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ECOLOGY AND POPULATION DYNAMICS OF BLACK BEARS IN MINNESOTA

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SUMMARY OF FINDINGS

During April 2004 – March 2005, 42 radiocollared black bears were monitored at 3 Minnesota study sites: Chippewa National Forest (CNF; central study site), Camp Ripley (southern) and Voyageurs National Park (northern). Prior to this year's monitoring, 781 individual bears were handled of which 474 were radiocollared at these 3 sites, beginning in 1981 in the CNF. In recent years, GPS radiocollars provided detailed information on movements of bears, yielding insights into establishment of home ranges, seasonal forays, dispersal, and wanderings after translocation. Mortality data were obtained through collars turned in by hunters or collars tracked to carcasses. Hunting is by far the largest source of bear mortality. In the past few years, however, hunters were asked not to shoot collared bears, so our study no longer provides representative mortality data. The study is now focused primarily on reproduction. Reproductive output varies among the 3 study sites in response to food conditions, but no upward or downward trends through time are evident. Most bears in Minnesota begin producing cubs at 3–7 years old (at 3 only in the southern area, 6–7 only in the central and northern areas), and produce an average of 2.6 cubs per litter (modal litter size = 3) every 2 years (mean = 2.06 years). Cub mortality, which is nearly twice as high for males as for females, varies by area from 17–33%. These data have been used to model and track the statewide population.

INTRODUCTION

A paucity of knowledge about bear ecology and effects of harvest on bear populations spurred the initiation of a long-term telemetry based bear research project by the Minnesota Department of

Natural Resources (MN DNR) in the early 1980s. For the first 10 years, the study was limited to the Chippewa National Forest (CNF), near the center of the Minnesota bear range. After becoming aware of significant geographic differences within the state in sizes, growth rates, and productivity of bears, apparently related to varying food supplies, we started other satellite bear projects in different study sites. Each of these began as graduate student projects, supported in part by the Minnesota DNR. After completion of these student projects, we continued studies of bears at Camp Ripley Military Reserve, near the southern fringe of the Minnesota bear range, and in Voyageurs National Park (VNP), on the Canadian border.

By comparing results from three study sites over a long term, we have gained insights into both spatial and temporal variation in bear life history parameters that are directly related to bear management. We tested and deployed a tetracycline-based mark-recapture program, and have since obtained three statewide population estimates over a span of 12 years (Garshelis and Visser 1997). However, confounding variables, related mainly to capture heterogeneity (e.g., Noyce et al. 2001) have necessitated further study for refinement of the technique. We developed a means of ascertaining reproductive histories from the spacing of cementum annulations in teeth (Coy and Garshelis 1992), which was used to investigate variation in reproductive output across the state (Coy 1999). We also developed a method for obtaining unbiased estimates of age of first reproduction and interval between litters (Garshelis et al. 1998, Garshelis et al. 2005). These data are needed for continued statewide population modeling. For many years we have focused our efforts on measuring and monitoring physical condition of bears (Noyce and

Garshelis 1994, Noyce et al. 2002) and their food supply (Noyce and Garshelis 1997). Results of this work have been instrumental in explaining variations in harvest numbers and sex-age structure (Garshelis and Noyce 2005). All of these represent areas of continued research and monitoring.

OBJECTIVES

- Monitor temporal and spatial variation in cub production and survival;
- Obtain additional, improved, measurements of body condition, heart function, and wound healing abilities; and
- Examine habitat use and detailed movements (dispersal, establishment of home ranges, fall excursions, etc.) with GPS telemetry.

METHODS

Radiocollars (with breakaway and/or expandable devices: Garshelis and McLaughlin 1998, Coy unpublished data) were attached to bears either when they were captured in barrel traps during the summer or when they were handled as yearlings in the den of their radiocollared mother. Limited trapping has been conducted in recent years. However, during December–March, all radio-instrumented bears were visited once or twice a year at their den site. Bears in dens were immobilized with an intramuscular injection of Telazol, administered with a jab stick or Dan-Inject dart gun. Bears were then removed from the den for processing, which included changing or refitting the collar, or attaching a first collar on yearlings, measuring, weighing, and obtaining blood and hair samples. We also measured bioelectrical impedance (to calculate percent body fat) and vital rates of all immobilized bears. Additionally, with the cooperation of investigators from the University of Minnesota (Dr. Paul Iaizzo) and Medtronic (Dr. Tim Laske), heart condition was measured with a 12-lead EKG and ultrasound on a select sample of

bears (these data are not presented in this report). Bears were returned to their den after processing.

Reproduction was assessed by observing cubs in dens of radiocollared mothers. Cubs were not immobilized, but were removed from the den after the mother was drugged, then sexed, weighed, and eartagged. We evaluated cub mortality by examining dens of these same mothers the following year: cubs that were not present as yearlings with their mother were presumed to have died.

During the non-denning period we monitored mortality of radio-instrumented bears from an airplane approximately once each month. We listened to their radio signals, and if a pulse rate was in mortality mode (no movement of the collar in >4 hours), we tracked the collar on the ground to locate the dead animal or the shed radiocollar. If a carcass was located, we attempted to discern the cause of death.

RESULTS AND DISCUSSION

From 1981 through completion of den visits in March 2004, a total of 634 individual bears were handled in and around CNF, 76 at Camp Ripley, and 71 at VNP. Of these, we collared and monitored 386 bears in CNF, 49 at Camp Ripley, and 39 in VNP. As of April 2004, the start of the current year's work, we were monitoring 22 collared bears in the CNF, 5 at Camp Ripley, and 8 in VNP. By April 2005, after deaths, failed radiocollars, and the addition of some new bears obtained through trapping, released orphaned cubs, and den visits, 37 bears were collared on the 3 study sites.

Movements

We have been using collars containing both VHF radios and GPS units during the past few years to obtain more reliable data on movements and habitat use than obtainable with standard VHF collars. Twelve bears (some in all 3 study areas) were equipped with GPS collars, but 5 collars failed, 1 was dropped by the bear, and 3 of the bears were shot; thus, we obtained a full year of GPS data on

only 3 bears, and a partial year of data on 4 other bears.

Four GPS-collared bears at Camp Ripley provided particularly interesting data. One 3-year-old female, the daughter of a bear who wore a GPS collar in 2002, used nearly the same area as her mother (Figure 1). Like her mother, she avoided the target impact area at the north end of camp where National Guard troops shoot live ammunition. It is virtually devoid of trees. The 3-year-old, however, did use the more southern impact area during the fall, as this area contains highly productive oak trees. The mother, who in 2002 had an older model GPS collar that collected less data was never located in the southern impact area, but about a month of fall data were missing from her record (only 370 locations were recorded for the mother vs 1072 for the daughter). The young female also spent some time outside the Camp, which was not evident in the mother's record.

Three GPS-collared males all spent time outside the Camp (Figure 2). An 8-year-old made a southward movement of 28 miles (45km) during the fall (8 August–17 September), and returned to the Camp to den. A 5-year-old that was trapped as a nuisance outside the Camp in early May was translocated 50 miles north. He immediately began moving westward, and in 10 days traveled 67 miles (109 km); he covered the last 46 miles (73 km) in 80 hours, moving mainly at night, ending at an unfenced beeyard where he was shot and killed. A 1-year-old, that was collared near the hunter's bait site where his mother was killed the previous year (and weighing 106 pounds as a cub), initiated a dispersal at the end of May. He moved 45 miles (72 km) northeastward, then retraced his route and settled 26 miles (42 km) from his natal range. From 21 August until the opening of bear season on 1 September he remained within an area of only $\frac{1}{8}$ mi² (possibly smaller – within the error of the GPS unit). As he was shot the first day of the season, we suspect that his small area of use was centered on a hunter's bait.

Mortality

Legal hunting has been the predominant cause of mortality among radiocollared bears from all 3 study sites (Table 1). In previous years, hunters were encouraged to treat collared bears as they would any other bear so that the mortality rate of collared bears would be representative of the population at large. With fewer collared bears left in the study, and the focus now primarily on reproduction rather than mortality, we sought to protect the remaining sample of bears. We asked hunters not to shoot radiocollared bears, and we fitted these bears with bright orange collars so hunters could more easily see them in dim light conditions. Nevertheless, 2 of 18 (11%) collared females from the CNF and 2 of 11 (18%) collared bears at Camp Ripley were shot by hunters (bear hunting is not allowed on Camp Ripley, but bears are vulnerable to hunters when they leave this area, as noted above). Four additional collars were lost track of during the hunting season, either as a result of premature battery failure or being destroyed and not reported by hunters.

In addition to these hunter-related mortalities, 4 bears were shot as nuisances; 2 of these were reported as required by statute, and 2 were found only because they were collared. One bear was killed in late April at a bird feeder, 1 was killed during opening fishing season for unknown reasons, 1 was killed at a beeyard that was not protected by electric fence, and 1 was killed because it purportedly attacked a pet dog on a porch. Nuisance-related deaths are the second-highest cause of bear mortality in the CNF (Table 1). Vehicle collisions are the second-leading source of mortality at Camp Ripley. Smaller patches of habitat and higher road densities, resulting in increased traffic-related deaths, probably limit the southward expansion of bears. Very few bears, other than cubs, die of natural mortality.

Reproduction

Two 5-year-old CNF females produced their first litters in 2005, and one 3 and one 4-year-old produced their first litters at Camp Ripley. At Camp Ripley, where hard mast (especially oak) is more abundant, bears have a somewhat earlier age of first reproduction than in CNF.

Litter size tends to be less responsive to food conditions than age of first reproduction. However, first litters by young females are often smaller and have higher cub mortality than subsequent litters (Noyce and Garshelis 1994). The younger age of first birthing by females at Camp Ripley thus explains their somewhat lower average litter size and higher cub mortality, compared to CNF (Tables 2 and 3). VNP, having lower natural food availability than either Camp Ripley or CNF, had the oldest age of first reproduction as well as smaller litters and higher cub mortality. Cub production and survival also appeared to be most variable from year to year at VNP (Table 4).

We investigated age and year-specific variation in cub production within our long-term dataset in CNF. We measured cub production as (1) the proportion of collared females that produced a surviving litter of cubs (i.e., a litter in which at least 1 cub survived at least 1 year), and (2) the reproductive rate, defined as the number of cubs (both sexes) produced per female (as described by Garshelis et al. 2005). For year-specific analyses we calculated productivity only for females at least 4 years old. We considered 4 years old the minimum age of sexual maturity in CNF, as only 2 of 81 (2%) collared bears in this area produced cubs at 3. Age-specific cub production increased until about 7 years old (Figure 3), at which point nearly all bears had produced their first cubs. From age 7 to 25 years, 47.5% of females produced surviving litters of cubs. If all bears produced cubs every other year, then 50%, on average, would have cubs in any given year. Of 104 observed intervals between successful litters, all but 6 were 2 years duration, yielding an average litter interval of 2.06 years ($1/2.06$ yields an expected 48.5% of females

bearing cubs each year).

The reproductive rate includes both the proportion of females producing cubs and litter size. If litter size were constant by age and year, the proportion producing cubs and the reproductive rate would be redundant. Litter size, though, varied by age, averaging 2.0 for 3-year-old mothers, 2.3 for 4–6 year-olds, 2.7 for 7–9 year-olds, and 2.9 for 10–20 year-olds. We observed no cub production after age 25, but we observed only 1 collared bear that lived that long.

Cub production among radiocollared females in CNF did not show an upward or downward trend during our 25 years of monitoring, but exhibited a strong 2-year cycle since 1995 (Figure 4). Other black bear studies indicated that such cycles are instigated when productivity is synchronized by a poor food year that causes reproductive failures, especially among potentially primiparous females (McLaughlin et al. 1994, Miller 1994). However, the cycling in our study began just prior to a food failure during the summer and fall of 1995. Thus, the poor cub production in 1996 was a consequence of both good productivity the year before (as bears cannot produce surviving litters in 2 consecutive years) as well as poor food production in 1995. The continued cycling, though, is somewhat an artifact of our sample. Once a sample of reproductive bears becomes synchronized on a 2-year cycle, this synchrony continues through time, being diluted only by deaths of some of these bears, the inclusion of newly-collared bears, or newly maturing collared bears producing cubs in the off years. Since the late-1990s, we collared fewer new bears each year than in the early years of the study, so apparent reproductive cycles within our sample tend to persist. Nevertheless, a matching cycle of productivity is also evident in the age structure of harvested bears from a wide area in northern Minnesota (Garshelis and Noyce 2005).

Cub mortality also has not shown any upward or downward trend over the course of our study (Tables 2–4). Mortality of male cubs has averaged

about twice that of females in all areas (24% M vs 11% F in CNF; 33% M vs 17% F in Camp Ripley; 40% M vs 25% F in VNP). However, sex ratios at birth were skewed towards males in all areas (51–53%; Tables 1–3). These results have been used as inputs in a statewide population model.

ACKNOWLEDGMENTS

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Table 1. Causes of mortality of radiocollared black bears ≥ 1 years old from the Chippewa National Forest (CNF), Camp Ripley, and Voyageurs National Park (VNP), Minnesota, 1981–2005. Bears did not necessarily die in the area where they usually lived (e.g., hunting was not permitted within Camp Ripley or VNP, but bears were killed by hunters when they traveled outside these areas).

	CNF	Camp Ripley	VNP
Shot by hunter	207	8	8
Likely shot by hunter ^a	8	1	0
Shot as nuisance	22	2	1
Vehicle collision	12	5	1
Other human-caused death	9	0	0
Natural mortality	7	3	1
Died from unknown causes	3	1	0
Total deaths	268	20	11

^a Lost track of during the hunting season.

Table 2. Black bear cubs examined in dens of radiocollared mothers in or near the Chippewa National Forest during March, 1982– 2005.

Year	Litters checked	No. of cubs	Mean cubs/litter	% Male cubs	Mortality after 1 yr ^a
1982	4	12	3.0	67%	25%
1983	7	17	2.4	65%	15%
1984	6	16	2.7	80%	0%
1985	9	22	2.4	38%	31%
1986	11	27	2.5	48%	17%
1987	5	15	3.0	40%	8%
1988	15	37	2.5	65%	10%
1989	9	22	2.4	59%	0%
1990	10	23	2.3	52%	20%
1991	8	20	2.5	45%	25%
1992	10	25	2.5	48%	25%
1993	9	23	2.6	57%	19%
1994	7	17	2.4	41%	29%
1995	13	38	2.9	47%	14%
1996	5	12	2.4	25%	25%
1997	9	27	3.0	48%	23% ^b
1998	2	6	3.0	67%	0%
1999	7	15	2.1	47%	9%
2000	2	6	3.0	50%	17%
2001	5	17	3.4	76%	15%
2002	0	0	—	—	—
2003	4	9	2.3	22%	0%
2004	5	13	2.6	46%	33%
2005	6	18	3.0	33%	—
Overall	168	437	2.6	51%	17%

^a Cubs that were absent from their mother's den as yearlings were considered dead. Blanks indicate no cubs were born to collared females.

^b Excluding 1 cub that was killed by a hunter after being translocated away from its mother.

Table 3. Black bear cubs examined in dens of radiocollared mothers in Camp Ripley Military Reserve during March, 1992–2005.

Year	Litters checked	No. of cubs	Mean cubs/litter	% Male cubs	Mortality after 1 yr ^a
1992	1	3	3.0	67%	0%
1993	3	7	2.3	57%	43%
1994	1	1	1.0	100%	—
1995	1	2	2.0	50%	0%
1996	0	0	—	—	—
1997	1	3	3.0	100%	33%
1998	0	0	—	—	—
1999	2	5	2.5	60%	20%
2000	1	2	2.0	0%	0%
2001	1	3	3.0	0%	33%
2002	0	0	—	—	—
2003	3	8	2.7	63%	33%
2004	1	2	2.0	50%	—
2005	3	6	2.0	33%	—
Overall	18	42	2.3	52%	25%

^a Cubs that were absent from their mother's den as yearlings were considered dead. Blanks indicate no cubs were born to collared females or collared mothers with cubs died before the subsequent den visit. Presumed deaths of orphaned cubs are not counted here as cub mortality.

Table 4. Black bear cubs examined in dens of radiocollared mothers in Voyageurs National Park during March, 1999–2005.

Year	Litters checked	No. of cubs	Mean cubs/litter	% Male cubs	Mortality after 1 yr ^a
1999	5	8	1.6	63%	20%
2000	2	5	2.5	60%	80%
2001	3	4	1.3	50%	75%
2002	0	0	—	—	—
2003	5	13	2.6	54%	8%
2004	0	0	—	—	—
2005	5	13	2.6	46%	—
Overall	15	30	2.0	57%	33%

^a Cubs that were absent from their mother's den as yearlings were considered dead. Blanks indicate no cub mortality data because no cubs were born to collared females.

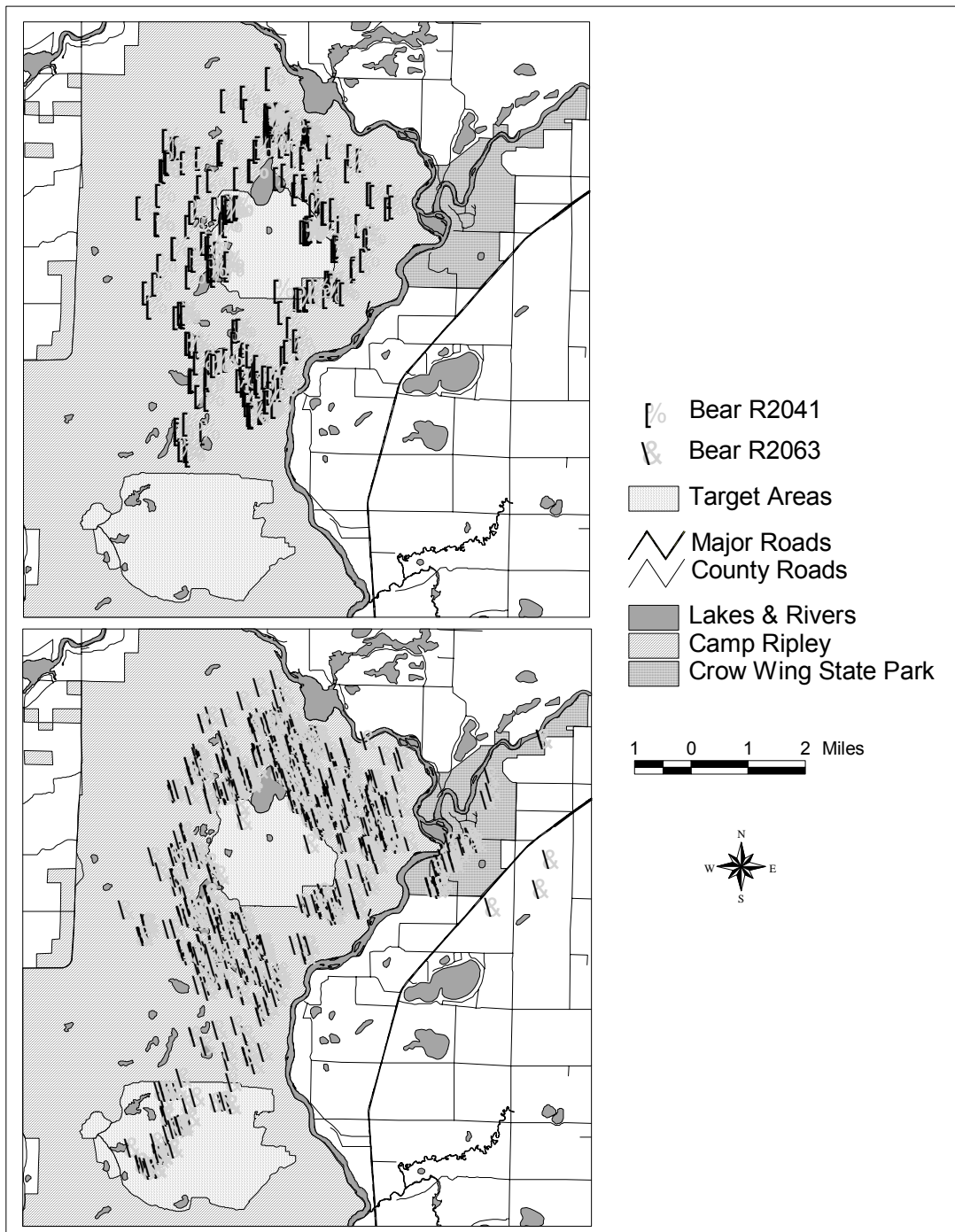


Figure 1. Movements of a GPS-collared female (top) in Camp Ripley during 2002 compared to her 3-year-old daughter (bottom) in 2004. Both bears avoided the northern impact target area (with few trees), but the daughter was attracted to productive oaks in the southern target area during the fall. More data were obtained in 2004 because of a newer model GPS collar.

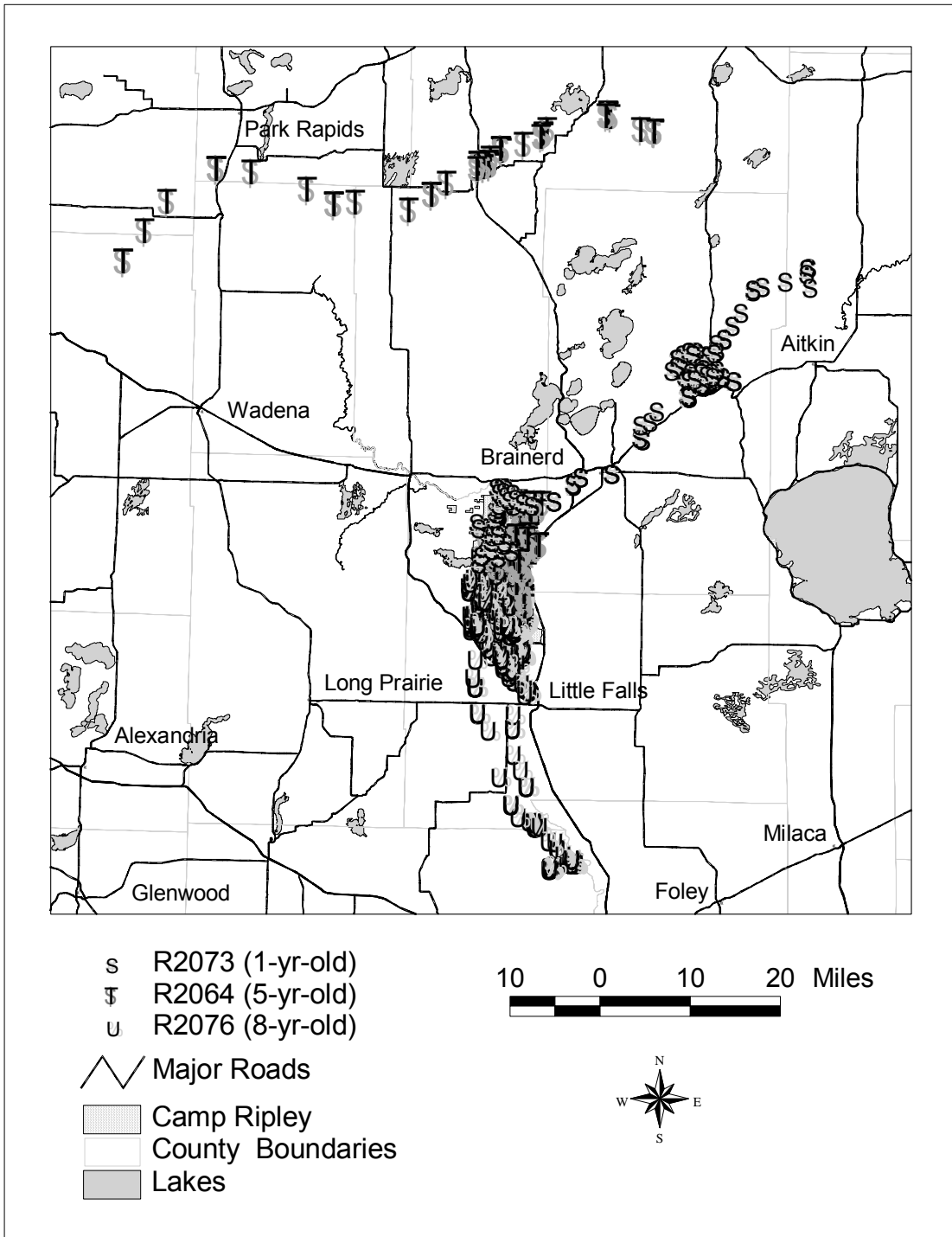


Figure 2. Movements of 3 GPS-collared males in Camp Ripley (southern Minnesota bear range) during 2004. The 8-year-old made a fall foray south of Camp, the 5-year-old was translocated north and then moved westward and was killed in a beeyard, and the 1-year-old dispersed northeastward and was shot by a hunter.

