnerable-prey biomass. Keith (1983) found a strong, significant, linear relationship between prey biomass and wolf density based on data from 7 studies. Fuller (1989) confirmed the relationship based on 25 studies, and Fuller et al. (2003), based on 32. These investigations strongly suggested that food supply rather than social factors was regulating wolf density. However, these researchers did not specifically investigate alternative models that might also provide an equivalent or improved fit to the data. Thus, specific testing of competing hypotheses had not occurred.

Recently Cariappa et al. (2011) reanalyzed the data that Fuller et al. (2003:Table 6.2) used in their analysis and found that nonlinear asymptotic models fit the data at least as well as a linear model. Those authors tested Type 1 (linear), Type 2 (monotonically increasing with a monotonically decreasing slope and an asymptote), and Type 3 (sigmoid with an asymptote) models (Messier 1995). Asymptotic relationships between prey biomass, represented by a biomass index (BMI), and wolf density imply that at greater wolf densities,

factors other than food supply, presumably social factors, regulate wolf density. Furthermore, Cariappa et al. (2011) found that when they excluded 4 data points that represented exploited or expanding wolf populations, Types 2 and 3 asymptotic models better fit the data than the Type 1 linear model. Cariappa et al. (2011:726) concluded that "... the data suggested that wolf populations are self-regulated rather than limited by prey biomass by at least a 3:1 margin."

We agreed with the removal of the 4 data points, but we found 2 more points from the Fuller et al. (2003) table that we believe should also be removed, those representing Algonquin Provincial Park in 1969 (Pimlott et al. 1969, Kolenosky 1972) and in 1988–1992 (Forbes and Theberge 1995). We think these data are not valid for inclusion because the wolf involved there is smaller (Way 2013) than the wolves in the rest of the study areas and is generally thought to represent a different species more closely related to the coyote (*Canis latrans*; Wilson et al. 2000, Fain et al. 2010, Chambers et al. 2012, but cf vonHoldt et al. 2011 and Rutledge et al. 2012).

To replicate the analyses of Cariappa et al. (2011), we first reanalyzed both the original data (designated Cariappa-all) and the pruned data from Fuller et al. (2003) (designated Cariappa-pruned) that Cariappa et al. (2011) used, and then we conducted the same analysis with the 2 Algonquin Park points pruned (designated Present-pruned). Because of the heteroskedasticity that Cariappa et al. (2011) recognized but did not deal with, we also reanalyzed the data using weighted regressions. These analyses yielded a different conclusion.

METHODS

The analyses included fitting the 3 models used by Cariappa et al. (2011),

$$\text{Type 1: } y_i = \beta_1 \cdot x_i + \varepsilon_i \quad (1)$$

$$\text{Type 2: } y_i = \frac{\beta_1 \cdot x_i}{\beta_2 + x_i} + \varepsilon_i \quad (2)$$

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$$\text{Type 3: } y_i = \frac{\beta_1 \cdot x_i^2}{\beta_2 + x_i^2} + \varepsilon_i \quad (3)$$

where y_i denotes wolves/1,000 km², x_i denotes BMI, the β_s are parameters to be estimated, and ε_i is a residual term assumed to follow a Gaussian (normal) distribution, $N(0, \sigma_i^2)$. We also fit a fourth, quadratic model,

$$\text{Quad: } y_i = \beta_1 \cdot x_i + \beta_2 \cdot x_i^2 + \varepsilon_i \quad (4)$$

to facilitate a statistically rigorous test for curvature in the relationship between wolf density and BMI.

