

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

USGS Northern Prairie Wildlife Research Center Wildlife Damage Management, Internet Center for

2014

Re-Evaluating the Northeastern Minnesota Moose Decline and the Role of Wolves

L. David Mech

USGS Northern Prairie Wildlife Research Center, david_mech@usgs.gov

John Fieberg

University of Minnesota, jfieberg@umn.edu

Follow this and additional works at: <http://digitalcommons.unl.edu/usgspwrc>

Mech, L. David and Fieberg, John, "Re-Evaluating the Northeastern Minnesota Moose Decline and the Role of Wolves" (2014). *USGS Northern Prairie Wildlife Research Center*. 291.

<http://digitalcommons.unl.edu/usgspwrc/291>

This Article is brought to you for free and open access by the Wildlife Damage Management, Internet Center for at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in USGS Northern Prairie Wildlife Research Center by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.



Commentary

Re-Evaluating the Northeastern Minnesota Moose Decline and the Role of Wolves

L. DAVID MECH,^{1,2} U.S. Geological Survey, Northern Prairie Wildlife Research Center, 8711–37th St. SE, Jamestown, ND 58401, USA
JOHN FIEBERG, University of Minnesota, Department of Fisheries, Wildlife and Conservation Biology, St. Paul, MN 55108, USA

ABSTRACT We re-evaluated findings from Lenarz et al. (2009) that adult moose (*Alces alces*) survival in northeastern Minnesota was related to high January temperatures and that predation by wolves (*Canis lupus*) played a minor role. We found significant inverse relationships between annual wolf numbers in part of the moose range and various moose demographics from 2003 to 2013 that suggested a stronger role of wolves than heretofore believed. To re-evaluate the temperature findings, we conducted a simulation study, mimicking the approach taken by Lenarz et al. (2009), to explore the potential for concluding a significant relationship exists between temperature and survival, when no association exists. We found that the high R^2 s and low probabilities associated with the regression models in Lenarz et al. (2009) should be viewed cautiously in light of the large number of fitted models ($m = 45$) and few observations ($n = 6$ for each of 5 response variables). Published 2014. **This article is a U.S. Government work and is in the public domain in the USA.**

KEY WORDS *Alces alces*, *Canis lupus*, climate change, Minnesota, moose, predation, temperature, survival, wolf.

A moose (*Alces alces*) population that has long inhabited northeastern Minnesota has been declining since 2006, and considerable research has been ongoing to determine the cause(s) of the decline (Lenarz et al. 2009, 2010; DelGiudice et al. 2011). Climate change has been implicated as playing a leading role in the recent moose declines in Minnesota (Murray et al. 2006, Lenarz et al. 2009). For example, temperatures above a critical threshold in January were found to explain >78% of the variability in estimated spring, fall, and annual moose survival rates (Lenarz et al. 2009). Lenarz et al. (2010:1020) analyzing the same data considered that “Although it is premature to conclude that climate change is ultimately responsible for the decline of moose in northeastern Minnesota, it is clear that proximate sources of mortality, independent of climate change, probably played a minor role in their decline.” This conclusion is consistent with the authors’ attribution of only 5 deaths to wolf predation out of the 85 radio-collared adult male and female moose that died during the study. However, 18 scavenged carcasses and 7 mortalities that could not be examined (Lenarz et al. 2009) could have been killed by wolves. A secondary reason Lenarz et al. (2009, 2010) considered wolves to have played a minor role in the moose decline is that they believed that wolf numbers had remained constant from 2000 to 2010.

This assumption, however, needs elaboration. The wolf numbers Lenarz et al. (2010) referred to as being constant were statewide, not specific to the study area and were estimated 5 years apart with wide confidence intervals (Erb 2008, Erb and DonCarlos 2009). In actuality, wolf numbers in an area that overlaps the Lenarz et al. (2010) study area by 20% (Fig. 1) had increased after the year 2000 to the highest levels in 40 years (Mech 2009; L. D. Mech, U.S. Geological Survey, unpublished data), after having just gained resistance to canine parvovirus (Mech et al. 2008).

Wolves can reduce moose populations in the region, as well-documented in Isle Royale National Park 98 km from the northeastern Minnesota study area and at the same latitude (Peterson et al. 1984), and wolves regularly prey on moose in northeastern Minnesota (Mech and Nelson 2013). In several areas, predation on calves limits moose populations (Larsen et al. 1989, Testa et al. 2000, Bertram and Vivion 2002). The extent to which northeastern Minnesota wolves prey on moose calves during summer is unknown, although moose calves do form part of their diet there (Frenzel 1974, Van Ballenberghe et al. 1975); the Minnesota Department of Natural Resources has been conducting adult and calf mortality studies that will shed further light on possible causes of the moose decline (Severud et al. 2012). During the moose-population decline in the Lenarz et al. (2009, 2010) study area and the wolf increase in our wolf-survey area, the proportion of moose calves decreased steadily (Lenarz et al. 2010). Furthermore, in at least the northern part of the Lenarz et al. (2009, 2010) study area, the primary prey of northeastern Minnesota wolves—the white-tailed deer (*Odocoileus virginianus*)—are almost non-existent

Received: 12 February 2014; Accepted: 7 July 2014
Published: 26 August 2014

¹E-mail: mechx002@umn.edu

²Present address: The Raptor Center, University of Minnesota, 1920 Fitch Ave, St. Paul, MN 55108

