

Wolf and bear predation on white-tailed deer fawns in northeastern Minnesota

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White-tailed deer (*Odocoileus virginianus*) fawn mortality was studied during the summers of 1989 and 1990 in northeastern Minnesota. Estimated pooled mortality rates for 21 radio-tagged fawns were 0.44 for the May–June, 0.13 for the July–October, and 0.51 for the May–October intervals. Predation accounted for all mortalities, with wolves (*Canis lupus*) responsible for 51% of them and black bears (*Ursus americanus*) for 49%. Fawns from mothers >4 years old weighed more and survived better than fawns from young mothers, which weighed less. Of various related factors (doe age, doe mass, fawn mass, fawn birth date, and fawn blood serum urea nitrogen (SUN)), only SUN was significant between surviving and perishing fawns; fawns with low SUN survived significantly less. Fawn SUN may have been only an indirect indicator of a doe physical or behavioral factor that was more important to fawn survival.

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La mortalité dans faons du Cerf à queue blanche (*Odocoileus virginianus*) été étudiée au cours des étés de 1989 et 1990 dans le nord-est du Minnesota. Les taux de mortalité compilés chez 21 faons porteurs d'un émetteur radio ont été évalués à 0,44 pour la période de mai–juin, à 0,13 pour la période juillet–octobre et à 0,51 pour la période totale mai–octobre. Tous les cas de mortalité ont dû être attribués à la prédation par le Loup gris (*Canis lupus*) (51%) et par l'Ours noir (*Ursus americanus*) (49%). Les faons nés de mères >4 ans étaient plus lourds et ils ont survécu mieux que les faons plus légers, nés de mères plus jeunes. Parmi toutes les variables associées aux faons (âge de la mère, masse de la mère, masse du faon, date de naissance du faon et azote sous forme d'urée dans le sang (SUN) chez le faon), seule cette dernière variable accusait une différence significative entre les faons victimes et les faons survivants; les faons à valeur de SUN faible ont survécu significativement moins bien. La variable SUN des faons peut n'être qu'un indice indirect d'une caractéristique physique ou comportementale de la mère plus critique pour la survie des faons.

[Traduit par la Rédaction]

Introduction

White-tailed deer numbers in northeastern Minnesota have fluctuated dramatically during the past 20 years (Nelson and Mech 1986b; M.E. Nelson and L.D. Mech, personal communication). Deer are the primary prey of wolves there, and many aspects of the interaction between these 2 species have been studied (Mech and Frenzel 1971; Mech and Karns 1977; Nelson and Mech 1981; Fuller 1989, 1990). However, no investigation has identified factors influencing wolf predation on deer neonates, and no study of black bear (*Ursus americanus*) predation on deer neonates has been conducted.

Predation on neonates has a significant effect on the recruitment and dynamics of many cervid populations by limiting potential rates of increase (Garner et al. 1978; Schlegel 1976; Ballard et al. 1981; Hamlin et al. 1984; Miller et al. 1988). Understanding factors affecting fawn mortality will further our knowledge of wolf–prey dynamics and increase our predictive capabilities in these systems.

The potential for predators to affect fawn survival in northern Minnesota is substantial. The wolf population there has increased from 1200 to 1500–1750 from 1979 to 1989 (Fuller

et al. 1992) and the density of black bears is 5–10 times that of wolves (Rogers 1987).

The objectives of this study were to determine (i) the causes, extent, and timing of fawn mortality, and (ii) whether the age and condition of the mother affects fawn vigor and survival.

Study area

This study was conducted in a 2000-km² region in the east-central Superior National Forest in northeastern Minnesota (48°N, 92°W) during 1989 and 1990. The area is located about 150 km south of the north-central edge of white-tailed deer distribution in North America and is characterized by gently rolling terrain ranging from 400 to 700 m in elevation. Climate is cool temperate (Hovde 1941), with weekly snow depths averaging 25–60 cm during 5 months beginning in mid-November. Forests of the region are mixed coniferous–deciduous (Nelson and Mech 1981).

Deer densities decline from the southwestern portion of the study area toward the northeast. Nelson (1990) estimated the 1987 summer density in the northern part of the range to be 5 deer/km² and projected a minimum density of 2 deer/km² in the southeastern part. Wolves inhabit the entire area at an estimated density of 28 wolves/1000 km² in 1989 and 24 wolves/1000 km² in 1990 (L.D. Mech, United States Fish and Wildlife Service, unpublished data); pack territory sizes range from 125 to 310 km² (Mech 1973, 1974). Black bears reach a density of approximately 159–244 bears/1000 km² (Rogers 1987). Moose (*Alces alces*) also inhabit the study area at a density of approximately 0.5–0.7 moose/km² (Minnesota Department of Natural Resources files) and provided alternative prey (especially calves in summer) for wolves.

