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DO WOLVES AFFECT WHITE-TAILED BUCK HARVEST IN NORTHEASTERN MINNESOTA?

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Abstract: We used simple linear regression to analyze 8–23 years of data on a wolf (*Canis lupus*) population and human harvest of white-tailed deer (*Odocoileus virginianus*) bucks in northeastern Minnesota to determine any effects of wolves on buck harvesting. Over the long term, wolves accounted for at least 14–22% of the inter-year variation in buck harvest in the region, but an unknown amount of variation in hunter effort may have obscured any more precise estimate. For part of the area with poorest habitat, we found strong inverse relationships ($r^2 = 0.66$–0.84) between annual wolf numbers and buck harvests from 1988 to 1995 when hunting pressure was considered relatively constant. However, in better habitat, where our buck harvest sample was larger, we found no evidence of wolves influencing buck harvest. Our findings tend to confirm the suitability of the Minnesota Department of Natural Resource's deer harvest regulations for a sustainable yield.

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Wolf numbers in Minnesota, Wisconsin, and Michigan have exceeded the criteria for recovery and removal from the federal list of endangered species in those states (Michigan Department of Natural Resources 1997, Wisconsin Department of Natural Resources 1998, Berg and Benson 1999). After delisting, each state will regain management responsibility with temporary federal oversight. One biological and political issue important to the design of a sound wolf management plan is the question to what extent wolves affect deer hunting, for deer are the primary prey of wolves in all 3 states. Minnesota alone hosts some 400,000 deer hunters (Fuller 1990).

Many aspects of wolf–deer interactions have been studied (Stenlund 1955, Pimlot et al. 1969, Mech and Frenzel 1971, Kolenosky 1972, Potvin et al. 1988, Mech et al. 1991). However, the resulting information is only partly relevant to the question of wolf effects on deer hunting. The latter subject has had little scientific attention. In the Superior National Forest (SNF) of northeastern Minnesota, Stenlund (1955) concluded that wolves reduced deer browsing pressure, and thus in some ways, benefitted the herd while at other times wolves competed with hunters. In part of this region where deer habitat was poorest, wolves and severe winters extirpated the wintering deer herd during 1968–74 and reduced deer numbers in the surrounding area (Mech and Karns 1977). This area included 3,000 km^2 of wilderness largely inaccessible during the hunting season. Because deer declined throughout northern Minnesota, the Minnesota Department of Natural Resources closed the deer hunting season for 1971 and implemented more restrictive antlerless deer hunting regulations in 1972 and 1973, and restricted the take to bucks only since 1974 (Mech and Karns 1977).

A few attempts have been made to numerically examine the interactions among wolves, deer, and hunters. For the area described above, a simple model using wolf and deer numbers predicted the deer demise (Mech and Karns 1977). A more complex model, utilizing data on hunter harvest and winter severity, indicated for the region around the void, that "without wolf predation the deer herd would have declined very little by 1976 but that with the known wolf densities the deer population would drop to less than 0.4 deer/km^2" (Mech and Karns 1977:21). The actual density dropped to 0.3–0.7 deer/km^2 (Nelson and Mech 1986*a*), with wolves killing 20% of the legal bucks in