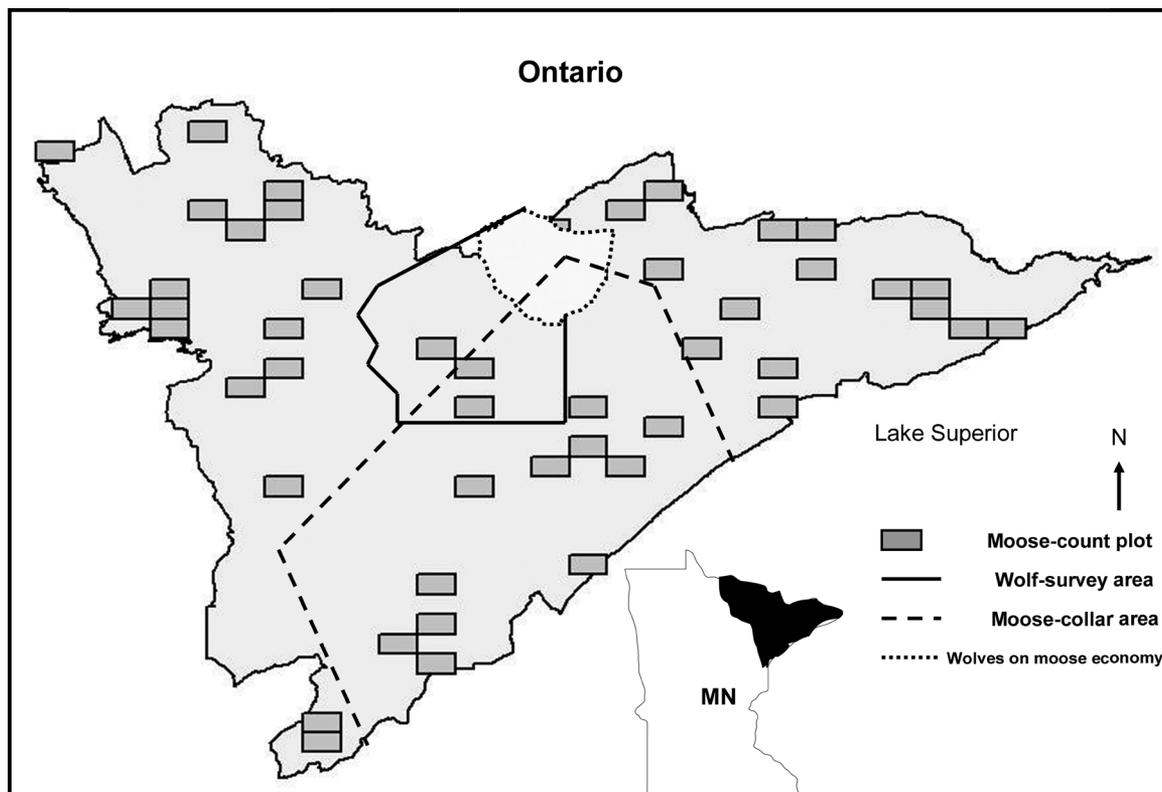


Figure 1. Moose-survey area. The Lenarz et al. (2009, 2010) studies were conducted in the moose-collar area. Wolves throughout the moose-survey area feed on moose, but in the part of the wolf-survey area where wolves are on a moose economy, moose constitute the only available prey during winter, with beavers and a few white-tailed deer available during the rest of the year. The locations of the moose-count plots vary by year, with those indicated here representing the distribution for only 2013 as an example.

(Mech and Karns 1977, Nelson and Mech 2006), so moose and beavers (*Castor canadensis*) are the wolves' only important prey there. Adult moose survival was also unusually low during the decline (Lenarz et al. 2010). The degree to which wolves caused adult mortality was unknown but could have been as high as 55% of the non-anthropogenic mortality if all scavenged carcasses were included (Lenarz et al. 2009). A further consideration is that wolves sometimes only injure moose that might die later of complications from the attack (Mech 1966), which would leave little evidence of wolf predation on a scavenged carcass.

Thus to gain insights into any possible effect of wolves on moose numbers in northeastern Minnesota, we examined the relationships between wolf numbers in the wolf-survey area and various aspects of moose demographics in the region surrounding that area. Given the possible important role wolves might have had in the moose decline, we also re-evaluated the earlier findings that related declining moose survival to temperature (Lenarz et al. 2009).

NORTHEASTERN MINNESOTA STUDY AREAS

The wolf-survey area encompassed some 2,060 km² immediately east of Ely in the east-central Superior National Forest (48°N, 92°W; Fig. 1). The area represents only about 3% of the total range of wolves in Minnesota. The following description of this area is verbatim from Mech (2009:16–17).

“Topography in the study area varies from large stretches of swamps and uneven upland to rocky ridges, with elevations ranging from 325 to 700 m above sea level. Winter temperatures below -35°C are not unusual, and snow depths (usually from mid-November through mid-April) generally range from 50 to 75 cm on the level. Summer temperatures rarely exceed $+35^{\circ}\text{C}$. Conifers predominate in the forest overstory, including jack pine (*Pinus banksiana*), white pine (*P. strobus*), red pine (*P. resinosa*), black spruce (*Picea mariana*), white spruce (*P. glauca*), balsam fir (*Abies balsamea*), white cedar (*Thuja occidentalis*), and tamarack (*Larix laricina*). However, as a result of extensive cutting and fires, much of the coniferous cover is interspersed with large stands of white birch (*Betula papyrifera*) and aspen (*Populus tremuloides*). Heinselman (1993) presented a detailed description of the forest vegetation.”

