10-2001

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L. David Mech

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

Douglas W. Smith

National Park Service

Kerry M. Murphy

National Park Service

Daniel R. MacNulty

University of Minnesota

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Mech, L. David; Smith, Douglas W.; Murphy, Kerry M.; and MacNulty, Daniel R., "WINTER SEVERITY AND WOLF PREDATION ON A FORMERLY WOLF-FREE ELK HERD" (2001). *USGS Northern Prairie Wildlife Research Center*. 337.
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WINTER SEVERITY AND WOLF PREDATION ON A FORMERLY WOLF-FREE ELK HERD

L. DAVID MECH,^{1,2} Biological Resources Division, U.S. Geological Survey, Northern Prairie Wildlife Research Center, 8711 37th Street, S.E., Jamestown, ND 58401, USA

DOUGLAS W. SMITH, National Park Service, Yellowstone Center for Resources, P.O. Box 168, Yellowstone National Park, WY 82190, USA

KERRY M. MURPHY, National Park Service, Yellowstone Center for Resources, P.O. Box 168, Yellowstone National Park, WY 82190, USA

DANIEL R. MACNULTY, Department of Fisheries and Wildlife, University of Minnesota, St. Paul, MN 55108, USA

Abstract: We studied wolf (*Canis lupus*) predation on elk (*Cervus elaphus*) in Yellowstone National Park from 17 March to 15 April 1997 (severe winter conditions) and from 2 to 31 March 1998 (mild winter conditions) 2–3 years after wolves were reintroduced to the park. Elk composed 91% of 117 kills. Data comparisons for 1997 versus 1998 were: hunting success rate, 26% versus 15%; kill rate, 17.1 kg/wolf/day versus 6.1; percent of kill consumed in first day, 7 versus 86; percent femur marrow fat of adult kills, 27 versus 70; calf:adult ratios of kills, 2:33 versus 17:23; sex ratio of kills, 14M:19F versus 17M:6F; mean age of elk killed, males 6.1 years, females 15.2 versus males, 4.8, females 13.0. Winter severity influenced the wolf–elk relationship more than the naivete of the elk herd to predation by wolves.

JOURNAL OF WILDLIFE MANAGEMENT 65(4):998–1003

Key words: *Canis lupus*, *Cervus elaphus*, elk, nutritional condition, predation, snow, winter severity, wolf, Yellowstone National Park.

The reintroduction of wolves into Yellowstone National Park (YNP) has provided new opportunities to study several aspects of wolf predation, such as effects of winter severity on predation patterns (Mech and Frenzel 1971, Mech and Karns 1977, Peterson 1977, DelGiudice 1998, Mech et al. 1998). However, except in the Glacier National Park area (where colonizing wolves preyed primarily on white-tailed deer [*Odocoileus virginianus*]; Boyd et al. 1994), previous studies have involved long-extant wolf–prey systems. Conceivably, winter severity could be so overwhelming a factor that regardless of the high prey:wolf ratio or number of uncultured prey in such a herd, winter severity still might strongly influence wolf predation.

The reintroduction of wolves in YNP provided an opportunity to pose the following 5 questions: (1) How would winter severity affect wolf predation on a previously wolf-free elk herd? (2) Would introduced wolves tend to take older, malnourished, or otherwise vulnerable elk as they do with other prey (summarized by Mech 1970 and Mech et al. 1998)? (3) What is the kill rate and amount of prey consumed? Usually the degree to which wolves consume each kill depends on prey vulnerability at the time. During rare periods when

prey are especially vulnerable and abundant, wolves kill often and may not completely consume each carcass (Pimlott et al. 1969, Mech and Frenzel 1971, Peterson and Allen 1974, Carbyn 1983, Miller et al. 1985, Boyd et al. 1994, DelGiudice 1998, Mech et al. 1998). This pattern also is common in other carnivores (Kruuk 1972). (4) Would reintroduced Yellowstone wolves find predation so easy that they would eat small amounts from each kill? (5) Finally, how would these relationships be affected by winter severity?

