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Michael E. Nelson

U.S. Fish and Wildlife Service

L. David Mech

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

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RELATIONSHIP BETWEEN SNOW DEPTH AND GRAY WOLF PREDATION ON WHITE-TAILED DEER

MICHAEL E. NELSON,¹ U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, MD 20708
L. DAVID MECH,² U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, MD 20708

Abstract: Survival of 203 yearling and adult white-tailed deer (*Odocoileus virginianus*) was monitored for 23,441 deer days from January through April 1975–85 in northeastern Minnesota. Gray wolf (*Canis lupus*) predation was the primary mortality cause, and from year to year during this period, the mean predation rate ranged from 0.00 to 0.29. The sum of weekly snow depths/month explained 51% of the variation in annual wolf predation rate, with the highest predation during the deepest snow.

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Wolves capture more prey during severe winters with deep snow (Pimlott et al. 1969, Mech and Frenzel 1971, Haber 1977, Mech and Karns 1977, Peterson 1977, Eide and Ballard 1982). However, except for extreme snow conditions, the relationship between degree of winter severity and wolf predation rate has only begun to be studied. Increased wolf kill of moose (*Alces alces*) has been related to increasing snow depths (Peterson and Allen 1974, Haber 1977, Gasaway et al. 1983), but no quantitative measure of this relationship between wolves and white-tailed deer has been made. This paper is the 1st attempt at analyzing such a relationship.

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METHODS

This study was conducted in eastcentral Superior National Forest in northeastern Minnesota (48°N, 92°W) from 1975 to 1985. The area is near the northeastern limit of white-tailed deer range and is cool temperate, with maximum snow depths ranging from 30 to 100 cm from mid-November through mid-April. The forests of the region are mixed coniferous-deciduous (Nelson and Mech 1981). During a se-

ries of several severe winters, including the most severe on record, the deer herd declined from 1968 through 1977 (Mech and Karns 1977) and then stabilized at a year-round density of 0.2–0.4 deer/km² (Floyd et al. 1979, Nelson and Mech 1986a). A combination of severe winters, deteriorating habitat, and wolf predation apparently caused the decline (Mech and Karns 1977). During winter, wolf predation is the only major source of deer mortality, with monthly mortality rates ranging from 0.08 to 0.22 for fawns and from 0.02 to 0.11 for yearlings (1 year old) and adults (≥ 2 years old) (Nelson and Mech, 1986b).

We captured, examined, and radiocollared deer from January 1975 through April 1985 (Nelson and Mech 1981, 1986a). We radiolocated them from the air (Mech 1974) 1–3 times/week and examined them for cause of mortality generally within 1–3 days after death. We considered predation the cause of death only when there was evidence of blood and a struggle, typical of observed kills by radioed wolves. There are no major predators of deer in the study area other than wolves. Deer dying from other causes or within 12 days after capture were excluded from this analysis because capture myopathy can still cause death that long after capture (Harthorn 1977).

Monthly survival and mortality rates (Heisey and Fuller 1985) were determined for all radioed deer, but only pooled yearling and adult data provided adequate data for yearly analysis (Nelson and Mech, 1986b). For each year, monthly survival rates for January–April were multiplied to estimate January–April survival and then subtracted from 1 to estimate January–April mortality from wolf predation (also referred to as wolf predation rate).

¹ Mailing address: 305 W. Harvey Street, Ely, MN 55731.

² Mailing address: North Central Forest Experiment Station, 1992 Folwell Avenue, St. Paul, MN 55108.

Table 1. Gray wolf predation rates (WPR)^a of radio-collared white-tailed deer, snow index (SI),^b and monthly mean minimum daily temperatures (T) from January through April in northeastern Minnesota, 1975–85.

Year	WPR	95% CI	SI	T (C)
1975	0.22	0.00–0.44	36	–14.3
1976	0.22	0.00–0.43	34	–12.7
1977	0.00		14	–12.5
1978	0.29	0.05–0.53	33	–15.8
1979	0.20	0.03–0.38	38	–16.4
1980	0.05	0.00–0.16	25	–14.3
1981	0.06	0.00–0.18	18	–11.5
1982	0.13	0.00–0.27	32	–16.5
1983	0.14	0.01–0.26	21	–8.6
1984	0.06	0.00–0.15	32	–12.3
1985	0.09	0.00–0.21	14	–13.5

^a Based on 27 deaths of 203 radio-collared adult (≥ 2 years old) and yearling (1-year old) white-tailed deer monitored for 23,441 deer days.

^b Sum of weekly snow depths (ft), Jan–Apr.