The only significant prey of wolves in the wolf-survey area are deer and moose, with beavers available primarily from May through November, similar to the rest of northeastern Minnesota. In the northeastern half of the wolf-survey area, as well as immediately north and east of it, the overwintering population of white-tailed deer was extirpated by about 1975 by a combination of severe winters, maturing vegetation, and high numbers of wolves (Mech and Karns 1977), and the area has remained devoid of wintering deer ever since (Nelson and Mech 2006). Moose inhabit the entire area but occur at a higher density in the northeastern half. Beavers live throughout the area.

The moose-survey area encompassed 15,500 km² of northeastern Minnesota (Giudice et al. 2012) that also included the wolf-survey area. Lenarz et al. (2009, 2010) radio-collared moose in an area that included approximately the southeastern 40% of the wolf-survey area, plus a large region east and south of the wolf-survey area encompassed by the moose-survey area (Fig. 1). Both the moose-collaring area and the moose-survey area are generally of the same basic habitat as described above for the wolf-survey area. However both moose and deer densities vary considerably throughout the larger moose-survey area, with fewer deer in the northeastern parts of both the wolf-survey and moose-collaring area (Nelson and Mech 2006, DelGiudice 2013; Fig. 1).

EVALUATING THE WOLF AND TEMPERATURE DATA

To assess the relationships between the population trajectories of the wolves and moose, we used published wolf numbers from 1997 to 2007 (Mech 2009) and L. D. Mech (unpublished data) from 2008 to 2012 (Table 1) in

simple-linear regressions with the following moose data: 1) moose-count data from 1997 to 2003 (Lenarz 2006) and 2005 to 2013 (no data available for 2004; DelGiudice 2013); 2) adult-moose-survival data from Lenarz et al. (2009); and 3) calf:cow ratios in the moose-survey area from 1984 to 2013 (Lenarz 1998, 2006; DelGiudice 2013). We considered calf:cow ratios to be approximate because of the difficulty of distinguishing cows from bulls during winter, so we also used available calf:population data (2004–2011). We used the calf:population data from the entire moose-survey area as well as from the wolf-survey area combined with an equal-sized area just to the south of there. R. A. Moen (University of Minnesota Duluth, personal communication) after personal communication with M. S. Lenarz (Minnesota Department of Natural Resources) selected the latter area for us to generate a larger sample that was also representative of the wolf-survey area. The regressions between wolf numbers and adult moose included counts in the same winters. The regressions with calf ratios involved wolf numbers during the winters preceding the calf ratios because those wolf numbers would be most relevant to calves born the following spring.

Table 1. Wolf numbers in a 2,060-km² survey area of northeastern Minnesota 1997–2012 (Mech 2009; L. D. Mech, U.S. Geological Survey, unpublished), annual moose estimates and calf:population ratios in the moose-survey area, and calf:cow ratios in the wolf-survey area and an equal-sized area just south of there and in the moose-survey area (Lenarz 1998, 2006, 2008; DelGiudice 2013; M. S. Lenarz, Minnesota Department of Natural Resources, personal communication).

Year	Wolves		Moose survey data ^a		Calf:population		
	Wolf-survey area	NE moose economy area ^b	Point estimate	90% CI	Calf:cow	Wolf-survey area ^c	Moose survey area
1984	35				0.43		
1985	54				0.57		
1986	47				0.75		
1987	48				0.65		
1988	59				0.64		
1989	79				0.39		
1990	51				0.3		
1991	56				0.45		
1992	53				0.53		
1993	55				0.55		
1994	55				0.62		
1995	55				0.9		
1996	69				0.52		
1997	56		3,960	(1,386–5,346)	0.49		
1998	55		3,464	(1,247–4,711)	0.71		
1999	50		3,915	(1,370–5,285)	0.57		
2000	44		3,733	(933–4,666)	0.7		
2001	52		3,879	(1,086–4,965)	0.61		
2002	53		5,214	(1,199–6,413)	0.93		
2003	58	31	4,161	(1,540–5,701)	0.7		
2004	62	26			0.42		
2005	74	35	8,160	(5,960–11,170)	0.52	0.28	0.17
2006	81	49	8,840	(6,670–11,710)	0.34	0.27	0.23
2007	81	41	6,860	(5,230–9,000)	0.29	0.31	0.17
2008	84	39	7,890	(5,970–10,420)	0.36	0.2	0.14
2009	97		7,840	(6,190–9,910)	0.32	0.17	0.18
2010	91		5,700	(4,480–7,250)	0.28	0.2	0.15
2011	82		4,900	(3,810–6,290)	0.24	0.12	0.15
2012	92		4,230	(3,190–5,600)	0.36	0.14	0.15
2013			2,760	(2,120–3,580)	0.33		

^a Data collection methods and adjustments for visibility bias differed between 1997–2003 (fixed-wing aircraft, double-sampling) and 2005–2013 (helicopter, sightability model).

^b In northeastern part of wolf-survey area where wolves prey primarily on moose.

^c For the wolf-survey area and an equal-sized area directly south of there.