We sought to answer these questions by studying wolf predation on elk in YNP 2–3 years after the first wolves were reintroduced. Except for possible loners passing through the area, wolves were extinct in YNP after 1930 (Weaver 1978) but were reintroduced in 1995 and 1996 (Bangs and Fritts 1996, Bangs et al. 1998). Until wolf reintroduction, the mortality of most Yellowstone ungulates in winter, especially elk, was due to malnutrition (Houston 1982, Singer et al. 1997). Furthermore, the YNP elk herd was near or at ecological carrying capacity (Singer et al. 1997) and undoubtedly contained at least as many old and vulnerable individuals (Mech 1970:248–261, Mech et al. 1998:121–137) as other elk herds.

STUDY AREA

Yellowstone National Park is an 891,000-ha protected area primarily in northwestern Wyoming, USA, with a variety of habitats from high alpine

¹ Mailing address: University of Minnesota, Gabbert Raptor Center, 1920 Fitch Street, St. Paul, MN 55108, USA.

² E-mail: mechx002@tc.umn.edu

(3,800 m) to sagebrush grasslands (1,500 m; Despain 1990, Cook 1993). The climate is characterized by long, cold winters with substantial snow, and short, cool summers. Annual precipitation varies from 26 to 205 cm and falls mostly as snow. Average monthly temperatures range from -12°C to 13°C (Cook 1993).

The park is home to approximately 22,000 elk, 4,000 mule deer (*Odocoileus hemionus*), 2,800 bison (*Bison bison*), 700 moose (*Alces alces*), 300 bighorn sheep (*Ovis canadensis*), 600 pronghorns (*Antilocapra americana*), and scattered mountain goats (*Oreamnus americanus*; Singer and Mack 1993). During our study, 48 wolves occurred in 9 packs during 1997, whereas 68 wolves occurred in 8 packs during 1998. About half of the wolves wore radiocollars. In the northeastern corner of the park (Fig. 1), where most of the elk spend late winter and spring, we studied the Druid Peak pack (5 members in 1997, 8 in 1998), the Rose Creek pack (10 members in 1997, 15 in 1998), and the Leopold pack (5 in 1997, 9 in 1998). Wolf density in this northern range was 25 wolves/1,000 km² in 1997 and 46/1,000 km² in 1998.

METHODS

We conducted our study from 17 March to 15 April 1997 and from 2 to 31 March 1998. These are periods when prey generally are in their poorest nutritional condition and thus most vulnerable to wolf predation (Mech and Frenzel 1971, Mech 1977, DelGiudice 1998, Mech et al. 1998).

Daily, we attempted to locate each pack. Three teams (1 per pack) of 2 people each were assigned to find and observe the wolf packs between dawn and dusk each day with radiotracking equipment and spotting scopes. When weather permitted, a fixed-wing aircraft was used daily to locate and observe the 3 study packs. If wolves were seen hunting elk, we attempted to monitor the hunts and determine outcomes. The distances between ground observers and wolves varied from about 200 to 2,000 m. Carcass locations were recorded on 1/24,000-scale USGS maps. Four other YNP packs were located from aircraft as often as time and weather allowed, but the only data we used from these wolves involved kill rates.

After it appeared that a pack had abandoned a kill, we attempted to determine whether the wolves were scavenging or had made the kill (from fresh blood and tracks; Mech et al. 1998:35). Probable kills were defined as carcasses for which such evidence was not quite as certain. The crews also checked each carcass for

Fig. 1. The northern range study area in northeastern Yellowstone National Park with wolf pack territories defined, 1997–1998.

species, age (calf or adult), and sex; estimated amount eaten; and collected bone marrow and mandibles. Kill rates and amounts eaten were estimated based on the following assumed weights (kg) for elk: cow, 226; yearling, 165; calf, 103; and bull, 266 (K. M. Murphy, National Park Service, unpublished data). Femur marrow was assayed to determine fat content (Neiland 1970). Prey age was estimated by examining annulations in incisiform teeth (Matson's Laboratory, Milltown, Montana, USA).

