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A 3-decade Dearth of Deer (*Odocoileus virginianus*) in a Wolf (*Canis lupus*)–dominated Ecosystem

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ABSTRACT.—Some 30 y after wolves (*Canis lupus*) were implicated in decimating wintering white-tailed deer (*Odocoileus virginianus*) in a 3000-km² area of northeastern Minnesota, wintering deer still have not recolonized the area. From 1976 to 2004, we aerially radio-tracked wolves there during 250 h and recorded 2 deer (in 1985 and 2000) killed or eaten by wolves during February and March. We observed no other deer or deer sign, but regularly observed deer, deer sign and wolf-killed deer in adjacent wolf-pack territories. Although habitat in the study area generally remains poor, some regeneration has taken place, and deer have increased adjacent to the area. However, wolf numbers have persisted by preying on moose (*Alces alces*). We could detect no reason other than wolf predation and deer migration traditions for why wintering deer have not recolonized the area.

INTRODUCTION

Wolf-prey systems generally persist for long periods, and it is rare for a prey population to be decimated from an area for a long period (Mech and Peterson, 2003). Wolves (*Canis lupus*) nearly decimated black-tailed deer (*Odocoileus hemionus sitchensis*) on a 73-km² island, but the wolves had been introduced there (Klein, 1995). The only documented natural decimation of prey that we know of involving wolves occurred in a 3000 km² area of mature forest in northeastern Minnesota where overwintering white-tailed deer (*Odocoileus virginianus*) were eliminated (Mech and Karns, 1977).

In that region deer wintering in a 3000-km² area of the Superior National Forest disappeared between 1964 and 1974 after being present for at least 30–40 y. Severe winters, maturing forests and wolf predation were implicated in the demise of the wintering population (Mech and Karns, 1977). Because forest maturation was a gradual process, a series of seven severe winters from 1966 through 1972, along with a wolf density of 39 wolves/1000 km² (Mech, 1973) was thought to be the trigger for the disappearance of wintering deer. A bounty on wolves had been removed in 1965, and legal protection of wolves in the area was instituted in 1970. The killing of hundreds of deer by wolves was documented (Mech and Karns, 1977). The migratory behavior of deer in the study area was unknown, but their lower numbers and sparser distribution compared to that of the hundreds of deer occupying major deeryards in the region suggest that large numbers of deer did not migrate into the area from more distant summer ranges to spend winter there. Migratory deer wintering 19 km south and 26 km west continued to occupy the area from April to December each year (Hoskinson and Mech, 1976; Nelson and Mech, 1987). Furthermore, the putative non-migratory behavior of the decimated deer suggested that migratory behavior confers higher survival because migration leads to congregation which helps dilute predation risk (Nelson and Mech, 1981, 1991).

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The rarity of such a localized prey decimation and the opportunity to study its aftermath for three more decades presented a valuable chance to examine the role of various factors involved in preventing deer recolonization of local areas. Current knowledge about deer recolonization and population recovery is limited to deer reintroductions to eastern North America where severe winters and wolf predation were lacking (Halls, 1984), and to one study that artificially removed deer from a local wolf-free area (Oyer and Porter, 2004). Thus, it is unknown what habitat, population, behavioral and predator-prey dynamics must occur before wintering deer can recolonize areas occupied by wolves.

The migratory deer population adjacent to the area devoid of deer maintains strong migratory traditions passed from mothers to offspring (Nelson, 1998). Thus, most deer migrate to the same winter range during their entire lives. The most likely colonizers of vacant areas would be either orphaned fawns or dispersing juveniles breaking with learned migration patterns (Nelson, 1993). Such colonization could be rare in the presence of wolves because deer are vulnerable when moving alone through deep snow with no associates to share the risk (Nelson and Mech, 1981, 1991). Furthermore, because deer numbers in northern Minnesota are highly influenced by winter severity (Lenarz, 1992, 2003), so too would be the number of deer available to recolonize suitable habitat.

Herein, we document a 30-y absence of wintering deer after decimation involving wolves, severe winters and poor habitat; we describe the occurrence, movements and population change of deer in the adjacent area during that time; and we discuss the influence of forest maturation, winter severity, wolf predation, deer migration behavior and regional deer population change on potential recolonization by deer. We assess these factors in an attempt to explain the lack of deer wintering in the area.