For example, we regressed wolf numbers for winter 2002–2003 with calf:population ratios obtained in January 2004, which reflected predation since spring 2003. The wolf data were based primarily on complete winter counts of radio-tagged wolves and their packs, although numbers from a few non-radioed wolves in the same standard study area were estimated from tracks or occasional winter aerial observations of the wolves as described earlier (Mech 2009).

The moose data were based on winter observations from fixed-wing aircraft from 1997 to 2003 and helicopter from 2005 to 2013. Counts from the fixed-wing surveys were adjusted for non-detection using a double-sampling procedure (Gasaway and DuBois 1987, Lenarz 1998). By contrast, counts from the helicopter surveys were adjusted for non-detection using a sightability model developed using radiocollared animals (Steinhorst and Samuel 1989, Fieberg 2012, Giudice et al. 2012). Although the change in survey methods makes it difficult to compare data from the 2 different periods, the data within each period provide estimates of moose-population trend (M. S. Lenarz, personal communication). Each year's moose point estimate has large and variable confidence limits (Table 1, Giudice et al. 2012, DelGiudice 2013, Fieberg et al. 2013).

To re-evaluate the temperature findings (Lenarz et al. 2009), we conducted a simple simulation study, mimicking the approach taken by Lenarz et al. (2009), to explore the potential for type I error – i.e., concluding there is a significant relationship between temperature and survival, when no association exists. Survival estimates from Table 2 of Lenarz et al. (2009) ranged from 0.86 to 0.99 in the spring and fall and from 0.91 to 1 in the summer and winter. To reflect these values, we generated survival rates using a continuous, uniform, random-number generator with support on the (0.8, 1) interval (spring and fall) or (0.9, 1) interval (in summer and winter). We determined annual survival as the product of the survival rates in each of the 4 seasons. We generated a set of 9 predictor variables, representing different temperature measurements, using a

multivariate, normal random-number generator, via the `mvrnorm` function in the MASS library of Program R (Venables and Ripley 2002, R Core Team 2013). We set the means and standard deviations of the random-number generator to the values reported for the temperature variables in Table 3 of Lenarz et al. (2009) excluding “LS14M,” “LS20M,” and “WS20M;” these latter 3 statistics exhibited little variability and were thus not considered in the original analyses conducted by Lenarz et al. (2009). We set the pairwise correlations among all predictor variables equal to 0.7 (scenario A) but repeated the analyses with all pairwise correlations equal to 0.1 (scenario B) to capture a range of plausible variables.

We fit a linear-regression model to each combination of survival rate (4 seasons, annual) and simulated temperature measurement (9 variables), for a total of $9 \times (4 + 1) = 45$ models. Importantly, the predictors were generated independent of the response variables. Thus, any relationships detected in the simulated data are spurious. We repeated the data generation and model-fitting processes 1,000 times. For each simulation, we recorded the R^2 and P -value for each fitted model as well as the maximum R^2 and minimum P -value across the 45 candidate models. Lastly, we counted the number of models that had an $R^2 > 0.5$. We overlaid the values of these statistics (maximum R^2 , minimum P -value, and number of models with $R^2 > 0.5$) from Lenarz et al. (2009) on the sampling distributions for these statistics obtained from the simulation study under the null hypothesis that survival is independent of temperature (Fig. 2).

THE ROLES OF WOLVES AND TEMPERATURE

Both wolf and moose numbers fluctuated considerably during the study, with wolf numbers in the 2,060-km² wolf-survey area varying between 44 and 97 (21–47 per 1,000 km²) and moose numbers from 3,960 to 5,214 from 1997 to 2003 and 2,760 to 8,840 from 2005 to 2013 (Table 1). Calf:cow

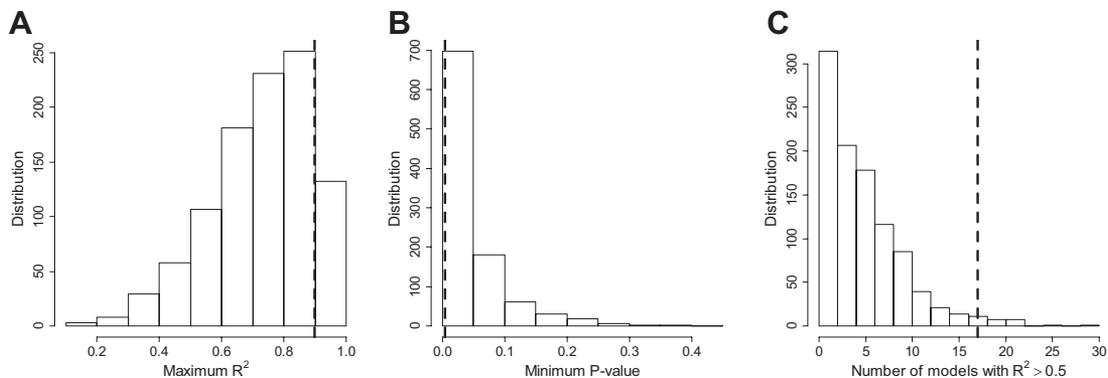


Figure 2. Summary statistics from 1,000 simulations, mimicking the data collection and analysis approach taken in Lenarz et al. (2009). In each case, we simulated 6 years of survival and temperature data. Specifically, we generated 9 temperature variables, representing different characterizations of heat stress, from a multivariate normal distribution in which predictors had pairwise correlations of 0.7. We then generated 5 sets of survival estimates, representing the 4 seasons and annual survival, independent of the temperature data. Thus, the simulated data were consistent with the null hypothesis that temperature and survival were not correlated. We then fit a linear regression model to all 45 combinations of predictor (temperature) and response (survival) variables. Histograms display the null sampling distribution (across the 1,000 simulations) of: A) the maximum R^2 among the 45 models, B) the minimum P -value among the 45 models, and C) the number of models that had an $R^2 > 0.5$. Results from Lenarz et al. (2009) are given by vertical dashed lines.

ratios varied from 0.24 to 0.93 and calf:population ratios (2004–2011) from 0.12 to 0.31.