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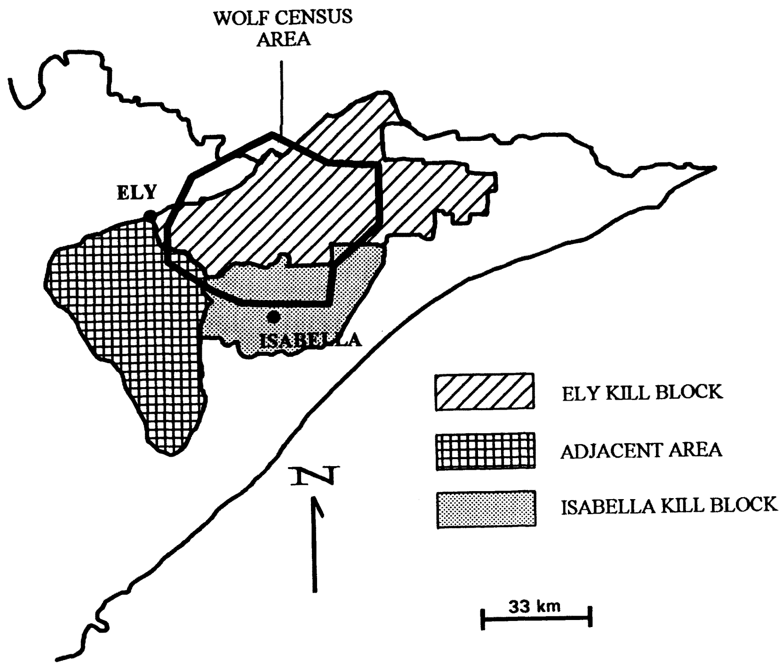

Fig. 1. The study area in northeastern Minnesota, including the wolf census area and areas from which deer harvest figures were obtained. Because of the inaccessibility of most of the eastern half of the Ely kill block area, the figures apply mostly to the western half.

the area and hunters taking 30% (Nelson and Mech 1986*b*).

For an area 130 km west of ours, Fuller (1989) modified a model by Keith (1983) to examine interactions among wolves, human hunters, and deer and showed graphically the minimal hypothetical effect of wolves on human harvesting of deer. The most direct study of wolf competition with human hunting was conducted in Quebec where wolf numbers were experimentally reduced by 40–71%; the authors concluded that "the harvest of bucks was not affected" (Potvin et al. 1992:1595).

These studies yielded certain insights into the effects of wolf predation on deer harvesting by humans. However, they also had limitations. The deer decline on SNF in the early 1970's was extreme, and the exact role of poor habitat and several severe winters was unknown. The Keith-Fuller models were hypothetical and based on assumptions that might not be valid. For example, wolf predation and hunting mortality were considered completely additive to other mortality factors. Furthermore, in Fuller's (1989,1990) study area, only 10% of the deer mortality was due to wolves, whereas some 77% was due to humans, so wolf predation was relatively light. In the Quebec wolf-removal experiment, wolves had repopulated the removal areas within 8 months, greatly confounding that study (Potvin et al. 1992).

Thus, additional information is needed on the question of wolf competition with human harvests of deer. One approach to the subject is to examine data on wolf numbers and deer harvests in an area where wolves and humans have both killed deer over a long enough period to include a good representation of weather conditions and their effects on deer numbers. We use such data from the central SNF of northeastern Minnesota from 1975 to 1997 to test the extent to which wolves might influence deer hunting there.

STUDY AREA

Our wolf census area encompasses some 2,060 km^2 immediately east of Ely in the east-central SNF (48°N, 92°W) of Minnesota (Fig. 1). The topography varies from large stretches of swamps to rocky ridges, with elevations ranging from 325 to 700 m above sea level. Winter temperatures $< -35°C$ are not unusual, and snow depths (usually from about mid-Nov through mid-Apr) generally range from 50 to 75 cm on the level. Temperatures in summer rarely exceed +35°C.

Conifers predominate in the forest overstory, with the following species present: 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 conifer cover is interspersed with large stands of white birch (*Betula papyrifera*) and aspen (*Populus tremuloides*). Detailed descriptions of the forest vegetation were presented by Ohmann and Ream (1969).

Deer inhabited the entire wolf census area until about 1975. By then, deer had been decimated in the northeastern half of the area and in the region north and east of it, although they persisted in the southwestern half (Mech and Karns 1977). Moose (*Alces alces*) inhabit the entire study area but at a higher density in the northeastern half (Peek et al. 1976). In spring, the deer inhabiting the southwestern half of the study area migrate northeastward and return in fall (Hoskinson and Mech 1976; Nelson and Mech 1981, 1986*a*). Beaver (*Castor canadensis*) are available throughout the study area, but generally only during April–November because of ice during the rest of the year.

