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Original Article

An Historical Overview and Update of Wolf–Moose Interactions in Northeastern Minnesota

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ABSTRACT Wolf (*Canis lupus*) and moose (*Alces americanus*) populations in northeastern Minnesota, USA, have fluctuated for decades and, based on helicopter counts, moose numbers declined to a new low from 2006 to about 2012. Other steep declines were found in 1991 and 1998 during periods when moose counts were done with fixed-wing aircraft; these declines also appeared to be real. Winter wolf numbers, monitored in part of the moose range, had been increasing since about 2002 to the highest population in decades in 2009. However, from 2009 to 2016, wolves decreased precipitously, and the moose-population decline leveled off from 2012 to 2017. Calf:population ratios from 1985 to 1997 and from 2005 to 2016 were inversely related to wolf numbers in the wolf-study area the previous winter both as wolves increased and decreased in abundance. Similarly, log annual growth rates of moose numbers were negatively correlated with counts of wolves in the prior year. Other factors such as nutrition and parasites, and possibly climate change, likely have been involved in the recent moose decline. However, wolves, as in other areas, appear to have contributed to the decline in the northeastern Minnesota moose population at least in part through predation on calves, supporting earlier reports. Published 2018. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS *Alces americanus*, Minnesota, moose, population, predation, survival, wolf.

Moose (*Alces americanus*) in northeastern Minnesota, USA, have been declining, and substantial effort is being expended to determine the reason (Lenarz et al. 2009, 2010; DelGiudice et al. 2015; Severud et al. 2015; Carstensen et al. 2017). Lenarz et al. (2009) considered the moose population stable at approximately 7,600 animals until about 2006, although it also could be considered stable until after 2009 (G. DelGiudice, Minnesota Department of Natural Resources, personal communication). Lenarz et al. (2009) also suggested warming weather might be a cause of the moose decline and did not conclude that predation by wolves (*Canis lupus*) was important. However, Mech and Fieberg (2014) challenged the weather findings, and provided evidence of a concurrent wolf increase in at least part of the area, suggesting that wolf predation might have been at least partly responsible

for a calf decline through 2013. Moose calves were an important summer food of wolves in the area; in 2013, the only year for which such data were available, wolves were a major source of moose-calf mortality (Severud et al. 2015, Barber-Meyer and Mech 2016). These new findings, continued concern about the moose-population trajectory, and more recent changes in wolf and moose numbers, prompted us to review the relationships between wolves and moose in northeastern Minnesota over the past several decades and to update, extend, and refine the analyses of Mech and Fieberg (2014).

STUDY AREA

Our data are from 2 overlapping study areas, the primary northeastern Minnesota moose range where the Minnesota Department of Natural Resources (MN DNR) surveys the population annually, and a long-term, wolf-study area comprising 13% of the moose-survey area. The moose-survey area comprised 15,300 km^2 of northeastern Minnesota between the Lake Superior shore and Ontario, Canada, centered about 48°N, 92°W (Fig. 1). Peek et al. (1976) summarized literature suggesting that moose numbers there varied between approximately 500 and >4,000 between 1915 and 1970. From 1984 to 2016, aerial estimates have ranged
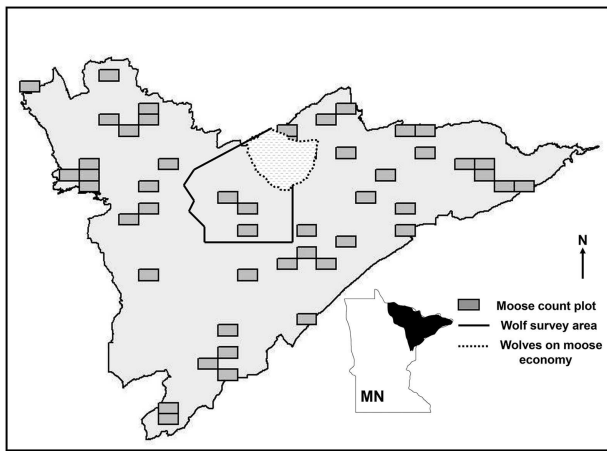
Figure 1. Moose range in northeastern Minnesota, USA, and a long-term wolf-study (2,060-km²) area in the middle of the moose range. The northeastern part of the wolf-study area was likely devoid of deer in winter, so wolves there fed primarily on moose. Distribution of moose-count plots vary each year; shown is a sample of a single year's distribution.