From 1997 through 2003, wolf and moose numbers were unrelated ($P=0.86$). However, from 2005 to 2013, moose numbers were inversely correlated with wolf numbers the year previous ($R^2=0.44$; $P=0.05$). Annual moose survival from 2002 to 2007 of a sample of radio-collared moose (Lenarz et al. 2009) was weakly inversely related to wolf numbers ($R^2=0.48$; $P=0.12$) in the part of the wolf-survey area where wolves prey primarily on moose and which overlaps the moose-survey area. Calf:cow ratios in relation to wolf numbers varied considerably from 1984 through 2013 (Fig. 3). From 1984 to 2000, the calf:cow ratio was weakly related inversely to the previous winter's wolf numbers ($R^2=0.21$; $P=0.07$), whereas from 2001 to 2013, the inverse relationship was much stronger ($R^2=0.68$; $P<0.0001$). Calf:population ratios from 2004 through 2011 for the wolf-survey area and adjacent area just south of it were inversely related to wolf numbers the winter before ($R^2=0.75$; $P<0.01$), as were the ratios from the entire moose-survey area ($R^2=0.43$; $P=0.08$).

Although the response data in our simulation were generated independent of the predictors, at least 1 model was statistically significant (i.e., $P<0.05$) in 70% of the simulations under scenario A (pairwise correlations among predictor variables equal to 0.7). Type I error rates were higher under scenario B (pairwise correlations equal to 0.1), with 87% of the simulations producing a significant result. Further, mean maximum R^2 values were 0.73 (scenario A) and 0.79 (scenario B), where the maximum is taken with respect to the 45 models, fit to each simulated data set, and the mean is taken over the 1,000 simulations. Lastly, although the results from Lenarz et al. (2009) are in the tails of the null sampling distribution (Fig. 2), they are not at all extreme. In fact, generating temperature and survival rates independently resulted in models with more highly significant P -values and R^2 in 14% (scenario A) and 16% (scenario B) of the simulations.

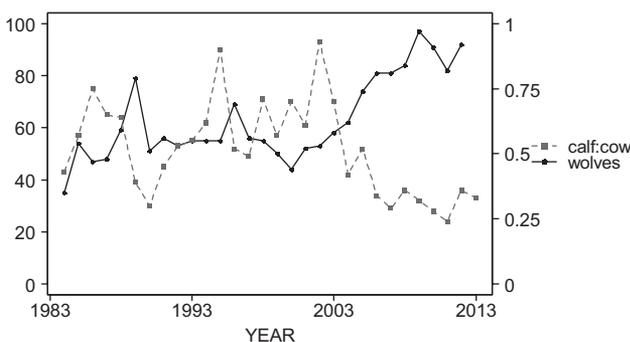


Figure 3. Wolf numbers in a 2,060-km² wolf-survey area of northeastern Minnesota, 1983–2012 (Mech 2009; L. D. Mech, U. S. Geological Survey, unpublished data) and calf:cow ratio in that area and an equal-sized area just south of there (Lenarz 1998, 2006, 2008; DelGiudice 2013; M. S. Lenarz, Minnesota Department of Natural Resources, personal communication).

WHY ARE MINNESOTA MOOSE NUMBERS DECLINING?

The correlations we found between various moose parameters and wolf numbers in overlapping study areas for the period of the moose decline suggest that an increasing wolf population may have contributed at least partly to the moose decline. Although the wolf-population trend in the wolf-survey area does not necessarily represent that in the entire moose-survey area, it is likely more representative of the wolf-population trend in northeastern Minnesota than in the entire state. The relationships we found are consistent with a hypothesis that from 1997 to about 2003 annual moose numbers were relatively unaffected by wolves and that wolf numbers tended to parallel moose numbers. However, starting in about 2004, after wolves increased 41% from 44 in 2000 to 62 in 2004 and 84% to 81 in 2006, moose numbers began declining. The moose-population estimate was inversely related to the number of wolves each year. The strongest relationship was between wolf numbers 1 year and the calf: population ratio the next year, explaining 75% of the calf population variance. Furthermore, the annual calf survival of 0.40 in northeastern Minnesota (Lenarz et al. 2010) during 2002–2008 was about 63% of that of eastern Ontario, where wolf density was about 67% of the density in northeastern Minnesota (Patterson et al. 2013).