Although wolves eat all 3 prey species mentioned above (Frenzel 1974), their primary prey in the northeastern 50–70% of our wolf-census area has increasingly been moose since winter 1976–77 (Mech 1986 and L. D. Mech, U.S. Geological Survey, unpublished data). In the southwestern remainder of the area, the main prey has been deer.

In August 1974, wolves in Minnesota were protected by the Endangered Species Act of 1973, and they remain legally protected. However, in accessible parts of the study area, light to moderate illegal killing of wolves continues, primarily in fall and winter (Mech 1977; L. D. Mech, U.S. Geological Survey, unpublished data).

In most of the wolf-census area, only buck deer could legally be taken during this study, but east, south, and west of the census area, limited numbers of anterless deer could be harvested as well (Fig. 1). The topography and weather of the latter area is similar to that of the census area, but has been subject to timber harvesting and deer numbers generally have been higher (M. S. Lenarz, Minnesota Department of Natural Resources, unpublished data.)

METHODS

We used 2 sources of data for our analyses: direct aerial counts of individual packs in the wolf-census area, and buck-harvest statistics for parts of the census area and the area immediately to the west. We conducted the wolf census by aerially tracking and counting radiocollared wolf packs from December through March each winter and aerially counting tracks of any noncollared packs in the census area (Mech 1977, 1986). For each pack, we considered the highest number of wolves (or tracks in nonradioed packs) seen as being the pack size for that winter. The total population for the census area was the sum of all of the packs living there. This approach does not include assessment of numbers of lone wolves. However, the fact that we used the highest figure for each pack greatly minimizes any inaccuracy caused by lone wolves because most lone wolves are individuals that recently dispersed from packs (Fritts and Mech 1981, Messier 1985, Fuller 1989).

To maintain the same size census area each year while individual wolf packs shifted their use of the area somewhat, we only counted the number of wolves proportionate to the percent of the census area that a given pack used that winter, based on radiotracking data. We subtracted the number of wolves killing primarily moose from our total wolf census to derive the number of wolves dependent on deer (Mech 1986; L. D. Mech, U. S. Geological Survey, unpublished data).

Information on buck harvest was obtained from the mandatory registration of bucks with the Minnesota Department of Natural Resources by hunters in various "kill blocks" in and adjacent to our wolf-census area (Lenarz 1997 and M.S. Lenarz, Minnesota Department of Natural Resources, personal communication). These kill blocks included an area east of Ely, an area around Isabella, and an area south of Ely (Fig. 1). There was a good relationship between the trends of the harvests in the latter 2 areas ($r^2 = 0.60$, $P < 0.001$), but not between the harvest in the first area and in either of the other two. We did not use numbers of antlerless deer harvested because those numbers fluctuated with the number of permits granted.

No measure of hunting effort was available for our study area to test whether variable hunting pressure obscured effects of wolves. Nevertheless, we hypothesized that if wolves had a

Table 1. Estimated size of the wolf population in the 2,060-km² census area of the central Superior National Forest (Mech 1986 and unpublished), and buck harvest for areas in and near the wolf census area (Lenarz 1997).

	Wolf numbers[a]		Buck harvest		
Year	Deer-dependent	Total	Isabella area	Ely area	Adjacent area[b]
1975	44	44	58	—	—
1976	56	56	52	—	—
1977	45	45	54	—	—
1978	48	50	34	—	—
1979	39	46	38	—	—
1980	47	54	50	—	—
1981	41	48	51	—	—
1982	36	47	43	—	—
1983	38	50	36	—	584
1984	23	35	28	16	479
1985	30	54	60	5	634
1986	27	47	63	8	697
1987	22	48	96	17	930
1988	28	59	87	83	814
1989	46	79	77	69	672
1990	21	51	77	106	771
1991	20	56	93	111	588
1992	23	53	97	98	765
1993	26	55	45	96	472
1994	28	55	38	88	482
1995	26	55	62	101	390
1996	33	69	28	70	250
1997	28	56	39	63	200

[a] In previous winter. All wolf packs in the census area fed on deer in 1975, but as deer were depleted in some areas (Mech and Karns 1977), fewer packs relied on deer. The difference between total wolves and deer-dependent wolves represents packs dependent on moose.
[b] Minnesota Department of Natural Resources permit blocks 122–124 immediately west of the wolf census area.