Temperatures were measured daily by the U.S. Weather Bureau at Winton, and snow depths were recorded weekly by the Minnesota Department of Natural Resources (P. D. Karns, pers. commun.) at Isabella, 45 km southeast of Winton. We quantified winter severity during January–April by averaging monthly mean minimum temperatures and summing weekly snow depths (in ft) to form yearly indexes. We then ran simple and multiple regressions of January–April predation rates for each year against respective snow indexes and average temperatures to determine the relationship between wolf predation rates and both measures of winter severity.

RESULTS

A total of 203 yearling and adult deer (39 yearling males, 47 yearling females, 41 adult males, and 76 adult females) was monitored from 1975 to 1985 yielding 23,441 deer days of January–April survival data. Twenty-seven of these deer were killed by wolves, providing yearly estimates of January–April wolf predation rates (Table 1). Because deer could only be captured from January to April, the total amount of time that fawns could be monitored (as fawns) was insufficient to allow their inclusion in this study. After May of their 1st year, they were included as yearlings.

Mean minimum temperatures during January–April averaged from -16.5 to -8.6 C, and snow indexes varied from 14 to 38 (Table 1). Snow indexes < 26 resulted from weekly snow

depths generally < 60 cm and indexes > 30 resulted from weekly snow depths of 60–100 cm. Snow depths and indexes were considered mild for 1977, 1980, 1981, 1983, and 1985 and severe for 1975, 1976, 1978, 1979, 1982, and 1984. Four of the 6 deep snow winters also had the lowest average temperatures.

We found a significant positive relationship between January–April wolf predation rates and January–April snow indexes, which explained 51% of the variation in predation rate ($R^2 = 0.51$, $E[y] = -0.063 + 0.007x$, $P < 0.02$). Simple and multiple regressions with temperatures failed to explain significant variation in mortality.

Monthly differences in predation rate were compared between mild and severe winters because monthly deer-day samples were too small for yearly comparisons. Snow index was the only criterion used for rating winter severity because temperature was not directly related to mortality. Predation rates were higher in January, March, and April during severe winters but were only significantly higher in April (Table 2). Mean weekly snow depths were $1.7\times$ deeper in severe winters than in mild winters during January–March but $2\times$ as deep in April.

DISCUSSION

Our findings support earlier reports that wolves tend to kill more deer during severe winters. However, winter severity influences wolf predation on deer even under less severe conditions, and it appears that the kill rate is more directly related to snow depth than to temperature. The data suggest that the effect of snow depth is most pronounced in late winter (Apr) during severe winters when snow depth averages $2\times$ that in milder winters.

Snow depth influences deer vulnerability to predation in 2 ways. First, it acts as a physical impedence to escape. Wolves have a lighter track load (Formozov 1946) and they sink less in deep snow than deer (Kelsall 1969, Mech and Frenzel 1971, Telfer and Kelsall 1984). Second, restricted mobility and increased energy costs from travel in deep snow reduce deer fat reserves (Mattfeld 1974, Parker et al. 1984). While not directly related to predation, cold temperature has the same effect on fat supplies, depleting fat deposits because of increased heat production needed to offset heat losses. Temperature effects are particularly acute in March

Table 2. Monthly gray wolf predation rates (WPR)^a of radio-collared white-tailed deer and mean weekly snow depths (SD) (cm) during mild and severe winters in northeastern Minnesota, 1975–85.^b

Winter severity ^c	Jan		Feb		Mar		Apr	
	WPR	SD	WPR	SD	WPR	SD	WPR	SD
Mild	0.01	37	0.05	43	0.01	46	0.02 ^c	21
Severe	0.03	61	0.04	73	0.03	76	0.07 ^c	43

^a Defined in Table 1.

^b Mild winters were 1977, 1980, 1981, 1983, and 1985; severe winters were 1975, 1976, 1978, 1979, 1982, and 1984.

^c $P = 0.04$.

and April when deer undergo a negative energy balance because of increased metabolism (Silver et al. 1969, Thompson et al. 1973) and restricted forage intake (Silver et al. 1969, Ozoga and Verme 1970). In some individuals increased energetic costs from gestation result in reduced serum nonesterified fatty acids (Seal et al. 1978). Thus, the cumulative effect of this energy drain, especially in late winter, decreases deer physical condition and predisposes them to wolf predation. The effect of temperature then is manifested through deer physical condition, which is more directly related to ability to escape predation (Pimlott et al. 1969, Mech and Frenzel 1971).

These results have important implications for wolf ecology and population dynamics because they indicate that, to a considerable degree, wolf food supply during winter is determined by external factors. This finding is particularly important because wolves breed in mid-winter and produce pups in spring. Therefore, it is conceivable that litter size and pup survival could be affected by the vagaries of winter weather.

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