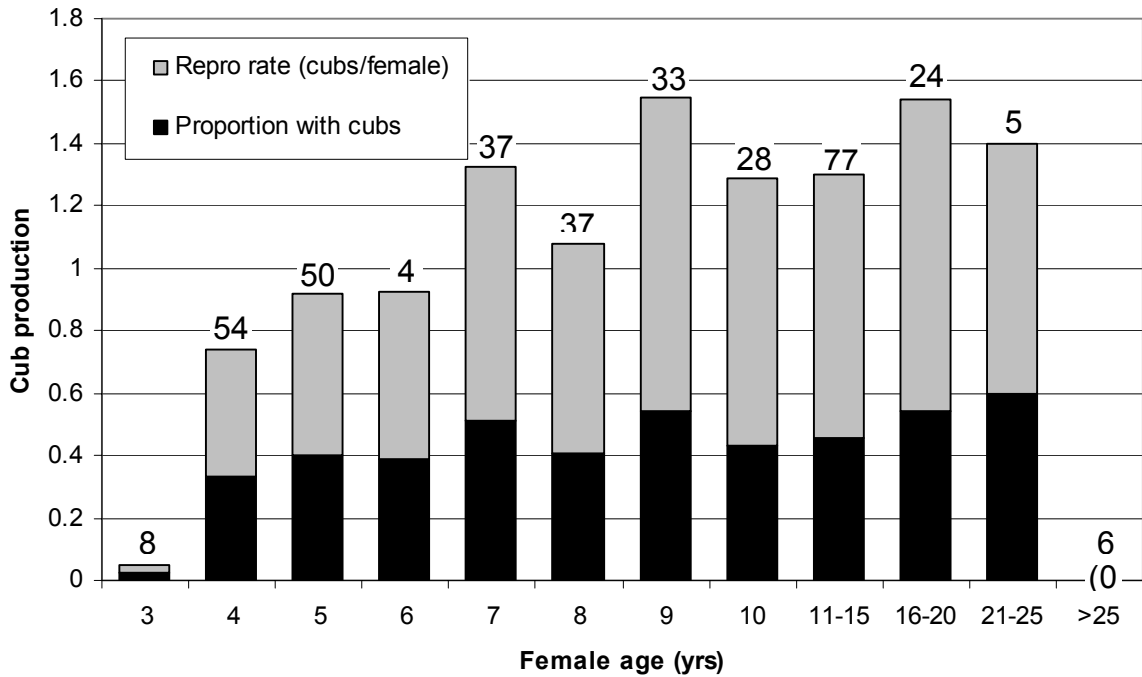


Figure 3. Age-specific cub production of bears in the Chippewa National Forest (central Minnesota) measured as the proportion of females with cubs during March den visits, 1982–2005, and cubs (M+F) per female. Sample sizes shown above bars represent bear-years (bears x years). However, only one individual bear was monitored past age 20 (for 11 years).

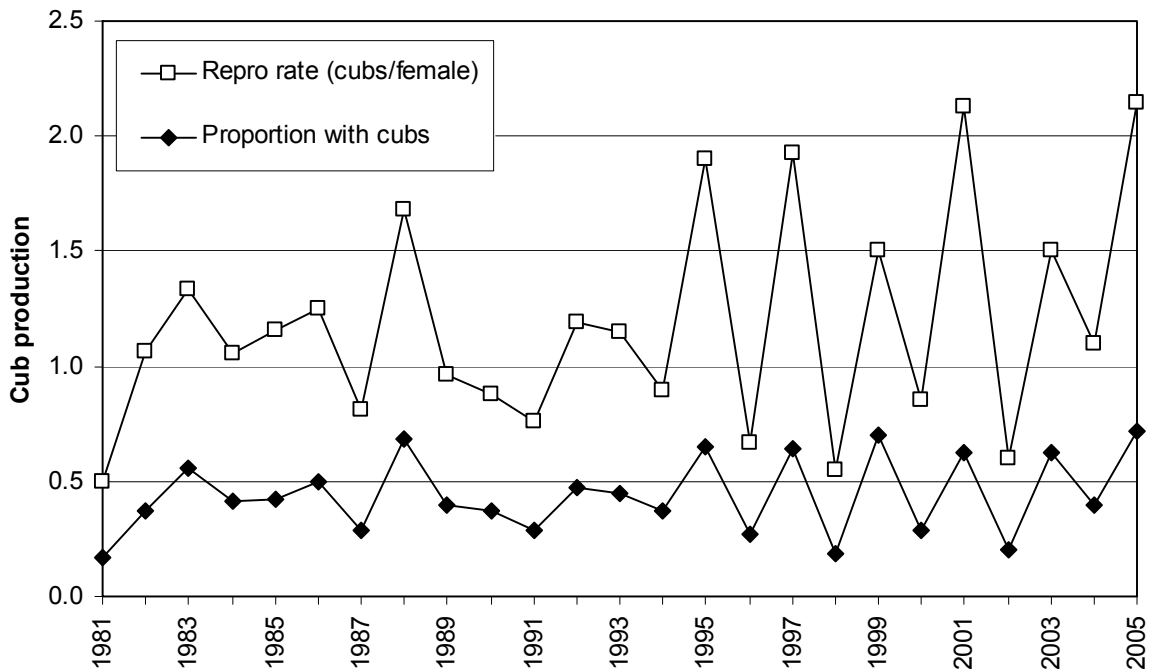


Figure 4. Year-specific cub production of bears in the Chippewa National Forest measured as the proportion of females with cubs during March den visits and cubs (M+F) per 4+ year-old female. Sample sizes vary from 5–25 females monitored per year (mean = 16).

GRIZZLY BEAR DEMOGRAPHICS IN AND AROUND BANFF NATIONAL PARK AND KANANASKIS COUNTRY, ALBERTA

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Abstract: The area in and around Banff National Park (BNP) in southwestern Alberta, Canada, is one of the most heavily used and developed areas where grizzly bears (*Ursus arctos*) still exist. During 1994–2002 we radiomarked and monitored 37 female and 34 male bears in this area to estimate rates of survival, reproduction, and population growth. Annual survival rates of bears other than dependent young averaged 95% for females and 81–85% for males. Although this area was largely un hunted, humans caused 75% of female mortality and 86% of male mortality. Females produced their first surviving litter at 6–12 years of age ($\bar{x} = 8.4$ years). Litters averaged 1.84 cubs spaced at 4.4-year intervals. Adult (6+ year-old) females produced 0.24 female cubs per year and were expected to produce an average of 1.7 female cubs in their lifetime, based on rates of reproduction and survival. Cub survival was 79%, yearling survival was 91%, and survival through independence at 2.5–5.5 years of age was 72%, as no dependent young older than yearlings died. Although this is the slowest reproducing grizzly bear population yet studied, high rates of survival seem to have enabled positive population growth ($\lambda=1.04$, 95% CI = 0.99–1.09), based on analyses using Leslie matrices. Current management practices, instituted in the late 1980s, focus on alleviating human-caused bear mortality. If the 1970–80s style of management had continued, we estimated that an average of 1 more radiomarked female would have been killed each year, reducing female survival to the point that the population would have declined.

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ASSESSING THE RELATIONSHIP OF CONIFER THERMAL COVER TO WINTER DISTRIBUTION, MOVEMENTS, AND SURVIVAL OF FEMALE WHITE-TAILED DEER IN NORTH CENTRAL MINNESOTA

Glenn D. DelGiudice

SUMMARY OF FINDINGS

During 8 February–23 March 2005, we had 91 captures, which included 66 initial captures (26 adult and 11 fawn females, 10 adult and 19 fawn males), and 25 recaptures (9 adult and 9 fawn females, 7 fawn males). As of 31 March 2005, a total of 452 female deer, including 43 female newborns, have been recruited into the study. The fawn:doe capture ratio during winter 2004–05 was the highest of the 15-year study (111 fawns:100 does); it followed 3 consecutive mild winters. Previously, the highest fawn:doe capture ratio (105:100) occurred during moderately severe winter 2000–01, which also followed an historically unprecedented 3 consecutive mild winters. The fawn:doe ratio was as low as 32:100 (winter 1996–97), attributable primarily to historically severe winter 1995–96. After the first year of the study, mean age of females remained stable and ranged from 5.0 (\pm 0.4 [SE], $n = 90$) in 2001 to 7.1 (\pm 0.6, $n = 62$) years old in 1993. During 2004, mean age was 6.5 (\pm 0.4) years old, compared to 6.0 (\pm 0.1) years old during the remainder of the study overall. The pregnancy rate of captured adult (≥ 1.0 years old) females has remained consistently high (95.2%, $n = 218$) with pregnancy rates for does 1.5–15.5 years old of 87.5 to 100%. There was a difference ($P \leq 0.05$) in mean body mass at capture for pregnant (63.0 ± 0.7 , range = 45.7–82.5 kg, $n = 171$) versus non-pregnant ($54.6 \text{ kg} \pm 2.8$, range = 43.3–69.1 kg, $n = 10$) does, which is indicative of an effect of inadequate nutrition on conception during the breeding season. The winter severity index (WSI) for our study sites has now ranged from 38 (winters 2003–04) to 185 (winter 1995–96) during the past 15 winters. The WSI of winter 2004–05 (108)

was attributable in part to 57 snow-days, whereas, during 5 of the past 7 winters accumulated snow-days were only 0–6. Winter mortality of adult females (≥ 1.0 year old) has ranged from 2.0 to 29.3% during 1990–91 to 2004–05, and it is significantly related to WSI ($r^2 = 0.47$, $P = 0.005$). Annual mortality of females (including fawns) has ranged from 9.1 to 47.6% through 2004. Wolf predation (24.5%), hunter harvest (21.8%), and “censored” (38.2%, i.e., lost to monitoring or still alive) accounted for the fates of most of the collared females through 2004.

INTRODUCTION

The goal of this long-term investigation is to assess the value of conifer stands, as winter thermal cover/snow shelter, to white-tailed deer (*Odocoileus virginianus*) at the population level. Historically, conifer stands have declined markedly relative to numbers of deer in Minnesota and elsewhere in the Great Lakes region. The level of logging of all tree species collectively, and conifer stands specifically, has recently reached the estimated allowable harvest. Most land management agencies and commercial landowners typically restrict harvests of conifers compared to hardwoods, because of evidence at least at the individual level, indicating the seasonal value of this vegetation type to various wildlife, including deer. However, agencies anticipate greater pressure to allow more liberal harvests of conifers in the future. Additional information is needed to assure future management responses and decisions are ecologically sound. Both white-tailed deer and the forests of the Great Lakes region have significant positive impacts on local and state economies, and they are highly regarded for their recreational value.

OBJECTIVES

The null hypothesis in this study is that conifer stands have no effect on the survival, movement, and distribution of white-tailed deer during winters of varying severities. Relative to varying winter severities, the specific objectives of the comprehensive, quasi-experimental approach of this study are to: (1) monitor deer movements between seasonal ranges by aerial radio-telemetry, and more importantly, within winter ranges, for determination of home range size; (2) determine habitat composition of winter home ranges and deer use of specific vegetation types; (3) monitor winter food habits; (4) monitor winter nutritional restriction and condition via sequential examination of deer weights, body composition, blood and bladder urine profiles, and urine specimens suspended in snow (snow-urine); (5) monitor age-specific survival and cause-specific mortality of all study deer; and (6) collect detailed weather data in conifer, hardwood, and open habitat types to determine the functional relationship between the severity of winter conditions, deer behavior (e.g., use of habitat), and survival.

METHODS

This study employs a replicated manipulative approach, which is a modification of the Before-After-Control-Environmental Impact design (BACI; Stewart-Oaten et al. 1986; see DelGiudice and Riggs 1996). The study involves 2 control (Willow Lake, Dirty Nose Lake) and 2 treatment sites (Inguadona Lake, Shingle Mill Lake), a 5-year pre-treatment (pre-impact) phase, a conifer harvest serving as the experimental treatment or impact (4-year phase), and a 6-year post-treatment phase. The 4 study sites are located in the Grand Rapids-Remer-Longville area of north central Minnesota and are 10.4-22.0 km² (4.0-8.5 mi²) in area. The study began with the Willow Lake and Inguadona Lake sites during winter 1990-91 with the Shingle Mill Lake

and Dirty Nose Lake sites included beginning in winter 1992-93.

The objective of the experimental treatment (impact) was to reduce moderate (≥ 40 -69% canopy closure) and optimum (≥ 70 % canopy closure) conifer thermal cover/snow shelter to what is considered a poor cover class (< 40 % canopy closure). We just completed our 15th winter of data collection and the 6th year of the post-treatment phase. This report is not a comprehensive summary of the study, rather I discuss the progress of numerous aspects, and I update various summary descriptive statistics.

Deer Capture

We captured white-tailed deer primarily with collapsible Clover traps (Clover 1956) during January-March along the eastern and southern boundaries of the Chippewa National Forest, Minnesota (46°52'-47°08'N and 93°45'-94°08'W). We augmented our capture efforts during some winters (not in 2004-05) with rocket-netting (Hawkins et al. 1968) and net-gunning from helicopter (Wildlife Capture Services, Marysvale, Utah). Generally, handling of each deer included chemical immobilization (intramuscular injection of a xylazine HCl/ketamine HCl combination), weighing, blood and urine-sampling (for assessment of nutritional, stress, and reproductive status [Warren et al. 1981, 1982, Wood et al. 1986, DelGiudice et al. 1987*a,b*, 1990*a,b*, 1994]), extraction of a last incisor for age-determination (Gilbert 1966), various morphological measurements, and administration of a broad-spectrum antibiotic. All does were checked for pregnancy by dop-tone or visual ultrasound. Female fawns and does were fitted with VHF radiocollars (Telonics, Inc., Mesa, Arizona¹) for monitoring their movements and survival 9 does also were fitted with global positioning system (GPS) radiocollars (Advanced Telemetry Systems, Inc., Isanti, Minnesota¹). Upon completion of handling, all deer immobilizations were

¹ disclaimer

reversed with an intravenous injection of yohimbine HCl. Additional details of deer capture and handling are provided elsewhere (DelGiudice et al. 2001, 2005b, Carstensen Powell 2004).

We live-captured wolves (*Canis lupus*) with Newhouse no. 14 steel leghold traps during May–September 1993–2004 to maintain radio contact for monitoring the movements of packs that ranged over the 4 deer study sites. Captured wolves were lightly anesthetized (xylazine/ketamine), weighed, blood-sampled, ear-tagged, radiocollared, injected with a broad-spectrum antibiotic, and released.

RESULTS AND DISCUSSION

Capture and Handling of Study Deer

During this study, we have had 1,208 deer captures, including recaptures. Because the study focuses on females, male fawns (< 1.0 year old in their first winter) and adult (≥ 1.0 year old) males were eartagged and released. As of 31 March 2005, a total of 452 female deer, including 43 female newborns, have been recruited into the study. Additionally, 47 male newborns were captured and radiocollared to monitor their survival and causes of mortality through early fall when collars dropped off. Additional information concerning the newborn deer portion of the study may be observed in Carstensen Powell (2004).

During 8 February–23 March 2005, we had 91 captures, which included 66 initial captures (26 adult and 11 fawn females, 10 adult and 19 fawn males), and 25 recaptures (9 adult and 9 fawn females, 7 fawn males). This winter's winter severity index (WSI = 108) was the highest since winter 2000–01 (WSI = 153). Consequently, nearly all of our radiocollared does that are seasonal migrators (i.e., mean distance between winter and spring-summer-fall home ranges is 8–16 km [5–10 miles]), which is about 72% of the total (DelGiudice, unpublished data), were induced to move to our winter range study sites this winter. This indicates that many more uncollared

deer migrated to winter ranges and facilitated our relatively high capture success.

The fawn:doe capture ratio was the highest of the 15-year study (111 fawns:100 does), which was likely attributable to age-specific pregnancy rates of 90–100% for does ≥ 1.5 years old (DelGiudice, unpublished data), and positive effects on survival of 3 consecutive very mild winters (2001–02 to 2003–04, WSIs = 38–58) previous to this winter. Previously, the highest fawn:doe capture ratio (105:100) occurred during winter 2000–01, which was moderately severe (WSI = 153), but similarly followed an historically unprecedented 3 consecutive mild winters (WSI range = 45–57) (P. Bouley, State Climate Office, personal communication). Although the mortality rate of winter 2000–01 was relatively high (16.2%), its weather conditions had only a moderate negative effect on the subsequent reproductive success in spring 2001, as the fawn:doe capture ratio of winter 2001–02 remained relatively high (81:100). Actual fawn:doe capture ratios for 2000–01, 2001–02, and 2003–04 would be expected to be somewhat higher, as a portion of the deer were captured by net-gun, which involves a level of selection for adult females. During the study, the fawn:doe capture ratio has declined to as low as 32:100 (winter 1996–97), likely attributable to the preceding historically severe winter (1995–96, WSI = 183), during which the highest mortality rate (29.3%) of collared does occurred. Further, observations indicated that reproductive success of surviving does following severe winter 1995–96 was exceptionally low, thus a small number of fawns would have entered winter 1996–97.

Of the 91 deer captured during winter 2004–05, 35 new females (11 fawns, 24 adults) were recruited into the radiocollared study cohort. Including does already radiocollared when this winter began, 82 females have been monitored during December 2004–May 2005.

Ages and Reproductive Status of Study Deer

Measured at the end of each calendar year, or at death (or at last contact for “lost signals”) within a specific year, mean age of collared female deer remained similar among the 4 study sites during the 5-year pre-treatment phase (1991–1995), the 4-year treatment phase (1996–1999), and thus far during the 6-year post-treatment phase (2000–2005). Consequently, observed differences in deer survival among sites within each of the study phases will not be confounded by differences in age among sites (DelGiudice and Riggs 1996). Equally as important, after 1991, mean age of deer on all 4 sites (pooled) also remained stable, and has ranged from 5.0 (\pm 0.4 [SE], $n = 90$) in 2001 to 7.1 (\pm 0.6, $n = 62$) years old in 1993 (Figure 1). During 2004, mean age was 6.5 (\pm 0.4) years old, compared to 6.0 (\pm 0.1) years old during the remainder of the study overall.

According to progesterone concentrations (≥ 1.6 ng/ml, Wood et al. 1986, DelGiudice, unpublished data), the pregnancy rate of captured adult (≥ 1.0 years old) females has remained consistently high (95.2%, $n = 218$) throughout the study, ranging from 79 to 100% during winters 1990–91 to 2001–02. Only 1 fawn has been assessed as pregnant by this method. However, pregnancy rates for does 1.5–15.5 years old have ranged from 87.5 to 100% (Figure 2). Mean serum progesterone concentrations differed ($P < 0.05$) between pregnant (3.8 ± 0.09 , range = 1.6–8.9 ng/ml, $n = 218$) and non-pregnant (0.7 ± 0.16 , range = 0–1.4 ng/ml, $n = 11$) does. There was no relationship ($r^2 = 0.01$, $P = 0.52$) between progesterone concentrations and julian day. However, there was a difference ($P \leq 0.05$) in mean body mass at capture for pregnant (63.0 ± 0.7 , range = 45.7–82.5 kg, $n = 171$) versus non-pregnant ($54.6 \text{ kg} \pm 2.8$, range = 43.3–69.1 kg, $n = 10$) does, which may be indicative of an effect of inadequate nutrition on conception during the breeding season.

Capturing the Variability of Winter Severity

Weather is one of the strongest environmental forces impacting wildlife nutrition, populations, and their numbers. For northern deer in the forest this becomes most evident during winter when diminished quantity, availability and quality of food resources, and severe weather conditions impose the most serious challenge to their survival. This long-term study continues to document highly variable winter weather conditions, which permits a more complete examination and understanding of the relationship between winter severity, conifer cover, and the many aspects of white-tailed deer ecology that we are investigating (e.g., movements, distribution, food habits, cause-specific mortality, and age-specific survival). We are examining the variability of weather conditions in several different ways. Specifically, Figure 3 illustrates the Minnesota Department of Natural Resources’ (MNDNR) WSI, which is calculated by accumulating a point for each day (temperature-days) with an ambient temperature $\leq -17.8^\circ \text{C}$ (0°F), and an additional point for each day (snow-days) with a snow depth ≥ 38.1 cm (15"). The WSI for our study sites has now ranged from 38 (winters 2003–04) to 185 (winter 1995–96) over the past 15 winters. The WSI of winter 2004–05 was attributable in part to 57 snow-days, whereas, during 5 of the past 7 winters, accumulated snow-days were only 0–6. The biological significance of this is that depth of snow cover is the component of the WSI that has the greatest negative effect on deer survival (DelGiudice et al. 2002). However, the average snow depth just exceeded the WSI snow threshold (38 cm) throughout much of winter 2004–05; depth of cover was actually rather moderate compared to all other winters (Figure 4). The wide range of winter weather conditions captured during this study will enhance the value of all data interpretations relative to deer survival, other aspects of their ecology, and management implications. A severe

winter during the post-treatment phase of the study remains elusive, and would undoubtedly prove valuable.

Mean daily minimum temperatures by month have been highly variable (Figure 4). To relate the variability of ambient temperature to deer in a more biologically meaningful or functional way, I calculated the *effective critical temperature* for an averaged size adult female deer (-7°C or 19.4°F), and the number of days per month when the maximum ambient temperature was at or below this threshold (Figure 5). At or below this temperature threshold, heat losses may exceed energy expenditure for standard metabolism and activity, with additional heat generated to maintain homeothermy (McDonald et al. 1973). On these days, a physiological (e.g., accelerated mobilization of fat reserves) or behavioral response (e.g., change in habitat use) by the deer would be necessary to meet this environmental challenge. Interestingly, the potential physiological challenges of ambient temperatures during January–March 2005 were greater than during this interval in any other year of the study (Figure 5). Similarly, I used a snow depth threshold of ≥ 41 cm (16.1"), about two-thirds chest height of adult female deer, because energetically expensive bounding often becomes necessary at this depth, and overall movements become markedly restricted (Kelsall 1969, Kelsall and Prescott 1971, Moen 1976). This threshold is slightly higher than that used for the WSI, but similarly, this winter's snow conditions are considered moderate. Importantly, these snow-days (6) were minimal during March, which can be a most critical time relative to deer survival (DelGiudice et al. 2002). Clearly, there has been a pronounced variability of days during the study's 15 winters when it is biologically reasonable to expect that there were potentially serious energetic implications associated with ambient temperature or snow depth. It is noteworthy that extensive statistical analyses of age-specific survival and weather data from the first 6 years of this study (DelGiudice et al. 2002) showed

that snow conditions (depth and density) impose a far greater challenge to survival than ambient temperature. However, during a very severe winter (e.g., 1996), the consequences of cold temperatures on individual deer with rapidly depleting or exhausted fat reserves should not be underestimated. Our analyses of 13 years of data have shown that variation in winter severity has direct and indirect influences on the age-specific hazard (i.e., instantaneous probability of death) of deer (DelGiudice et al. 2005a).