between 2,757 and 8,854, though changing survey methods likely contributed to the variability (Fig. 2; Table 1). The 2,060-km² wolf-study area was in the north-central part of the moose-survey area and included high, medium, and low moose densities (Mech 2009, DelGiudice 2016; Fig. 1). Wolf numbers between winter 1966–1967 and 2014–2015 varied between 35 and 97 (Mech 1986, 2009; Mech and Fieberg 2014).

Wolves were legally protected on federal land in the Superior National Forest, which comprises much of the northeastern Minnesota moose range, in 1970 and throughout Minnesota beginning in 1974. From late 2012 through late 2014, they were subjected to regulated harvest and then completely protected again. Wolves in

both the wolf-study area and the larger moose range preyed primarily on white-tailed deer (*Odocoileus virginianus*), beavers (*Castor canadensis*), and moose, generally calves and older adults (Stenlund 1955, Mech and Frenzel 1971, Peek et al. 1976, Mech and Nelson 2013, Barber-Meyer and Mech 2016).

Deer and moose originally inhabited the entire wolf-study area during both summer and winter. However, during a series of severe winters from 1968 to 1974, wolves depleted the deer that remained during winter in the northeastern part, where habitat was of lowest quality (Mech and Frenzel 1971, Mech and Karns 1977). That area has remained devoid of wintering deer ever since (Nelson and Mech 2006). A few deer that inhabit the northeastern part of the wolf-study area during summer migrated west-southwesterly to near Ely, Minnesota, during winter, which also hosts resident deer year-around (Nelson and Mech 1981, 1987). Wolves that inhabited the northeastern part of the study area during summer mimicked the migrating deer by focusing their winter activity to the west-southwest near the deer (Mech and Boitani 2003; L.D. Mech and S. H. Barber-Meyer, U.S. Geological Survey, unpublished data). In addition, fire burned 376 km² of the east-central part of the wolf-study area in 2011; moose are only now beginning to reoccupy that area. The decline in moose left a near void of prey and wolves during winter from the central to the northeastern part of the wolf-study area.

The only other predator of moose in the area was the black bear (*Ursus americanus*). In 2013, bears accounted for 16% of the natural mortality of radiotagged moose calves (Severud et al. 2015); other than the 2013 data, no information is available about bear predation in the area. Both male and female moose were legally harvested from 1993 until 2007. However, from 2007 to 2012, only males were killed except
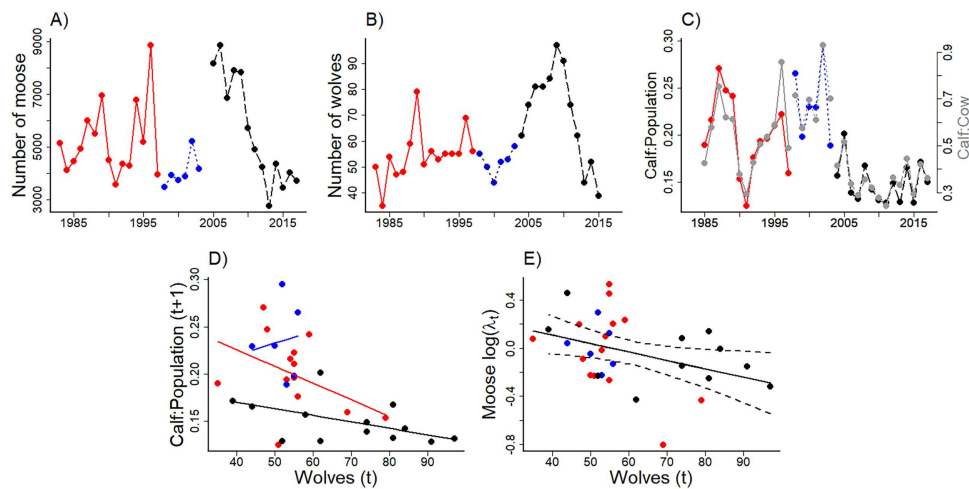