STUDY AREA

Our study, spanning 1976–2004, lay in the 10,750 km² Superior National Forest of northeastern Minnesota (91°W longitude and 48°W latitude). Our observations and conclusions apply to the western half (1500 km²) of Mech's and Karns' (1977: Fig. 2) "Interior Area"; roadless wilderness east of Ely in parts of Lake and Cook counties (Fig. 1). The topography is gently rolling with numerous low rocky ridges and elevations from 400–700 m, typical of the region. Climate is cool temperate (Hovde, 1941) with snowfall averaging over 150 cm during 5 mo of winter starting in mid-November. In 8 of 29 winters during 1976–2004, weekly snow depths in broadleaf-conifer forests were consistently >60 cm during February–March (Mean = 64 cm, SD = 11, n = 29 wk). Six of those winters came 2–4 y apart and 2 in consecutive years. February–March weekly snow depths generally 40–60 cm occurred during 7 winters (Mean = 49 cm, SD = 9, n = 56). February–March weekly snow depths generally <40 cm occurred in the remaining 14 winters (Mean = 31 cm, SD = 12, n = 111), 8 preceding or following 1–2 other light-snow years.

Upland coniferous and coniferous-broadleaf communities predominate (Heinselman, 1993), comprised of white pine (*Pinus strobus*), red pine (*P. resinosa*), jack pine (*P. banksiana*), black spruce (*Picea mariana*), white spruce (*P. glauca*), balsam fir (*Abies balsamea*), aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*) and red maple (*Acer rubrum*). Common shrubs include alder (*Alnus* sp.), cherry (*Prunus virginianus*), dogwood (*Cornus* sp.), beaked hazelnut (*Corylus cornuta*), fly honey suckle (*Lonicera canadensis*), juneberries (*Amelanchier* spp.), mountain maple (*A. spicatum*), bush honeysuckle (*Dierovilla lonicera*), red raspberry (*Rubus strigosus*) and blueberry (*Vaccinium angustifolium*). The forests are transitional, comprising all the major tree species of the central Canadian boreal forest but lacking dominant tree species of the eastern Great Lakes forests (Rowe, 1972; Heinselman, 1993).

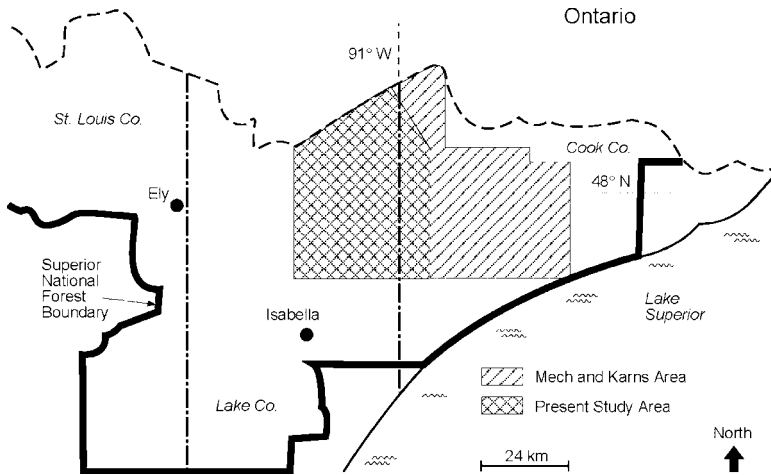


FIG. 1.—The study area in northeastern Minnesota

This is equally true for the shrubs and herbs, reflecting a “nearly boreal character” when compared to northeastern forests (Heinselman, 1993).

The northern 19% of the study area was logged for pine sawtimber during 1900–1916 and the southern 46% for jack pine and spruce pulpwood during 1948–1968. The remaining 35% was 150-y-old virgin forest originating from 1864 and 1875 fires (Heinselman, 1993). A 1999 windstorm destroyed nearly all the canopy trees in the northern third of the area, comprising all of the early-logged forests and 25% of the virgin forests. Shade-tolerant balsam fir and spruce from the pre-storm understory now dominate the tree canopy. However, dense aspen root suckering is evident in mixed forests. All of the forests 40 km to the east and most 16 km to the west, share this same vegetation and disturbance history, but some adjacent forests to the west and all to the south are intensively managed commercial forests with various ages of conifer plantations and post-logging stands.