Status and Cause-Specific Mortality of Study Deer

The status/fate of study deer through 31 December 2004 is shown in Figure 6. The "crude mortality rate" of our study deer was calculated by dividing the number of collared deer that died during a reference period (e.g., winter defined as Dec–May) by the total number of deer that were collared and monitored during that period. With each year, new data collected from the field, including recaptures of does with expired collars (i.e., "lost signals"), permit revision of mortality statistics. During 1 January 1991–31 December 2004, annual mortality rates of collared females ranged from 9.1 to 47.6% (Figure 7). The mortality rate for 2004 was rather typical at 23.3%. As has been mentioned in previous reports, the atypical mortality of 1992 (47.6%) was largely attributable to elevated hunter harvest (37.1%) associated with an increase in antlerless permits, whereas during 1994 and 1996, a preponderance of older females, severe weather conditions, and wolf predation contributed to the higher mortality rates (Figure 7). The number of antlerless permits issued varied considerably from 1991 to 2004. As reflected by the hunter-caused mortality rates in Figure 7, no antlerless permits were issued in the vicinity of our winter study sites or of the spring-summer-fall ranges of our study deer during 1996 and 1997, and very few were issued during the 1998 season. However, in 1999 there was an increase in hunter-caused mortality, and this

increased further to the study's second highest level during 2000 (19.4%, Figure 7). During 2003 and 2004, antlerless permits were unlimited, and hunter-caused mortality rates were among the highest of the study (17.0 and 16.1%). Although hunter harvest mortality is primarily a function of antlerless permit numbers, the more than 2 times higher percent harvest mortality in 1992 compared to 2003 was likely influenced by the markedly smaller sample of collared does entering the 1992 hunting season ($n = 35$) than in 2003 and 2004 ($n = 53$ and 62). Wolf-caused mortality of females in 2004 was the second lowest of the study (Figure 7). Except for during 1994 and 1996, when winters were moderately severe to severe, annual wolf-caused mortality of female deer was 4.1–14.5%, with the maximum occurring during 2001. Typically, wolf predation has had its greatest impact on the older segment of the study cohort of does (DeGiudice et al. 2002). Mean age of female deer killed by wolves during 11 of the first 14 winters of the study was 6.0 (+ 1.8, $n = 9$)– 11.7 (+ 1.7, $n = 8$) years old. Mean age of deer killed by wolves during winter 2003–04 was 9.9 (± 2.7 , $n = 4$) versus 7.9 (± 0.6 , $n = 63$) during the previous 13 years.

Most of the annual non-hunting mortality of study deer occurred during winter. Typically, winter mortality of collared adult female deer has been low (2.0–12.5%, Figure 8). The highest winter mortality rates (16.2–29.3%) of does have occurred during 3 of the 4 most severe winters (1993–94, 1995–96, and 2000–01, Figure 8). Mortality during winter 2004–05 was among the lowest of the study (5.4%). The relationship between WSI and percent winter mortality of adult female deer continued to be reasonably strong ($r^2 = 0.47$, $P = 0.005$, Figure 9). Predation, and wolf predation specifically, were responsible for a mean 77.1% (± 7.2 , range = 0.00–100%, $n = 15$) and 68.05% (± 7.8 , range = 0–100%, $n = 15$), respectively, of the winter (Dec–May) mortality of collared fawn and adult females throughout the 15-year study period. Monthly wolf predation of females

was greatest during March and April (Figure 10).

Monitoring Wolf Activity

Over the past 15 years, wolf activity on the 4 sites appears to have increased. Wolves were extirpated from the area of the study sites during the 1950–60s, but just 5–6 years prior to initiation of the study, had re-entered and became re-established. When the study began in winter 1990–91, this area was on the leading edge of wolf range expansion in Minnesota. Since spring 1993, we have captured and radiocollared 50 (28 females, 22 males) wolves from 7–9 packs which range over the 4 study sites (Table 1). Fates of these wolves include being killed by a variety of human-related and natural causes.

During 1993–2001, median survival of 31 wolves from date of capture was 1,328 days (3.7 years, 90% confidence interval = 686–1,915 days) (DeGiudice, unpublished data). Human-caused mortality (e.g., shot, snared, car-kills) has accounted for 11 wolf deaths versus 5 deaths by natural causes (Figure 11).

Based on aerial observations, pack sizes have ranged from 2 to 7 members. Current status of each of the collared wolves is listed in Table 1. As is somewhat typical of wolf packs, the territories of our collared wolves have been relatively stable and have ranged in size from 62 to 186 km² (24–72 mi²). Radio location data are being used to more closely monitor wolf activity and distribution relative to the distribution and movements of collared deer. We will capture and radiocollar additional wolves this summer. As described above, year-round monitoring and examination of mortalities of collared deer provide additional important information concerning wolf activity on the study sites.

Habitat Analyses and Updates

Detailed baseline habitat analyses using stereoscope interpretation of color infrared air photos and geographic information systems (GIS, Arc/Info and

ArcView) were completed. Forest stand types were classified by dominant tree species, height class, and canopy closure class. Open habitat types, water sources, and roads were also delineated. We are updating the coverage to account for any changes in type classification associated with succession during the past 14 years. The experimental treatment (i.e., conifer harvest) impacted 157 and 83 hectares (388 and 206 acres) of conifer canopy closure classes A (< 40%), B (40-69%), and C ($\geq 70\%$) on the Inguadona Lake and Shingle Mill Lake sites. A very preliminary analysis has shown that during phases of the study associated with mild to average winter conditions, deer distribution over the study sites was more dispersed and use of vegetative cover was more variable, whereas when influenced by severe winters, locations were more concentrated in dense conifer cover. Data will be analyzed more rigorously in the upcoming year.

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Table 1. History of radiocollared gray wolves, north central Minnesota, 1993–2005. (Ad=adult, juv=juvenile).

WOLF NO.	Pack	CAPTURE DATE	SEX	AGE CLASS	FATE	DATE
2093	WILLOW	MAY 1994	F	AD	SHOT	MAR 1996
2094	WILLOW	MAY 1994	M	AD	SHOT	NOV 1997
2056	WILLOW	MAY 1996	M	AD	NOT COLLARED	
2058	WILLOW	MAY 1996	F	AD	PROB. SHOT	AUG 1996
2052	NORTH INGY	MAY 1993	M	AD	UNKNOWN	DEC 1996
2087	SOUTH INGY	MAY 1993	F	AD	DIED FROM NATURAL CAUSES (EMACIATED, MANGEY)	AUG 2, 1998
2062	SOUTH INGY	AUG 1997	F	AD	SHOT	FEB 1998
2089	SHINGLE MILL	MAY 1993	F	AD	KILLED BY WOLVES	SEP 1994
2050	SHINGLE MILL	MAY 1993	M	AD	COLLAR CHEWED OFF	AUG 1993
2095	SHINGLE MILL	MAY 1995	F	AD	LOST SIGNAL	NOV 1995
2064	SHINGLE MILL	AUG 1996	F	JUV	ON THE AIR	
		MAY 2004				
2060	SHINGLE MILL	AUG 1996	F	JUV	LOST SIGNAL	FEB 1, 2000
		JUL 1998 - RECAPTURED				
2059	SHINGLE MILL	AUG 1996	M	JUV	LOST SIGNAL	OCT 1996
2085	DIRTY NOSE	MAY 1993	M	AD	DISPERSED	OCT 1993
2054	DIRTY NOSE	MAY 1993	M	AD	DISPERSED	SEP 1993
2091	DIRTY NOSE	APR 1994	F	AD	RADIO FAILED	MAY 27, 1998
2092	DIRTY NOSE	APR 1994	F	AD	RADIO FAILED	MAY 27, 1998
2096	MORRISON	MAY 1995	F	AD	DROPPED TRANSMITTER	NOV 22, 1996
2252	WILLOW	APR 1998	M	AD	ROAD-KILL	JUN 1998
2253	DIRTY NOSE	APR 1998	F	AD	UNKNOWN MORTALITY	AUG 3, 1998
2254	SHINGLE MILL	JUL 1998	M	AD	DROPPED TRANSMITTER	JUL 17, 2001
2066	MORRISON	JUL 1998	M	AD	KILLED BY WOLVES	JUN 4, 1999
2067	SHINGLE MILL	JUL 1998	M	JUV	COLLAR CHEWED OFF	JUL 1998
2068	HOLY WATER	JUL 1998	M	AD	LOST SIGNAL	AUG 27, 1999
2069	SOUTH INGY	JUL 1998	M	AD	LOST SIGNAL	DEC 4, 1998
2070	SOUTH INGY	JUL 1998	F	AD	LOST SIGNAL	JUL 3, 2002
2255	SOUTH INGY	JUL 1998	F	AD	DISPERSED	MAR 22, 1999
2256	DIRTY NOSE	AUG 1999	M	AD	DROPPED TRANSMITTER	JUL 6, 2001
2257	E. DIRTY NOSE	MAY 1999	M	AD	LOST SIGNAL	JAN 14, 2001
2258	WILLOW	AUG 1999	M	AD	DISPERSED	MAR 16, 2000
2259	DIRTY NOSE	JUL 2000	M	AD	DISPERSED	JUL 2001
2261	SHINGLE MILL	AUG 2000	M	AD	DROPPED TRANSMITTER	APR 10, 2002
2074	SOUTH INGY	AUG 2001	F	AD	SHOT BY FARMER	OCT 23, 2002
2073	SHINGLE MILL	AUG 8, 2001	F	JUV	DROPPED TRANSMITTER	AUG 28, 2001
2071	SHINGLE MILL	SEP 2000	F	AD	SNARED	JAN 13, 2001
2139	SHINGLE MILL	AUG 2002	F	AD	DISPERSED	MAR 17, 2004
		RECAPTURED JUN 2003				
2141	INGUADONA	SEP 2002	F	JUV	DROPPED TRANSMITTER	SEP 22, 2002
2149	INGUADONA	MAY 2003	M	AD	SHOT	NOV 2003
2143	WILLOW	MAY 2003	M	AD	KILLED BY WOLVES	JUN 20, 2004
2144	MORRISON BROOK	JUN 2003	F	AD	SHOT	NOV 12, 2004
2145	INGUADONA	JUL 2003	F	AD	DIED, MANGE	JAN 3, 2004
2148	WILLOW	AUG 2003	F	AD	DISPERSED	DEC 2, 2003
2291	SMITH CREEK	AUG 2003	F	AD	ON THE AIR	
2146	WILLOW	AUG 2003	F	JUV	ON THE AIR	
2262	DIRTY NOSE	SEP 2003	F	AD	SHOT	NOV 14, 2003
2263	SHINGLE MILL	MAY 2004	F	AD	ON THE AIR	
2264	DIRTY NOSE	MAY 2004	F	AD	ON THE AIR	
2266	WILLOW	MAY 2004	F	AD	ROAD-KILL	NOV 6, 2004
2267	INGUADONA	MAY 2004	M	AD	DISPERSED	JAN 2005
2268	INGUADONA	MAY 2004	M	AD	UNKNOWN MORTALITY	JAN 19, 2005
2269	WILLOW	MAY 2004	M	AD	DISPERSED	JUN 2004

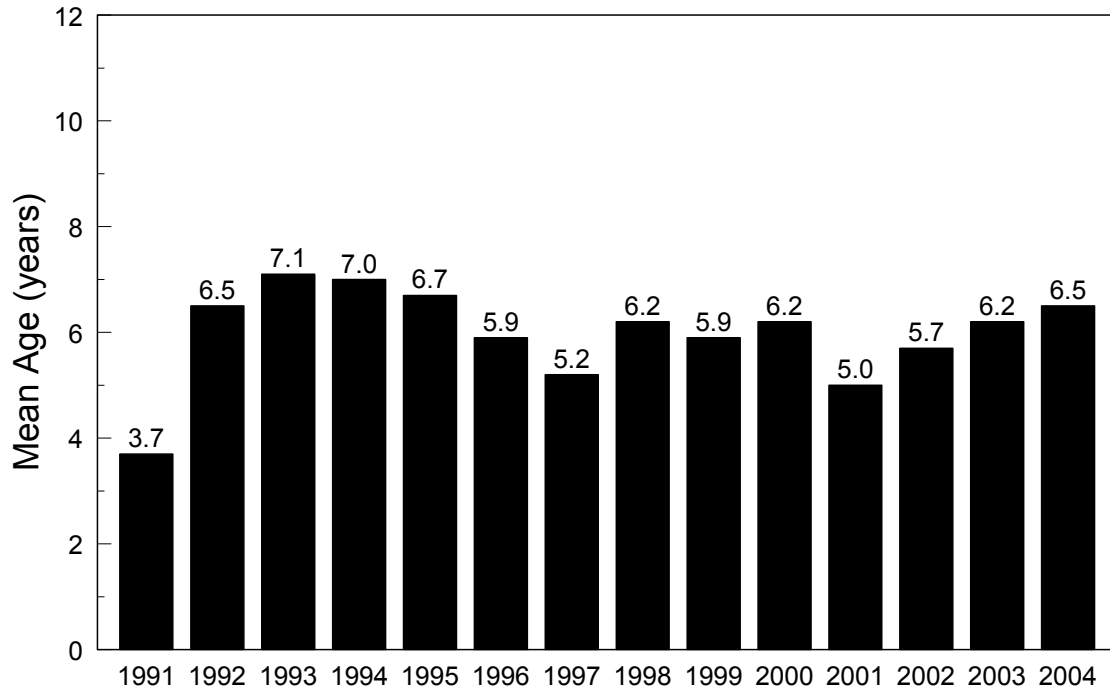


Figure 1. Mean age of radiocollared female white-tailed deer among years, north central Minnesota, 1 January 1991–31 December 2004. (Sample sizes were 22, 34, 62, 66, 54, 76, 74, 49, 55, 48, 90, 84, 75, and 81, respectively.)

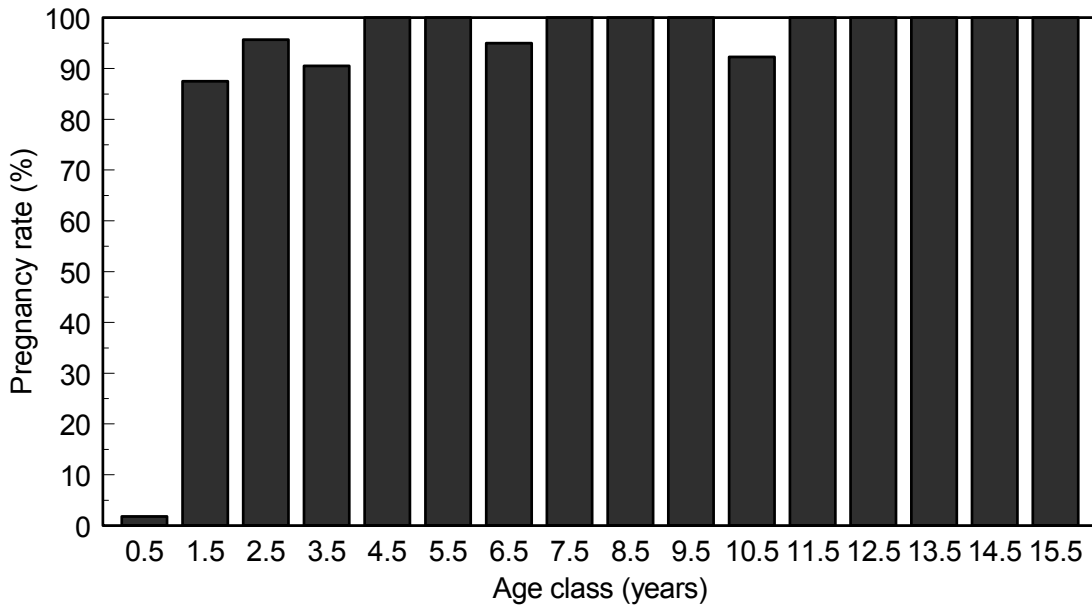


Figure 2. Age-specific pregnancy rate of radiocollared white-tailed deer (4 study sites pooled) in north central Minnesota, winters 1991–2002. (Sample sizes were 55, 48, 23, 21, 18, 21, 20, 13, 9, 11, 13, 8, 11, 5, 4, and 4 for yearly age classes, respectively.)

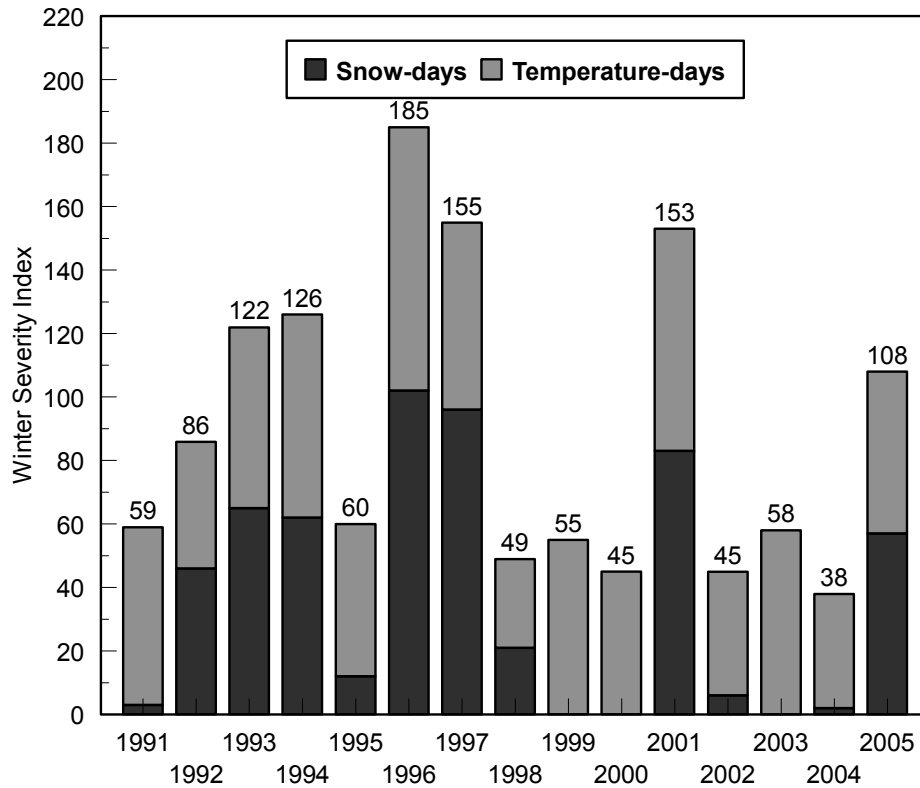


Figure 3. Winter severity index for white-tailed deer study sites, north central Minnesota, winters 1990–91 to 2004–05. One point is accumulated for each day with an ambient temperature $\leq -17.8^{\circ}\text{C}$ (temperature-day), and an additional point is accumulated for each day with snow depths $\geq 38.1\text{ cm}$ (snow-day).

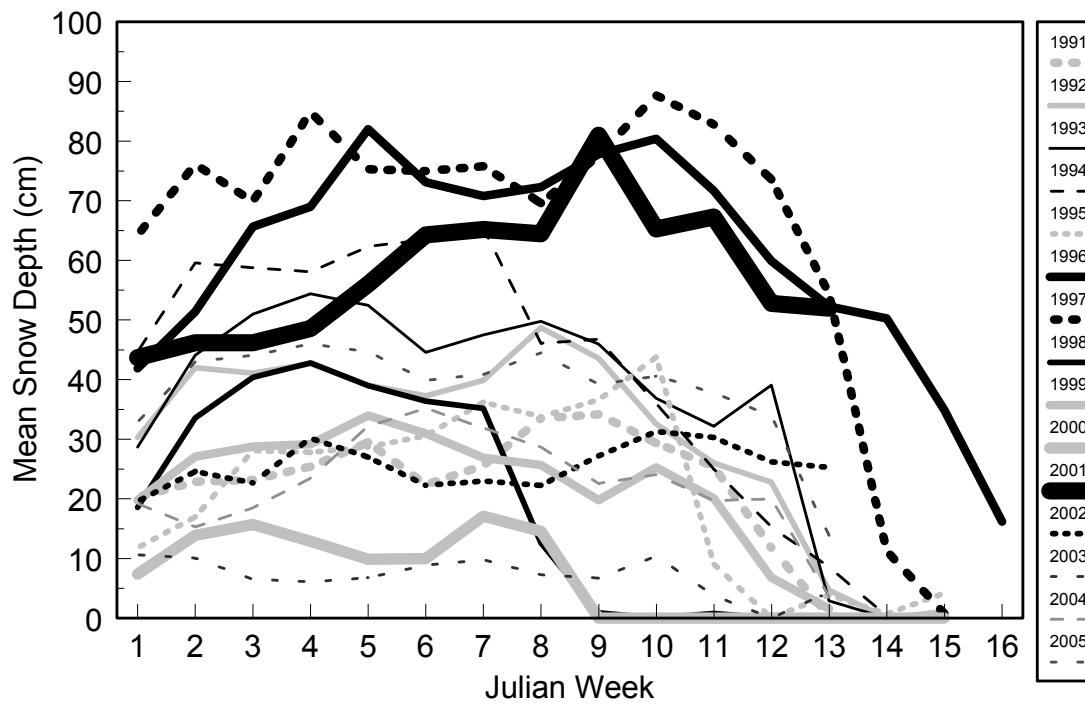
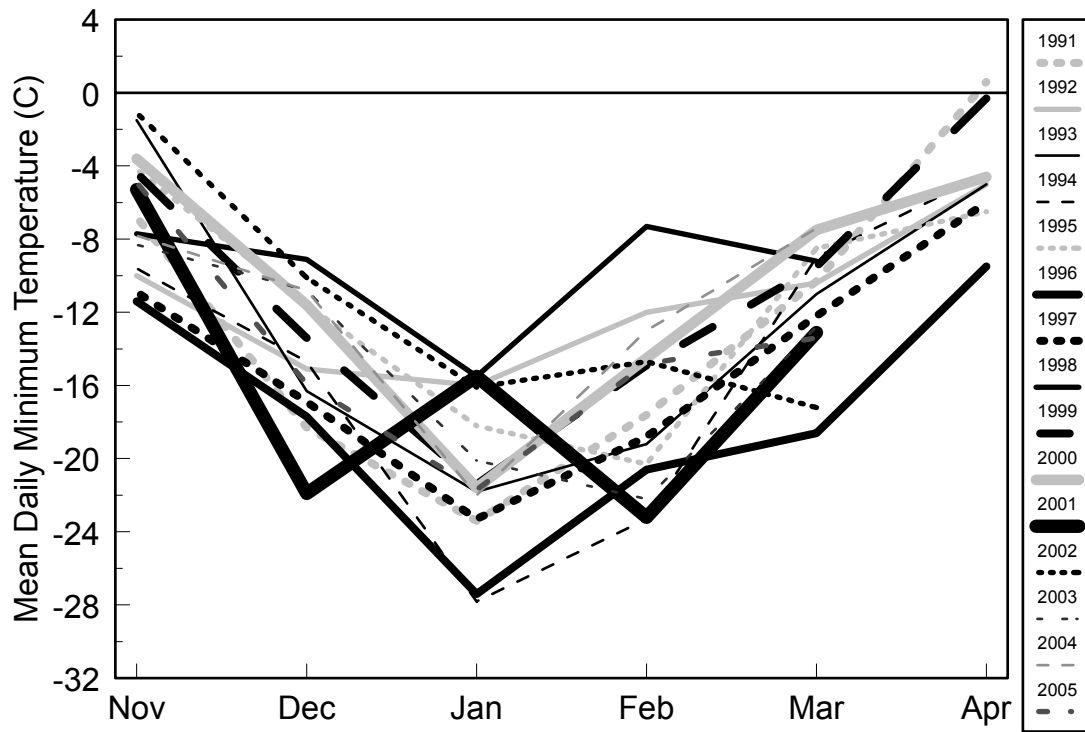


Figure 4. Mean daily minimum ambient temperature (top, Nov–Apr 1990–2005) and mean weekly (julian) snow depths (bottom, Jan–Apr 1991–2005) for white-tailed deer study sites, north central Minnesota.