Thus, even though there appeared to be evidence of a climate-change relationship to moose survival from 2002 to 2008 (Lenarz et al. 2009), the increased temperatures used in the analyses coincided with an increasing wolf population. Could the significant relationship Lenarz et al. (2009) found of moose-population decline to high temperatures be a correlate of wolf predation rather than the cause of the variation in adult-moose survival? Recent and prior studies linking ambient temperatures to increased metabolism, heart, and respiration rates in moose (Renecker and Hudson 1986, 1990; McCann et al. 2013) provide a mechanistic basis and explanation for the relationships between temperature and survival reported in Lenarz et al. (2009). Nonetheless, the high R^2 values and low P -values associated with the regression models summarized in Table 4 of Lenarz et al. (2009) should be viewed cautiously in light of the large number of fitted models ($m=45$) and small number of observations ($n=6$ for each of 5 response variables; Fig. 2). Similar to stepwise model-selection procedures, there are hidden costs associated with looking at a large number of models. A reasonable guideline when fitting models to a single response variable is that one should limit the number of candidate degrees of freedom (i.e., number of predictors considered in all fitted models) to $< n/10$ to $n/20$ (Harrell 2001). Lenarz et al. (2009) considered 9 different temperature variables in conjunction with each model response, whereas this guideline would suggest considering at most 1 (i.e., $n/10=3/5$). As our simulation results illustrate, the likelihood of making a type I error increases as one considers additional (related) response variables.

Although our analyses were also motivated by and grounded in ecological theory, we recognize that some of

the same criticisms (i.e., high potential for type I error) may limit the strength of our inferences regarding the role of wolves in the moose decline. We also considered 7 different 1-variable regression models, with sample sizes ranging from 6 to 16 (i.e., $n/10$ ranged from $3/5$ to $1\ 3/5$). At minimum however, the present findings raise the possibility that proximate causes of mortality (e.g., wolf predation) may play a larger role in the moose decline than previously thought. Wolf predation does not always reduce moose numbers as evidenced by the lack of a relationship between wolf and moose numbers from 1997 through 2003 and by other studies (Peterson et al. 1998, Mech and Peterson 2003). However, when predisposing factors such as adverse snow conditions prevail, wolves can reduce moose populations (Peterson and Allen 1974).

One common factor that predisposes adult moose to wolf predation is old age (Mech 1966, Mech et al. 1998, Peterson et al. 1998, Lenarz et al. 2010, Mech and Nelson 2013). In a relatively stable moose population, each year a certain older cohort would begin reaching an age vulnerable to wolf predation. If relatively low wolf density such as predominated from about 1997 to 2002 in the wolf-survey area allowed high calf survival for several consecutive years, then 8–12 years later a large proportion of the moose population would reach the age vulnerable to wolves. If that vulnerable period corresponded to years of high wolf density such as after 2005, the combination of a high proportion of old moose and heavy predation on calves could cause a drop in moose numbers. This possibility may not be a suitable explanation for the northeastern Minnesota moose decline because the adult moose that died in the Lenarz (2010) study included several that were of younger and medium ages. Nevertheless in searching for a cause or causes of a moose decline, it will be important to examine any available data on moose age, including live-captured or hunter-killed moose.

Other factors predisposing adult moose to wolf predation could be physiological or pathological such as poor nutritional condition, hydatid cysts (*Echinococcus granulosus*), arthritis (Mech 1966, Peterson 1977), possibly ambient temperature-related problems (Lenarz et al. 2009, 2010), or unknown conditions. Several such problems recently plagued moose in northwestern Minnesota (Murray et al. 2006).

Wolf predation is one of the primary, proximate mortality factors of moose calves (Larsen et al. 1989, Testa et al. 2000, Patterson et al. 2013), and the relatively strong, inverse relationship we found between wolf density 1 year and calf: population ratio the next year suggests that this relationship played a role in the recent northeastern Minnesota moose decline. Little is known about factors that might influence or predispose moose calves to predation by wolves, but generally the higher the wolf density, the more calves would be taken.

Wolf-population density in the wolf-survey area was able to remain high even as moose numbers were declining because throughout much of the wolf-survey area as well as the larger moose-survey area, deer and beavers continued to be available, probably subsidizing wolves while they also preyed on declining numbers of moose. Some wolf packs even occupied narrow territories stretching as far as 42 km

from the northeastern part of the wolf-survey area where few deer live in summer and none in winter to the southwestern part where deer live in summer and congregate in winter (L. D. Mech and S. Barber-Meyer, U.S. Geological Survey, unpublished data).

The possible role of any predisposing factor(s) in promoting moose-population reduction by wolf predation highlights the key question yet to be answered as to why northeastern Minnesota's moose began declining in 2006. In seeking the answer, researchers need to appreciate that wolf predation is as an ever-present potential contributor, especially with calves. In 3,000-km² of the northeastern Minnesota moose range, wolf predation was one of the main causes of a near extirpation of deer during a series of severe winters between 1964 and 1974 (Mech and Karns 1977), and 30 years later, the deer population had not yet recovered (Nelson and Mech 2006). Conceivably, a high wolf population preying on moose calves, coupled with the usual maladies that beset adult Minnesota moose (Murray et al. 2006, Lenarz et al. 2009, DelGiudice et al. 2011) that may predispose them to wolf predation, could reduce the moose population. The Minnesota Department of Natural Resources and the Bois Forte 1854 Authority have been radio-collaring large samples of cow and newborn-calf moose in northeastern Minnesota in an attempt to determine both proximate and ultimate causes of mortality (G. D. DelGiudice, Minnesota Department of Natural Resources, personal communication). We recommend continuing such studies along with the annual moose count as well as monitoring annual wolf numbers in a larger portion of the northeastern Minnesota moose range.