Wolves (*Canis lupus*) (Mech, 1973, 1986) and moose (*Alces alces*) (Dexter, 2003) inhabit all of the Superior National Forest. Although wolf density was unknown for 25% of the study area, in the other 75%, it ranged from 20 to 40 wolves/1000 km², measured from counts of four wolf packs (L. D. Mech, unpubl.). Six adjacent packs to the west and south ranged from 22 to 51 wolves/1000 km² (L. D. Mech, unpubl.). Before depletion of wintering deer, wolf density ranged from 36 to 39 wolves/1000 km² (Mech, 1973).

Deer (*Odocoileus virginianus*) occupy the entire region except that in winter, they are vacant from the study area as well as from much of the area north and east of it (Fig. 1). The nearest wintering deer are single animals or small groups sparsely distributed 3–6 km west and south of the study area. The closest large concentrations of wintering deer are 26 km west and 19 km south of the study area. An aerial deer survey in deciduous forests during November 1986 estimated 5 deer/km² west of the study area and 2 deer/km² south of it (Nelson, 1990). Calculations based on percentage of radioed deer migrating into the study area estimated summer density at 0.5 deer/km². Summer deer density in the area north and east of the study area is unknown. Inaccessibility precludes the annual deer hunting in November that occurs to the south and west.

Moose density is 0.5 moose/km² in the adjacent managed forests (M. S. Lenarz, Minnesota Department of Natural Resources, pers. comm.). Moose density may be somewhat lower

in the study area due to maturing habitat, although forest aging dynamics and the 1999 windstorm effects likely favored conditions for moose. Moose population change in the region is unknown.

Black bears (*Ursus americanus*) also inhabit the region and may prey upon neonatal fawns at a similar rate as wolves during the first 2 wk of life, after which time fawns readily escape bears (Kunkel and Mech, 1994). Compared to wolf predation which is a continual threat to fawns (Nelson and Mech, 1986a), bear predation is a minor contributor to fawn mortality.

METHODS

Two to five times weekly during February–March 1976–2004, we aerially radio-tracked 3–4 wolf (*Canis lupus*) packs that occupied the study area in addition to radio-tracking six adjacent packs (Mech, 1986). In years when a specific wolf pack was not radio-collared, the abundance of lakes and interconnecting streams allowed estimating its numbers by aerial observations of wolves and wolf trails in the snow (Mech, 1986).

We attempted to document the occurrence of wintering deer (*Odocoileus virginianus*) by recording all wolf-killed deer (bloody snow, fresh tracks) observed while circling radio-collared wolves 150 m above ground level (AGL). We assumed that if deer were present in a wolf pack's territory in winter, we would see the deer, or wolves would kill some, and we would discover them, as happens regularly when radio-tracking adjacent wolf packs. We restricted our observations to February and March when radio-collared migratory deer were on their winter ranges (Nelson and Mech, 1981). Thus, we concluded that deer killed by wolves in February or March were wintering deer and not lingering migratory deer still on summer ranges (Nelson, 1995). We additionally scanned for deer and their trails while flying 400 m AGL. We developed our aerial search image for deer sign by observing known deer wintering areas with varying densities of deer (Nelson and Mech, 1986b). We also recorded any wolf-killed moose we found in the study area.

We examined the probability of deer recolonization of the study area by monitoring the survival and movements of deer (mostly migratory) captured and radio-collared 26 km west and 19 km south of the study area during 1975–2004 (Nelson and Mech, 1981, and unpubl.). Many of these deer migrate to, or live adjacent to, the study area during summer.

We measured deer population changes from 1985 to 2003 by examining buck harvests in 13,000 km² encompassing the study area (Lenarz, 1992, 2003), and used simple linear regression to examine the relationship between percent change in buck harvest and mean weekly snow depths. We conducted low-level aerial reconnaissance to observe the canopy structure and regeneration of 1999 storm-damaged forests. Ground surveys of vegetation of the storm-damaged-forest also were conducted by Superior National Forest personnel (unpubl.).