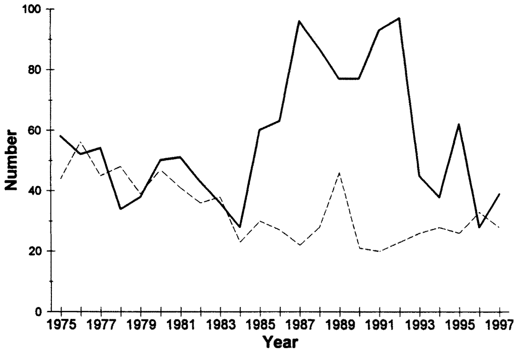

Fig. 2. Buck harvest (solid line) in the Isabella area and population trend of wolves that were dependent on deer in the census area (Fig. 1).

strong negative effect on number of bucks harvested, we should find an inverse relationship between wolf numbers in the deer-killing packs one winter and the buck harvest the following fall. Thus, we used simple linear regression (Statistix 4.1 1994) to compare harvest statistics to wolf numbers.

So as not to overlook possible relationships that might support our hypothesis, we deliberately ran regressions on whatever combinations of our 2 variables we thought logical. This approach would assure that if we did not find significant relationships, that negative finding would tend to indicate either that wolves were having little effect or that variable hunting effort might be masking any wolf effect. We analyzed data from each pack and from our entire census area against harvest statistics in 2 kill blocks partly in the wolf-census area and harvest data from the zones immediately west of our wolf-census area (Fig. 1). We assumed that annual changes in estimates of wolf density represented changes in the surrounding area as well. We also examined relationships between buck harvest in each kill block and wolf populations in and near each of those blocks.

With our largest data set, we also examined the individual annual changes in wolf and deer numbers (Table 1) and examined plots for any lag between wolf numbers and buck harvest that might confound regression analyses (Fig. 2). Annual numbers of deer hunters fluctuated widely in our study area before 1988 and after 1995, but remained reasonably constant from 1988 to 1995 (M. S. Lenarz, Minnesota Department of Natural Resources, personal communication). Therefore, we conducted separate analyses for 1988 to 1995.

RESULTS

From 1975 through 1997, we counted 4–6 wolf packs that were dependent on deer in our census area, and their numbers ranged from 2 to 14 per pack each winter (Mech 1986; L. D. Mech, U.S. Geological Survey, unpublished data). Annual buck harvest varied from 28 to 97 for the Isabella kill block, and 5 to 111 for the Ely kill block (Table 1). Total buck harvest for the zones west of our wolf-census area varied from 200 to 930 each year (Table 1).

We found no significant relationship between any of our individual wolf pack sizes and either the Isabella or Ely buck harvest over the entire 23-year period, even though some of the wolf packs inhabited those kill blocks. The total number of wolves from all packs showed a marginally significant ($P = 0.08$) inverse relationship ($r^2 = 0.14$) with the Isabella buck harvest (Table 2).

Upon inspecting the scatter plots of the re-

Table 2. Results of simple linear regressions to test the hypothesis that buck harvest should be inversely related to wolf numbers the previous winter if wolves strongly influence deer harvest. Only packs that prey on deer were included; all relationships are inverse.