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Methods

Fawns were captured in May and June during searches on foot, usually after movement patterns indicative of parturition were made by radio-collared adult does observed via daily aerial locations (Huegel et al. 1985b). Mothers of the radio-tagged fawns had been captured, weighed, and radio-tagged during winters preceding fawn capture (Nelson and Mech 1981). Captured fawns were handled for an average of 22 min each, and age was determined on the basis of new hoof growth measurements and texture, umbilicus condition, and behavioral characteristics (Haugen and Speake 1958) in combination with the timing of doe range constriction. The presence of afterbirth, wet hair, and twins bedded together indicated that fawns were <1 day old. Fawns were sexed, weighed, and ear-tagged and blood samples were taken. We collected blood in ethylenediamine tetraacetic acid vials and serum tubes by venipuncture of the jugular vein. Blood samples were stored in an ice cooler in the field and then placed in a refrigerator. Measurements were also made of hind-foot length, head length, neck circumference, and total length. Rectal temperatures and swabs were obtained. The general condition of each fawn was subjectively assessed on the basis of appearance and behavior. Fawns were fitted with a breakaway radio collar (Telonics Inc., 932 East Impala Avenue, Mesa, AZ 85204, U.S.A.) that doubled its signal rate after a 4-h period with no movement (indicative of mortality).

Radio-tagged fawns were checked for mortality signals 1–2 times daily from May through August, and less often (3–4 times/week) during September and October. When a mortality signal was received, the collar was located and the site and any fawn remains were examined to determine cause of death. Any carcasses located were necropsied by the senior author. Predation was considered to be the cause of death when blood, subcutaneous hemorrhaging at wound sites, and (or) signs of a struggle were found at the site. Evidence such as bear or wolf hair, tracks, scats and vomit, the presence of a buried carcass, and the percentage of carcass found was used to determine the species of predator responsible for death (O'Gara 1978). These data were incorporated into a key similar to that of Hatter (1984) to aid in ascertaining the type of predator involved.

Blood samples obtained from captured fawns were analyzed for hematological components and serum chemistry procedures and hormone assays were performed. Hematology methods are described by DelGiudice et al. (1990) and serum chemistry procedures and hormone assays by Seal et al. (1972a, 1972b, 1975, 1978). Levels of serum urea nitrogen (SUN), thyroxine, creatinine, cortisol, and triiodothyronine were compared among fawns.

Rectal swabs obtained from fawns were refrigerated until they could be cultured for enteric bacteria and analyzed by the University of Minnesota Veterinary Diagnostic Laboratory.

Data analysis

Birth mass of fawns was estimated by taking the average daily mass gain of northern white-tailed deer fawns (0.2 kg; Verme and Ullrey 1984), multiplying it by the estimated age of a fawn at capture, and subtracting that value from the mass of the fawn at capture (Haugen and Speake 1958). Fawn mothers were divided into 2 classes, those <4 years old (young) and those ≥ 4 years old (mature), on the basis of differences in fawn survival found by Ozoga et al. (1982) and Ozoga and Verme (1986).

Survival and cause-specific mortality rates were determined using the microcomputer program MICROMORT (Heisey and Fuller 1985). Initially, each month was considered as an interval with a constant daily survival rate. Daily survival rates for each interval were then compared and data from intervals pooled if the rates were not significantly different (Heisey and Fuller 1985). MICROMORT allows radio-tagged animals to be separated into classes so that comparisons of their respective survival rates can be made with Z tests (Heisey and Fuller 1985). Log likelihood ratio analysis was used to compare daily survival rates among months. All radio-tagged fawns were included in survival estimates.

Survival rates of fawns in the general deer population were also determined using fawn : radio-tagged doe ratios obtained during aerial surveys conducted each year in January. Fawn:doe ratios were adjusted to compensate for adult mortality during the same period by multiplying the number of fawns seen by the survival rates of radio-tagged does (Nelson and Mech 1986b). These fawn:doe ratios were compared with fecundity rates of road-killed does in and near the area and the difference was assumed to be a measure of fawn survival between parturition (June 1) and January. Sizes and configurations of summer wolf territories were estimated by the minimum home range method (Mohr 1947). Survival of fawns living outside versus anywhere inside wolf pack territories was tested by χ^2 analysis.