Figure 2. Estimates of (A) moose numbers in northeastern Minnesota, USA (J. Giudice, Minnesota Department of Natural Resources, personal communication), (B) wolf numbers in a wolf-study area in the middle of the moose range (Fig. 1) that comprises 13% of the moose range, (C) moose calf:adult female ("cow"; gray dots) and calf:population ratios (black dots) in northeastern Minnesota, and estimated relationships between wolf numbers and (D) moose calf:population ratios and (E) moose log growth rates (dotted lines depict pointwise 95% CIs for the regression line). Methods for surveying moose changed over time. From 1983 to 2003 surveys were conducted using a fixed-wing aircraft with a single observer (1983–1997, in red) or with 2 observers (1998–2003, in blue), and estimates since 1983 were adjusted using a sightability correction factor estimated using a double-sampling approach (Gasaway et al. 1986). Since 2005, moose have been surveyed from helicopters with estimates adjusted for visibility bias using a sightability model (Fieberg 2012, Giudice et al. 2012).

Table 1. Wolf numbers in a 2,060-km^2 study area of northeastern Minnesota, USA, 1983–2016 (Mech 1986, 2009; L. D. Mech and S. H. Barber-Meyer, U.S. Geological Survey, unpublished data)[a] and annual moose counts in a 15,300-km^2 area in and around that area (J. Giudice, Minnesota Department of Natural Resources, personal communication)[b]. Year refers to the year at the end of winter (e.g., 1983 = winter 1982–1983). Calf:cow, ratio of calves to adult females.

Year	Number of wolves (prior year)[a]	Moose estimate[b] (SE)[c]	Calf:cow	Calf:total
1983	47	5,148 (608)	.[d]	.[d]
1984	50	4,112 (559)	.[d]	.[d]
1985	35	4,451 (729)	0.43	0.19
1986	54	4,918 (1,751)	0.58	0.22
1987	47	5,994 (1,325)	0.75	0.27
1988	48	5,492 (1,094)	0.62	0.25
1989	59	6,938 (1,812)	0.61	0.24
1990	79	4,492 (1,040)	0.38	0.15
1991	51	3,572 (1,088)	0.29	0.12
1992	56	4,362 (1,076)	0.43	0.18
1993	53	4,292 (1,088)	0.51	0.19
1994	55	6,768 (1,198)	0.54	0.20
1995	55	5,193 (1,240)	0.59	0.21
1996	55	8,854 (.)	0.86	0.22
1997	69	3,960 (851)	0.49	0.16
1998	56	3,464 (754)	0.71	0.27
1999	55	3,915 (760)	0.57	0.20
2000	50	3,733 (571)	0.70	0.23
2001	44	3,879 (663)	0.61	0.23
2002	52	5,214 (729)	0.93	0.30
2003	53	4,161 (924)	0.70	0.19
2004	58	.[e]	0.42	0.16
2005	62	8,158 (1,574)	0.52	0.20
2006	74	8,840 (1,523)	0.34	0.14
2007	81	6,860 (1,139)	0.29	0.13
2008	81	7,887 (1,345)	0.36	0.17
2009	84	7,835 (1,127)	0.32	0.14
2010	97	5,699 (840)	0.28	0.13
2011	91	4,896 (749)	0.24	0.13
2012	74 (82)[a]	4,226 (730)	0.36	0.15
2013	62 (92)[a]	2,757 (444)	0.33	0.13
2014	44	4,351 (878)	0.44	0.17
2015	52	3,446 (637)	0.29	0.13
2016	39	4,023 (583)	0.42	0.17
2017	25–34[f]	3,708 (508)	0.36	0.16

[a] Wolf data through 2012 as per Mech and Fieberg (2014), except for those in parentheses (see Methods). Numbers in parentheses represent the figures used by Mech and Fieberg (2014).