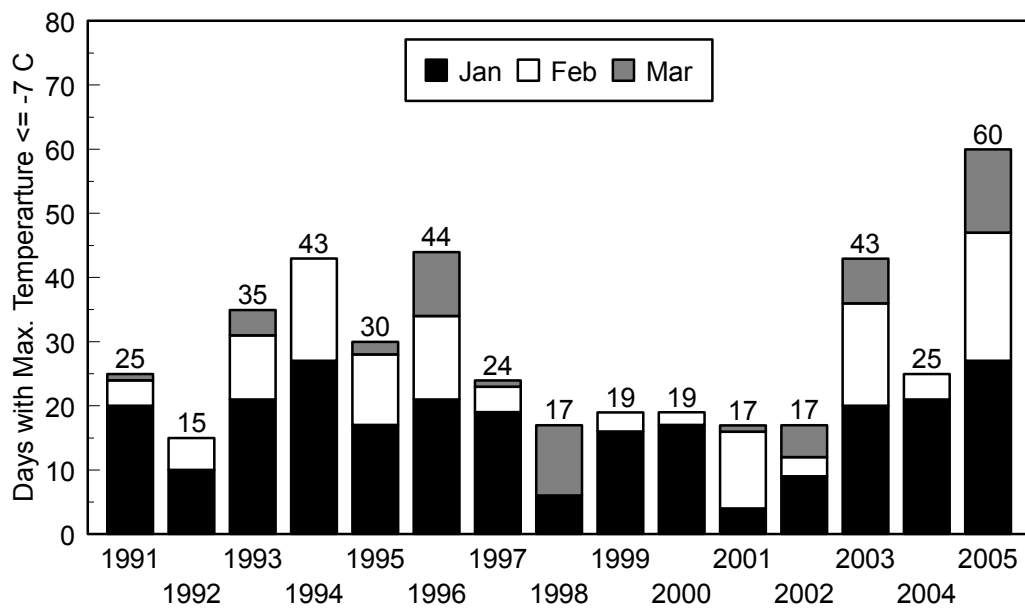
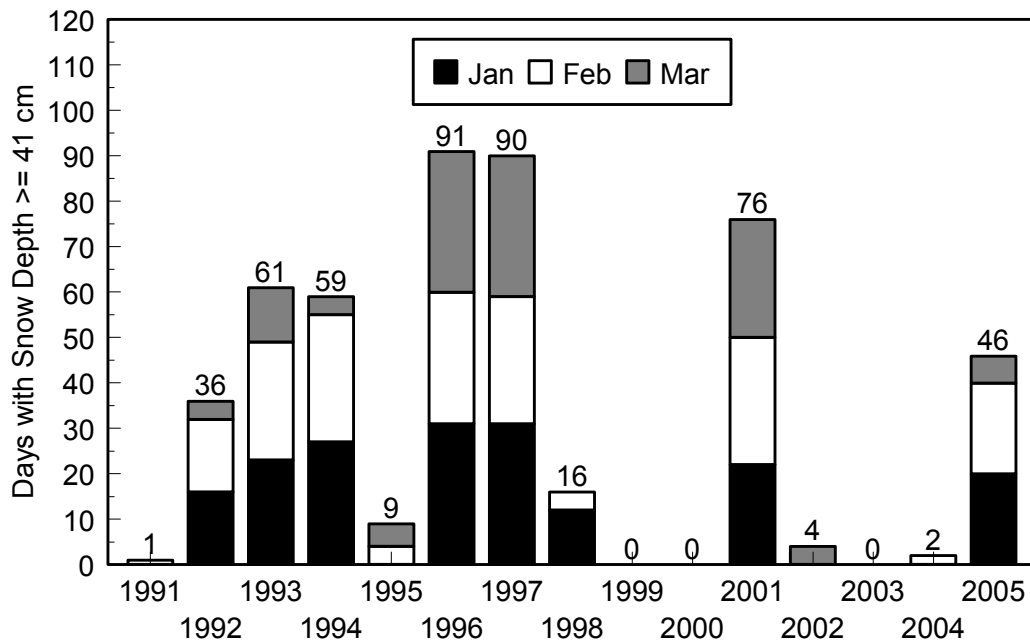


Figure 5. Number of days with snow depths ≥ 41 cm (top) and maximum ambient temperatures $\leq -7^\circ\text{C}$ (bottom, *effective critical temperature* for an average size doe [60 kg]), north central Minnesota, January–March 1991–2005.

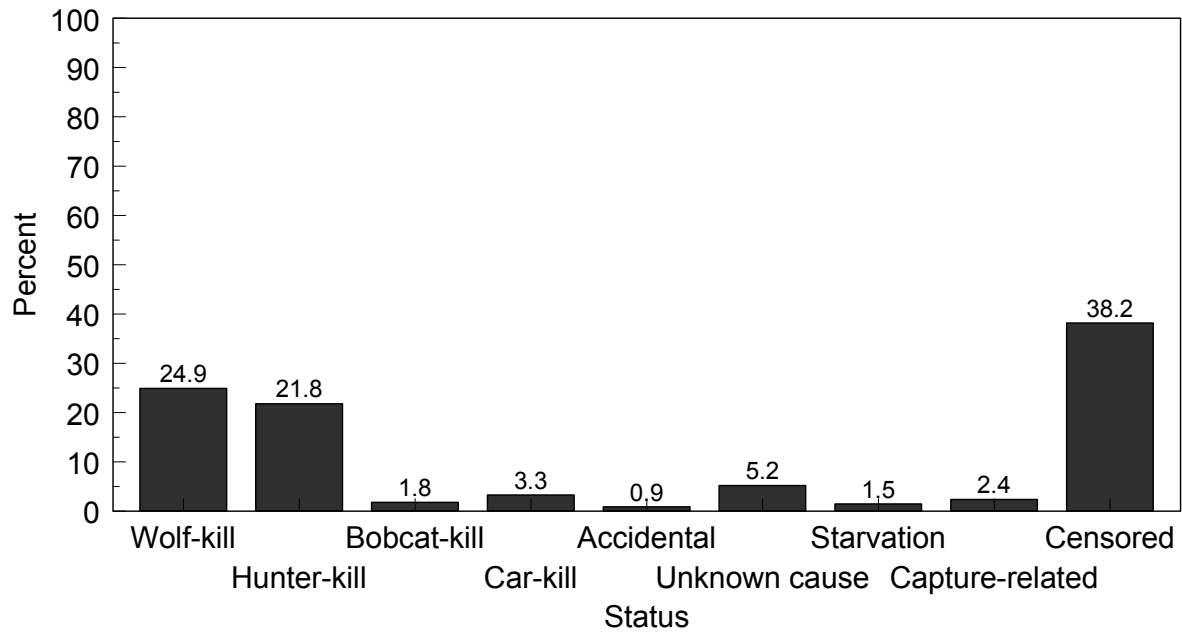


Figure 6. Status of radiocollared female deer, north central Minnesota, January 1991–December 2004. Censored deer include those that were still alive on 31 December 2004, or whose radio signals have been lost to monitoring (e.g., radio failure, dispersal from region of the study sites).

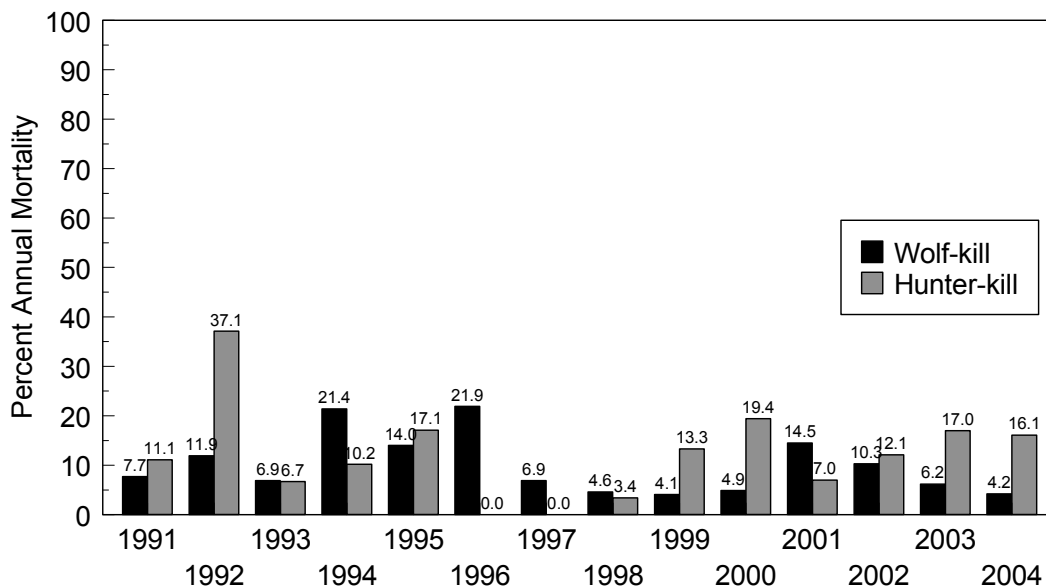
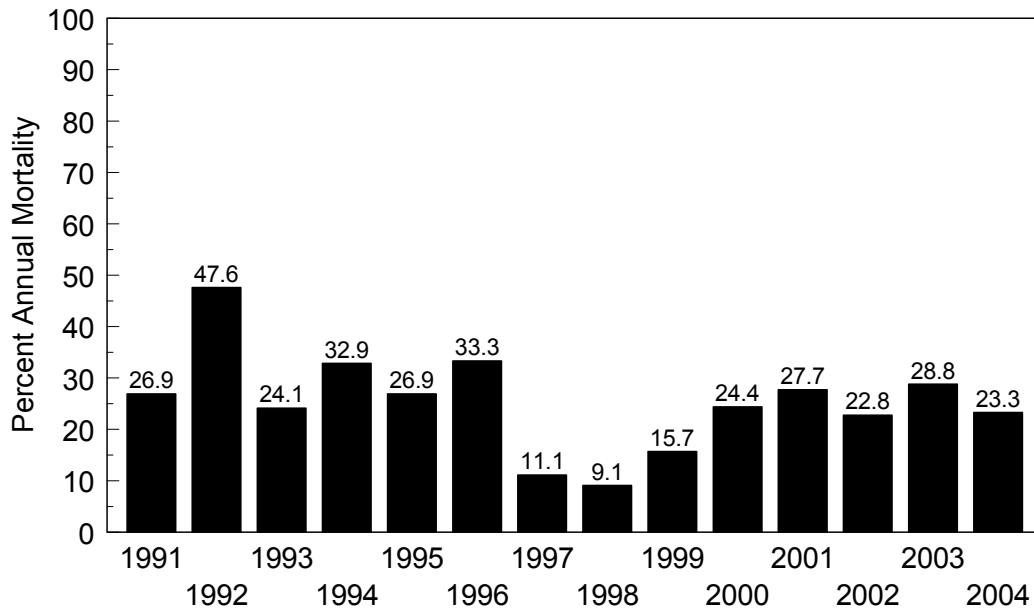


Figure 7. Annual (1 Jan–31 Dec) percent mortality of radiocollared, female white-tailed deer (top) and annual percent mortality attributable to wolf predation and hunter harvest (bottom, 4 sites pooled), north central Minnesota, 1991–2004. (Sample sizes were 26, 42, 58, 70, 52, 66, 72, 44, 51, 41, 83, 79, 66, and 73, respectively. Hunter harvest was calculated with the maximum number of collared females entering November; no antlerless permits were issued in 1996 and 1997, and very few were issued in 1998.)

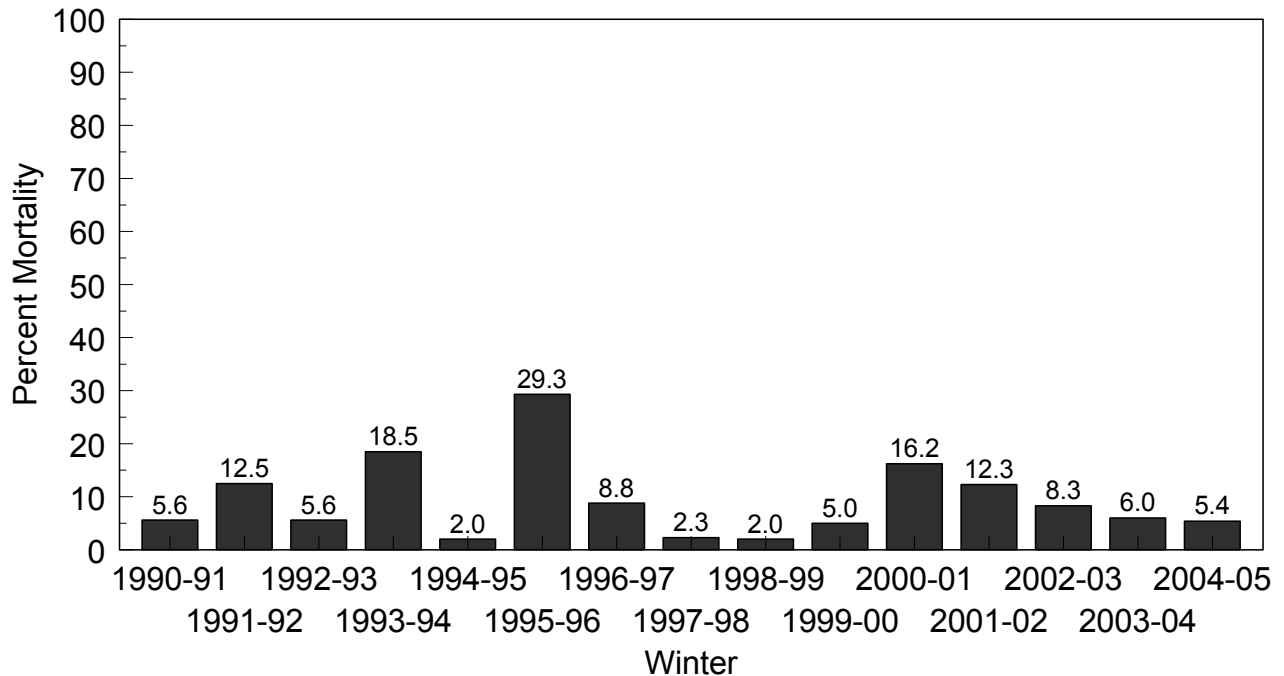


Figure 8. Percent winter mortality (Dec–May) of radiocollared, adult (≥ 1.0 year old) female white-tailed deer (4 sites pooled), north central Minnesota, winters 1990–91 to 2004–05. (Sample sizes were 18, 40, 54, 65, 50, 58, 68, 43, 49, 40, 68, 73, 60, 67, and 74, respectively; no deer were radiocollared during Dec 1990.)

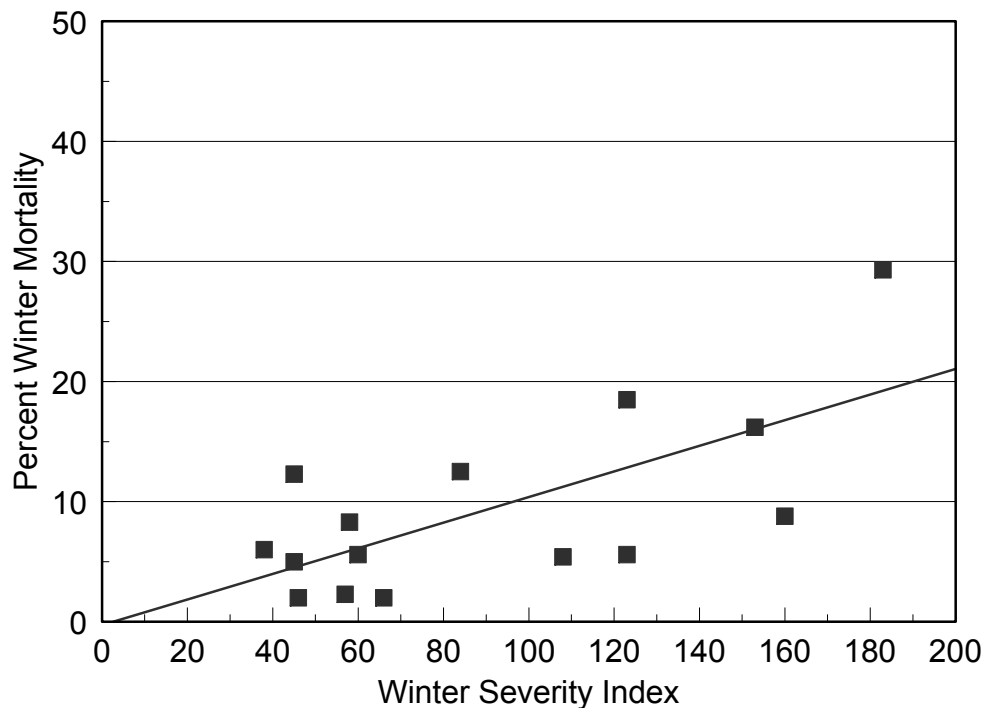


Figure 9. Relationship between MNDNR winter severity index (Nov–May) and percent winter (Dec–May) mortality ($Y = -0.2820 + 0.1068x$, $r^2 = 0.47$, $P = 0.005$) of radiocollared, adult (≥ 1.0 year old), female white-tailed deer (4 sites pooled), north central Minnesota, winters 1990–91 to 2004–05.

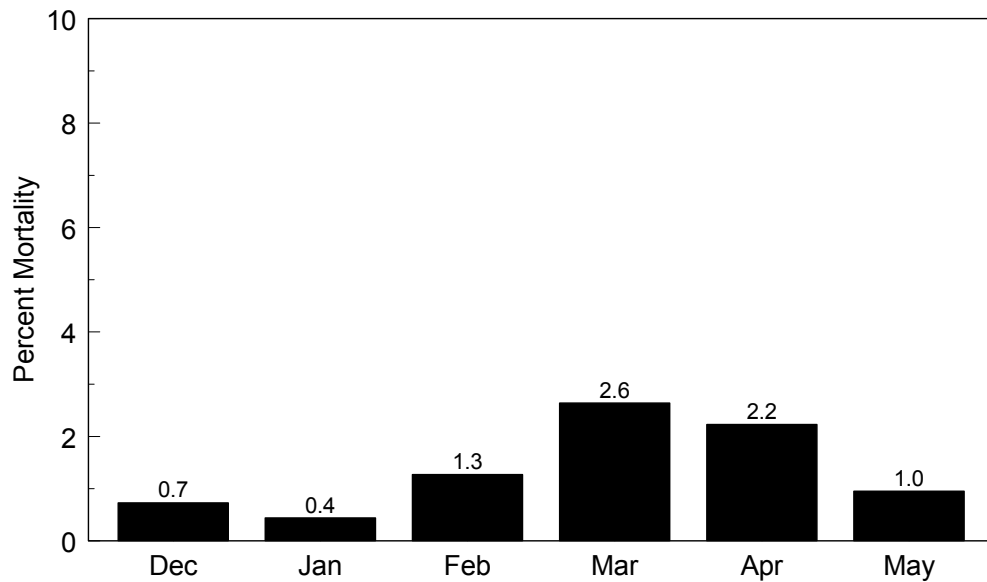


Figure 10. Monthly mortality of radiocollared female (fawns and adults) white-tailed deer by wolves (4 sites pooled), north central Minnesota, winters 1990–91 to 2004–05.

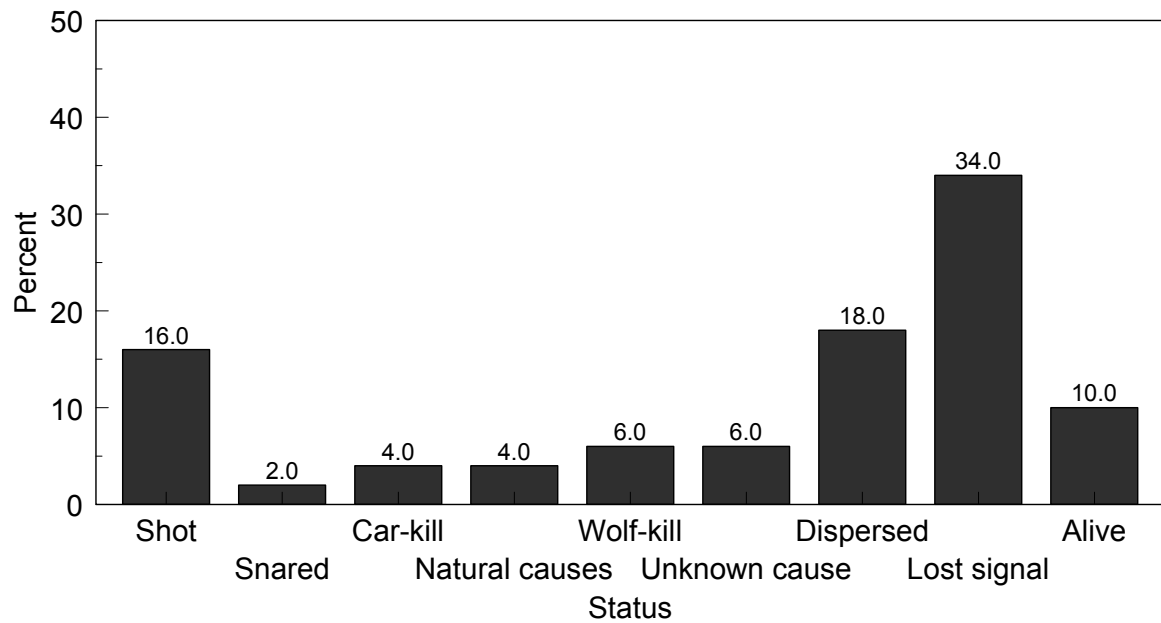


Figure 11. Status of radiocollared wolves, north central Minnesota, 1993–2005.