RESULTS AND DISCUSSION

Wolves and deer.—Wolf (*Canis lupus*) pack use of the study area has been dynamic, with the Malberg Lake pack from 1978 to 2005, numbering 2 to 12 ($\bar{x} = 8$, $n = 28$), usually having most of its territory in the study area. Also, the Ensign Lake pack and two or three other packs used parts of the area (Mech, 1986; L. D. Mech, unpubl.). During 250 h of winter flying over the study area from 1976 to 2004, we recorded only two deer (*Odocoileus virginianus*) (in 1985 and 2000) killed or eaten by wolves during February and March in the study area but 65 moose so killed. We observed no other deer or deer sign, but we regularly observed moose and their tracks. In contrast, we regularly observed deer, deer sign and wolf-killed deer in adjacent areas to the west and south.

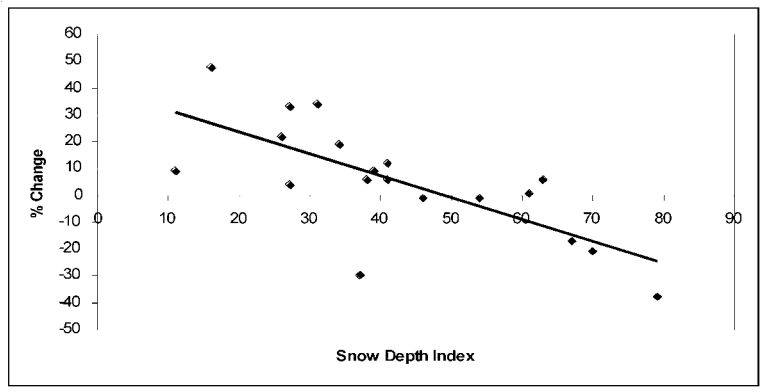


FIG. 2.—Relationship between fall harvest of buck deer (*Odocoileus virginianus*) in the region adjacent to the study area and mean weekly snow depths in February and March the preceding winter ($r = -0.7$; $P = 0.005$)

From 1975 to 2004 we captured and radio-collared 284 deer west and south of the study area, in the two nearest wintering areas, and radio-tracked each deer >1 summer (Nelson and Mech, 1981). Thirty-five (12.3%) migrated 19–64 km to spend summer within the study area, typical migration distance for this area. We followed 30 of the deer through >2 winters; all migrated to wintering areas outside the study area. Two other radioed deer summering outside the study area wintered 5 km west of the study area at sites with little or no deer sign. One was 1-year-old male that remained on his dispersal summer range, but resumed migrating to his original winter range each year until killed by a hunter when 5-y-old. The other was a 5-y-old nonmigratory female that moved 22 km to a site where we observed her with another deer before she was killed by wolves 67 d later. Two years earlier, the same wolf pack had killed a non-radioed deer near that site.

Regional buck harvests indicated that deer numbers in the region south and west of the study area increased and generally remained high after 1984 (Lenarz, 1992, 2003; Mech and Nelson, 2000). Increases in the buck harvest during 1985–2004 were related to lower mean weekly snow depths during February–March the previous winter ($r = -0.7$, $P = 0.005$, $n = 19$ y, Fig. 2). Given that buck harvests are reliable indicators of population trends in northern Minnesota (Lenarz, 1992, 2003), this indicated that winter severity was a primary determinant of deer population change near our study area.

Forest maturation.—Before the loss of deer, Stenlund *et al.* (1952) considered plant succession to balsam fir as a primary factor in reducing deer habitat in the region. At the time the last wintering deer disappeared in 1975, Grigal and Ohman (1975) confirmed the vegetation trend from the dominance of broadleaf tree species to balsam fir. Supporting Stenlund *et al.*'s (1952) conclusions, Peek *et al.* (1976) measured increased height, decreased density and decreased nutrient levels of shrubs in mature stands within and adjacent to our study area. Although succession to balsam fir has created ubiquitous winter cover, its effect reduced the quantity and quality of browse.