[b] As explained in the Methods, the following moose data in this table differ slightly from those used by Mech and Fieberg (2014): moose estimates from 2005 to 2013 differ due to rounding; calf:cow ratios from 1985–1996, which are also shifted later by a year relative to those in Mech and Fieberg (2014); and calf: total ratios from 2004 to 2011, which are also shifted earlier by a year relative to those in Mech and Fieberg (2014).

[c] Counts after 2004 used helicopters; fixed-wing aircraft were used previously, with a single observer from 1983 to 1997 and 2 observers since 1998.

[d] Moose were only classified as cow/calf, antlered adult male (bull), or unknown adult in 1983 and 1984.

[e] Moose population estimate was deemed unreliable in 2004 due to changing survey methodology, but the calf:population ratio was useable because that was based on raw proportions of calves and adults not subject to inter-year bias.

[f] Range based on known pack numbers for some packs plus estimates for others.

for a few females killed by Native American hunters; annual harvest averaged 197 from 2002 through 2008 (Lenarz et al. 2010). Lenarz et al. (2010) gave details about the vegetation, topography, and weather in the area.

Teasing out the role of wolf predation in ungulate declines is difficult because many factors can predispose prey to wolf (and to varying extents other predators, such as bear) predation. Malnutrition, diseases, and parasites are examples, yet one can seldom determine from prey remains whether any of these factors were involved in the predation. With calves, there are additional predisposing factors (Barber-Meyer and Mech 2008). Nevertheless, the more wolves there are (perhaps up to a point) to take advantage of any of these factors, the greater the wolves' possible effect on the population.

METHODS

Wolf numbers in the wolf-study area have been monitored since winter 1968–1969 via counts of radiomarked packs and aerially snow-tracking nonradioed wolves on the numerous waterways (Mech 1973, 1986, 2009; Mech and Fieberg 2014). Until 2010, this technique allowed complete counts of the resident (i.e., nonfloater) wolves. However, during 2011–2016, dispersal and mortality resulted in fewer radioed wolves in some parts of the wolf-study area. Weather extremes produced either too little snow or too much powdery snow to allow us to fully estimate the wolf population with these methods.

Therefore, we re-examined the 2011–2016 wolf-count data, including 2011 and 2012 wolf numbers of Mech and

Fieberg (2014), which we had derived by extrapolating differences in annual mean sizes of packs radioed in consecutive years. As the wolf population dropped, we had fewer radioed packs and fewer packs radioed for consecutive years, so this extrapolation became less accurate. During our re-examination, we supplemented our known counts from radioed packs with information about prey density where we had no radioed packs. Results from decades of annual winter wolf-survey flights indicated that the area held no deer during winter (Nelson and Mech 2006), and few moose (S. H. Barber-Meyer and L. D. Mech, unpublished data). Thus we examined the number of moose and deer seen in 10 individual, annual, 34-km² moose-census plots in that area since 2010 (DelGiudice 2016). We found that the area held no deer (Nelson and Mech 2006) and so few moose (a biomass index of 0.78/km² as per Fuller et al. [2003]) that it would support a wolf density of only 4.8/1,000 km² based on the formula of Mech and Barber-Meyer (2015). Our aerial wolf radiotracking and observations had also shown that radioed wolves dispersed during winter, and there were only infrequent, if any, wolf tracks (i.e., no consistent use by a resident pack). We then used our known wolf counts and track observations in the rest of the wolf-study area to derive known minimum wolf counts for 2011–2016 that approximated the actual number, but in the case of the 2011 and 2012 figures, they were lower than those first reported by Mech and Fieberg (2014; Table 1).