WINTER SEVERITY, BODY COMPOSITION, AND SURVIVAL OF WHITE-TAILED DEER

Michelle Carstensen Powell, and Glenn D. DelGiudice

Abstract: Understanding the relation between winter severity and survival of free-ranging deer (*Odocoileus* spp.) requires close examination of the functional relation between environmental conditions and the nutritional status of deer. In this study, we determined the body composition of free-ranging adult (>1.0 year old) female white-tailed deer (*O. virginianus*) and fawns (< 1.0 year old) during 2 winters of varying severity; winter 2000–01 was severe (Winter Severity Index [WSI] = 153), and winter 2001–02 was mild (WSI = 45). We used deuterium-dilution to estimate total body water of 39 adult females and 37 fawns (18 females, 19 males) and employed predictive equations derived from 15 sacrificed deer (7 adults, 8 fawns) to calculate their ingesta-free body composition (i.e., total body water, fat, protein, and ash). Mean total fat (%) decreased from mid- to late-winter for adults and fawns in 2001 (adults = 7.9, \pm 0.1% [SE] to 7.2 \pm 0.3%; fawns = 6.9 \pm 0.4% to 5.3 \pm 0.4%) and 2002 (adults = 7.9 \pm 0.3% to 6.5 \pm 0.2%; fawns = 6.2 \pm 0.3% to 5.0 \pm 0.7%). These changes were accompanied by declines in protein mass (0.6 and 1.0 kg for adults and 1.6 and 0.2 kg for fawns in 2001 and 2002, respectively). Fat reserves did not differ between years for either adults or fawns. Similarly, there was a minimal effect of winter severity on blood profiles of deer; however, cholesterol (in combination with julian day) was inversely related ($R^2 = 0.43$) to fat (%) of adults and serum urea nitrogen (in combination with julian day) was inversely related ($R^2 = 0.36$) to fat (%) of fawns. Survival of adult females was similar between years with the majority of deaths occurring between February and April; wolf (*Canis lupus*) predation was the primary cause of death. Age appeared to influence adult survival as 70% of adults that died were >10 years old. Winter severity may have played a role in fawn survival. Nearly half (47%) of the fawns died during late-winter to early-spring of 2001, while all survived in the same interval of 2002. Fat reserves were not reliable predictors of deer survival in this study. Eighty-two percent and 71% of adults in 2001 and 2002 that were determined to have low fat reserves in mid- or late-winter (i.e., below the median body fat percentage of animals sampled) survived winter and early-spring; 75% of fawns with low fat reserves in 2001 also survived. Absence of a biologically significant relation of body condition of deer relative to winter severity may be a result of a cumulative effect of several mild winters preceding 2000–01, that enabled deer to accumulate sufficient energy reserves to withstand prolonged and severe climatic stress. Further study of the relation between winter severity and body condition of northern deer during several successive winters of varying severity may be warranted, as well as consideration of other potentially influential factors (e.g., migration behavior, predator density, habitat quality).

**From the abstract of Chapter 1 of Michelle Carstensen Powell's Ph.D. Dissertation ,
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SURVIVAL AND CAUSE-SPECIFIC MORTALITY OF WHITE-TAILED DEER NEONATES IN RELATION TO WINTER SEVERITY AND NUTRITIONAL CONDITION OF THEIR DAMS

Michelle Carstensen Powell, and Glenn D. DelGiudice

Abstract: Winter severity is thought to play a key role in newborn white-tailed deer (*Odocoileus virginianus*) survival, yet few studies of free-ranging ungulate populations have been able to establish a link between maternal body condition and subsequent survival of offspring. Free-ranging deer neonates ($n = 66$) were captured from radiocollared dams that survived winters of varying severity; winter 2000–01 was severe (Winter Severity Index [WSI] = 153) and 2001–02 was historically mild (WSI = 42). Mean dates of birth (26 May \pm 1.7 [SE] days and 26 May \pm 1.3 days) and estimated birth-mass (2.8 \pm 0.1 kg and 3.0 \pm 0.1 kg) of neonates were similar between springs 2001 ($n = 31$) and 2002 ($n = 35$). Neonate survival was similar between years; pooled mortality rates for neonates were 14, 11, and 20% at 0–1, 1–4, and 4–12 weeks of age, respectively. Predation accounted for 86% of mortality, the remaining 14% of deaths were attributed to unknown causes. Black bears (*Ursus americanus*) were responsible for 57 and 38% of predator-related deaths of neonates in springs 2001 and 2002; whereas, 50% of neonate mortality in 2002 was caused by bobcats (*Felis rufus*). Wolves (*Canis lupus*) played a minor role in neonate mortality, accounting for only 5% of predator-related deaths. Birth characteristics and blood profiles of neonates were examined as possible predictors of survival. Serum urea nitrogen:creatinine (SUN:C) ratio was associated with neonate survival to 1, 4, and 12 weeks of age; with elevated levels reported in survivors (28.6–35.2) compared to nonsurvivors (22.1–27.0). No relation between winter fat reserves (i.e., percent ingesta-free body fat) of dams and survival of their neonates the subsequent spring was observed; however, dams ($n = 5$) of neonates that died within 4 weeks of age had greater ($P < 0.05$) concentrations of SUN (19.8 \pm 3.4 vs 11.1 \pm 1.1 mg/dL), C (2.7 \pm 0.1 vs 2.3 \pm 0.1 mg/dL), and SUN:C (7.2 \pm 0.9 vs 4.8 vs 0.4) than dams ($n = 20$) of survivors. Even though a direct relation between winter severity and birth or blood characteristics of neonates was not detected in this study, evidence suggested that body mass at birth and key serum indices of neonate nutrition were associated with their survival. Further, we were able to link winter severity and nutritional restriction of dams to reduced survival of their offspring. Clearly, additional study of free-ranging populations is needed to allow a greater understanding of the factors that may predispose neonates to natural sources of mortality.

**From the abstract of Chapter 2 of Michelle Carstensen Powell's Ph.D. Dissertation, Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul.*

BIRTH-SITE CHARACTERISTICS, HABITAT USE, AND SPATIAL RELATIONS OF WHITE-TAILED DEER NEONATES

Michelle Carstensen Powell, and Glenn D. DelGiudice

Abstract: Little is known about birth-site characteristics of free-ranging white-tailed deer (*Odocoileus virginianus*) in northern climates, or whether use of fawning habitat is related to neonate survival. In this study, we located 31 birth-sites of fawns in north central Minnesota during springs 2001 ($n = 17$) and 2002 ($n = 14$), and captured 41 neonates. Seven dams lost 1 or more fawns within 1 week of birth; 5 neonates were killed by predators and 3 died of unknown causes. Birth-site characteristics, including vegetative cover-types, distances to roadways and water, and concealment cover were highly variable; and none of these factors had an apparent influence on neonate survival. Neonates used a variety of cover-types within 3 weeks post-parturition, including hardwood and conifer stands, open areas, and they also used residential communities. Spatial relations of neonates to their dam, birth-site and siblings were assessed.

**From the abstract of Chapter 3 of Michelle Carstensen Powell's Ph.D. Dissertation, Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul.*

A LONG-TERM AGE-SPECIFIC SURVIVAL ANALYSIS OF FEMALE WHITE-TAILED DEER

Glenn D. DelGiudice, John Fieberg, Michael R. Riggs¹, Michelle Carstensen Powell, and Wei Pan²

Abstract: We conducted a 13-year survival (i.e., time survived since birth) and cause-specific mortality study, divided into 2 phases (Phase I = yr 1-6; Phase II = yr 7-13), of 302 female white-tailed deer (*Odocoileus virginianus*) ≥ 0.6 years old at capture. The study spanned a period of extreme variability in winter severity (maximum winter severity indexes of 45-195) and hunting pressure. Most studies of survival and cause-specific mortality of northern deer have assumed constant survival rates for adults (≥ 1.0 yr old pooled) of a sex and examined fawns ($0.6 \leq x \leq 1.0$ yr old) separately. We observed U-shaped hazard (i.e., instantaneous risk of death) curves for both phases of the study, indicating the risk of death is highest for younger and older individuals. The estimated hazard for Phase II was generally lower and relatively constant for adults 2-10 years old compared to Phase I, where the curve began ascending at age 6 years. This difference likely reflected differences in winter severities, associated changes in the magnitude of wolf (*Canis lupus*) predation, and changes in hunting pressure between the 2 phases. The age distribution of our study cohort was relatively stable over the study period. Subsequently, when 76 neonates (i.e., ≤ 0.6 yr old) were included in the study cohort, the descending arm of the all-causes hazard began its descent at a hazard rate of 2.3 (vs 1.0 without neonates), clearly demonstrating that the greatest risk of mortality occurs in the first 1 year of life. We compared cumulative survival estimates for these data using the generalized Kaplan-Meier (GKM) and the iterative Nelson estimator (INE) and illustrate the potential for bias when applying the GKM to left-truncated data. Median age of survival for females was 0.8 years old (90% confidence interval [CI] = 0.79-1.45 yr old) using the INE and 0.4 years old (90% CI = 0.8-1.4 yr old) using the GKM. Lastly, we use a simulation approach to examine the potential for bias resulting from pooling adults (using the U-shaped hazard function to determine reasonable "age classes" for pooling). These simulations suggest that models using the constructed discrete time variable give nearly unbiased estimates and provide support for using age-specific hazards to determine the reliability of adult age-pooled survival estimates. However, we caution that assessed cause-specific mortality may vary with environmental variability, variation of human-related activities, and age distribution of the study cohort.

**Abstract of paper accepted by the Journal of Wildlife Management.*

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MYCOBACTERIUM AVIUM SUBSP PARATUBERCULOSIS FROM FREE-RANGING DEER AND RABBITS SURROUNDING MINNESOTA DAIRY HERDS

Eran A. Raizman¹, Scott J. Wells¹, Peter A. Jordan², Glenn D. DelGiudice, and Russell R. Bey³

Abstract: The objectives of this study were to (1) estimate the prevalence of *Mycobacterium avium subsp paratuberculosis* (MAP) among white-tailed deer (*Odocoileus virginianus*) and eastern cottontail rabbits (*Sylvilagus floridanus*) surrounding infected and noninfected Minnesota dairy farms using fecal culture and (2) describe the frequency of use of farm management practices that could lead to potential transmission of infection between these species. Fecal samples from cows and the cow environment were collected from 108 Minnesota dairy herds, and fecal pellets of free-ranging deer and rabbits were collected from locations surrounding 114 farms; all samples were tested using bacterial culture. In addition, a questionnaire was administered to 114 herd owners. Sixty-two percent of the dairy herds had at least 1 positive fecal pool or environmental sample. A total of 218 rabbit samples were collected from 90% of the herds, and 309 deer samples were collected from 47% of the herds. On each of 2 sampled farms (4%), 1 deer fecal sample was MAP positive. Both farms had culture positive cow fecal pool and cow environment samples. On each of 2 other farms (2%), 1 rabbit fecal sample was culture positive to MAP, with 1 of these farms having positive fecal pools and environmental samples. Pasture was used on 79% of the study farms as a grazing area for cattle, mainly for dry cows (75%) and bred or prebred heifers (87%). Of the 114 farms, 88 (77%) provided access to drylot for their cattle, mainly for milking cows (77/88; 88%) and bred heifers (87%). Of all 114 farms, 20% and 25% estimated as daily the probability of physical contact between cattle manure and deer or rabbits, respectively. Possible contact between cattle manure and deer or rabbits was estimated to occur primarily from March through December. The frequency of pasture or drylot use and manure spreading on crop fields may be important risk factors for transmission of MAP among dairy cattle, deer, and rabbits. Although the MAP prevalence among rabbits and deer is low, their role as MAP reservoirs should be considered, especially in proximity to cattle herds with very low or zero prevalence.

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CHRONIC WASTING DISEASE SURVEILLANCE PROGRAM 2002–2004

Michael DonCarlos, Michelle Carstensen Powell, and Lou Cornicelli

SUMMARY OF FINDINGS

In response to the discovery of chronic wasting disease (CWD) in wild Wisconsin white-tailed deer (*Odocoileus virginianus*) and a Minnesota captive elk (*Cervus elaphus*) herd in 2002, the Minnesota Department of Natural Resources (MNDNR) developed a comprehensive wild deer CWD monitoring program that included surveillance of targeted animals (e.g., suspect or potentially sick deer exhibiting clinical signs or symptoms consistent with CWD), opportunistic surveillance (e.g., vehicle-killed deer), and hunter-killed deer surveillance. From 2002–2004, nearly 28,000 deer have been tested for CWD statewide with no positive results. The MNDNR will continue to monitor for the presence of CWD in suspect deer statewide, and may revisit the need to sample hunter-killed and opportunistic deer if the disease is detected in captive or wild deer in the future.

INTRODUCTION

Chronic wasting disease is a transmissible spongiform encephalopathy (TSE) that affects elk, mule deer (*Odocoileus hemionus*), and white-tailed deer (Spraker et al. 1997, Miller et al. 2000). TSEs are infectious diseases that alter the morphology of the central nervous system, resulting in a “sponge-like” appearance of this tissue (Williams and Young 1993). The etiological agent of CWD is believed to be an infectious protein, called a “prion.” A healthy animal exposed to these prions may develop CWD (Miller et al. 1998); however, precise mechanisms and rates of CWD transmission are poorly understood. Incubation time of the disease, from infection to clinical signs, can range from a few months to nearly 3 years (Williams

and Young 1980, Spraker et al. 1997, Miller et al. 1998). Clinical signs may include a loss of body condition and weight, excessive salivation, ataxia, and behavioral changes. Currently, there is no known treatment for the disease, and it is always fatal.

Chronic wasting disease was first discovered in captive mule deer in 1967, and then recognized in captive white-tailed deer and elk in 1978 (Williams and Young 1980). The disease has been diagnosed in captive cervid populations from Nebraska, Oklahoma, Kansas, Montana, Colorado, Wyoming, South Dakota, Wisconsin, New York, and Minnesota, USA, and Alberta and Saskatchewan, Canada (United States Animal Health Association 2001, Canadian Food Inspection Agency 2002). Within wild populations, CWD was historically confined to free-ranging deer and elk in the endemic area of northeast Colorado and southeast Wyoming (Miller et al. 2000, Williams et al. 2002). Recently CWD has been detected west of the continental divide in Colorado, and within wild deer populations of Nebraska, Wisconsin, Illinois, South Dakota, Utah, New Mexico, and New York. Generally, wild cervid CWD occurrences outside the endemic area have been located in close proximity to captive cervid facilities with past or present infected animals, except for 4 positive deer located at White Sands Missile Base, New Mexico.

Public health officials and the Centers for Disease Control in Atlanta, Georgia, have concluded there is no link between CWD and any neurological disease in humans. Furthermore, there is no evidence that CWD can be naturally transmitted to animals other than deer and elk. Experimental and circumstantial evidence suggests that transmission of the disease is primarily through direct

contact with infected animals (Miller et al. 1998). However, because of the possibility of persistence of prions in the environment, transmission in a contaminated environment may also be possible.

Wildlife disease control strategies need to be based on an understanding of specific disease etiology and epidemiology. Once established, most infectious diseases are extremely difficult to eliminate from wild populations. Because the epidemiological attributes of CWD remain uncertain, the MNDNR has positioned itself to acquire as much information as possible about CWD, including effective control strategies. Since CWD has not been detected in Minnesota's free ranging white-tailed deer population, the opportunity to assess the progress of the disease in other states, and observe the outcomes of selected management alternatives is of great value. Given the extended incubation period associated with CWD, the apparent capacity for lateral transmission, and the potential contributions from environmental contamination (Miller et al. 2004), it is imperative that CWD be identified, isolated, and controlled as rapidly as possible following detection within a population.

OBJECTIVES

- Determine if CWD is present in Minnesota's wild deer population; and
- Continue to monitor occurrences of CWD in wild or captive cervids in bordering states.

METHODS

Hunter-Killed Deer Surveillance

Power analysis was used to determine sample sizes for each Deer Permit Area (DPA) to ensure a $\geq 95\%$ probability of detecting CWD, given a 1% infection rate (assuming a random distribution of the disease among individuals within each sampling area). Approximately 300 deer were needed in

each sampling area (Table 1). Due to the prolonged incubation period of CWD, only deer ≥ 1.5 years of age were selected. Also, an attempt was made to collect samples equally across sex classes, as both sexes are susceptible to CWD (Miller et al. 2000). To optimize the time spent collecting samples, collections occurred primarily during the Minnesota firearms deer season. Hunters voluntarily submitted all samples.

During the 2002 Minnesota deer hunting seasons, 16 sampling areas consisting of 17 DPAs were selected for CWD monitoring of hunter-killed deer (Figure 1a). Sampling areas were selected based on the following criteria: 1) proximity to cervid farms with known or suspected CWD positive animals, 2) proximity to CWD infected states, and 3) a statewide distribution. Approximately 100 registration stations within the selected DPAs were staffed for sample collection. Staff were trained to collect hunter data, including the specific harvest location, and to remove deer heads. All heads were given a unique ID number and transported to "extraction" sites. A total of 57 DNR wildlife research staff and veterinary students were trained to extract a portion of the brain, called the obex. All samples were transported to the Farmland Wildlife Population and Research Station in Madelia where they were inventoried, entered into a database, and sent to the University of Minnesota Veterinary Diagnostic Laboratory (VDL) for immunohistochemical (IHC) testing of the obex tissue for the presence of the abnormal prion protein.

During the 2003 Minnesota deer hunting seasons, 37 sampling areas consisting of 59 DPAs were selected for CWD monitoring of hunter-killed deer (Figure 1b). The sampling plan was modified from the 2002 scheme to include blocks of adjacent DPAs that enabled greater utilization of available personnel, and enhanced the efficiency of collection efforts. Approximately 130 registration stations within the selected DPAs were staffed for collection of deer heads, which were then transported to 11 extraction sites. Over 90 DNR wildlife management

and research staff and veterinary students were trained to extract the medial retropharyngeal lymph nodes (MRPLN) from collected deer heads. The removal of MRPLN instead of obexes was another enhancement from the 2002 collection year, which resulted in a faster extraction process and less expensive testing protocol. All samples were transported to the Farmland Wildlife Population and Research Station in Madelia where they were inventoried, entered into a database, and sent to the University of Minnesota VDL for enzyme-linked immunosorbent assay (ELISA) testing of the lymph node tissue for the presence of the abnormal prion protein.

During the 2004 Minnesota deer hunting seasons, 50 sampling units consisting of 60 DPAs were selected for CWD monitoring of hunter-killed deer (Figure 1c). The sampling plan was meant to include all DPAs that were not previously sampled during the 2002 and 2003 collections. Nearly 130 registration stations within the selected DPAs were staffed for collection of MRPLN. This was a major change from previous collection years, where deer heads were removed at the registration stations and then transported to extraction sites for subsequent MRPLN removal. Removal of MRPLN on-site marked a vast improvement in the efficiency of sample collection and use of personnel (see Surveillance Costs section). Over 500 DNR wildlife staff, veterinary students, and volunteers were trained to extract MRPLN and gather relevant sample information from the hunters. Samples were transported to either the Farmland Wildlife Population and Research Station in Madelia or the Carlos Avery Wildlife Management Area in Forest Lake where they were inventoried, entered into a database, and sent to the University of Minnesota VDL for ELISA testing of the lymph node tissue for the presence of the abnormal prion protein.

Suspect Deer Surveillance

Suspect deer, which included animals in any DPA that displayed clinical symptoms thought to be consistent with

CWD, as well as escaped captive cervids, were also tested for CWD. Obexes (2002) or MRPLNs (2003 and 2003) were extracted from suspect animals and submitted to the

RESULTS

Hunter-Killed Deer Surveillance

A total of 4,533 usable samples were collected from the selected sampling areas in 2002 and all were negative for the presence of CWD. Approximately 4.8% of collected samples were not usable. Females composed 40% of the samples, while males contributed the remaining 60%. Assuming that the samples were randomly collected from each DPA, results indicate that CWD infection rates $\geq 1\%$ would have been detected in 7 of 16 sampling areas with $\geq 95\%$ confidence, in 4 of 16 sampling areas with 92-95% confidence, and in 5 of 16 sampling areas with $< 90\%$ confidence (Figure 2).

No positive results were detected in the 10,054 usable samples collected from the selected sampling areas in 2003. Approximately 2.8% of collected samples were not usable. Females composed 44% of the samples, while males contributed the remaining 56%. Assuming that the samples were randomly collected from each DPA, results indicate that CWD infection rates $\geq 1\%$ would have been detected in 19 of 37 sampling areas with $\geq 95\%$ confidence, in 13 of 37 sampling areas with 90-95% confidence, and in 5 of 37 sampling areas with $\leq 90\%$ confidence (Figure 2).

In 2004, there were no positive results detected in the 13,038 usable samples collected from the selected sampling areas. The percentage of unusable samples (0.7%) marked a vast improvement in sample quality compared to the previous collection years. Females and males comprised 35% and 64% of the samples, respectively. Sex was not recorded in the remaining 1% of samples. Assuming that the samples were randomly collected from each DPA, results indicate that CWD infection rates $\geq 1\%$ would have been detected in 21 of 50

sampling areas with $\geq 95\%$ confidence, in 13 of 50 sampling areas with 90-95% confidence, and in 16 of 50 sampling areas with $\leq 90\%$ confidence (Figure 2).

Suspect Deer Surveillance

From 2002 to 2004, 120 deer were sampled as suspects (Figure 3). All suspect samples were negative for the presence of the abnormal prion protein.

Surveillance Costs

The MNDNR conducted CWD surveillance for three deer seasons. Over that time, the protocol was changed to reflect new information about CWD (e.g., extraction of the obex versus MRPLN), and an overall desire to increase efficiency and decrease costs. In 2002, obexes were removed at centralized extraction stations. In total (including diagnostic fees), \$857,600 was expended to collect 4,533 samples (\$189/sample). In 2003, MRPLN were removed (again at centralized extraction stations) and \$1.14 million was expended to collect 10,054 samples (\$113/sample). In 2004, the protocol was changed to collect MRPLN at the registration stations, which eliminated the need to remove deer heads and transport them to centralized extraction stations. Ultimately, we expended \$1.046 million and collected 13,038 samples (\$80.50/sample). Diefenbach et al. (2004) reported spending \$56/sample to remove heads and transport them to a centralized location in Pennsylvania for CWD testing. In Minnesota, excluding the diagnostic fees (\$25/sample) and the veterinary student contract (\$7.70/sample), it cost an estimated \$48/sample to collect the sample (there were no head removal or transportation costs).

FUTURE CWD SURVEILLANCE EFFORTS

The MNDNR's effort to sample hunter-killed deer for the presence of CWD was highly successful, with the collection of nearly 28,000 samples statewide from 2002–2004. As the disease has not been detected in wild deer, there is no immediate need to continue the surveillance of hunter-killed deer. However, the sampling of suspect animals will continue throughout the state. If CWD is detected in wild or captive deer in the future, the MNDNR may revisit the need to sample hunter-killed or opportunistic deer.

We have attempted to collect CWD samples from the metro permit areas (228 and 337), but have been unsuccessful in obtaining statistically significant numbers. Consequently, an effort will be made again in 2006 to collect approximately 500 metro deer samples.

ACKNOWLEDGEMENTS

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Table 1. 2004 CWD sampling areas and sample size required to detect an infection rate of 1% with 95% confidence (98% confidence in combined DPAs)

Sampling Area (DPA)	Modeled Pre-Fawn Population Size	CWD Sample Size
Block 1		
104	14,564	295
107	15,160	295
110/283	5,940	377
205/214	6,000	377
211	10,986	294
213 (Red Lake)	18,500	300
Block 2		
167	10,560	294
168	12,308	294
170	17,095	295
172	15,785	295
197	9,600	293
242	14,003	295
243	9,734	294
245	16,907	295
246	19,708	296
Block 3		
244/251/287	23,594	386
297/298	9,997	382
402	1,939	276
407	2,657	282
408	2,519	281
409	3,936	287
420/421	3,261	367
Block 4		
152/157	23,287	386
156	13,216	295
159	12,496	295
174	10,020	294
183	10,605	294
222	5,562	290
225	9,656	294
249	9,538	293
337/338/339	5,442	376
228	3,555	286

Table 1. Continued.