Simple linear regression analysis was used to determine the relationships between birth date and fawn mass and between doe mass and fawn mass. Differences between mean masses of old and young does and between dying and surviving fawns were determined by a *t* test. Comparisons of fawn-blood data were made by one-way analysis of covariance using fawn age as the covariate. We also compared fawn survival rate among the following variables, singly and together, by our Mann–Whitney Wilcoxon test: fawn mass, doe mass, doe age, fawn birth date, and fawn SUN. Statistical differences were considered significant when $P < 0.05$ unless otherwise indicated.

Results

Searches for fawns from 19 does in 1989 and 16 does in 1990 resulted in the capture of 23 fawns, of which 21 were radio-tagged, 8 in 1989 and 13 in 1990 (Table 1). The capture success rate was 0.53 fawns/doe in 1989 and 0.81 fawns/doe in 1990.

Mean estimated age at capture was 8.5 days in 1989 and 3.7 days in 1990 (range for both years, 1–13 days). Back-dating indicated that fawning occurred from 19 May through 10 June (median = 28 May). All fawns were judged to be in good health at capture on the basis of physical and behavioral characteristics. No doe abandoned any radio-tagged fawn.

Timing, causes, and extent of mortality

A total of 2145 radiolocation days of data was obtained from 21 radio-tagged fawns from 24 May to 21 October 1989 and 1990. Daily mortality rates were similar for all months except the 37-day May–June monthly interval, which was higher (G^2 test, $P = 0.008$). Therefore, 2 intervals were defined during which survival was assumed to be constant, May–June and July–October. The mortality rate for both summers combined was 0.44 (range = 0.19–0.57) for May–June, which was higher ($P = 0.03$) than the 0.13 rate (range = 0.12–0.13) for July–October. The overall mortality rate (May–October) was 0.51.

Two of 8 radio-tagged fawns died in 1989 and 7 of 13 died in 1990; predation accounted for all deaths. Seven of the deaths (78%) occurred before 28 June. The cause-specific mortality rates for the May–June interval (1989 and 1990 pooled) were 25% attributable to bears and 19% to wolves and for the July–October interval were 0% and 13%, respectively (Table 2). Overall, wolves caused 51% of fawn mortalities and black bears 49%.

During the aerial fawn:doe survey in January 1990, 16 fawns were found with 14 radio-tagged does, which, when adjusted for doe mortality, gave a fawn:doe ratio of 101:100. Fourteen fawns were found with 15 radio-tagged does in January 1991, yielding an adjusted fawn:doe ratio of 82:100. Using these estimates, the June–January survival rates, based on a fecundity rate of 160 fetuses : 100 does from our road-killed deer sample, were 0.63 and 0.51 for 1989 and 1990, respectively, with a mean of 0.57. The June–October survival

TABLE 1. Characteristics and fate of 23 fawns captured in northeastern Minnesota in 1989 and 1990 and characteristics of their mothers at capture

Fawns									Does			
Number	Sex	Mass at capture (kg)	Date of capture	Estimated birth date	Estimated birth mass (kg)	SUN (mg/dL)	Survival (days)	Fate	Number	Date of capture	Mass at capture (kg)	Age at capture (years)
176	M	3.6	89-05-28	05-28	3.6	28.2	156	Survived	7278	89-03	54	6+
178	M	3.8	89-05-28	05-28	3.8	—	Not radio-tagged		7278	89-03	54	6+
180	F	3.7	89-05-29	05-23	2.7	19.1	155	Survived	7286	89-03	53	1+
182	M	4.4	89-05-29	05-20	2.5	—	Not radio-tagged		7096	89-03	77	3+
184	F	4.8	89-05-30	05-22	3.6	—	154	Survived	7266	89-03	63	10+
186	F	4.0	89-06-08	05-31	2.7	9.5	3	Bear	7282	89-04	48	1+
188	M	4.8	89-06-08	05-25	2.0	17.8	145	Survived	Unknown			
190	M	6.9	89-06-09	05-30	4.8	16.3	144	Survived	6728	89-04	62	4+
192	F	6.3	89-06-10	05-28	4.4	—	133	Wolf	6992	87-03	66	5+
162	M	5.7	89-06-12	06-03	3.9	9.2	141	Survived	7258	89-03	54	2+
226	M	4.2	90-05-24	05-19	3.1	13.9	160	Survived	6876	86-03	59	1+
228	M	3.9	90-05-27	05-23	3.0	10.6	12	Wolf	7282	89-04	48	1+
230	M	4.0	90-05-27	05-23	3.1	6.1	6	Bear	7282	89-04	48	1+
232	M	3.4	90-05-28	05-28	3.4	—	145	Wolf	6706	89-03	56	6+
234	F	3.3	90-05-28	05-28	3.3	—	4	Wolf	6706	89-03	56	6+
238	M	3.7	90-05-30	05-30	3.7	—	154	Survived	6884	86-04	49	1+
240	F	3.5	90-05-30	05-30	3.5	—	7	Bear	6884	86-04	49	1+
242	M	3.4	90-06-01	05-25	2.2	—	13	Bear	7286	89-03	53	1+
244	F	—	90-06-01	05-22	—	21.2	152	Survived	7258	89-03	54	2+
248	M	3.8	90-06-03	06-03	3.8	—	150	Survived	7020	88-02	65	4+
250	M	4.3	90-06-03	06-03	4.3	—	25	Wolf	7020	88-02	65	4+
252	F	4.2	90-06-10	06-10	4.2	24.4	143	Survived	7346	90-04	68	4+
254	M	4.1	90-06-10	06-10	4.1	26.6	143	Survived	7346	90-04	68	4+