Variables					
Dependent	Independent[a]	Years	n	r^2	P
Isabella buck kill	Individual packs[b]	1975–1997	23		NS
Isabella buck kill	Isabella packs	1975–1997	23		NS
Isabella buck kill	Total population	1975–1997	23	0.14	0.08
Isabella buck kill	Total population	1975–1997	22[c]	0.22	0.03
Ely buck kill	Individual packs	1984–1997	14		NS
Ely buck kill	Ely wolves	1984–1997	14		NS
Ely buck kill	Total population	1984–1997	14		NS
Ely and Isabella buck kill	Total population	1984–1997	14		NS
Adjacent buck kill	Total population	1983–1997	15		NS

[a] Winter before the deer harvest.
[b] Six individual packs were tested.
[c] With 1984 removed as "outlier".

gressions, we noticed an apparent outlier in one of the plots. Although we knew of no reason to remove the outlier from the analysis, we did so arbitrarily to see how much this maneuver would force the data to fit our hypothesis. The result was an increase to an r^2 of 0.22 for the total of the wolf packs on a deer economy versus the Isabella buck kill (Table 2).

Plotting annual total wolf numbers against Isabella buck harvest from 1975 to 1997 showed no lag effect (Fig. 2). In fact, from 1975 through 1984, the wolf population tracked the decreasing deer harvest but continued downward through 1991 after deer harvest increased. Wolf numbers then increased again.

Annual decreases or increases of ≥5 each of wolves and deer were inversely related in only 9 (41%) of the 22 years. Inverse relationships occurred in 7 other years but in those years the increase or decrease for one species was <5 animals. In the remaining 6 years, wolves and deer increased or decreased similarly in 5 years, and in one year the largest decrease (n = 25) in the wolf population (from 1989 to 1990) was followed by no change in the buck harvest. Among all years, the greatest decrease in the buck harvest (from 1992 to 1993) was preceded by only a small wolf increase, and large increases in buck harvest (from 1979 to 1980 and 1984 to 1985) were preceded by wolf increases.

From 1988 to 1995 when hunting pressure was deemed relatively constant, we found inverse relationships (r^2 = 0.36–0.48) between size of individual wolf packs and buck harvest, and between the Ely buck kill and the wolves in the Ely-buck-kill area (r^2 = 0.66; Table 3). The strongest relationship was between the total population of wolves in all our deer-killing packs and the harvest of bucks in the Ely area (r^2 = 0.84, P = 0.001). Nevertheless, we found

Table 3. Results of simple linear regression analysis of data from 1988 to 1995[a] to test the hypothesis that buck harvest should be inversely related to wolf numbers the previous winter if wolves strongly influence deer harvest. Only packs that prey on deer are included; all relationships are inverse.

Variables			
Dependent	Independent	r^2	P
Isabella buck kill	Isabella wolves		NS
Isabella buck kill	Jackpine pack	0.37	0.11
Isabella buck kill	Total population		NS
Ely buck kill	Birch L. pack	0.48	0.06
Ely buck kill	Little Gabbro pack		NS
Ely buck kill	Wood L. pack	0.36	0.11
Ely buck kill	Ely wolves	0.66	0.01
Ely buck kill	Total population	0.84	0.001
Ely and Isabella buck kill	Total population		NS
Adjacent buck kill	Total population		NS

[a] Deer hunting pressure relatively constant during this period (M. S. Lenarz, Minnesota Department of Natural Resources, personal communication.)

no relationships between total population of deer-killing wolves and either the combination of Ely and Isabella buck harvest or size of buck harvest from adjacent areas (Table 3).

DISCUSSION

Because deer constitute the main prey of wolves in our study area, it is reasonable to think that wolves would affect the number of deer harvested by humans (Mech 1971, 1984; Fuller 1989). In fact, any major factor that adds to total deer mortality would have some effect, especially if a high percentage of the deer population is harvested. An extreme example was the decimation of deer in the eastcentral part of the SNF and reduction of the surrounding population in the early 1970's. Although poor habitat and a series of severe winters contributed to the deer decline, it was exacerbated by wolves (Mech and Karns 1977). To whatever extent wolf predation added to any direct weather-caused losses, that predation affected deer hunting.

The more heavily harvested a deer population, the greater the potential for other mortality factors, including wolves, to affect the number of harvestable deer (Mech 1971, 1984; Fuller 1989). Thus, a wolf-free area should support more harvestable deer than a similar area with wolves. The degree to which wolf predation and human hunting actually compete, however, is dependent on the intensity of each and how compensatory are those factors. The greater the proportion of the herd removed by each mortality factor, the greater the probability for competition.