Moose in northeastern Minnesota have been aerially counted since 1959 (Peek et al. 1976; Lenarz 1998, 2008; DelGiudice 2016, 2017). Starting in 1983, population estimates were derived by adjusting counts using a sightability correction factor estimated using a double-sampling approach (Gasaway et al. 1986, Lenarz 1998). From 1983 to 1997, fixed-wing surveys were conducted at various times over winter with a single observer; whereas, since 1998, the survey was conducted at a consistent time each winter and used 2 observers. Since 2004, Minnesota Department of Natural Resources survey teams flew 2 Bell Jet Ranger OH-58 helicopter (Bell Helicopter, Fort Worth, TX, USA) transects within a stratified random sample of survey plots (from a total of 436) that differed each year (DelGiudice 2016). Since 2005, moose estimates were then derived using a modified Horvitz–Thompson estimator that adjusted for sightability and sampling (Fieberg 2012, Giudice et al. 2012). Calf:population estimates were based on raw counts. Moose population estimates from 2004 onward, however, required observers to accurately record a measure of visual obstruction, which was later used to estimate and adjust counts for imperfect detection. In 2004, observers were inconsistent in how they recorded visual obstruction; therefore, we did not include the abundance estimate from 2004 in our analysis. We did, however, include the 2004 calf:population estimate in our analysis.

The double-sampling approach, used with fixed-wing flights during the early and middle survey periods, assumed that more intensive flights (which follow initial counts) result in perfect detection. By contrast, counts during the last survey period were adjusted using a model fit to detection–nondetection data collected using radiomarked individuals. These latter surveys also relied on helicopters, which although more costly, should produce more reliable counts. Estimates of detection probabilities from the latter surveys tended to be lower and generally thought to be more accurate (J. Giudice, MN DNR personal communication).

As a result of MN DNR staff turnover, differences among staff in the assignment of years to winters (e.g., some assigned 1983 to winter 1983–1984, whereas others assigned 1984 to that winter) resulted in data files with slightly different numbers. The MN DNR data we used are the most up-to-date and corrected (J. Giudice, MN DNR, personal communication; Table 1) and differ somewhat from those used by Mech and Fieberg (2014). In particular, to correct Table 1 in Mech and Fieberg (2014), the calf:adult female (hereafter, calf:cow) data from 1984 to 1995 were shifted later by 1 year, and the calf:population data from 2005 to 2012 were shifted earlier by 1 year. These changes now appropriately align the calf:cow and calf:population data with the wolf counts in the prior year. The original analysis of calf:population ratios in Mech and Fieberg (2014) were correct (i.e., they used data that were properly aligned, but data were transcribed incorrectly when forming Table 1); the original analysis of calf:cow ratios used counts that were not properly aligned.

We used the new wolf-count figures and updated moose estimates and calf:population data from 2013 to 2016 to update the regression between the proportion of calves one year and the wolf numbers the previous year with which Mech and Fieberg (2014) assessed the wolf–moose relationship. We extended the calf analysis back to 1985 to include the period of wolf increase and then decline. As a further refinement, we used calf:population ratios rather than calf:cow ratios in our analyses because of the difficulty of distinguishing adult females from adult males with shed antlers. Using calf:population ratios assumes a constant adult male:adult female ratio, and variation in that ratio could cause spurious differences between calf:cow and calf:population ratios. However, our calf:cow and calf:population ratios were correlated ($r = 0.92$). We also reran and extended the Mech and Fieberg (2014) analysis of the moose count and wolf numbers the previous year for 1983–2016. We conducted the analyses in Program R (R Core Team 2016).

Statistical Methods

Let c_t represent the moose calf:population ratio, $r_t = \log(M_t/M_{t-1})$ the estimated log-transformed annual growth rate of moose, and W_t the estimated number of wolves in year t, scaled and centered to have mean 0 and standard deviation of 1. Further, let $S_t = (S_{1t}, S_{2t}, S_{3t})$ be a vector of indicator variables used to identify the unique survey periods: $S_t = (1, 0, 0)$ for fixed-wing surveys conducted from 1983 to 1997, $S_t = (0, 1, 0)$ for fixed-wing surveys conducted from 1998 to 2003, and $S_t = (0, 0, 1)$ for helicopter surveys conducted since 2004. We used generalized least squares, implemented using the gls function in the nlme package of Program R (Pinheiro and Bates 2000, Pinheiro et al. 2016, R Core Team 2016), to model the relationship between c_t, and (W_{t-1}, S_t).