The 1997 winter was 1 of the severest on record with a Winter Severity Index (WSI) of -2.6 on a scale of -4.0 to $+4.0$. The 1998 winter was relatively mild with a WSI of $+2.9$ (P. Farnes, Snowcap Hydrology, personal communication). Winter severity in 1997 was exacerbated by freezing rain on 1 January that limited ungulates from accessing forage until spring thaw.

The data for much of our study represented complete counts or nearly complete counts rather than random samples. For example, we located nearly all of the kills that each of our 3

Table 1. Success rates of Yellowstone National Park wolves hunting elk, 17 March to 15 April 1997 and 2 to 31 March 1998.

Pack	Hunting attempts observed		Prey encountered		Prey killed		Prey killed/hunting attempts		Prey killed/total prey encountered	
	1997	1998	1997	1998	1997	1998	1997	1998	1997	1998
Leopold	35	15	620	71	7	1	0.20	0.07	0.01	0.01
Rose Creek	8	8	32	322	2	2	0.25	0.25	0.06	0.01
Druid	22	14	400	87	7	2	0.32	0.14	0.02	0.02
Total	65	37	1,052	480	16	5				
Weighted mean (SE)							0.26 (0.05)	0.15 (0.06)	0.03 (0.004)	0.01 (0.005)

main study packs made during our study. Thus, any differences we observed are real and not a result of sampling error.

RESULTS

Observational Effort

We located and/or observed the 3 study packs on an average of 28 days and 29 days in 1997 and 1998, respectively. We were able to fly on 19 days in 1997 and 17 days in 1998. On many of these flights, we also observed the 4 other wolf packs that could not be located from the ground. We observed 24 wolves in 1997 and 57 wolves in 1998 at the remains of 55 and 62 kills or probable kills, respectively.

Wolf Hunting Success

During the 1997 study, the 3 main study packs made at least 65 attempts to kill elk. They succeeded in 16 ($26 \pm 5[\text{SE}]\%$) attempts. Most elk chased by wolves were in herds of up to 150, totaling 1,052 animals. Of those 1,052 elk, the wolves killed 16, or $3.0 \pm 0.4(\text{SE})\%$ (Table 1).

During the 1998 study, wolves made at least 37 attempts to kill an elk and succeeded in 5 ($15 \pm 6[\text{SE}]\%$) attempts. Most of the elk that were chased were in herds of up to 147, totaling 480 animals. Of those 480 elk, the wolves killed 5, or $1 \pm 0.5(\text{SE})\%$ (Table 1).

Composition of Kills

Elk constituted 45 (87%) of the kills in 1997 and 61 (98%) in 1998. Other kills included 6 moose and 1 mule deer in 1997 and 1 bison in 1998. A greater proportion of male elk were killed in 1998 than in 1997 (Table 2).

Kill Rate

The mean 1997 kill rate of 17.1 kg of prey/wolf/day was higher than the 1998 rate of 6.1, a

difference that was consistent among packs (Table 3). In addition to killing more prey on a biomass/wolf basis in 1997, the wolves also killed more individual animals (1.9/wolf in 1997 vs. 1.1/wolf in 1998).

During our 1997 study, the Druid Peak pack, Rose Creek pack, Leopold pack, and scavengers consumed an average of 7% of the available food from their kills on the day they made the kill ($n = 5$), and 23% after 1 more day ($n = 15$; Table 4); 5 kills were untouched to about 5% eaten. During 1998, wolves and scavengers consumed an average of 86% of the available food from their kills the day they made the kill ($n = 14$), and 89% after 1 more day. All kills were fed upon ($n = 23$).

Condition of Kills

Mean marrow fat content for 22 adult elk killed was 27% in 1997 and 70% for 20 adult elk in 1998. In 1998, marrow fat of the 12 calf and yearling kills averaged 22% (range from 7 to 50%).

Table 2. Sexes and ages (yr) of adult elk killed by 3 wolf packs on the northern range of Yellowstone National Park from 17 March to 15 April 1997 and from 2 to 31 March 1998. (Elk of unknown sex not included.)

Variable	7 March to 15 April 1997 ^a		2 March to 31 March 1998 ^b	
	Bulls	Cows ^c	Bulls	Cows ^c
<i>n</i>	14 ^c	19	17	6
mean ^d	6.1	15.2	4.8	13.0
range ^d	2.0–16.0	9.0–21.0	1.0–8.0	2.0–19.0

^a Plus 2 calves and 1 yearling.