NOTE: SUN, serum urea nitrogen.

TABLE 2. Survival and cause-specific mortality rates of 21 radio-tagged fawns captured in northeastern Minnesota for May–October 1989 and 1990

	Year	May–June				July–October				May–October	
		Rate	95% CI	<i>n</i> ^a	<i>n</i> ^b	Rate	95% CI	<i>n</i> ^a	<i>n</i> ^b	Rate	95% CI
Survival	1989	0.81*	0.54–1.00	180		0.87	0.65–1.00	851		0.70	0.43–1.00
Mortality											
Bear		0.19	0.00–0.52		1	0.00	0.00–0.00		0	0.19	0.00–0.51
Wolf		0.00	0.00–0.00		0	0.13	0.00–0.38		1	0.11	0.00–0.31
Survival	1990	0.43**	0.21–0.84	264		0.88	0.69–1.00	972		0.38	0.18–0.78
Mortality											
Bear		0.29	0.02–0.56		3	0.00	0.00–0.00		0	0.29	0.02–0.56
Wolf		0.29	0.02–0.56		3	0.12	0.00–0.34		1	0.34	0.07–0.61
Survival	1989–1990	0.56 [†]	0.36–0.86	444		0.87 ^{††}	0.72–1.00	1823		0.49	0.30–0.78
Mortality											
Bear		0.25	0.04–0.47			0.00	0.00–0.00			0.25	0.04–0.47
Wolf		0.19	0.00–0.38			0.13	0.00–0.29			0.26	0.06–0.46

NOTE: Rates followed by 2 superscript symbols are significantly different ($P < 0.10$) from rates with only 1 similar superscript.^aNumber of transmitter-days^bNumber of deaths.

rate estimated from radio-tagged fawns was 0.49 (95% CI = 0.30–0.78). Although the estimates from the aerial surveys fall within the 95% confidence intervals of the telemetry estimates, any fawn mortality occurring during November and December (e.g., 6–15%/month; Nelson and Mech 1986a) would make these point estimates even more different.

Factors affecting predation

Predation on fawns was related to fawn mass and SUN level, age and mass of doe in winter, and possibly the location

of doe and fawn relative to wolf pack territory edges. Estimated fawn birth masses ($\bar{x} = 3.5$ kg; range = 2.0–4.8) did not differ ($P = 0.77$) by year or sex. However, a significant positive linear correlation was apparent between fawn birth date and fawn birth mass ($r = 0.61$, $P = 0.002$; Fig. 1), with late-born fawns weighing more. Survival rates of male and female fawns did not differ significantly during the May–June interval ($P = 0.58$), the July–October interval, or overall (Table 3). Both bears and wolves killed fawns of both sexes.

TABLE 3. Survival rates for May–October 1989 and 1990 of 21 radio-tagged fawns captured in northeastern Minnesota classed by sex, mass, and doe age

Class	May–June			July–October			May–October	
	Rate	95% CI	<i>n</i> ^a	Rate	95% CI	<i>n</i> ^a	Rate	95% CI
Male	0.61	0.37–0.99	298	0.90	0.74–1.00	1218	0.55	0.32–0.93
Female	0.46	0.19–1.00	146	0.82	0.55–1.00	605	0.38	0.15–0.98
<3.6 kg	0.26	0.09–0.75	169	0.77	0.47–1.00	480	0.20	0.06–0.66
≥3.6 kg	0.86*	0.64–1.00	246	0.90	0.74–1.00	1220	0.78	0.54–1.00
Doe <4 years	0.17	0.03–0.93	85	1.00	1.00–1.00	236	0.17	0.03–0.97
Doe ≥4 years	0.73 [†]	0.52–1.00	359	0.86	0.69–1.00	1587	0.63	0.42–0.95

^aNumber of transmitter-days.