We fit all regression models using maximum likelihood methods for each of the 3 datasets under the homoscedasticity assumption of a Gaussian distributed, constant residual variance (i.e., for all i , $\sigma_i^2 = \sigma^2$). Under this assumption, maximum likelihood and least squares parameter estimates are identical. We calculated the same metrics reported by Cariappa et al. (2011): the natural logarithm of the Gaussian likelihood,

$$\ln(\lambda) = -\frac{n}{2} \ln(2 \cdot \pi \cdot \sigma^2) - \frac{1}{2 \cdot \sigma^2} \sum_{i=1}^n (y_i - \hat{y})^2 \quad (5)$$

where λ denotes likelihood and n denotes sample size; Akaike's Information Criterion,

$$\text{AIC} = 2 \cdot p - 2 \cdot \ln(\lambda) \quad (6)$$

where p denotes the number of estimated parameters: for the Type 1 model, $p = 2$ (β_1 , σ); for the Type 2, Type 3, and Quad models, $p = 3$ (β_1 , β_2 , σ); small sample Akaike's Information Criterion,

$$\text{AIC}_c = \text{AIC} + \frac{2 \cdot p \cdot (p + 1)}{n - p - 1} \quad (7)$$

and

Akaike weights,

$$\text{WT}_j = \frac{\exp(-(1/2)\Delta_j)}{\sum_{i=1}^3 \exp(-(1/2)\Delta_i)} \quad (8)$$

where j denotes a Type j model, $\Delta_j = \text{AIC}_{c,j} - \text{AIC}_{c,\min}$, and $\text{AIC}_{c,\min}$ is the minimum AIC_c value among the 3 models. The Akaike weights represent normalized, relative likelihoods and are useful for comparing models (Burnham and Anderson 2002:Section 2.9.1). Comparison of metrics for the Cariappa-all and Cariappa-pruned datasets as we calculated them and as reported by Cariappa et al. (2011) constituted a consistency check for the methods.

Graphs of residuals versus BMI for the 12 combinations of the 3 datasets and the 4 models all exhibited clear evidence of heteroskedasticity (Fig. 1). In such cases, the assumption that $\sigma_i^2 = \sigma^2$ is violated, and weighted analyses should be used whereby each observation is weighted by the inverse of its residual variance, that is, the weight for the i th observation is $w_i = \sigma_i^{-2}$ (Draper and Smith 1966). Preliminary analyses indicated that residual variances were approximately proportional to BMI for all datasets and models. Therefore, to accommodate heteroscedasticity, we weighted all observa-

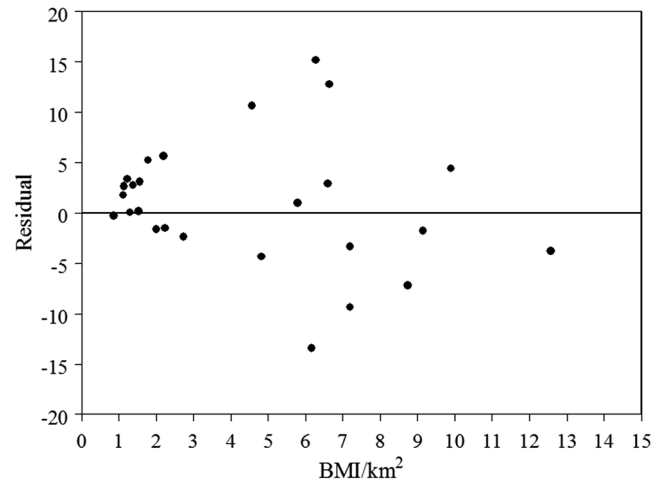


Figure 1. Residuals versus ungulate biomass index (BMI) in white-tailed deer equivalents/km² (Fuller et al. 2003:Table 6.2) for the type-1 unweighted linear model and the present-pruned dataset. The present-pruned data set includes all 28 North American wolf populations used by Cariappa et al. (2011) except 2 from Algonquin Park, Ontario (Fuller et al. 2003:Table 6.2).

tions by the inverse of their corresponding BMI for all analyses. We recalculated the same metrics described in Equations (5)–(8) using the heteroscedastic form of $\ln(\lambda)$:

$$\ln(\lambda) = -\frac{1}{2} \sum_{i=1}^n \left[\ln(2 \cdot \pi \cdot \sigma_i^2) + \left(\frac{y_i - \hat{y}}{\sigma_i} \right)^2 \right] \quad (9)$$

In addition, for the Types 2 and 3 models, we explicitly estimated the asymptotes, β_1 , and their standard errors.