During the period when the deer declined (1964–1974), the upland conifer and broad-leaf virgin forests reached ages when windfall, insect damage and disease creates openings in the forest canopy which in turn stimulates shrub production (Heinselman, 1993). Since then, these forests have frequently sustained these kinds of stand-level disturbances that reverse or retard succession to balsam fir and its negative nutritional effects for deer. Aerial

TABLE 1.—Relationship between February–March mean weekly snow depths and percent change in the harvest of white-tailed (*Odocoileus virginianus*) bucks in the central Superior National Forest

Year	Snow depth (cm)	% change in buck harvest
1985	31	34
1986	54	-1
1987	27	33
1988	41	6
1989	70	-21
1990	34	19
1991	46	-1
1992	61	1
1993	37	-30
1994	41	12
1995	27	4
1996	79	-38
1997	67	-17
1998	16	48
1999	38	6
2000	11	9
2001	63	6
2002	39	9
2003	26	22

reconnaissance confirmed the dominance of coniferous-broadleaf communities with abundant canopy and understory conifers interspersed with small disturbance openings. Thus, wintering habitat appears equally abundant inside the study area as it is outside the study area where deer spend winter.

More recent logging of jack pine and black spruce in the southern part of the study area also improved deer habitat by converting previous conifer forests to a mosaic of uneven-aged broadleaf-conifer forests comprised of mature uncut aspen, birch and balsam fir originating after a fire in 1864 as well as second-growth aspen, birch and fir (Heinselman, 1993). By 1975, when the last deer were observed in the interior, these forests were 7–27 y old, less than half the age when balsam fir can be a significant understory in broadleaf-conifer forests (Heinselman, 1993). The two wolf-killed deer we found occurred in these forests.

The 1999 windstorm created a 35×12 -km path of damage through the virgin and early-era logged forests of the interior. We observed the damage from aircraft in May 2004 before green-up and could readily see to ground level in most areas, despite the presence of the fir that comprised the pre-storm understory in many, but not all, stands. Vegetation surveys 3 and 4 y after the storm found winter deer forages [mountain maple, dogwood, red maple, and beaked hazel (Wetzel *et al.*, 1975; DelGiudice *et al.*, 1989)], abundant in the shrub layer in broadleaf-conifer forests (Superior National Forest, unpubl.). These observations suggest that the edge of the damaged forest should provide a new source of browse combined with winter cover in adjacent undamaged areas. However, during the five winters since the storm damage, we have not observed wintering deer along this edge. The 1999 windstorm did not affect the adjacent areas where deer increased and from which some deer migrated into the study area to spend summer.

Recolonization dynamics.—After being absent during winter for three decades, deer that inhabited the study area in spring, summer and autumn continued to vacate the study area during February–March. Given our frequent radio-tracking and unsuccessful systematic

searching for deer sign, the number of deer wintering and surviving more than one winter must have been extremely small if there were any at all. During radio-tracking flights for wolves in adjacent areas we regularly observed wolf-killed deer, live deer and deer trails in the snow. Despite the presence of some wintering deer in adjacent areas and presumably suitable habitat for them 10 and 25 y after the population decline, the forest dynamics creating deer browse failed to prevent summering deer from vacating the area during winter.

Mech and Karns (1977) presented evidence that wolves were the immediate agents of deer mortality, but proposed that severe winters and forest maturation interacted to predispose the deer to depredation by wolves and cause the decline and disappearance of wintering deer in this study area. Because generally mild and moderate winters have led to higher deer numbers nearby since 1984, forest maturation and wolf predation now remain as likely factors contributing to the lack of deer recolonization.

The lower quantity and nutritional content of browse due to forest maturation has reduced ungulate populations in other ecosystems (Cowan *et al.*, 1950; Leopold *et al.*, 1951) and the same vegetation processes were documented in our study area (Peek *et al.*, 1976). However, the dynamics of forest aging including fires, windfall, diseases and insect infestation can reverse or retard maturation of deer browse (Heinselman, 1993) and the 5 y of shrub growth in the wind-damaged forest that we documented demonstrate how this can happen. Thus, forest maturation probably has not prevented recolonization during the last 5 y, at least for some sites comparable in size to a deer home range.