Sampling Area (DPA)	Modeled Pre-Fawn Population Size	CWD Sample Size
Block 5		
440	2,515	281
442	3,143	284
443	1,852	275
448	3,263	285
449	4,187	288
450	1,795	275
451	2,198	279
452	1,592	272
453	2,770	283
454/455	4,134	372
456	2,349	280
457	1,964	275
458	1,644	273
459	3,701	286
461	2,597	282
463	1,494	270
464	1,885	276
466	2,979	284

Table 2. Summary of CWD samples collected by sampling area. Sample numbers include hunter-killed and opportunistic deer.

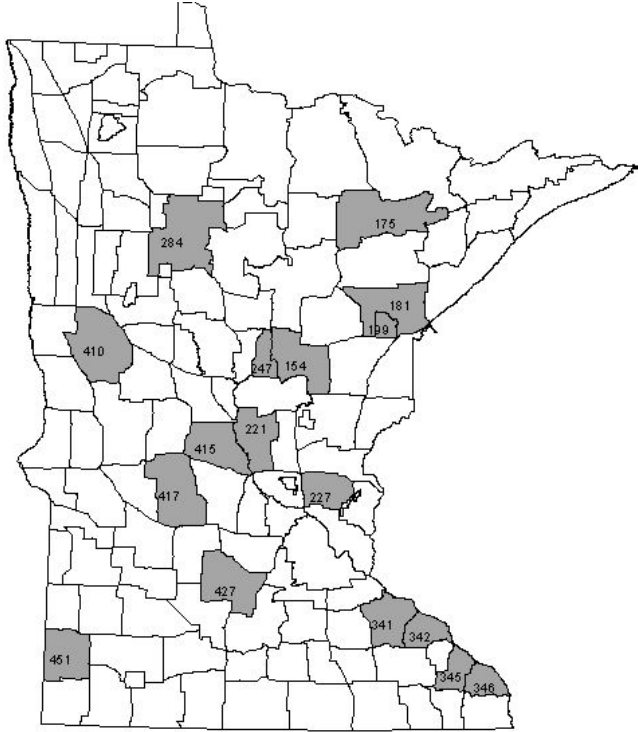
Sampling Area (DPA)	Total # of Samples Collected	Total # of Usable Samples	Negative Samples	Positive Samples	Unusable Samples	Female (%)	Male (%)	Unknown Sex (%)	Total Unusable Samples (%)	Confidence Level (1% Infection Rate)
BLOCK 1										
104	321	316	316	0	5	32.30	66.15	1.55	1.56	95.82
107	325	325	325	0	0	26.15	72.00	1.85	0.00	96.19
110/283	327	327	327	0	0	46.20	53.80	0.00	0.00	96.26
205/214	352	351	351	0	1	34.66	63.35	1.99	0.28	97.06
211	301	300	300	0	1	29.90	69.10	1.00	0.33	95.10
213	11	11	11	0	0	9.09	90.91	0.00	0.00	10.47
BLOCK 2										
167	245	245	245	0	0	28.16	69.80	2.04	0.00	91.48
168	344	344	344	0	0	33.72	64.53	1.75	0.00	96.85
170	358	358	358	0	0	30.45	69.55	0.00	0.00	97.26
172	381	376	376	0	5	37.53	61.68	0.79	1.31	97.72
197	253	252	252	0	1	28.02	67.70	4.28	0.43	92.06
242	191	191	191	0	0	46.07	53.40	0.53	0.00	85.33
243	292	289	289	0	3	43.15	56.85	0.00	1.03	94.52
245	328	328	328	0	0	36.67	63.03	0.30	0.00	96.30
246	399	399	399	0	0	40.35	59.40	0.25	0.00	98.19
BLOCK 3										
244/251/287	412	412	412	0	0	35.59	63.44	0.97	0.00	98.41
297/298	312	312	312	0	0	36.42	61.98	1.60	0.00	95.65
402	171	168	168	0	3	43.27	54.97	1.76	1.75	81.52
407	345	345	345	0	0	45.00	54.44	0.56	0.00	96.88
408	258	257	257	0	1	42.25	57.36	0.39	0.39	92.44
409	315	315	315	0	0	39.05	60.95	0.00	0.00	95.78
420/421	330	327	327	0	3	44.35	55.65	0.00	0.91	96.26
BLOCK 4										
152/157	514	513	513	0	1	30.29	68.93	0.78	0.19	99.42
156	295	295	295	0	0	34.69	64.97	0.34	0.00	94.84
159	290	290	290	0	0	40.34	57.93	1.73	0.00	94.58
174	296	294	294	0	2	34.46	65.54	0.00	0.68	94.79

Table 2. Continued.

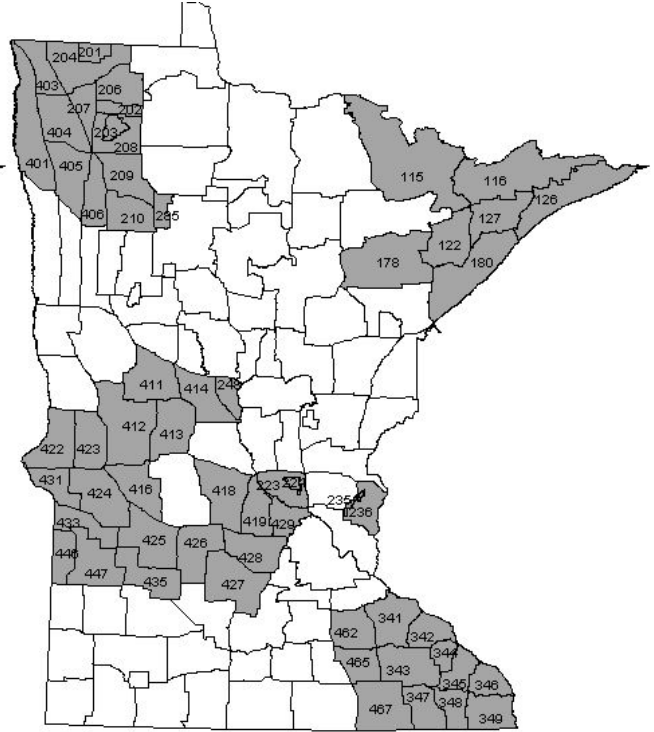
Sampling Area (DPA)	Total # of Samples Collected	Total # of Usable Samples	Negative Samples	Positive Samples	Unusable Samples	Female (%)	Male (%)	Unknown Sex (%)	Total Unusable Samples (%)	Confidence Level (1% Infection Rate)
183	359	359	359	0	0	29.53	69.64	0.83	0.00	97.29
222	291	291	291	0	0	33.68	65.98	0.34	0.00	94.63
225	299	299	299	0	0	33.78	65.22	1.00	0.00	95.05
249	296	295	295	0	1	40.54	57.09	2.37	0.34	94.84
337/338/339										
228										
BLOCK 5										
440	198	193	193	0	5	39.00	61.00	0.00	2.53	85.63
442	302	300	300	0	2	29.14	69.21	1.65	0.66	95.10
443	181	178	178	0	3	28.73	70.17	1.10	1.66	83.29
448	186	185	185	0	1	34.41	63.44	2.15	0.54	84.42
449	288	288	288	0	0	26.48	72.47	1.05	0.00	94.47
450	128	127	127	0	1	29.46	70.54	0.00	0.78	72.10
451*	324	300	300	0	24	29.33	70.67	0.00	7.41	95.10
452	145	144	144	0	1	37.93	62.07	0.00	0.69	76.48
453	173	170	170	0	3	27.96	71.51	0.53	1.73	81.89
454/455	377	373	373	0	4	31.65	66.75	1.60	1.06	97.65
456	294	293	293	0	1	42.81	57.19	0.00	0.34	94.74
457	237	234	234	0	3	35.86	63.29	0.85	1.27	90.48
458	167	167	167	0	0	23.35	76.65	0.00	0.00	81.33
459	284	281	281	0	3	24.30	75.35	0.35	1.06	94.06
461	226	223	223	0	3	42.15	57.40	0.45	1.33	89.37
463	135	133	133	0	2	41.61	58.39	0.00	1.48	73.73
464	86	84	84	0	2	37.21	61.63	1.16	2.33	57.01
466	184	181	181	0	3	36.67	62.78	0.55	1.63	83.78
2004 Totals	13,126	13,038	13,038	0	88	35.0	64.0	1.0	0.67	

*Includes 215 samples (191 usable, 24 unusable) samples collected in 2002.

a) 2002 DPAs



b) 2003 DPAs



c) 2004 DPAs

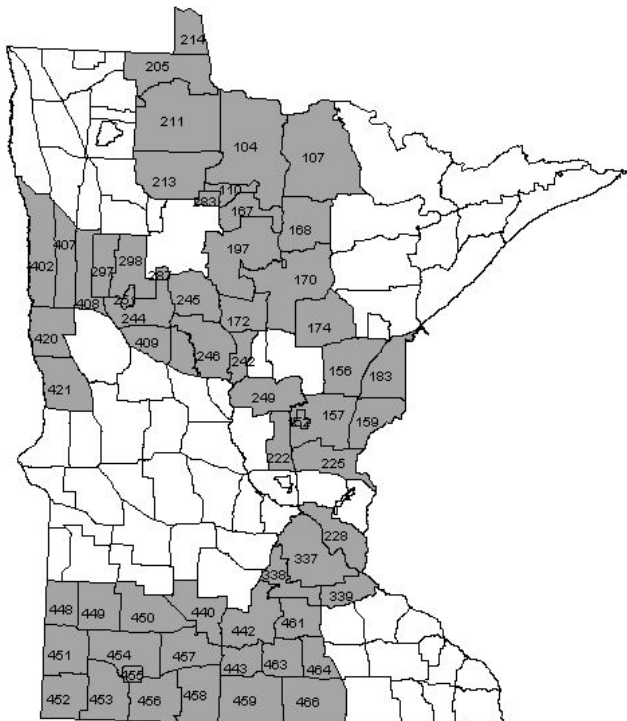


Figure 1. Sampling areas, denoted by Deer Permit Area (DPA), selected for chronic wasting disease surveillance of hunter-killed deer in 2002 (a), 2003 (b), and 2004 (c).

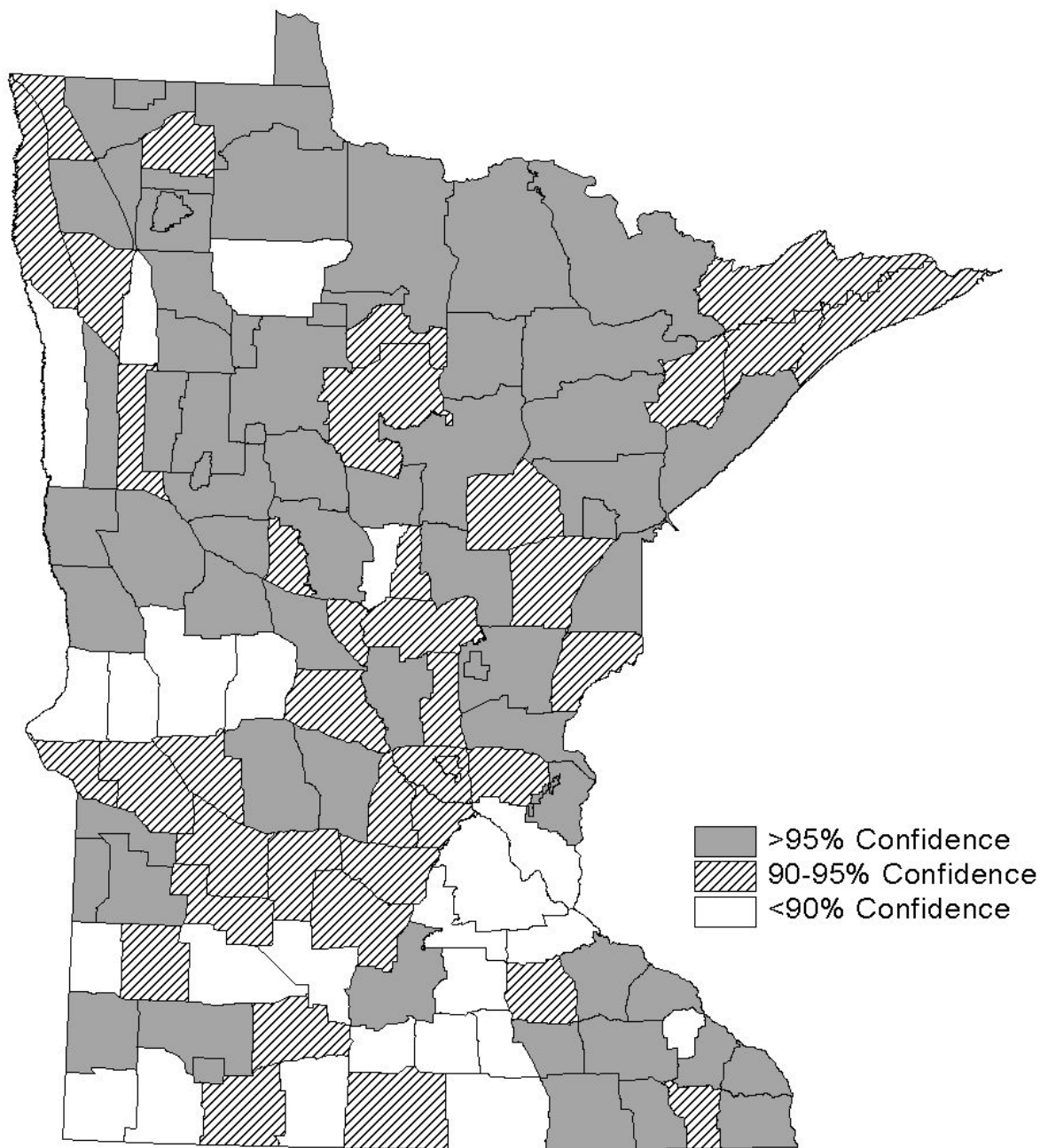


Figure 2. Probability of detecting the presence of chronic wasting disease (CWD), given a 1% infection rate, in white-tailed deer sampled in Deer Permit Areas in Minnesota, 2002–2004. Confidence level was based on the assumption of a random distribution of CWD among individuals within each sampling area.

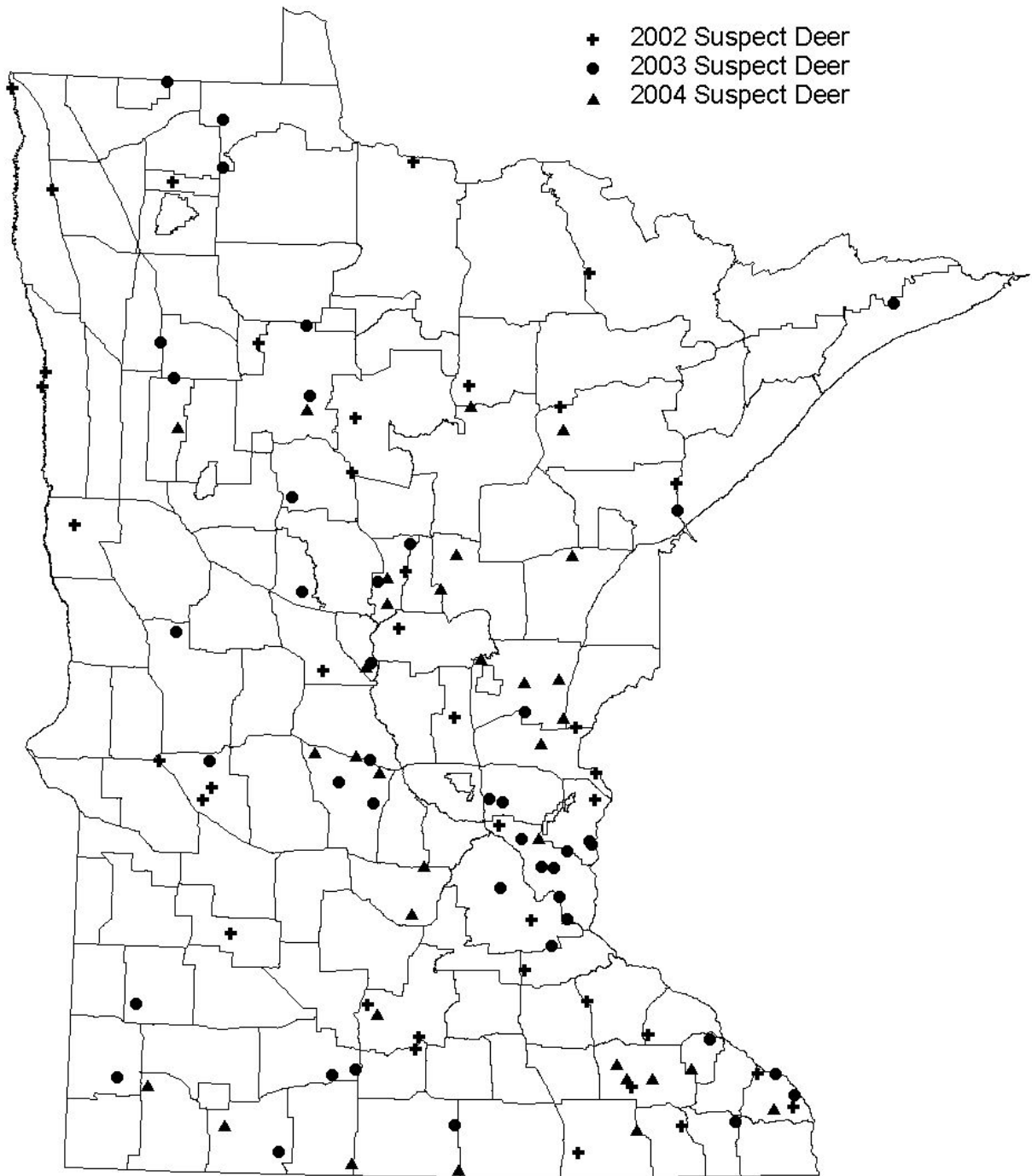


Figure 3. Locations of suspect deer sampled for chronic wasting disease in Deer Permit Areas of Minnesota, 2002–2004.

SURVIVAL AND CAUSE-SPECIFIC MORTALITY OF A PROTECTED POPULATION OF RIVER OTTERS IN SOUTHEASTERN MINNESOTA*

Thomas A. Gorman¹, Brock R. McMillan¹, and John D. Erb

Abstract: Determining causes of mortality and estimating survival rates can provide insight into the status of a species whose population trends are not well understood. Legal harvest of river otters (*Lontra canadensis*) has been prohibited in southern Minnesota since 1917. Thus, this region provided an opportunity to examine the influences of incidental trapping and natural causes of mortality on a protected population of river otters. From October 2001 through April 2004, 39 (13 adult males; 6 sub-adult males; 8 adult females; 12 sub-adult females) river otters were captured and radio-marked along a portion of the Mississippi River watershed to estimate survival and determine causes of mortality. For each mortality event, we determined the cause of death (e.g., incidental captures from trappers, automobile collisions, and natural mortality). To assess which factors were most influential on survival, we developed a suite of a priori models incorporating age (i.e., sub-adults < 2 years old and adults > 2 years old), sex, and/or season. Program MARK was used for model selection and survival estimation and we estimated population growth using a Leslie projection matrix. Human induced mortalities, including accidental captures by fur-harvesters targeting other species (n = 6) and automobile collisions (n = 1), accounted for the majority of deaths, while natural mortality was low (n = 1). Annual survival of adult females (S = 0.733, SE = 0.122) was similar to survival of sub-adult females (S = 0.709, SE = 0.132), but survival of adult males (S = 0.889, SE = 0.086) and sub-adult males (S = 0.891, SE = 0.088) was higher than females. The population was estimated to be increasing ($\lambda = 1.146$) despite females having a lower overall survival rate than males. A perturbation analysis of the matrix indicated that the survival of juvenile and adult females has the greatest influence on λ . River otters and other furbearers need to be monitored to assess population status, and measures should be taken to ensure that demographic parameters are sufficient for the population to persist.

** From the Abstract of Chapter 1 of Thomas A. Gorman's Master's Thesis, Biology Dept., Minnesota State University, Mankato.*

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HOME RANGE AND SPATIAL CHARACTERISTICS OF RIVER OTTERS IN SOUTHEASTERN MINNESOTA*

Thomas A. Gorman¹, Brock R. McMillan¹, and John D. Erb

Abstract. The river otter (*Lontra canadensis*) has been re-occupying portions of its native range across North America for more than 25 years due to extensive reintroduction programs, improved water quality, and wetland restoration. In southeastern Minnesota, there is a native population of river otters that is believed to be increasing in distribution and numbers. We examined the spatial characteristics, overlap, and interactions between river otters in southeastern Minnesota. We captured 39 river otters (13 adult males; 6 sub-adult males; 8 adult females; 12 sub-adult females) and equipped them with radio transmitter implants. Otters were monitored from spring 2002 to spring 2004 along portions of the Mississippi River, the Whitewater River, and the Zumbro River. We estimated annual and seasonal home ranges and annual core areas for individual otters, and compared home range characteristics between sexes and among age classes. Further, we evaluated the static and dynamic interactions between individuals to evaluate the social structure of the population. Annual home ranges of male river otters were 2.73 times larger than females, and annual core areas of males were 2.52 times larger than females. Within each sex, we did not detect a difference in home range size between seasons, but there was a seasonal difference between sexes ($F = 14.419$; $p = 0.0003$). The static interactions (home range overlap) between river otters were extensive, and occurred between 94.9% of the individuals analyzed at the 95% home range scale, and occurred between 69.2% of the individuals analyzed, at the 50% core area scale. Dynamic interactions between male: female comparisons and female: female comparisons were positive (78.5% and 75.5% were positive, respectively), revealing that one animal's movements influenced the others. River otter sociality and space use varied between the sexes, with minimal influence of age and season.

* From the Abstract of Chapter 2 of Thomas A. Gorman's Master's Thesis, Biology Dept., Minnesota State University, Mankato.

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NATAL DEN SITE CHARACTERISTICS OF RIVER OTTERS IN SOUTHEASTERN MINNESOTA*

Thomas A. Gorman¹, Brock R. McMillan¹, and John D. Erb

Abstract: Several factors may influence the selection of natal dens by female river otters (*Lontra canadensis*). Den use may be influenced by the availability of dens sites as well as specific den characteristics that protect young from other river otters and weather extremes. Otters have been reported to use a variety of existing burrows created by other animals. We monitored 8 adult (>2 years old) female river otters during the natal denning season (March – May). We measured 12 micro- and macro-habitat characteristics to best describe the physical characteristics of their natal dens. Females began to actively den on 27 March, with a mean denning date of 31 March, and were in natal dens for an average of 49 days (SE = 3.03). Two females used natal dens that consisted of brush piles, 4 females located dens in caves that may have been improved by other animals, but otherwise were natural features that occurred in the limestone bluffs, 1 female used a den that was created by the roots of a big-toothed aspen (*Populus grandidentata*), and 1 female placed her den in a beaver bank den. Dens were located an average of 315.9 m (SE = 78.5, n = 9) from the nearest body of water and were on average at 274.1 m (SE = 15.7m, n = 9) of elevation above sea level. All females used natal dens that were protected from rapid changes in water levels, and 7 of 8 females placed dens outside of their normal activity areas. Management for river otters should not only consider habitats within normal areas of activity, but also adjacent uplands likely to be used for natal denning habitat.