The issue of whether the Type 1 linear model or either of the Type 2 or Type 3 nonlinear asymptotic models better represents the relationship between wolf density and BMI is closely related to the issue of whether the relationship is linear or exhibits curvature. If the quality of fit of an asymptotic model is statistically significantly greater than the fit of a linear model, then curvature in the relationship could be concluded; otherwise, curvature cannot be concluded and in the interest of parsimony the simpler linear model would generally be selected. Statistically rigorous tests of whether the fit of a more complex model is better than the fit of a less complex model are possible only if the less complex model form is nested within the more complex model form. For example, the Type 1 linear model is nested in the Quad model because the latter can be reduced to the former simply by eliminating the quadratic term. Therefore, if the fit of the Quad model is statistically significantly better than the fit of the Type 1 model, then a conclusion of curvature in the relationship is justified. However, because the Type 1 linear model is not nested in either the Types 2 or 3 models, statistical significance cannot be assessed by comparing the fits of these models; hence the use of the Quad model. Although the Quad model is not necessarily asymptotic, it does permit a considerable degree of flexibility and is appropriate for assessing curvature. Of importance, the Quad model is used only for this purpose of assessing curvature; we

do not suggest that it should be used instead of either the Type 2 or Type 3 models in the case that significant curvature is detected.

When models are nested, the likelihood ratio test may be used to test whether the fit of a more complex model is statistically significantly greater than the fit of a less complex nested model (Strawderman 1983). The test statistic is calculated as,

$$D = 2 \cdot [\ln(\lambda_1) - \ln(\lambda_2)], \quad (10)$$

where λ_1 and λ_2 are the likelihoods for the fits of the less complex and more complex models, respectively. We used the likelihood ratio test to test for curvature by testing whether the fit of the Quad model, which can accommodate curvature, was statistically significantly better than the fit of the Type 1 linear model, which cannot accommodate curvature. For this study, D may be assumed to follow a χ^2 distribution with degrees of freedom, df , equal to the difference in the number of parameters for the models being compared; in this case, $df=1$.

RESULTS

For the unweighted analyses, using $p=1, 2$, and 3 for the Type 1, 2, and 3 models as did Cariappa et al. (2011), our estimates of the metrics described in Equations (5)–(8) for the Cariappa-all and Cariappa-pruned datasets were, with 1 minor exception, within rounding errors of those reported by Cariappa et al. (2011) indicating consistency with respect to methods. When using $p=2, 3$, and 3 for the Type 1, 2, and 3 models as is correct, the Type 1 linear model was superior for the Cariappa-all and Present-all datasets, but the Type 2 asymptotic model was superior for the Cariappa-pruned dataset (Table 1). For each dataset, $0.50 \leq WT \leq 0.60$ for

the superior model, but at least 1 other model had $WT \geq 0.20$.

For the weighted analyses, the Type 2 model had greater WT for the Cariappa-all and Present datasets, whereas the Type 3 model had greater WT for the Cariappa-pruned dataset. For each dataset, $0.48 \leq WT \leq 0.67$ for the asymptotic model, but $0.20 \leq WT \leq 0.30$ for the Type 1 linear model. Thus, the evidence was not compelling that either of the Type 2 or Type 3 models was superior to the Type 1 linear model for any of the datasets.

The differences in $\ln(\lambda)$, AIC, and AIC_c between the unweighted and weighted analyses can be attributed to accommodating or not accommodating the effects of heteroscedasticity when calculating $\ln(\lambda)$. The only difference between Equations (5) and (9) is whether a separate or common value of σ^2 is used for each observation.

For the weighted analyses, none of the likelihood ratio tests for curvature in the relationships between wolf density and BMI for any of the 3 datasets indicated that the quality of fit of the Quad model was statistically significantly greater at the $\alpha = 0.05$ level than for the Type 1 linear model. This result, in combination with the similarities in the likelihood estimates for the Quad model and both the Types 2 and 3 models, suggests lack of significant curvature in the relationships.