*Significant difference ($P = 0.002$) between mass classes for the May–June interval.

[†]Significant difference ($P = 0.005$) between doe age classes for the May–June interval.

TABLE 4. Mean (\pm SE) concentrations of serum components for white-tailed deer fawns captured in northeastern Minnesota in 1989 and 1990

	No. of fawns	Serum urea nitrogen (mg/dL)	Creatinine (mg/dL)	T ₄ (μ g/dL)	T ₃ (mg/dL)
1989	9	17.8 (6.1)	0.88 (0.17)	17.8 (4.7)	361 (61)
1990	6	17.1 (8.2)	1.56 (0.33)	23.2 (9.7)	317 (50)
Killed	3	8.8 (2.4)	0.70 (0.03)	13.7 (4.6)	360 (50)
Survived	9	19.6* (6.2)	1.41 [†] (0.80)	20.4 (9.4)	326 (64)
Young mothers	5	10.9 (4.8)	0.70 (0.10)	13.1 (5.4)	370 (63)
Mature mothers	6	21.8 [‡] (5.7)	1.70 [§] (0.70)	24.1 (8.8)	311 (57)

*Significant difference ($P = 0.006$) in serum urea nitrogen level between killed and surviving fawns.

[†]Significant difference ($P = 0.07$) in creatinine level between killed and surviving fawns.

[‡]Significant difference ($P = 0.06$) in serum urea nitrogen level between young and mature mothers.

[§]Significant difference ($P = 0.02$) in creatinine level between young and mature mothers.

^{||}Significant difference ($P = 0.02$) in T₄ level between young and mature mothers.

A majority (78%) of the fawns that died weighed <3.6 kg at birth and a majority of those that survived (73%) weighed more than this. The survival rate of fawns <3.6 kg (0.26) was significantly less ($P = 0.002$) than that of fawns \geq 3.6 kg (0.86) during the May–June interval, indicating a possible threshold mass for survival (Table 3). The mean birth mass of fawns killed by predators (3.3 kg, SE = 0.2) did not, however, differ significantly ($P = 0.43$) from that of survivors (3.6 kg, SE = 0.2). The small sample may have prevented the detection of significance.

The ages of 22 fawn mothers ranged from 2 to 11 years (median = 4). For May–June, the survival rate of fawns born to mature mothers was significantly greater ($P = 0.005$) than that of fawns from young mothers (0.73 vs. 0.17; Table 3). This was likely related to the fact that older does weighed more (62 vs. 52 kg; $P = 0.001$; Mech and McRoberts 1990b) and had heavier fawns ($r = 0.70$, $P = 0.03$).

Fawn SUN values (adjusted for age, 1989 and 1990 pooled) were lower ($P = 0.006$) in fawns killed by predators than in surviving fawns (Table 4), and SUN was the only significant variable ($P = 0.03$) in our Mann–Whitney Wilcoxon multiple-variable test. Thyroxine (T₄) and creatinine levels also tended to be lower in predator-killed fawns (Table 4), which also did not differ significantly in mass ($P = 0.33$). Fawns from young does had significantly lower T₄, SUN, and creatinine values than fawns from mature does (Table 4).

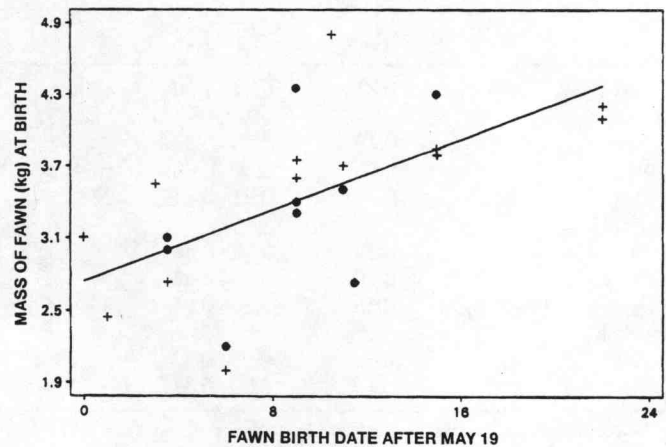


FIG. 1. Relationship between estimated birth date (x) and fawn mass (y) for 22 radio-tagged fawns in northeastern Minnesota in 1989 and 1990 ($y = 2.740 + 0.075x$; $r = 0.61$, $P = 0.002$). Dots represent fawns killed by bears or wolves.