* From the Abstract of Chapter 3 of Thomas A. Gorman's Master's Thesis, Biology Dept., Minnesota State University, Mankato.

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IDENTIFYING PLOTS FOR SURVEYS OF PRAIRIE CHICKENS IN MINNESOTA

Michael A. Larson

SUMMARY OF FINDINGS

Collection of data for this project will begin on 4 April 2005, so no results are available.

INTRODUCTION

Nearly all methods for monitoring populations of greater prairie chickens (*Tympanuchus cupido pinnatus*), including those currently employed by the Minnesota Department of Natural Resources (MN DNR), depend upon locating leks, or concentrations of the birds at their arenas for breeding displays (i.e., booming grounds), during spring. Surveying a statistically valid sample of leks requires identifying all areas where leks may occur and then sampling to find a number of plots occupied by active leks. The range of prairie chickens in Minnesota covers approximately 10,000 km², so a major limitation to monitoring leks of prairie chickens is determining where to survey within that range.

The availability of GIS technology and databases of spatially explicit land cover have made it feasible to use landscape-scale habitat criteria to identify areas where leks may occur. Although land cover associated with prairie chicken leks in Minnesota and Wisconsin have been quantified during previous studies (Merrill et al. 1999, Niemuth 2000, 2003), interpretation and application of those data are problematic. In particular, the previous studies were based on a case-control sampling design, which does not allow inferences about relative probabilities of occurrence (Keating and Cherry 2004), and they did not select active leks randomly or verify nonuse at the randomly selected control locations. A study design that selects all samples randomly or at least allows for concurrently estimating the proportions of locations that are and are not occupied by leks, as I propose below, would preclude

those problems (Keating and Cherry 2004).

Inferences about trends in the abundance of grouse throughout the state require statistically valid samples of survey locations from defined areas in which the species may occur. This study will build upon existing knowledge of landscape-scale habitat criteria that may be useful for identifying plots where prairie chicken leks may occur, thereby dramatically reducing the area needed to be included in monitoring programs. It will also serve as a pilot project for a new survey design that may prove to be more efficient than current survey methods for detecting changes in the abundance of prairie chickens. Results of this study may benefit management programs for prairie chickens by improving the quality of inferences drawn from spring surveys and developing resource selection functions for using landscape characteristics to estimate the relative probability of an area being occupied by a lek.

OBJECTIVES

- To determine landscape-scale characteristics associated with plots of land occupied by prairie-chicken leks in Minnesota.
- To evaluate potential within-year sources of variation in the probability of detecting prairie-chicken leks in Minnesota.

METHODS

In Minnesota, prairie chickens occur in 3 distinct ranges (i.e., Northwest, Southwest, and Central; Giudice 2004; Figure 1). The study area will be established in the Northwest prairie chicken range because the Northwest range contains the largest population of prairie chickens, is where the hunting

permit areas are, and is the focus of all current prairie chicken monitoring effort by the DNR. The Northwest prairie chicken range is linear, and most known lek locations are between southwest Red Lake County in the north and eastcentral Wilkin County in the south (Figure 1). The study area includes the northern 96% of the Northwest range as defined by Giudice (2004) based upon land type associations of the Ecological Classification System. The size of the study area was limited by a maximum distance of 90 km from Crookston and Moorhead, where field technicians reside. All study areas will encompass many large areas of open grasslands that could serve as suitable habitat for prairie grouse leks.

Methods for this study are based on recently developed analytical techniques for estimating the probability of site occupancy (MacKenzie et al. 2002). Multiple visits to sample plots, only a portion of which will be occupied by the object of interest, are the basis of such studies. The main benefit of this method for estimating the probability of site occupancy is that the models used to analyze the data simultaneously account for covariates of site occupancy and the fact that the probability of detecting the object of interest is <1 . Although logistic regression may seem simpler and more straightforward than occupancy modeling, it does not account for errors in the response variable (occupied or unoccupied) due to detection probabilities <1 , and it is not necessary because occupancy models incorporate the same logistic function to relate covariates to the probabilities of detection and occupancy.

Throughout this report notation follows that of MacKenzie et al. (2002): ψ , probability that a sample plot is occupied by a lek; p , probability of detecting a lek within a sample plot, given that the plot is occupied; N , number of sample plots in a study area; T , number of surveys, or distinct sampling intervals during which all plots are visited once; and the "hat" character (e.g., $\hat{\psi}$) denotes the estimated value of a quantity. Additionally, c is the

probability of detecting a lek during visits that occur after a lek already has been detected within a plot (i.e., recapture).

A sampling unit, or plot, will be defined as a Public Land Survey (PLS) section, most of which are 1.6×1.6 km squares (i.e., $2.59 \text{ km}^2 = 1 \text{ mi}^2$). In portions of the prairie chicken range in Minnesota some PLS sections are more rectangular and much smaller than 2.59 km^2 . Variability in the size of plots is accounted for by the possible inclusion of habitat area within a plot as a covariate for ψ . The spatial scale of sampling units is a trade-off between being relatively large, so a reasonable proportion of them can be surveyed each year and ψ is "large" (Figure 1), and being relatively small, so that each unit can be surveyed rapidly and is likely to contain ≤ 1 lek (few PLS sections contain >1 lek [DNR, unpublished data]).

Access to and within plots by automobiles may be limited or infeasible in some areas. Time constraints will prevent extensive surveying by foot, so failing to detect a lek within a plot, even after multiple visits and accounting for detection probabilities <1 , will not ensure that the plot is not occupied. That will cause the estimated probability of occupancy to be biased relative to true occupancy throughout the study area. Inferences, therefore, will be limited to portions of each study area that are within some distance of roads that are accessible by automobiles during spring. The distance will be equal to the maximum distance at which leks may be detected by sight or sound.

I applied a dual frame sampling design, in which samples were drawn from a list frame consisting of plots known to have been occupied by a lek during 2004 and a much larger area frame consisting of the statistical population of plots to which the estimate of occupancy can be inferred (Haines and Pollock 1998). Dual frame sampling is appropriate for this situation because an area frame is necessary for sample plots to be representative of other plots in the population, and a list frame is useful for

focusing adequate sampling effort in plots where leks are known to have occurred recently. The locations of leks, especially those attended by more than a few males, are relatively consistent among years (Schroeder and Braun 1992), which makes them amenable to the use of a list frame. Dual frame sampling is essentially a form of stratification because parameter estimates and variances are weighted by the size of each frame and then added across frames (Haines and Pollock 1998), just as they are for stratified random samples.

An observer will visit each sample plot once during each of $T = 3$ consecutive biweekly periods from 4 April until 15 May 2005 (Svedarsky 1983). A visit will consist of a 20-minute interval between 0.5 hours before until 2 hours after sunrise (Cartwright 2000) during which a plot is surveyed with the purpose of detecting the presence of a lek (i.e., ≥ 2 male prairie chickens) by sight or sound. During each visit the observer will record whether or not a lek was detected, the value of time-dependent covariates that may affect p , and, if time is still available, the value of covariates of p and ψ that vary only spatially. Observers will also compare printed maps of land cover with actual land cover in and near sample plots (i.e., within 1.6 km) and mark corrections, including whether or not roads are paved, on the maps.

Occupancy models often require an assumption that p is homogeneous (i.e., does not vary among plots). Using covariates of p in the model may ameliorate the negative effects of potential heterogeneity in p , but the following 2 steps also will be taken to prevent the sampling design from introducing heterogeneity during this study. First, each observer will visit a different set of plots during each biweekly survey period, so differences among observers in their ability to detect leks will not be correlated with specific plots. Second, 1 visit to each plot will occur during each of 3 periods of the morning—early (-30–20 minutes from sunrise), middle (21–70 minutes after sunrise), and late (71–120 minutes after

sunrise). This will minimize the correlation between plot-specific p 's and differences in detection rates caused by time of day.

The probability of detecting a lek, p , may be affected by many different covariates (Table 1). The value of some time-dependent covariates of p will be recorded during each visit, whereas the value of other covariates that vary only spatially will be recorded only once for each plot.

The probability that a plot is occupied by a lek, ψ , also may be affected by many different covariates (Table 2). Prairie chickens may respond to landscape characteristics at several spatial scales (Niemuth 2000), so each covariate will be quantified at 2 different spatial scales (Keppie and Kierstead 2003)—the 2.59-km² sampling plot and a 9-plot area (≤ 23.3 km²) centered on the sample plot. The sampling plot roughly corresponds to home range sizes of prairie chickens (<400 ha; Robel et al. 1970) during spring. The larger scale roughly corresponds to areas of nesting and brood-rearing, which usually occur within 1.6 km from a lek (Schroeder and Braun 1992, Ryan et al. 1998). Most of the covariates of ψ will be measured using a GIS, but some will need to be verified by observers in the field.

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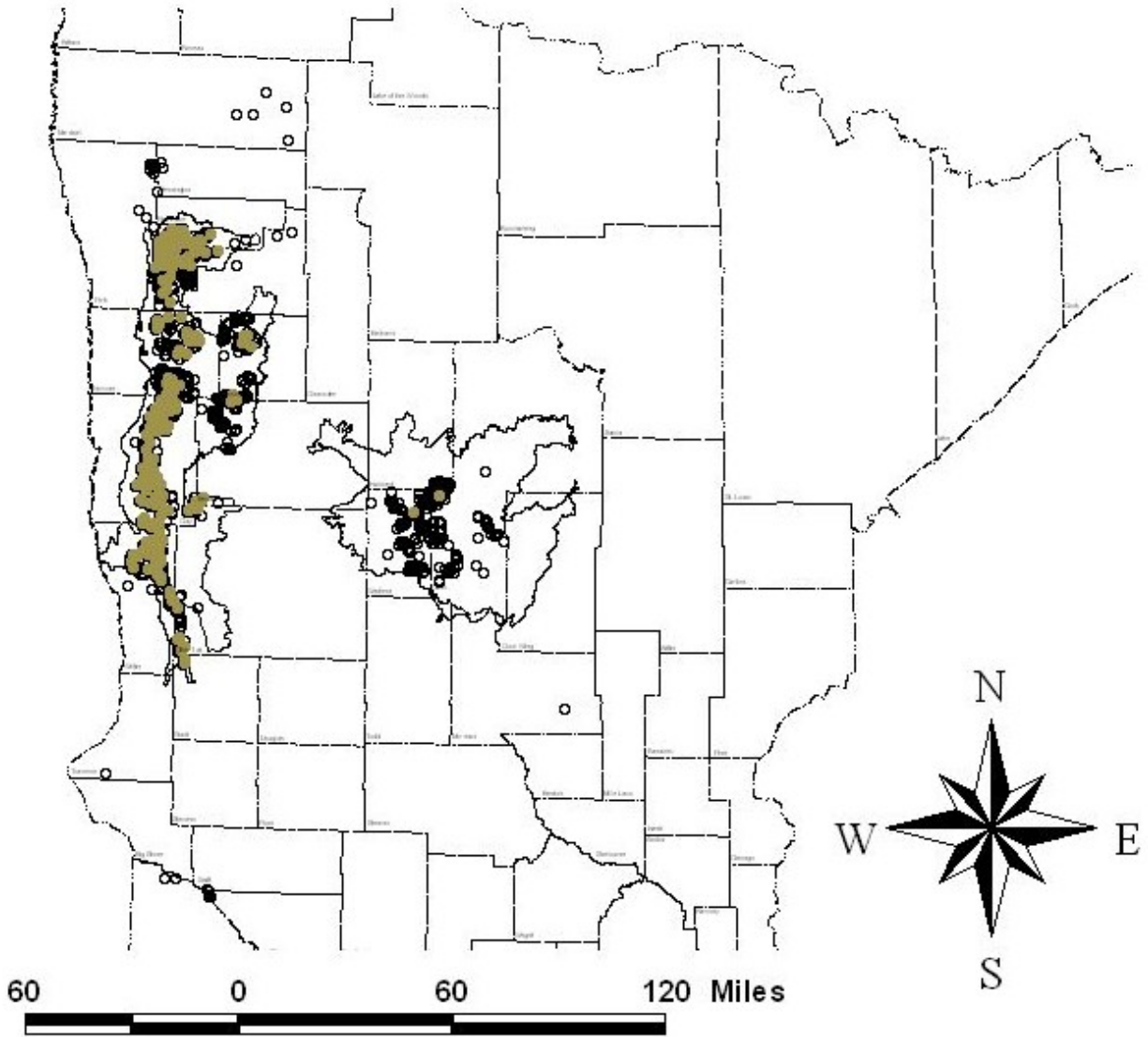


Figure 1. Locations of recent (gray circles) and historical (open circles) leks of greater prairie-chickens in Minnesota. Boundaries of the Northwest and Central ranges are based on land type associations of the Ecological Classification System. The Southwest range includes areas near the Minnesota River and in Big Stone County.

Table 1. Covariates that may affect the probability of detecting a lek, given that a lek was present within a sample plot (p).

Type ^a	Abbreviation	Description
t	OBS	observer
t	RECAP	whether or not a lek was detected previously this year
t	BIRDS	number of prairie grouse observed
s	LEKS	number of leks observed
t	DAY	day of the survey
t	TIME	minutes before or after sunrise
t	TEMP	ambient temperature
t	WIND	wind velocity
t	PREC	presence or absence of precipitation; type and intensity recorded also
t	CLOUD	proportion of the sky obscured by clouds
s	ROAD	density of roads accessible to a vehicle (km/km ²)
s	RDINT	density of accessible roads to the interior of the plot only
s	VIS	proportion of suitable land cover types that is visible to the observer
t	COV	proportion of suitable cover types under snow cover or water

^a Time-dependent covariates (t) will be quantified during each visit to a plot, whereas covariates that vary only spatially (s) during the study will be quantified only once for each plot.

Table 2. Covariates that may affect the probability of a plot being occupied by a lek (ψ).

Abbreviation	Description
HABAREA	area (ha) of all suitable land cover types combined
PROTECT	area of land in a conservation program or owned by a conservation organization
PRAIRIE	proportion of area in the Prairie cover type
GRASS	proportion of area in the Grassland cover type
SEDGE	proportion of area in the Sedge Meadow cover type
CROP	proportion of area in the Cropland cover type
SHRUB	proportion of area in the Lowland Deciduous Shrub & Upland Shrub cover types
BOGCON	proportion of area in the Stagnant Black Spruce & Stagnant Tamarack cover types
FOREST	proportion of area in the Forestland cover type
EDGE	density of edges (m/ha) between suitable and unsuitable cover types
LEKDIST	distance (m) to the nearest known lek, measured between plot centers
HOMES	number of occupied human residences (v)
TREE	presence of trees within suitable cover types (v)
ROAD	density of all roads (km/km ²) as an indicator of disturbance (v) ^a
PAVE	density of paved roads (v)
DISTURB	evidence of disturbance (e.g., prescribed burning, livestock grazing) (v)

^a The last 5 covariates will be verified (v) by observers in the field.

LINKING POPULATION VIABILITY, HABITAT SUITABILITY, AND LANDSCAPE SIMULATION MODELS FOR CONSERVATION PLANNING

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Abstract: Methods for habitat modeling based on landscape simulations and population viability modeling based on habitat quality are well developed, but no published study of which we are aware has effectively joined them in a single, comprehensive analysis. We demonstrate the application of a population viability model for ovenbirds (*Seiurus aurocapillus*) that is linked to realistic landscape simulations using a GIS-based habitat suitability index (HSI) model. We simulated potential future characteristics of a hardwood forest in southern Missouri under 2 tree harvest scenarios using LANDIS. We applied 3 different versions of the HSI model (lower, best, and upper estimates) to output from the landscape simulations and used RAMAS GIS to link estimates of temporally dynamic habitat suitability, through fecundity and carrying capacity, to ovenbird population viability. Abundances and viability differed more between the upper and lower HSI estimates than between the 2 forest management scenarios. The viability model was as sensitive to the relationship between reproductive success and habitat suitability as it was to rates of first-year survival and reproductive success itself. Habitat-based viability models and the wildlife studies they support, therefore, would benefit greatly from improving the accuracy and precision of habitat suitability estimates.

Combining landscape, habitat, and viability models in a single analysis provides benefits beyond those of the individual modeling stages. A comprehensive modeling approach encompasses all components and processes of interest, allows direct comparison of the relative levels of uncertainty in each stage of modeling, and allows analysis of the economic benefits and costs of different land use plans, which may be affected by landscape management, habitat manipulation, and wildlife conservation efforts. Using population viability, habitat suitability, and landscape simulation models in an integrated analysis for conservation planning is an important advancement because habitat quality is a critical link between human land use decisions and wildlife population viability.

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COMPARABILITY OF THREE ANALYTICAL TECHNIQUES TO ASSESS JOINT SPACE USE

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Abstract: The degree of space-use overlap among adjacent individuals is a central focus of many wildlife investigations. We studied the comparability of minimum convex polygon and fixed-kernel home-range overlap indices and Volume of Intersection (VI) scores using simulated data. We simulated pairs of point patterns to represent telemetry locations of adjacent individuals and varied the amount of potential overlap in the simulation region (100%, 50%, and 10%) and the point distribution (random, loosely clumped, and tightly clumped). We created 1,000 pairs of point sets (60 points in each individual set) for each of the 9 potential overlap and point distribution combinations. In all 9 treatment combinations, VI scores were highest followed by kernel and then polygon estimates. Raw differences among estimates within a treatment were greatest when there was 50% potential overlap, and overlap indices decreased as the degree of clumping increased. The relative differences among overlap indices within a treatment were affected most by potential overlap; differences generally were greatest at 10% and least at 100%. Correlation between index values was lowest for random point patterns, and highest for loosely clumped and tightly clumped point patterns. Although the VI tended to indicate the most overlap and minimum convex polygon the least, there was no consistent correction factor among techniques because of the interacting effects of the overlap index, distribution pattern, and potential overlap. Interpretation of overlap measures requires careful consideration of assumptions and properties of animals under study.

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MOOSE POPULATION DYNAMICS IN NORTHEASTERN MINNESOTA

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SUMMARY OF FINDINGS

A total of 114 moose (54 bulls and 60 cows) have been captured and collared since beginning the study in 2002. As of 31 March 2005, 36 collared moose (20 bulls and 16 cows) have died. Annual mortality rates varied between sexes and among years, and generally were higher than found elsewhere in North America. Pregnancy rates of captured cows were variable, but higher than found in northwestern Minnesota. Radio collared moose were used to develop a "sightability model" to correct observations during the annual aerial moose survey. This model will likely improve the accuracy and precision of the aerial survey.

INTRODUCTION

Moose formerly occurred throughout much of the forested zone of northern Minnesota, but today, most occur within two disjunct ranges in the northeastern and northwestern portions of the state. The present day northeastern moose range includes all of Lake and Cook counties, and most of northern St. Louis County. In recent years, population estimates based on aerial surveys suggest that moose numbers have stabilized around 4,000 animals.

That moose numbers in northeast Minnesota have not increased in recent years is an enigma. Research in Alaska and northern Canada has indicated that non-hunting mortality in moose

populations is relatively low. When these rates are used in computer models to simulate change in Minnesota's northeastern moose population, moose numbers increase dramatically, counter to the trend indicated by aerial surveys. Several non-exclusive hypotheses can be proposed to explain this result: i) average non-hunting mortality rate for moose in northeastern Minnesota is considerably higher and/or more variable than measured in previous studies; ii) recruitment rates estimated from the aerial surveys and used in the model are biased high; and/or iii) moose numbers estimated by the aerial survey are biased low.

OBJECTIVES

- Determine annual rates of non-hunting mortality for northeastern moose;
- Determine annual rates of reproduction in northeastern moose; and
- Determine the proportion of moose observed during aerial surveys and the factors that influence observability.

METHODS

Moose were immobilized with a combination of carfentanil and xylazine delivered by a dart gun from a helicopter. A radio-collar was attached, and blood, hair and fecal samples were collected from each moose. Beginning in 2003, a canine tooth also was extracted for aging.

Mortality was determined by monitoring a sample of up to 77 radio-collared moose. The transmitter in each radio-collar contained a mortality sensor that increased the pulse rate (mortality mode) if it remained stationary for more than 6 hours. When a transmitter was

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detected in mortality mode, we located the moose and conducted a necropsy to determine, if possible, the cause of death. Mortality rates were calculated using Kaplan-Meier survival functions (Pollock et al. 1989). During the first year of the study, the GPS location of each moose was determined weekly from the air. Beginning in March 2003, GPS locations were determined for one-half of the moose each week, and a mortality check was conducted on the remaining moose. After moose were located on 30 or more occasions, only mortality checks were conducted.

Pregnancy was determined from serum progesterone levels (Haigh et al. 1981). Following birth, the presence/absence of a calf with a radio-collared cow was determined, when possible during the telemetry flights.

During the aerial moose survey in January 2005, a sightability model (Anderson and Lindzey 1996, Quayle et al. 2001) was developed using the radio-collared moose. Following each relocation flight, a square test plot (6.7 mi²) that surrounded one or more collared moose was surveyed using procedures identical to those used in the operational survey. If the collared moose was observed within the plot, a suite of covariates including environmental conditions, group size, and visual obstruction were recorded. If the collared moose were not observed, they were located using telemetry, and the same set of covariates were recorded. Logistic regression was used to determine which covariates should be included in the sightability model.

RESULTS

During 7-11 February 2005, 30 adult moose (20 bulls and 10 cows) were immobilized to increase the sample of collared moose. A total of 114 moose (60 cows and 54 bulls) have been captured in northeastern Minnesota since February 2002 (Figure 1). No additional moose will be collared.

As of 31 March 2005, 36 radio-collared moose (20 bulls and 16 cows)

have died. The cause of death in 16 cases could be identified (8 hunter kill, 1 poached, 1 train, 3 trucks, 2 wolf predation, and 1 natural accident). Three deaths were censored from the study because they occurred within 2 weeks of their capture (1 wolf predation and 2 unknown). We were unable to examine remains of 2 additional moose that died within BWCAW. Fifteen appear to have died from unknown non-traumatic causes. In 8 cases, scavengers had consumed the carcasses, but evidence suggested predators did not kill them. In the remaining 7 cases, moose had little or no body fat (rump, kidney, abdominal, or heart), and were often emaciated. Moose dying of unknown causes died throughout year (1 - January, 2 - April, 4 - May, 1 - June, 1 - July, 3 - August, 2 - November, 3 - December). To date, samples from unknown cases have tested negative for CWD, Rabies, Eastern Equine Encephalitis, and West Nile Virus. Sera from captured moose were tested for BVD, borreliosis, leptospirosis, malignant catarrhal fever, respiratory syncytial virus, parainfluenza 3, infectious bovine rhinotracheitis, epizootic hemorrhagic disease, and blue tongue. All test results were negative except for borreliosis (21 of 64 serum samples had positive titers 1:320 or greater).

Annual non-hunting and total mortality varied considerably among years and between sexes (Table 1). It should be noted that only 7 bulls were collared during 2002. In both sexes, non-hunting mortality was substantially higher than documented for populations outside of Minnesota (generally 8 to 12%) (Ballard, 1991, Bangs 1989, Bertram and Vivion 2002, Kufeld and Bowden 1996, Larsen et al. 1989, Mytton and Keith 1981, Peterson 1977).