For the Type 2 model, estimates of the asymptote ranged from 89.39 to 107.33 with standard errors ranging from 52.88 to 65.47. Lower bounds for 95% confidence intervals for the estimates were less than 0, and upper bounds ranged from approximately 190 to 235. Thus, the asymptote estimates were so imprecise as to render them nearly meaningless. This result can be attributed to multiple causes including a model that is either poorly formulated or that has

Table 1. Comparison of weighted versus unweighted regressions for wolf density relationships with biomass index (BMI) used by Cariappa et al. (2011) and this study. Model 1 is linear, model 2 monotonically increases with a monotonically decreasing slope and asymptote, and model 3 is sigmoid with an asymptote. AIC is Akaike's Information Criterion, and AIC_c is the same adjusted for small samples. ΔAIC_c is the difference between nested models. Wt is a relative measure of the fit of a model to data, with larger values indicating better fits.

Dataset	Model	No. of model parameters (p)	Sample size	$\ln(\lambda)^a$	AIC	AIC_c	ΔAIC_c	Wt
Unweighted								
Cariappa all	1	2	32	−111.1	226.1	226.5	0.0	0.52
	2	3	32	−110.0	226.0	226.9	0.4	0.42
	3	3	32	−112.1	230.1	230.9	4.4	0.06
Cariappa pruned	1	2	28	−97.3	198.6	199.1	1.7	0.24
	2	3	28	−95.2	196.4	197.4	0.0	0.56
	3	3	28	−96.2	198.4	199.4	2.0	0.20
Present pruned	1	2	26	−84.5	172.9	173.4	0.0	0.62
	2	3	26	−83.7	173.4	174.5	1.1	0.36
	3	3	26	−86.4	178.7	179.8	6.4	0.03
Weighted								
Cariappa all	1	2	32	−105.8	215.5	216.0	1.0	0.29
	2	3	32	−104.1	214.1	215.0	0.0	0.48
	3	3	32	−104.8	215.6	216.5	1.5	0.33
Cariappa pruned	1	2	28	−92.0	187.9	188.4	1.5	0.22
	2	3	28	−90.4	186.8	187.8	0.9	0.30
	3	3	28	−90.0	185.9	186.9	0.0	0.47
Present pruned	1	2	26	−77.7	159.4	160.0	1.5	0.31
	2	3	26	−75.7	157.4	158.5	0.0	0.66
	3	3	26	−78.9	163.8	164.9	6.4	0.03

^a $\ln(\lambda)$, log likelihood.

too many parameters relative to attributes of the data. In particular, for this study, BMI values corresponding to 90% of the Type 2 model asymptote estimates ranged from approximately 140–175, whereas the greatest BMI value in any of the datasets was less than 15. Thus, any attempt to fit an asymptotic model to these data should be expected to produce imprecise estimates of the asymptote and inconclusive results regarding model superiority. Estimates of the asymptotes for the Type 3 model for the 3 datasets ranged from 27.64 to 31.71, all considerably less than the greatest wolf densities observed in the data. This anomalous result also suggests an inappropriate model relative to the nature of the data.

Overall, although a Type 2 or Type 3 asymptotic model produced slightly better representations of the relationship between wolf population density and BMI exhibited in the data than the Type 1 linear model, the degree to which they better represent the relationship is not great enough to be characterized as statistically significant. Further, the estimates of the asymptotes, particularly their imprecision, for the Types 2 and 3 models suggest insufficient observations for large BMI values to justify the asymptotic model forms and parameterizations. Thus, the general technical result is that based on the data available, no compelling argument can be made to reject the simpler, more parsimonious Type 1 linear model in favor of either the Type 2 or Type 3 nonlinear models.