Femur marrow-fat samples were obtained from 3 fawns (all killed by bears). The marrow from fawn 242 was red and gelatinous indicating a low fat percentage, but there was much fat around the kidney (kidney fat index = 21.2; Riney 1955). Fawn 230 had low levels of marrow fat (24%) but also had much fat around the kidneys and throughout the body. The

marrow-fat level in fawn 240 was 3%. The fat content in other areas of fawn 240 could not be determined, as very few other remains were found. Low femur marrow fat accompanied by high fat elsewhere is contrary to the situation in older deer (Harris 1945). The significance of this finding is unknown.

Bacteria were isolated on anal swabs from 12 of 22 captured fawns. None of the isolated bacteria were considered to be detrimental to the fawns, but were likely normal flora (M.E. Bergeland, University of Minnesota Veterinary Diagnostic Laboratory, personal communication). No external parasite was found on any fawn.

Ten of the 12 radio-tagged does (and their fawns) being studied for fawn-capture purposes, which were also in an area where we had data from radio-tagged wolf packs, had summer home ranges outside, or <1.0 km inside, summer wolf pack territories. This finding was not the result of a bias in the locations where we searched for fawns, because we used does that had been radio-tagged in winter yards many kilometres from their fawning ranges. Four of the 8 fawns living inside wolf territories were killed by wolves, whereas only 1 of the 6 fawns living outside wolf territories was killed by wolves ($\chi^2 = 1.7$, 1 df, $P = 0.20$).

Discussion

Causes of mortality

No other radiotelemetry study of white-tailed deer neonate mortality has been conducted where wolves are present, but other studies have found that coyotes (*Canis latrans*) have killed 9–52% of marked white-tailed and mule deer (*Odocoileus hemionus*) fawns (prewinter) in the midwestern and western U.S.A. (Cook et al. 1971; Garner et al. 1978; Steigers and Flinders 1980; Trainer et al. 1981; Smith 1983; Hamlin et al. 1984; Huegel et al. 1985a; Gerlach 1986; Nelson and Woolf 1987).

Overall, from 24 May to 31 October, wolves killed 26% (95% CI = 6–46%) of our fawns. In north-central Minnesota, Fuller (1990) indicated that wolves were only a minor source of neonate mortality (<10% of all fawns) and that other predators such as dogs, coyotes, black bears, and bobcats (*Felis rufus*) were probably as important. He based this conclusion on scat analysis, a method which, in our study, underestimated the mortality rate of radio-tagged fawns attributable to wolves by 83% (0.11 vs. 0.63 fawns/km² killed) (Kunkel 1992). On the other hand, the lower population of dogs and coyotes and the lower deer:wolf ratio in our study area compared with north-central Minnesota (35:1 vs. 140:1) (Fuller 1990) probably also accounted for higher wolf predation rates in our study area. The impact of wolves on deer in our study area may be magnified by the abundance of moose (0.5–0.7/km², Minnesota Department of Natural Resources files), which may serve as an alternative food source, and thus may help maintain the wolf population at a higher density than would deer alone.

Numerous studies during the past 15 years in Canada and Alaska have concluded that wolves are important predators of newborn ungulates (Gasaway et al. 1983; Keith 1983; Bergerud 1983 but cf. Van Ballenberghe 1985 and Bergerud and Ballard 1988; Messier and Crete 1985; Bergerud and Elliot 1986; Miller et al. 1988). Wolves were responsible for the mortality of 2–31% of neonates in studies in Canada and Alaska (Franzmann et al. 1980; Ballard et al. 1981; Hatter

1984; Page 1985; Whitten et al. 1992; Larsen et al. 1989). In these studies, >90% of mortalities occurred before November.

Black bears can be an important source of ungulate-neonate mortality. The bear population density in our study area (159–243/1000 km²; Rogers 1987) was similar to the densities of two black bear populations from the Kenai Peninsula, Alaska (171–223/1000 km²; Schwartz and Franzmann 1991), where black bears killed 34% of marked moose calves (Franzmann et al. 1980). Moose calves were available in our study area, which may have reduced bear predation on fawns to the 25% we observed. Elsewhere, black bears killed 3–47% of marked neonates (Schlegel 1976; Ozoga and Verme 1982; Smith 1983; Hatter 1984; Mathews and Porter 1988; Larsen et al. 1989).