^b Plus 17 calves.

^c Male:female versus expected 50:50—not significant.

^d Based on 10 bulls and 18 cows in 1997 and 17 bulls and 4 cows in 1998 whose ages could be determined by tooth sections.

Table 3. Yellowstone National Park wolf mean minimum kill rates from 17 March to 15 April 1997 and from 2 to 31 March 1998. (Only packs from which kill rate data were collected are included.)

Pack	No. wolves		No. elk kills		Biomass (kg) killed		Mean prey(kg/wolf/day)	
	1997	1998	1997	1998	1997	1998	1997	1998
Druid	5	8	11 ^a	16	3,324	3,676	22.2	15.3
Rose	8	14	14 ^b	19	3,645	2,522	15.2	6.0
Leopold	5	8	12	9	2,558	1,988	17.1	8.3
Thorofare	2	5	2 ^c	3	1,204	500	20.0	3.3
Soda Butte	4	8	6	4	1,342	547	11.2	2.3
Chief Joseph	-	6	-	6	-	615	-	3.4
Crystal	-	8	-	4 ^d	-	1,042	-	4.3
Total	24	57	45	61			17.1	6.1

^a Plus 2 moose.

^b Plus 1 moose and 1 mule deer.

^c Plus 3 moose.

^d Plus 1 bison.

Ages of Kills

In 1997, all but 2 of the elk kills during our study were adults (including 1 yearling), whereas in 1998, almost half the elk killed in March were calves. Of the adult elk killed, most were old females and males of various ages (Table 2).

DISCUSSION

Determining the amount of each carcass consumed by Yellowstone wolves was difficult because it was often unknown when the wolves abandoned a carcass. When wolves were away from a carcass, scavengers such as coyotes (*Canis latrans*), ravens (*Corvus corax*), eagles (*Haliaeetus leucocephalus*, *Aquila chrysaetos*), and grizzly bears (*Ursus arctos*) often fed on carcasses. Furthermore, even after we assessed a carcass, the wolves may have returned. Nevertheless, we were able to obtain information about the wolves' immediate use of carcasses

because wolves usually consume a large amount of most kills within a few hours (Mech 1970).

The wolves in our study killed elk at rates similar to wolves hunting caribou (*Rangifer tarandus*; Mech et al. 1998:110) and tended to kill calves, old cows, and individuals with low marrow fat. This pattern is similar to that found in other areas where wolves prey on a variety of ungulate species (Mech 1970, Mech et al. 1998). Furthermore, the annual difference in winter severity yielded results similar to those of other studies. During 1997, at the end of 1 of the most severe winters on record, YNP wolves had a higher killing success rate, killed more prey, and consumed less of each carcass than in the mild winter of 1998. The nutritional condition of the prey killed in 1997 was poorer than of prey killed in 1998.

In addition, the wolves killed more calves in March 1998 than in March 1997. There are sev-

Table 4. Percent of Yellowstone National Park wolf-killed elk eaten, from 17 March to 15 April 1997 and from 2 to 31 March 1998, based on carcasses that could be examined within 36 hr after being killed in 1997 and 1998. (AM = adult male; AF = adult female; C = calf.)

Pack	1997 kills examined			1998 kills examined		
	No. elk	Age-sex	% eaten	No. elk	Age-sex	% eaten
Druid	8	5AM, 3AF	19	8	5AM, 3AF	84
Leopold	4	1AM, 3AF	23	2	2AM	88
Rose Creek	3	2AM, 1AF	32	13	1AF, 12C	92
Weighted mean ± SE			23 ± 5			89 ± 5
Total	15	8AM, 7AF		23	7AM, 4AF, 12C	

eral possible reasons for this: (1) relative to adults, calves were disproportionately more vulnerable in 1998 than in 1997 because mild weather had less influence on 1998 adult condition; (2) the wolves killed more calves in fall 1996 than in fall 1997 and more calves died over winter, so there were fewer left in spring 1997 (D. W. Smith, unpublished data); and (3) calves were more abundant within wolf pack territories in spring 1998 than spring 1997 because more cows with calves migrate from wolf pack territories to lower elevations during severe winters (Shoesmith 1979, Coughenour and Singer 1996).