Serum samples from 18 additional radio-collared moose were tested for the presence of *P. tenuis*-specific antibodies using an enzyme-linked immunosorbent assay procedure (ELISA) (Ogunremi et al. 1999). Thirteen (11 cows and 2 bulls) of the 79 collared moose tested to date were sero-positive for antibodies against *P. tenuis*. Subsequently 3 died of unknown

causes and 1 was killed by a hunter.

Pregnancy rate was estimated at 92% in 2002, 57% in 2003, and 100% in 2004, based on serum progesterone. The samples from 2005 have not been analyzed yet. Similar estimates for the northwest moose population between 1996 and 1999 averaged 48% (Cox et al. *In press*).

Radio collared moose were located 41 times in the process of developing a sightability model. In 21 cases, the collared moose was observed using the standard survey protocol. In 17 cases, the collared moose was not observed, and telemetry had to be used to locate the collared moose. Six different models were evaluated, and the model with the highest predictive reliability incorporated a single covariate, visual obstruction, grouped into 6 equal intervals (Giudice and Fieberg, unpublished). Total population size based on this sightability model was $6,481 \pm 26\%$, higher than previous estimates calculated using the "Gasaway" protocol (Gasaway et al. 1986) and likely more accurate (Lenarz, unpublished). Ultimately, with additional data, this model will improve the accuracy and precision of the aerial survey.

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Table 1. Annual non-hunting and total mortality of collared moose. Number of collared moose in sample at beginning of calendar year is listed in parentheses.

Non-Hunting Mortality			
Year	Bulls	Cows	Combined
2002	0% (7)	29% (17)	21% (24)
2003	27% (27)	23% (33)	24% (60)
2004	14% (23)	6% (35)	9% (59)
Total Mortality			
Year	Bulls	Cows	Combined
2002	14% (7)	29% (17)	25% (24)
2003	33% (27)	23% (33)	28% (60)
2004	35% (23)	6% (35)	17% (59)

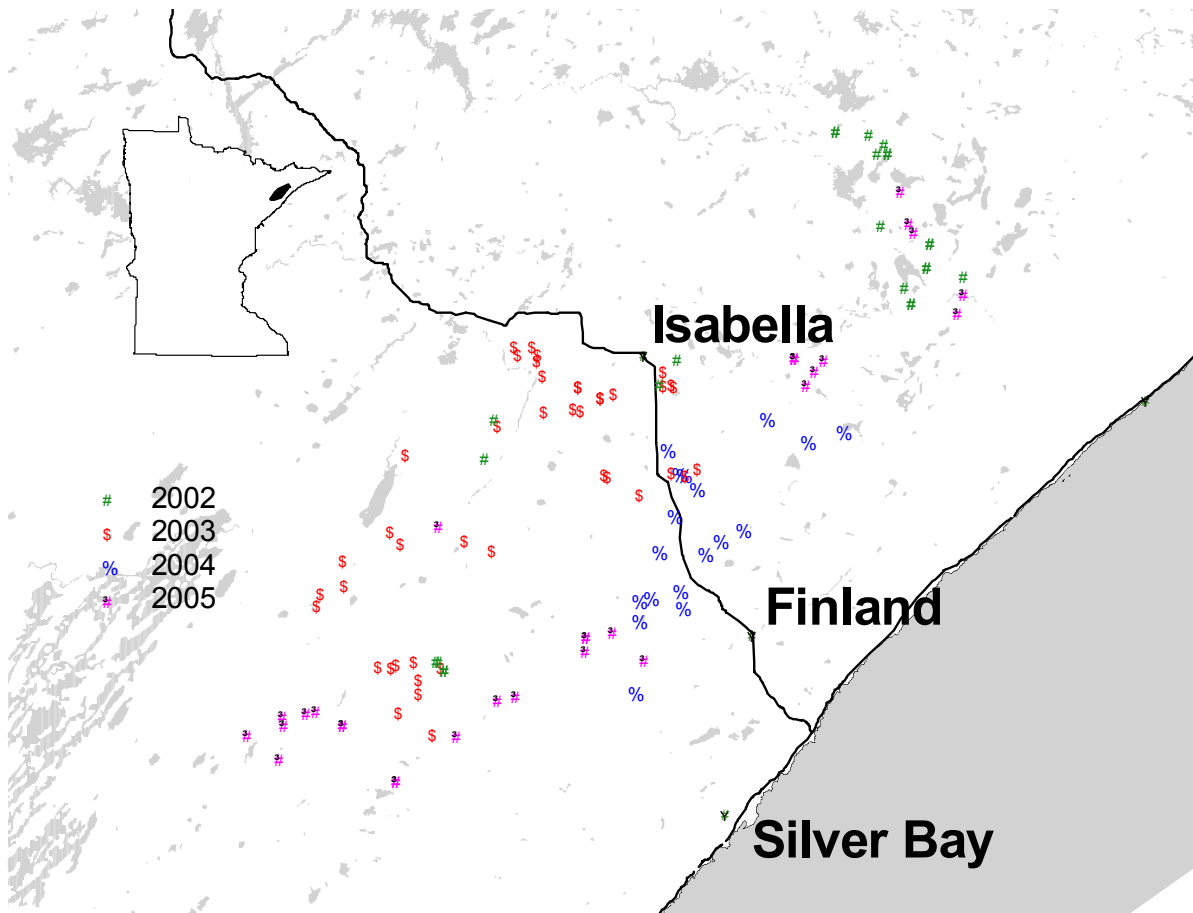


Figure 1. Capture locations of moose radio collared, 2002-2004.

CONDITION OF MOOSE (*ALCES ALCES*) IN NORTHEASTERN MINNESOTA

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Sampson

SUMMARY OF FINDINGS

During winters 2002–03, 2003–04, and 2004–05, body condition of 37, 17, and 26 free-ranging moose (*Alces alces*), respectively, was assessed by at least 1 of the following: (1) ultrasonic measurement of rump fat thickness, (2) Franzmann's condition classification (FCC), or (3) visual and palpation assessment of fat repletteness of the rump (BCS_r). Mean maximum rumps fat (Maxfat) thickness was 1.6 (SE = 0.16), 2.1 (SE = 0.38), and 2.2 (SE = 0.18) cm during these 3 winters, whereas mean ingesta-free body fat (IFBFAT) estimates were 8.9% (range = < 5.6–13.4%), 9.9% (range = 6.8–15.0%), and 10.1% (range = 6.5–14.2%). Maxfat and IFBFAT were less in bulls than in cows during winters 2003–04 and 2004–05. Mean FCC and BCS_r scores were 7.2 (scale of 10) and 3.4 (scale of 5), 7.3 and 3.8, and 6.5 and 3.2, respectively, during winters 2002–03 to 2004–05. Both scores tended to be lower in bulls than in cows during the first 2 winters, and were significantly ($P \leq 0.05$) lower during winter 2004–05. There were significant correlations between the FCC and BCS_r for all moose during all 3 winters ($r = 0.83, 0.75, \text{ and } 0.61; P \leq 0.002$). Additionally, Maxfat was correlated to FCC scores ($r = 0.56, 0.71, \text{ and } 0.56; P \leq 0.01$) and BCS_r scores ($r = 0.53, 0.68, 0.71; P \leq 0.02$).

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INTRODUCTION

A study of moose in northeastern Minnesota was begun in 2002, because aerial survey estimates suggested the population was stable despite a very conservative harvest (Lenarz et al., unpublished data). The study's goal is to generate data that will provide a clearer understanding of the ecological mechanism(s) underlying the population dynamics observed (Lenarz et al., unpublished data). One of the primary objectives was to "determine annual rates of non-hunting mortality..." for moose in this part of the state (Lenarz et al., unpublished data). Winter is the most nutritionally challenging season of the year for northern cervids, and nutrition has been shown to be a mechanistic link between environmental variation (e.g., winter tick [*Dermacentor albipictus*] infestation) and variation of moose populations (DelGiudice et al. 1997).

OBJECTIVES

- Assess winter condition of moose recruited into the study;
- Relate condition to winter severity; and
- Relate condition to sex and age.

METHODS

Logistical constraints and considerations associated with capture and handling of free-ranging moose during the study's first winter field season (2001–02) precluded condition assessments; however, such evaluations during capture operations of winter's 2002–03, 2003–04, and 2004–05 were feasible and successful.

During 26 February–2 March 2003, 9–11 February 2004, and 7–10 February 2005 adult (≥ 1.5 year old) moose were immobilized with a carfentanil-xylazine combination delivered by a dart rifle from a helicopter. Details of the capture/chemical immobilization procedure, as well as a description of the study area, are provided elsewhere (Lenarz et al., unpublished data).

Condition of moose was assessed by the following 3 methods: (1) ultrasonic measurements of rump fat thickness (Stephenson et al. 1998, 2002), (2) Franzmann's condition classification (FCC), developed specifically for moose (Franzmann 1977), and (3) the portion of a body condition scoring system developed for elk (*Cervus elaphus*), which concentrates on visual and palpation assessments of fat repletteness of the rump (BCS_r , Cook et al. 2001). We measured subcutaneous rump fat thickness (cm) with a portable ultrasound device (Sonovet 600 model, Universal Medical Systems, Inc., Bedford Hills, N.Y.1) and a 5-MHz 8-cm linear-array transducer. Measurements were made at the midway point ("Mid") between the tips of the iliums and the right or left tuber ischium (pin bone), and at the point of maximum fat thickness ("Maxfat"), which we located by scanning laterally along the sacral ridge towards the pin bone. Location of Maxfat was immediately anterior to the cranial process of the pin bone. Due to differences in body size of males and females, application of a scaling factor (0.83) to Maxfat measurements of males permitted comparison to adult females (Stephenson et al. 1998). The FCC and the BCS_r are described in Tables 1 and 2. Compared to the BCS_r , the FCC system includes a more complete assessment of the conformation of the moose's entire body related to condition. Captured moose were aged in the laboratory by counting of cementum annuli on the last incisor (extracted during capture). Age determinations of moose captured during

winter 2004–05 had not been made prior to the writing of this summary.

RESULTS AND DISCUSSION

By at least 1 of the 3 methods, we assessed the condition of 37 (19 females, 18 males) of the 42 adult moose captured and handled during winter 2002–03, 17 (12 females, 5 males) of 18 moose in winter 2003–04, and 26 (8 females, 18 males) of 30 moose in winter 2004–05. Overall, mean Maxfat was 1.6 (SE = 0.16, range = 0–3.8 cm), 2.1 cm (SE = 0.38, range = 0.58–4.6 cm), and 2.2 cm (SE = 0.18, range = 0.42–4.2 cm) during these 3 winters. In captive moose, Maxfat measurements have ranged between 0 and 7.0 cm, and were directly related ($Y = 5.61 + 2.05 x$, $r^2 = 0.96$, $P < 0.0001$) to ingesta-free body fat (IFBFAT) contents of approximately 2.5–17.5% (Stephenson et al. 1998). Applying the regression of Stephenson et al. (1998), Maxfat measurements of our free-ranging moose indicated an estimated mean IFBFAT of about 8.9% (range of < 5.6–13.4%), 9.9% (range = 6.8–15.0%), and 10.1% (6.5–14.2%) during winters 2002–03, 2003–04, and 2004–05, respectively. Studies of captive moose (and other cervids) have shown that at 5–5.6% IFBFAT, rump fat will be depleted (i.e., Maxfat = 0 cm). Maxfat and IFBFAT were less in bulls than in cows during all 3 winters with the difference significant ($P \leq 0.05$) in winter 2003–04 and 2004–05 (Table 3).

The mean FCC and BCS_r scores were 7.2 (range = 3–10, scale of 10) and 3.4 (range = 2–4.5, scale of 5) in winter 2002–03, 7.3 (range = 4–9) and 3.8 (range = 2.5–5.0) in winter 2003–04, and 6.5 (range = 4–8) and 3.2 (range = 2–4.5) in winter 2004–05. According to both of these scoring systems, although not significantly, mean condition scores were apparently lower for bulls than cows during winters 2002–03 and 2003–04 (Table 3). However, during winter 2004–05, the FCC and BCS_r scores were significantly lower ($P \leq 0.05$) in bulls than

¹ disclaimer

in cows (Table 3). There was no difference in age of moose between winters 2002–03 and 2003–04, and we observed no relation between moose condition, as assessed by FCC, BCS_r, Maxfat or estimated IFBFAT, and moose age during winters 2002–03 and 2003–04. There were significant correlations between the FCC and BCS_r scores for all moose during winters 2002–03 ($r = 0.83$, $P < 0.0001$), 2003–04 ($r = 0.75$, $P = 0.002$), and 2004–05 ($r = 0.61$, $P < 0.0001$). Additionally, during all 3 winters, Maxfat was significantly correlated to FCC scores ($r = 0.56, 0.71, \text{ and } 0.56$; $P \leq 0.01$) and BCS_r scores ($r = 0.53, 0.68, 0.71$; $P \leq 0.02$). The strength of the statistical relationship between the scoring systems and Maxfat measurements is inherently limited, because the scoring systems are characterized by discrete scores, whereas the Maxfat measurements are continuous. Consequently, a range of Maxfat measurements may be associated with a given condition score.

The late winter, mean Maxfat measurements (2002–03, 1.6 cm and 95% confidence limits [CL] = 1.3, 1.9 cm; 2003–04, 2.1 cm and 95% CL = 1.4, 2.9 cm; 2004–05, 2.2 cm and 95% CL = 1.8, 2.6) and associated estimated IFBFAT contents (roughly 9–10%) of our free-ranging moose indicate that most of them were in good condition, which was consistent with the unusually mild (2002–03) and moderate (2003–04 and 2004–05) weather conditions of these winters in northeastern Minnesota. It is noteworthy that snow depths were only 30–36 cm until mid-January 2004, but by early February when we conducted moose capture operations, snow depths were typically approaching 80 cm. Similarly, during early February 2005, snow depths were 74–91 cm; however, when assessing moose condition in late February–early March 2003, snow cover was only 23–33 cm. Clearly, the preponderance of bulls in the capture sample of 2005 lead to the overall increase in the animals assessed to be in fair-poor condition (46.2%) compared to moose assessed in 2003 and 2004

(24.3–25.0%, Table 4). Breeding bulls particularly are entering winter in poorer condition than females due to their diminished consumption of food during the fall rut (Schwartz and Renecker 1997).

The potential value of the condition assessments of the radiocollared moose may occur at the individual and population scales. They may provide insight relative to the survival or fate (i.e., cause of mortality) of each individual moose. There was a tendency for moose that died of non-hunting causes to be younger and exhibit lower winter condition scores than moose that survived; however, overall, we noted no significant differences. This may be attributable in part to a relatively small sample size of such mortalities.

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Table 1. Franzmann's condition classification for moose, used to assess winter condition of free-ranging adult moose during winters 2002–03 (19 females, 18 males), 2003–04 (11 females, 5 males), and 2004–05 (8 females, 18 males), northeastern Minnesota.

10	A prime, fat animal with thick, firm rump fat by sight. Well fleshed over back and loin. Shoulders round and full
9	A choice, fat moose with evidence of rump fat by feel. Fleshed over back and loin. Shoulders round and full.
8	A good, fat moose with slight evidence of rump fat by feel. Bony structures of back and loin not prominent. Shoulders well fleshed.
7	An average moose with no evidence of rump fat, but well fleshed. Bony structures of back and loin evident by feel. Shoulders with some angularity.
6	A moderately fleshed moose beginning to demonstrate one of the following conditions: (A) definition of neck from shoulders; (B) upper foreleg (humerous and musculature) distinct from chest; or (C) rib cage prominent.
5	A condition in which two of the characteristics listed in Class 6 are evident.
4	A condition in which three of the characteristics listed in Class 6 are evident.
3	A condition in which the hide fits loosely about neck and shoulders. Head is carried at a lower profile. Walking and running postures appear normal.
2	Signs of malnutrition are obvious. The outline of the scapula is evident. Head and neck are low and extended. The moose walks normally but trots and paces with difficulty, and cannot canter.
1	A point of no return. A generalized appearance of weakness. The moose walks with difficulty and can no longer trot, pace or canter.
0	Dead

Table 2. Body condition scoring system modified from Cook et al. (2001), used to assess the condition of free-ranging adult moose during winters 2002–03 (19 females, 18 males), 2003–04 (10 females, 4 males), and 2004–05 (8 females, 18 males), northeastern Minnesota.

5	Sacral ridge, ilium, ischium are virtually discernible.
4	Sacral ridge is discernible from ilium approximately midway to base of tail, Ischium and sacro-sciatic ligament are discernible.
3	Entire sacral ridge is discernible, but not prominent.
2	Sacral ridge is prominent to base of tail.
1	Sacral ridge, ilium, ischium, tuber coxae, and sacro-sciatic ligament (entire top of rump) are prominent.

Table 3. Mean (\pm SE) maximum rump fat (Maxfat) thickness measured by portable ultrasonography, and body condition scores (Franzmann's condition classification [FCC] and rump portion of body condition scoring system [BCS_r] modified from Cook et al. 2001) of free-ranging adult moose during winters 2002–03 (19 females, 18 males), 2003–04 (11 females, 5 males), and 2004–05 (8 females, 18 males), northeastern Minnesota.^a Range of values occurs in parentheses.

Sex	Maxfat (cm)		FCC		BCS _r	
	Mean	SE	Mean	SE	Mean	SE
Winter 2002–03						
Females	1.7 ^b	0.24	7.4	0.4	3.6	0.2
	(0.0–3.8)		(3.0–10.0)		(2.0–4.5)	
Males	1.5 ^b	0.20	7.0	0.3	3.2	0.1
	(0.3–2.6)		(4.0–9.0)		(2.0–4.3)	
Winter 2003–04						
Females	2.9 ^c	0.42	7.8	0.3	4.1 ^d	0.2
	(1.5–4.6)		(5.0–9.0)		(3.0–5.0)	
Males	1.1 ^c	0.38	6.2	0.8	3.1 ^d	0.3
	(0.6–2.6)		(4.0–8.0)		(2.5–4.0)	
Winter 2004–05						
Females	2.9	0.24	7.4	0.3	3.8	0.2
	(2.0–4.2)		(6.0–8.0)		(3.0–4.5)	
Males	1.8 ^e	0.18	6.1	0.3	2.9	0.1
	(0.4–2.8)		(4.0–7.5)		(2.0–3.5)	

^a Descriptions of the FCC and BCS_r systems are provided in Tables 1 and 2, respectively.

^b $n = 16$ for females and males due to temporary malfunctioning of portable ultrasound.

^c $n = 7$ and 5 for females and males, respectively, due to unavailability of portable ultrasound.

^d $n = 10$ and 4 for females and males, respectively; assessor did not have access to moose.

^e $n = 15$ due to unavailability of portable ultrasound.

Table 4. Qualitative condition assessment according to Franzmann's condition classification of free-ranging adult moose during winters 2002–03 (19 females, 18 males), 2003–04 (11 females, 5 males), and 2004–05 (8 females, 18 males), northeastern Minnesota.

Franzmann's Condition Score				
	≥ 8	$7 \leq x < 8$	< 7	Total
	(Very Good)	(Good)	(Fair-Poor)	
Winter 2002-03				
Number of moose	15	13	9	37
Percent of total	40.54	35.14	24.32	100
Winter 2003-04				
Number of moose	9	3	4	16
Percent of total	56.25	18.75	25.00	100
Winter 2004-05				
Number of moose	4	10	12	26
Percent of total	15.38	38.46	46.15	100

^aA description of Franzmann's condition classification is provided in Table 1.

PARASITE-MEDIATED DECLINE IN A MOOSE POPULATION AT THE SOUTHERN RANGE PERIPHERY

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Abstract: Several potential proximate causes may be implicated in a recent (1984-2001) decline in moose (*Alces alces andersoni*) numbers from their southern range periphery in northwest Minnesota, including increased: i) predation by wolves (*Canis lupus*) and black bears (*Ursus americanus*), ii) mortality from legal or illegal hunting, iii) malnutrition due to high intraspecific competition, iv) malnutrition from increased food competition with white-tailed deer (*Odocoileus virginianus*), v) deleterious effects of parasites and diseases, some of which are associated with deer, and vi) negative effects of climate change on survival and production. Ultimate causes potentially contributing to the moose decline include factors associated with marginal habitat (leading to malnutrition, immunosuppression, etc.). We examined survival among radiocollared ($n = 152$) adult cow and juvenile moose in 3 northwest Minnesota study areas during 1995–2000. We assessed cause of death and pathology through carcass necropsy of radioed animals, with additional necropsies being conducted on nonradioed animals collected opportunistically. Pregnancy and twinning rates were determined through radioimmunoassay of reproductive hormones in blood and feces, and calf observations post partum, respectively. Aerial moose surveys suggested that hunting was an unlikely source of the numerical decline because the level of harvest was relatively low (i.e., 3-25% per year) and the population usually grew in years following a hunt. The bull:cow and calf:cow ratios were markedly high throughout the population decline period but remained low following hunting cessation.

The majority of mortalities (62% of radioed moose [$n = 76$] 54% of non-radioed moose [$n = 94$]) are related to pathology associated with parasitism, infectious disease, and perhaps starvation, with few mortalities being associated with predation or poaching. Liver fluke infections, apparently the greatest single cause of death, were associated with pathology in the liver, thoracic and peritoneal cavities, pericardial sac, and lungs. Mortality due to meningeal worm (*Parelaphostrongylus tenuis*) appeared to be less prevalent. Bone marrow fat was lower for moose dying of natural causes than for those dying of anthropogenic factors or accidents, implying that acute malnutrition contributed to moose mortality. Blood profiles indicated that animals dying in the subsequent 18 months were chronically malnourished.

Average annual survival rates for adult cows (0.79 [0.74, 0.84; 95% CI]) and yearlings (0.64 [0.48, 0.86]) were low, whereas for calves (0.66 [0.53, 0.81]) survival rates were higher than in many other moose populations, with female calf survival rates being higher than for males. Moose exhibited low pregnancy (48%) and twinning (24%) rates, with reproductive senescence being observed as early as age 8 years among adult cows. Pregnancy status was related to indices of acute (bone marrow fat) and chronic (blood condition indices) malnutrition. Carcass recovery indicated that there likely were few prime-aged bulls (> 5 years old) in the population.

Analysis of protein content for the predominant browse species indicated that food quality was probably adequate to support moose over winter. Trace element analysis from necropsied moose livers revealed apparent deficiencies in copper and selenium concentrations, but there was limited association between trace elements and moose

¹ Deceased.

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disease, pathology, or mortality

Time series analysis of regional moose population censuses (1961–2000) suggested that annual growth rate in the surveyed population was negatively related to mean summer temperature, with winter and summer temperatures increasing by about 6.8°C and 2.1°C, respectively, during the 40-year period. This change may have contributed to increased moose thermoregulatory costs and disruption of energy balance. Population rate of change also was associated positively with population size, implying inverse density-dependence and the absence of resource limitation in the study population.

We concluded that the decline in moose numbers in northwest Minnesota likely was caused principally and proximally by fluke parasitism, with additional mortality and reduced productivity being related to infectious disease and poor nutritional status; these factors likely interacted synergistically. Climatic changes also may have contributed to the population decline, and when combined with recent increases in deer numbers and parasite transmission rates, may have rendered northwest Minnesota inhospitable to moose. Our results imply that the southern distribution of moose may become restricted in the future if the phenomena observed in northwest Minnesota are common elsewhere in the southern range.

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