Extent of mortality

Our mortality rates might be considered conservative, because 57% of our fawns were captured several days after birth. Ozoga and Clute (1988) found that many unmarked fawns died when <2 days old, which precluded their being found and tagged. As a result, Ozoga and Clute (1988) believed they had captured the healthiest individuals and had underestimated neonatal mortality. Because our mean capture age was 5 days, we may have missed some early mortality. However, we believe that this bias was insignificant, because captured fawns <1 day old (43% of our total) all survived to the average age of capture. Wolf scats analyzed during this study (Kunkel 1992) indicated that relatively few fawns were killed in May. None of our radio-tagged fawns died before June 1.

In dense vegetation, fawns are seemingly less vulnerable during their first month (Carroll and Brown 1977; Dood 1978; Bryan 1980; Giessman and Dalton 1981, 1982; Huegel et al. 1985a; Nelson and Woolf 1987). Mortality in these studies increased as the fawns aged and became more active. Nelson and Woolf (1987) suggested that fawns were most vulnerable during a transition period that occurred after the safe "hiding phase" and before they were too swift to be captured by coyotes (>8 weeks old).

Timing of mortality in our study did not follow the general trend of other studies with similar vegetation characteristics. Except for the 2 mortalities in October, all our fawns were <30 days old when they were killed. Even with relatively dense vegetation, predation by bears and wolves was intense during our fawn "hiding phase." Probably fawn vulnerability varies with varying conditions.

Bears did not appear to actively hunt fawns in our study area. Rather, they detected bedded fawns up to 10 m away incidentally while feeding upon insects and vegetation, and then rushed them (L. Rogers, United States Forest Service (USFS), personal communication). In most studies where black bears are present, predation by bears is limited to neonates <45 days old (Franzmann et al. 1980; Ballard et al. 1981; Ozoga and Verme 1982; Smith 1983; Mathews and Porter 1988). After this time moose calves and deer fawns can apparently outrun bears. No fawn >20 days old was killed by bears in our study, nor was any bear observed killing fawns after June in our study area (L. Rogers, USFS, personal communication).

Factors affecting predation

Fawn mass and nutritional status

Mean birth mass of our fawns (3.5 kg) was the same as that reported for captive fawns from does on a high nutritional

diet in Michigan (Verme 1963) and greater than the predicted birth mass of fawns born after a mild winter in upper Michigan (3.2 kg) (Verme 1977). Fawn birth masses in our study were typical of the northern subspecies of white-tailed deer (3.4 kg) (Haugen and Davenport 1950).

Verme (1962) reported that the lower the birth mass of captive deer fawns, the higher the mortality rate. While this relationship has generally been acknowledged, few studies of free-ranging ungulates have substantiated the finding. Furthermore, few studies have compared body masses of neonates that survive with those of neonates killed by predators, to determine whether neonates lost to predators would have perished from other causes (Boutin 1992). Nelson and Woolf (1987) reported that predator-killed fawns tended to be light to average in mass near birth and were not the heaviest fawns in the cohort. Guinness et al. (1987) and Clutton-Brock and Albon (1989) found that light red deer (*Cervus elaphus*) calves were more likely to die than heavier calves in their predator-free study area. Adams et al. (1994) showed that in caribou (*Rangifer tarandus*), neonate losses to wolves were inversely correlated with average birth mass. Lighter mass fawns in our study also had a lower survival rate than heavier fawns.

Guinness et al. (1978) suggested that the reason summer mortality may be related to birth mass is that mass may affect the fawn's vulnerability to predators. Heavier fawns are more healthy and vigorous (Verme 1962) and may be able to escape predation more readily. This factor becomes more important as fawns age and spend less time hiding. Even in their first week of life, however, greater vigor may be important in escape if they are detected. Verme and Ullrey (1984) suggested that a difference of even a few ounces in natal mass may be crucial to survival. Wolves and bears can no doubt capture and kill even the strongest newborn fawns under the right conditions but our results indicate that generally they end up with the lighter, and presumably weaker, fawns. Fawns killed by predators in our study were lighter than surviving fawns but, probably because of our small sample, not significantly so by the *t* test. Nevertheless, fawns <3.6 kg suffered a significantly higher incidence of mortality than heavier fawns.

On the predator-free Isle of Rhum, offspring of young mother red deer suffer increased summer mortality (Guinness et al. 1978). In a large enclosure, white-tailed deer fawns from older mothers sustained lower mortality rates, particularly when threatened by predation (Ozoga and Verme 1986).