The cows killed during both years were older than the bulls, in keeping with their greater longevity (Houston 1982) and similar to the findings of Boyd et al. (1994). Proportionately, ages of the cows killed averaged about 70% of their maximum life span of about 21 years, whereas those of the bulls killed averaged only about 40% of their maximum age of about 15 years (Houston 1982). This age disparity is similar to that in other ungulate populations preyed on by wolves (Mech 1970, Mech et al. 1998).

The average age of all elk killed and of all adult elk killed in 1997 was higher than in 1998. This is opposite of what might be expected in that the severe winter of 1997 may have predisposed younger adult elk to predation as in Denali Park caribou (Mech et al. 1998). On the other hand, during neither winter did young adult elk comprise a very large proportion of the elk killed by wolves.

Comparison of the severe 1997 winter with the mild 1998 winter allowed us to distinguish the conditions that may have contributed to incomplete carcass consumption. Originally, we hypothesized that regardless of the severity of the winter, there would be enough elk in poor nutritional condition that the wolves would kill more than they could eat at the time. The fact that the wolves behaved as expected in 1997 but not in 1998 tends to refute that hypothesis. Although YNP wolves killed prey in poor condition during both mild and severe winters, they had a lower success rate during the mild 1998 winter, and a lower kill rate (despite an increased wolf density), and they tended to promptly consume all that they killed. Their 1998 kill rate was still high compared with published data (Schmidt and Mech 1997). Further, they were not aggressive or persistent in defending their kills from scavengers, indicating they had adequate provisions. Nevertheless, the degree of consumption of their

kills showed that they did not kill more than they could immediately eat in 1998.

Snow conditions appeared to be the main factor influencing kill rate and the degree of carcass consumption in our study, and elsewhere (Pimlott et al. 1969, Mech and Frenzel 1971, Peterson and Allen 1974, Boyd et al. 1994, DelGiudice 1998, Mech et al. 1998). High elk density and lack of previous culling by wolves were insufficient to predispose elk to easy killing, even in late winter when elk are in their poorest condition of the year.

Our results also demonstrate that severe winters are not necessary for individual elk to become malnourished. Marrow fat content of adult wolf-killed elk during March 1998, after a mild winter, averaged 70, a direct indicator of low total body fat and marginal condition (Mech et al. 1998:136).

In summary, the relationships between reintroduced YNP wolves and previously wolf-free elk did not differ in any way that we could detect from wolf-prey relations in long-extant systems. This was true despite the high ratio of prey available to wolves and the large number of uncultured prey. Furthermore, the degree of winter severity affected the new wolf-elk system in much the same way it affects long-extant systems. These findings suggest a dominating influence of winter severity on wolf predation patterns (Mech et al. 1998).

MANAGEMENT IMPLICATIONS

As wolves recolonize areas of the West outside Yellowstone National Park, concerns will be voiced about the possible effects of wolves on elk populations. Although this article does not directly address that issue, it does emphasize that the effect of wolves on elk numbers will be related to winter severity. Thus, any population modeling, hunting regulation changes, or other management reactions to wolf predation must consider this important relationship.

ACKNOWLEDGMENTS

Our study was supported by National Geographic Society, Yellowstone National Park, and the Biological Resources Division of the U.S. Geological Survey. We thank the following volunteers and technicians who assisted with the study: M. E. Nelson, G. D. DelGiudice, C. A. Campbell, D. Guernsey, D. R. Stahler, S. Evans, T. Zeiber, and K. Honness; R. Stradly who safely piloted the aircraft; W. Brewster and J. Varley, Yel-

lowstone National Park, for administrative oversight; and L. Diekmann, Yellowstone Park Foundation, for fiscal management. We also appreciate the suggestions made by D. Maehr and the anonymous reviewers who greatly improved the paper.

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Received 17 July 2000.

Accepted 16 May 2001.

Associate Editor: Maehr.