Changes in survey aircraft and methods could have resulted in systematic differences in population estimates over time; therefore, to be conservative in our inference, we started with a global model in which the intercept and slope (associated with wolves in year $t-1$) varied by survey period:

$$c_t = \alpha_1 S_{1t} + \alpha_2 S_{2t} + \alpha_3 S_{3t} + \beta_1 S_{1t} W_{t-1} + \beta_2 S_{2t} W_{t-1} + \beta_3 S_{3t} W_{t-1} + \varepsilon_t \tag{1}$$

We then used Akaike's Information Criterion (AIC) to determine whether reduced models might be preferred, including an analysis of covariance model with constant slope and also the model with no effect of survey period. We assumed residuals followed an autoregressive (1) autocorrelation structure and modeled response heterogeneity by assuming the variance of the residuals increased as a power function of the mean (Pinheiro and Bates 2000):

$$\mathrm{Cor}(\varepsilon_t, \varepsilon_{t-j}) = \rho^{|t-j|} \tag{2a}$$

$$\mathrm{Var}[c_t | \ W_{t-1}, S_t] = \sigma^2 E[c_t | W_{t-1}, S_t]^{2\theta} \tag{2b}$$

We applied backwards stepwise selection using AIC, implemented using the stepAIC function in the MASS library, to determine an appropriate reduced model (Venables and Ripley 2002). We used the same approach to model the relationship between r_t and (W_{t-1}, S_t), except that we assumed residuals had constant variance, $\mathrm{Var}[c_t] = \sigma^2$. We evaluated model assumptions using residual versus fitted value plots and plots of residuals versus each predictor and versus year.

The 1996 moose estimate seemed unusually high, and possibly due to an artifact, so we refit the regression model relating estimated annual growth rates of moose to previous wolf counts after deleting this observation. Data and R code used to fit the models have been archived with the University of Minnesota's Digital Conservancy and made accessible through a permanent Universal Resource Locater (Fieberg et al. 2017). The wolf data are archived by Mech and Barber-Meyer (2017).

RESULTS

Published historical data indicate that estimated moose numbers in northeastern Minnesota have fluctuated between approximately 2,760 and 8,800 for the past few decades, and that from 1935 to 1955 estimates were below 1,000 (Table 1; Peek et al. 1976). Moose highs around 1989, 1996, and 2006 all came when wolf numbers in our wolf-study area were relatively low or increasing (Fig. 2A and B). Although historical calf:cow ratios once dropped to 0.29, generally they were much greater until about 2006 near the time when wolf numbers in our wolf-study area were heading toward their long-time highs and when helicopters replaced fixed-wing aircraft for the moose surveys. Calf:population ratios showed a similar trend, although not as extreme (Table 1; Fig. 2C).

Wolf numbers, after increasing from 53 in 2002 to 97 in 2009 (Mech and Fieberg 2014), dropped to an estimated 25–34 by 2016 (Table 1). Point estimates of moose numbers dropped from 8,840 (SE = 1,523) in 2006 to 4,226 (SE = 730) in 2012 and have since leveled off (Table 1; Fig. 2A; also see ArchMiller et al. [2017, in press]). Calf: population ratios in winter, which serve as a survival index of calves born the previous spring, were inversely related to wolf population estimates in the previous year (Fig. 2D). These ratios were also generally greater and exhibited more variability during early survey periods when wolf population sizes were lower. The best-fit model for c_t included S_t, W_{t-1}, and their interaction (ΔAIC = 2.48 for the full model relative to the model with main effects only). The regression coefficients for W_{t-1} were negative during the early (-0.027, SE = 0.012, $P = 0.04$) and late survey (-0.010, SE = 0.005, $P = 0.07$) periods and positive, but not statistically significant, during the middle survey period (0.018, SE = 0.078, $P = 0.82$; Table 2).

The best-fit model for the estimated, annual, log growth rate of moose (r_t) included only the previous year's wolf density (W_{t-1}). The estimated regression coefficient was negative (-0.105, SE = 0.048, $P = 0.04$), suggesting moose growth rates were negatively associated with wolf numbers in the previous year (Fig. 2E). These results changed very little when data from 1996 were dropped. Using backwards selection with AIC again led us to a model that only contained W_{t-1}, and the slope and its SE changed minimally ($\widehat{\beta} = -0.091$, SE = 0.040).