Temperature could still be a factor in the moose decline. As Lenarz et al. (2010) noted, heat stress on cattle can negatively affect food intake, body growth, milk production, and reproduction (Hahn 1999) as well as immune response (Kelley et al. 1982, Morrow-Tesch et al. 1996). Although these factors could affect moose survival independently of predation, they could also help predispose moose to predation (Mech and Peterson 2003). Moose declines in northwestern and northeastern Minnesota have coincided with warmer-than-average temperatures. The role increased temperatures might have played in determining ultimate and proximate causes of mortality, however, remain to be elucidated.

MANAGEMENT IMPLICATIONS

The Minnesota Department of Natural Resources regulates a public harvest of wolves throughout the 70,000-km² wolf range and has allowed annual quotas of 400 in 2012 and 220 in 2013. If current or future studies suggest that wolves contribute importantly to the moose population decline, the Minnesota Department of Natural Resources could allocate a certain portion of its annual public-wolf-harvest quota to part of the moose range and compare moose mortality and numbers in that area with a similar experimental control area where wolves are not taken. If that experiment confirms the importance of wolves to the moose decline, we recommend that the Minnesota Department of Natural Resources

allocate an increased portion of the wolf-harvest quota to the moose range until the moose population recovers.

ACKNOWLEDGMENTS

This study was funded by the United States Geological Survey. The following critiqued earlier drafts of the manuscript and offered helpful suggestions for improvements: G. D. DelGiudice, M. S. Lenarz, R. A. Moen, M. E. Nelson, M. W. Schrage, and J. Erb. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