Eliminating lack of browse due to forest maturation leaves wolf predation as a likely factor in helping prevent the recolonization of wintering deer. Wolf numbers in the area have remained relatively stable since the decline (Mech, 1986, 2000:23) because moose provided a readily available food supply. Thus, the population effects that wolf predation had on deer at the time of the decline have remained unchanged and at least partly explain why deer have failed to recolonize the area despite an available source population (Mech and Nelson, 2000) and mild winters. This direct predation effect could also be reinforced by the inter-generational learning of migration behavior during a deer's first year (Nelson, 1998) because migratory does would take their fawns away during winter and any remaining nonmigratory does with fawns would face increased vulnerability to wolf predation. If mortality exceeded recruitment in nonmigratory deer, eventually wintering deer would be extirpated.

Nonmigratory deer in a predominantly migratory population incur higher wolf predation rates when the migrants vacate an area during winter (Nelson and Mech, 1991). Nonyarded deer were at least nine times more likely to be killed by wolves than yarded deer, probably because they lacked the anti-predator benefits afforded by concentration behavior (Nelson and Mech, 1981). Nonyarded deer could be deer with no migration tradition such as orphan fawns, natal dispersers, adult dispersers or migrants that break with their learned movement pattern. Older fawns that become orphans before winter would have no knowledge about migrating even if their mothers had been migrators. Deer can learn migratory behavior, but it is not innate (Nelson, 1998). An orphan fawn would have to join other migratory deer to migrate to a wintering area shared with other deer. Thus, when discovered by wolves, orphans that did not do so would be the sole target of attack and possibly subjected to repeated chases and tracking until eventually killed. During periods of deep snow, the kill likely would occur immediately (Nelson and Mech, 1986c), but during milder conditions it could take repeated attempts because wolves only succeed in 20% of deer chases in winter (Nelson and Mech, 1993). Wolves can be persistent in following fresh scent and will chase deer for many kilometers (Mech and Korb, 1978), although this appears to be the exception.

Wolves also intimately know their territory and likely remember locations where they encounter prey. This ability to locate prey would be further enhanced by the rarity of a nonmigrant deer in a territory otherwise occupied by moose that can be more difficult to kill. However the scenario is played out, the result would be the same. The probability of a nonmigrant deer surviving not only more than one winter, but also producing offspring that survive and reproduce, would be low in the presence of wolves. The same likelihood of survival also would apply to any deer breaking with its previous tradition and moving into a wolf-occupied area where deer are rare and more vulnerable to wolf predation. It might be argued that prey rarity enhances concealment and minimizes detection by predators, but for wolves and deer, the evidence from our study suggests otherwise. For deer preyed upon by wolves, proximity to other deer and not solitariness increases deer survival during winter (Nelson and Mech, 1981, 1991). Thus, our study of deer migration, starting after the decimation of wintering deer, suggests that deer migration traditions probably exacerbated the effect of wolves in eliminating non-migratory wintering deer and that both factors likely continue to interact in preventing the reestablishment of wintering deer.

CONCLUSIONS

Our findings underscore the localized and multiple-decade effects of severe population decline in deer (*Odocoileus virginianus*) experiencing severe winters and wolf predation in mature forests near the northern edge of their range. Thirty y of a persistent deer population nearby, including 19 y of increasing deer numbers, failed to produce enough dispersers to recolonize the study area during winter. Given the knowledge of forest dynamics (Heinselman, 1993) and our understanding of wolf (*Canis lupus*)-deer interactions, the evidence also manifests the inter-generational influence of learned migration behavior on the spatial dynamics of northern white-tailed deer. As with the deer population artificially reduced locally in the Adirondacks (Oyer and Porter, 2004), the females immediately adjacent to our study area failed to change their home range or migratory patterns to colonize suitable nearby vacant areas or to produce enough dispersers to overcome predation by wolf packs supported by moose in the study area.

Most wolf-prey systems are self-sustaining (Mech and Peterson, 2003). However, it is clear from our study that local and/or temporary habitat and weather disruptions can affect a wolf-deer system for long periods, similar to situations found elsewhere with other wolf prey (e.g., Gasaway *et al.*, 1983, 1992).

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