DISCUSSION

Our findings indicate that, contrary to Cariappa et al. (2011), the hypothesis that wolf density is regulated by prey biomass has more support at all biomass values measured to date (Fuller et al. 2003). Although social factors such as territoriality and intraspecific strife, age of first reproduction, and dispersal, as discussed by Packard and Mech (1980) do operate in wolf populations, ultimately they might only fine tune basic wolf densities to biomass values at finer scales than have so far been measured. This conclusion is not all that surprising given reports of wolf densities in individual pack territories (Table 2) that far exceed those reported for population densities used in the Fuller (2003) table. Those large pack densities evince that at least within packs, social factors do not limit densities.

Cariappa et al. (2011) also speculated that a putative lower limit on wolf-territory size postulated by Jedrzejewski et al. (2007) might have led to the upper asymptote that Cariappa et al. (2011) found. However, the evidence for a lower asymptotic territory size is faulty. Jedrzejewski et al. (2007:74) maintained that “... wolves did not reduce their territories below a certain asymptotic value (approx. 80–100 km²), even if prey numbers continued to grow.” Their evidence Jedrzejewski et al. (2007:Table 5) cited both individual and territory size and mean population-pack territory size. Nevertheless, some of the mean territory sizes they cited included individual territories as small as 50 km² (Fuller 1989), and these authors overlooked reported territories as small as 20 km² (Mech and Tracy 2004; Table 2). Thus, although failure to reject a null hypothesis

Table 2. Wolf densities reported in individual wolf-pack territories that exceed mean wolf-population densities reported by Fuller et al. (2003)

Density wolves/1,000 km ²	Territory size (km ²)	No. of locations	Source
156	64	213	Scott and Shackleton (1982)
67	75	135	Scott and Shackleton (1982)
92 ^a			Peterson and Page (1988)
59 ^b	153 ^c	94 ^c	Fuller (1989)
175 ^c	23	39	Mech and Tracy (2004)
308 ^c	20	44	Mech and Tracy (2004)
182 ^c	33	88	Mech and Tracy (2004)
59 ^d	84	28	Mech and Barber-Meyer (unpublished)
106 ^e	38	30	Mech and Barber-Meyer (unpublished)

^a Mean of 5 packs.

^b Mean of 4 packs.

^c The same pack at different periods from October 1997–March 1999.

^d Wolf 7,172 pack of 5 during winter from 2 July 2012 to 15 July 2013.

^e Wolf 7,175 pack of ≥4 during winter from 27 July 2012 to 15 July 2013.

does not constitute proof of the hypothesis, the analyses do not support either the putative lower asymptote of 80–100 km² for wolf-pack-territory size or the proposal of Jedrzejewski et al. (2007) that social factors determine minimum pack territory size.

Our results also contradict the conclusion that an upper density bound of 69 wolves per 1,000 km² exists in wolf populations (Cariappa et al. 2011). Instead, we found no evidence for a maximum wolf density except that dictated by biomass.

Some subjectivity lies in the selection of data to use in determining the shape of models relating wolf density to BMI as evidenced by the different choices made by Fuller et al. (2003), Cariappa et al. (2011), and our analyses. Although we agree with the decision by Cariappa et al. (2011) to delete 4 points from the Fuller et al. (2003) data, other workers might not agree with them or with our rationale for deleting 2 more points. However, even if one agrees with our decision, and even if the questionable unweighted analyses are used, our analysis clearly demonstrates that the difference between concluding that wolf density is regulated by food or by social factors—a 5-decade controversy—depends on only 2 of 28 data points.

MANAGEMENT IMPLICATIONS

Our analyses indicate that the question of whether wolf density is regulated by prey biomass or social factors at high-prey densities should remain open. The most important information that managers should consider is that, regardless of what regulates wolf densities, such densities can far exceed the 69/1,000 km² proposed as an upper bound under the model of Cariappa et al. (2011; Table 2). Researchers, however, should closely examine all possible regulating factors. As Cubaynes et al. (2014) found, high wolf densities can increase intraspecific aggression. Although such aggression in itself may not regulate wolf populations because pup

survival and dispersal are also critically important (Mech et al. 1998, Adams et al. 2008), aggression remains a factor to be considered and warrants further research on its role in wolf population regulation.

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