LITERATURE CITED

- Bertram, M. R., and M. T. Vivion 2002. Moose mortality in eastern Interior Alaska. *Journal of Wildlife Management* 66:747–756.
- DelGiudice, G. D. 2013. 2013 Aerial moose survey. Minnesota Department of Natural Resources, St. Paul, Minnesota, USA: <files.dnr.state.mn.us/recreation/hunting/moose/moose_survey_2013.pdf>. Accessed 20 Jan 2014.
- DelGiudice, G. D., B. A. Sampson, M. S. Lenarz, M. W. Schrage, and A. J. Edwards. 2011. Winter body condition of moose (*Alces alces*) in a declining population in northeastern Minnesota. *Journal of Wildlife Diseases* 47:30–40.
- Erb, J. 2008. Distribution and abundance of wolves in Minnesota, 2007–2008. Minnesota Department of Natural Resources, St. Paul, Minnesota, USA.
- Erb, J., and M. W. DonCarlos 2009. An overview of the legal history and population status of wolves in Minnesota. Pages 49–64 in A. P., Wydeven T. R., Van Deelen, and E. J., Heske, editors. Recovery of gray wolves in the Great Lakes region of the United States: an endangered species success story. Springer, New York, New York, USA.
- Fieberg, J. 2012. Estimating population abundance using sightability models: R sightability model package. *Journal of Statistical Software* 51:1–20.
- Fieberg, J., M. Alexander, S. Tse, and K. St. Clair. 2013. Abundance estimation with sightability data: a Bayesian data augmentation approach. *Methods in Ecology and Evolution* 4:854–864.
- Frenzel, L. D. 1974. Occurrence of moose in food of wolves as revealed by scat analyses: a review of North American studies. *Naturaliste Canadien* 101:467–479.
- Gasaway, W. C., and S. D. DuBois 1987. Estimating moose population parameters. *Swedish Wildlife Research (Supplement)* 1:603–617.
- Giudice, J., J. Fieberg, and M. Lenarz. 2012. Spending degrees of freedom in a poor economy: a case study of building a sightability model for moose in northeastern Minnesota. *Journal of Wildlife Management* 76:75–87.
- Hahn, G. L. 1999. Dynamic responses of cattle to thermal heat loads. *Journal of Animal Science* 77:10–20.
- Harrell, F. E. Jr. 2001. Regression modeling strategies: with applications to linear models, logistic regression, and survival analysis. Spring-Verlag, New York, New York, USA.
- Heinselman, M. 1993. The boundary waters wilderness ecosystem. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Kelley, K. W., R. E. Greenfield, J. F. Evermann, S. M. Parish, and L. E. Perryman. 1982. Delayed-type hypersensitivity, contact sensitivity, and phytohemagglutinin skin-test responses of heat- and cold-stressed calves. *American Journal of Veterinary Research* 43:775–779.
- Larsen, D. G., D. A. Gauthier, and R. L. Markel. 1989. Causes and rate of moose mortality in the southwest Yukon. *Journal of Wildlife Management* 53:548–557.
- Lenarz, M. S. 1998. Precision and bias of aerial moose surveys in northeastern Minnesota. *Alces* 34:117–124.
- Lenarz, M. S. 2006. 2006 Aerial moose survey. Minnesota Department of Natural Resources, St. Paul, Minnesota, USA: <files.dnr.state.mn.us/recreation/hunting/moose/moose_survey_2006.pdf>. Accessed 20 Jan 2014.
- Lenarz, M. S. 2008. 2008 Aerial moose survey. Minnesota Department of Natural Resources, St. Paul, Minnesota, USA: <files.dnr.state.mn.us/recreation/hunting/moose/moose_survey_2008.pdf>. Accessed 20 Jan 2014.
- Lenarz, M. S., M. E. Nelson, M. W. Schrage, and A. J. Edwards. 2009. Temperature mediated moose survival in northeastern Minnesota. *Journal of Wildlife Management* 73:503–510.
- Lenarz, M. S., J. Fieberg, M. W. Schrage, and A. J. Edwards. 2010. Living on the edge: viability of moose in northeastern Minnesota. *Journal of Wildlife Management* 74:1013–1023.
- McCann, N. P., R. A. Moen, and T. R. Harris. 2013. Warm-season heat stress in moose (*Alces alces*). *Canadian Journal of Zoology* 91:893–898.
- Mech, L. D. 1966. The wolves of Isle Royale. National Parks Fauna Series No. 7. U.S. Government Printing Office, Washington, D.C., USA.
- Mech, L. D. 2009. Long-term research on wolves in the Superior National Forest. Pages 15–34 in A. P., Wydeven E. J., Heske, and T. R., Van Deelen, editors. Recovery of gray wolves in the Great Lakes region of the United States: an endangered species success story. Springer, New York, New York, USA.
- Mech, L. D., L. G. Adams, T. J. Meier, J. W. Burch, and B. W. Dale. 1998. The wolves of Denali. University of Minnesota Press, Minneapolis, USA.
- Mech, L. D., S. M. Goyal, W. J. Paul, and W. E. Newton. 2008. Demographic effects of canine parvovirus on a free-ranging wolf population over 30 years. *Journal of Wildlife Diseases* 44:824–836.
- Mech, L. D., and P. D. Karns 1977. Role of the wolf in a deer decline in the Superior National Forest. Research Report. NC-148. United States Department of Agriculture, Forest Service, North Central Forest Experimental Station, St. Paul, Minnesota, USA.
- Mech, L. D., and M. E. Nelson 2013. Age structure of moose (*Alces alces*) killed by gray wolves (*Canis lupus*) in northeastern Minnesota, 1967–2011. *Canadian Field Naturalist* 127:70–71.
- Mech, L. D., and R. O. Peterson 2003. Wolf-prey relations. Pages 131–157 in L. D., Mech, and L., Boitani, editors. Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, Illinois, USA.
- Morrow-Tesch, J., N. Woolen, and L. Hahn. 1996. Response of gamma delta T-lymphocytes to heat stress in *Bos Taurus* and *Bos indicus* crossbred cattle. *Journal of Thermal Biology* 21:101–108.
- Murray, D. L., E. W. Cox, W. B. Ballard, H. A. Whitlaw, M. S. Lenarz, T. W. Custer, T. Barnett, and T. K. Fuller. 2006. Pathogens, nutritional deficiency, and climate influences on a declining moose population. *Wildlife Monographs* 166:1–30.
- Nelson, M. E., and L. D. Mech 2006. Causes of a 3-decade dearth of deer in a wolf-dominated ecosystem. *American Midland Naturalist* 155:373–382.
- Patterson, B. R., J. F. Benson, K. R. Middel, K. J. Mills, A. Silver, and M. E. Obbard. 2013. Moose calf mortality in central Ontario, Canada. *Journal of Wildlife Management* 77:832–841.
- Peterson, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. United States National Park Service Scientific Monograph Series 11:1–210.
- Peterson, R. O., and D. L. Allen 1974. Snow conditions as a parameter in moose-wolf relationships. *Naturaliste Canadien* 101:481–492.
- Peterson, R. O., R. E. Page, and K. M. Dodge. 1984. Wolves, moose and the allometry of population cycles. *Science* 224:1350–1352.
- Peterson, R. O., N. J. Thomas, J. M. Thurber, J. A. Vucetich, and T. A. Waite. 1998. Population limitation and the wolves of Isle Royale. *Journal of Mammalogy* 79:487–841.
- R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria: <http://www.R-project.org/>. Accessed 20 Jan 2014.
- Renecker, L. A., and R. J. Hudson 1986. Seasonal energy expenditure and thermoregulatory response of moose. *Canadian Journal of Zoology* 64:322–327.
- Renecker, L. A., and R. J. Hudson 1990. Behavioral and thermoregulatory responses of moose to high ambient temperatures and insect harassment in aspen dominated forests. *Alces* 26:66–72.
- Severud, W. J., G. D. DelGiudice, and R. G. Wright. 2012. Evaluating the use of GPS collars to determine moose calving and calf mortalities in northeastern Minnesota. Summaries of wildlife findings 2012. Minnesota Department of Natural Resources, St. Paul, USA.
- Steinhorst, R. K. and M. D. Samuel. 1989. Sightability adjustment methods for aerial surveys of wildlife populations. *Biometrics* 45:415–425.

Testa, J. W., E. F. Becker, and G. R. Lee. 2000. Temporal patterns in the survival of twin and single moose (*Alces alces*) calves in southcentral Alaska. *Journal of Mammalogy* 81:162–168.

Van Ballenberghe, V., A. W. Erickson, and D. Byman. 1975. Ecology of the timber wolf in northeastern Minnesota. *Wildlife Monographs* No 43.

Venables, W. N., and B. D. Ripley 2002. *Modern applied statistics with S*. Fourth edition. Springer, New York, New York, USA.

Associate Editor: John Squires.