DISCUSSION

Throughout the past half century, northeastern Minnesota moose have lived with wolves and bears. Moose numbers have fluctuated greatly, contrary to Lenarz et al. (2009), including ≥2 major declines (1990 through 1993 and 1997 through 2001) before the current drop. Each of the 2 previous major declines reached nadirs almost as low as the current nadir between 2012 and 2016; in both previous cases, the population recovered when wolf numbers in our wolf-study area were at their concurrent lows. Conceivably the depth of these lows was related to the earlier methods used to estimate moose numbers. However, the 1990–1993 low was found during a period when the 1983–1997 estimation method was consistent, so this result was not due to difference in estimation method. The 1997–2001 low

Table 2. Regression coefficients relating moose calf:population ratios (c_t) in northeastern Minnesota, USA, from 1985 to 2016 in year t, to the estimated number of wolves in year $t-1$, W_{t-1} (scaled and centered to have mean of 0 and SD of 1). The vector $S_t = (S_{1t}, S_{2t}, S_{3t})$ was used to allow for different intercepts in each of the unique survey periods: $S_t = (1, 0, 0)$ for fixed-wing surveys conducted from 1983 to 1997, $S_t = (0, 1, 0)$ for fixed-wing surveys conducted from 1998 to 2003, and $S_t = (0, 0, 1)$ for helicopter surveys conducted since 2004.

Variable	Coeff.	SE	t	P
S_{1t}	0.191	0.011	16.82	<0.001
S_{2t}	0.245	0.050	4.89	<0.001
S_{3t}	0.156	0.008	18.82	<0.001
$S_{1t}W_{t-1}$	−0.027	0.012	−2.16	0.04
$S_{2t}W_{t-1}$	0.018	0.078	0.24	0.82
$S_{3t}W_{t-1}$	−0.010	0.005	−1.90	0.07

included the 1997 count made with the previous count method and remained similarly low even with the change in fixed-wing survey methods, so the difference in methods did not explain it either.

The latest moose decline shows a similar pattern. Wolves in our study area began increasing about 2001 and peaked in 2009. As wolves became resistant to canine parvovirus and increased substantially (Mech and Goyal 2011), moose numbers from 1985 to 2016 were inversely related to wolf numbers as was the calf:population ratio (except for 1998 to 2003 when the relationship was nonsignificant).

A good test of whether wolves contributed to low moose-calf survival would be whether calf survival increased coincident with the wolf decline. Our data since 2013 show that wolves declined drastically from winter 2008–2009 to winter 2015–2016, and the decreasing trend in both moose numbers and calf:population ratio leveled off or increased concurrently with the wolf decline. This recent trend supports the hypothesis that wolf predation on moose calves contributed to the decline of moose from 2005 to 2011 (Mech and Fieberg 2014, Severud et al. 2015).

We do not claim that wolf numbers only influence moose populations during declines nor that wolves are the only factor affecting moose numbers. We merely highlight the above periods because moose declines have gained public and researchers' attention. Obviously, recent years of both our wolf and moose data provide only suggestive information about the current moose population trajectory. However, our new and revised data signal a critical downward turn in the wolf population in our wolf-study area and an apparent response by moose. Viewed in the long history of the relationships between those wolf numbers and the moose population as well as wolf–moose relations elsewhere (Peterson et al. 1984, Larsen et al. 1989, Testa et al. 2000, Bertram and Vivion 2002, Patterson et al. 2013), current data strengthen growing findings that wolves are important to the direction of the moose population trend.

In 2013, wolves were the single greatest cause of mortality (52–72%) for radiocollared moose calves in northeastern Minnesota, taking 38–53% of 34 radiocollared calves (Severud et al. 2015). (The minimum figures are based on known wolf-caused mortality, whereas larger numbers include known, probable, and possible wolf-caused mortality.) The negative correlation between calf:population ratios and prior-year wolf counts during the early and late-survey periods, as well as the negative correlation between moose annual, log, growth rates and prior-year wolf counts are consistent with wolves having some effect. The positive relationship between calf:population ratios and prior-year wolf counts during 1998–2003 was more ambiguous and not statistically significant. Note that this period included relatively stable wolf numbers compared with the increasing wolf trend in the early period and decreasing trend in the late period.