In our census area, wolves kill about 20% and hunters about 30% of the legal bucks, and of all yearling and adult deer of both sexes, wolves take about 15% and hunters 7% (Nelson and Mech 1986*b*; M. E. Nelson and L. D. Mech, U. S. Geological Survey, unpublished data). The northeastern half of the area includes soil of low fertility and poor habitat that has been protected from cutting or burning and has supported a relatively low deer density for decades (Mech and Karns 1977, Nelson and Mech 1981). In such an area, wolves and hunters would probably compete more for the relatively few deer, which may explain the stronger relationship between size of the wolf population and deer harvest.

Our findings in the present study are ambiguous about the degree to which wolves compete with hunters for bucks, and the possible masking of relationships by the unknown effect of variable hunter effort each year. Only if we had found no relationships between wolf numbers and buck harvest in all the tests we ran could we have concluded that wolves probably did not have any strong direct effect on buck harvest.

However, we did find some significant relationships between wolf numbers and buck harvest, and it is revealing that the stronger relationships were for a period when hunter effort was considered relatively constant. This finding may demonstrate that variable hunter effort can indeed mask these relationships under some conditions. However, we found the strongest relationships when deer density was lowest and competition between wolves and hunters probably greatest. In fact, in the better habitat where we had the largest samples of buck harvest data, we found no significant relationships between wolves and buck harvest even when hunter effort appeared relatively constant. This suggests that generally hunter effort may not be so overwhelming a factor that it obscures strong relationships with wolves.

Our examination of annual changes in wolf and deer numbers showed inconsistent relationships. During some years after wolves increased, buck harvest increased. Furthermore, the wolf population actually declined while deer numbers, as reflected by the buck harvest (Lenarz 1997), increased (Fig. 2).

We are uncertain about the significance of the fact that during the 8-year period when wolves seemed to be most influential, the buck harvest for the Ely area was the highest for the 14 years of records (Table 1). However, this increased harvest might have resulted from increased hunting pressure responding to an increasing deer population.

Despite the ambiguities and uncertainties in our results, it is reasonable to conclude that, at least in poor quality habitat, wolves do negatively influence deer harvest: Stenlund (1955) and Mech and Karns (1977) also came to the same conclusion. However, there still is no evidence that in most areas wolves directly influence buck harvest significantly, at least under current hunting regulations.

MANAGEMENT IMPLICATIONS

Our conclusions must be viewed in the total context of Minnesota's deer hunting regulations. The Minnesota Department of Natural Resources adjusts deer harvesting levels for a sustainable yield based on simulation modeling of deer density (Lenarz 1997). Therefore, the effect of major mortality factors such as wolves and weather are automatically considered in setting harvest regulations. A wolf-inhabited area would have more restrictive regulations, and thus, a lower allowable harvest than an area free of wolves. In fact, continued restrictions against taking antlerless deer in the wolf-census area are in themselves a form of compensation for the combination of wolves, weather, and poorer quality of the area for deer. Given these considerations, our findings tend to confirm the suitability of the Minnesota Department of Natural Resource's harvest regulations for a sustainable yield in our study area.

If deer-hunting regulations are well adjusted to the wolf–deer–weather complex in the study area, what does this situation imply for other areas in wolf range where wolves may be less influential such as parts of northcentral Minnesota (Fuller 1989)? Throughout much of Minnesota's current wolf range (Fuller et al. 1992, Berg and Benson 1999), deer harvest has increased even as wolves were recolonizing new areas (Route 1998). This implies that during the expansion of the wolf's range, wolves were not impacting deer numbers enough to have prevented liberalizing harvest regulations.

How long recolonized wolf populations can thrive without affecting harvests will depend at least partly on whether harvest regulations are conservative or liberal. Fuller (1989) provided a theoretical approximation of this relationship. If harvest regulations are liberal enough, a point might be reached where wolves would strongly reduce deer harvest by humans (Mech 1971, 1984; Fuller 1989).

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