Whereas wolves were the most important predator, bears also killed 4 of 25 radioed moose calves that died of natural causes in a northeastern Minnesota study from May to December 2013 (the only year for which there are data;

Severud et al. 2015). Bears are also significant predators of moose calves in Ontario (Patterson et al. 2013). Thus, it is possible that bears could have an important effect on moose calf survival as well. Whereas bears mainly kill young moose, wolves also kill adult moose in the area (Mech and Frenzel 1971, Lenarz et al. 2009). Although many of these moose are old, or sustained other life-threatening conditions, at least some of the wolf-caused adult mortality probably also contributes to limiting moose numbers (Mech and Nelson 2013, Carstensen et al. 2017). If so, the recently decreased wolf population in our wolf-study area and possibly in the surrounding area should also increase survival of adult moose and thus contribute to an increase in the moose population.

Wolves in much of the northeastern Minnesota moose range fed primarily on deer, with moose and beavers being secondary (Stenlund 1955, Frenzel 1974, Barber-Meyer and Mech 2016). This prey suite allowed wolf numbers to build to 47/1,000 km^2 in our wolf-study area (97 wolves/2,060 km^2 in 2009), a relatively high density (Fuller et al. 2003). Thus, deer might have subsidized this high wolf density while wolves also preyed on moose and contributed to the moose decline (Barber-Meyer and Mech 2016). Also, the deer population hosted brain worm (*Parelaphostrongylus tenuis*) that then infected adult moose and killed them or predisposed them to wolf predation (Karns 1967, Lankester 2010, Barber-Meyer and Mech 2016). Some moose killed by wolves were predisposed to this predation by brainworm infections, although almost certainly calves were not (Carstensen et al. 2017).

The wolf decline in our wolf-study area after 2009 was probably due mostly to decreasing moose numbers, and later the decreasing deer population (Grund and Walberg 2012, Barber-Meyer and Mech 2016). Public wolf harvesting in autumn–winter 2012–2013, 2013–2014, and 2014 likely had an effect in the more accessible parts (~25%) of our wolf-study area, and possibly in other parts of the northeastern Minnesota moose range. However, most wolves taken by the public are killed in the more accessible areas, and much of the moose range is inaccessible during the autumn and winter wolf seasons.

As indicated earlier, changes in wolf numbers in our wolf-study area do not necessarily reflect changes in the entire northeastern Minnesota moose range. However, the basic trends in the wolf-study area and those in the rest of moose range may be similar because 1) the wolf-study area comprises 13% of the northeastern Minnesota moose range; 2) both the wolf-study area and the moose range include regions where deer form the main prey and other regions where only moose and beavers are available; 3) both areas include high, medium, and low moose densities; and 4) both areas include wilderness and areas easily accessible to humans.

Given the above relationships, would the northeastern Minnesota moose population be declining if there were no wolves? Our findings do not answer this question definitively. Other possible, important mortality factors such as brainworm, other parasites and diseases, malnutrition and climate-change-related factors might be affecting the

moose population as well. However, ungulate populations with wolves tend to occur at lower densities than wolf-free prey populations, especially where bears are also present and where human harvest of ungulates occurs (Ripple and Beschta 2012).

We found an inverse relationship between wolf-population trend and trend in moose calf:population both as wolves increased and decreased. We also found evidence that the historical northeastern-Minnesota wolf and moose population trends were similarly inverse. These results update, refine, and extend the conclusions of Mech and Fieberg (2014) and suggest that the decline of northeastern Minnesota moose since 2006 at least would not have been as steep without wolves' presence and influence.

MANAGEMENT IMPLICATIONS

The northeastern Minnesota moose population will no doubt continue to fluctuate for the foreseeable future. With all the possible mortality factors apart from wolves that affect that population, we strongly support continued radio-collaring studies of both adult female and calf moose to determine survival and cause-specific mortality. Also, given the relative paucity of data on black bear predation on moose calves in northeastern Minnesota, we recommend continued research to fill that important information gap.

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