In our study area, the fawn:doe ratio for older does was significantly higher than for younger does in both December and April (Mech and McRoberts 1990a). One explanation for the lower rates of mortality found in fawns of older does was that older does are heavier and produce heavier fawns that survive better, which our results support. Clutton-Brock et al. (1982) reported that 50% of the variation in summer mortality among calves born to mothers of different ages was attributable to differences in birth mass with maternal age. While our sample size was too small for this type of analysis, doe and fawn mass did appear to explain more of the variation in fawn survival than did doe age.

Maternal mass strongly influences birth mass in many mammals (Sadleir 1969), and our results and those of Mitchel et al. (1976), Blaxter and Hamilton (1980), and Clutton-Brock et al. (1982) confirm this for ungulates.

Guinness et al. (1978) believed that red deer calf mass was a more likely determinant of survival than was maternal experience, because they found no significant difference in summer mortality in calves of first breeders compared with those of parous 4–6 year olds, and they also found increased mortality among calves from old hinds. Additionally, Clutton-Brock and Guinness (1975) learned that several aspects of maternal behavior were similar between first breeders and experienced mothers. They believed it would be inefficient if behavioral changes that help protect young from predators depended on breeding experience. Maternal care in other ungulates improves with successive parturitions, however, (Zarrow et al. 1962) and younger mothers may exhibit behavior detrimental to their young (Alexander 1960). Unlike Clutton-Brock and Guinness (1975), Ozoga and Verme (1986) described significantly better maternal behavior in mature does. They concluded that a doe's fawn-rearing skills, including bedsite-habitat selection, movements, social and (or) spatial relationships, and predator evasion tactics, improve with age. Older does were especially more successful in the presence of predators. Ozoga and Verme (1986) did not, however, examine the effect of doe mass on fawn mass and survival, so possibly the fawns in their study from older does survived better partly as a result of greater mass.

Because heavy predation pressure does not occur on Rhum, age differences in maternal antipredator behavior may not have been readily apparent to Guinness et al. (1978). Unlike red deer, productivity of white-tailed deer >10 years old does not seem to decline in our study area (Nelson and Mech 1990). In the presence of significant predation like that in our study area, both maternal experience and mass may contribute to survival.

Mass generally is a reliable indicator of condition. High correlations have been found between live mass and quantities of gross energy, water, crude protein, and fat (Robbins et al. 1974; Huot 1982; McCullough and Ullrey 1983; Watkins et al. 1991). However, reliance on mass alone to predict body composition can yield spurious results (Watkins et al. 1991), so it should be used with other condition indicators. We also examined marrow-fat and blood characteristics.

SUN has been the most thoroughly tested and consistent serum indicator of nutritional condition in white-tailed deer (DelGiudice et al. 1987, 1990). SUN level appears to be closely related to the protein content of a diet, and thus can be used to discriminate between deer on low- and high-protein diets and to assess condition over time. The low SUN values in our predator-killed fawns may have indicated a dietary protein deficit in these animals. SUN was not significantly related to mass in our fawns ($r^2 = 0.10$; $P = 0.34$).

Few serum chemistry values have been reported for newborn fawns. Tumbleson et al. (1970) found that the mean SUN value for captive fawns 1–2 weeks old was 20 mg/dL (range = 19–21 mg/dL). Fawns <2 weeks old in southern Illinois had a mean SUN value of 11.8 mg/dL (range = 3–27 mg/dL; Nelson 1984). Fawns from both of these studies were considered to be in good condition based on appearance and behavior. The former value is similar to our SUN values from surviving fawns (range = 9.2–28.2 mg/dL; $\bar{x} = 19.6$ mg/dL). In our study, fawns killed by predators had lower SUN values (range = 6.1–10.6 mg/dL; $\bar{x} = 8.8$ mg/dL).

Spatial relationships of deer and wolf ranges

Deer survival can be related to the spatial relationship between deer and wolf home ranges (Hoskinson and Mech

1976; Mech 1977; Rogers et al. 1980; Nelson and Mech 1981). Our findings on fawn survival were suggestive of such a relationship but were not statistically significant. Hatter (1984) found that black-tailed deer fawn survival was relatively high in 1980, when most fawns were located either outside or on the edge of wolf territories where wolf scat transects indicated little wolf activity. In 1981, 4 or 5 of the fawns in Hatter's study located within the "50% wolf location boundary" were killed by wolves; 2 or 3 fawns located just outside the "50% boundary" were also killed by wolves.

Conclusions

Because of our small sample and the high degree of relatedness among the variables we measured, it is difficult to sort out the roles of the above factors in fawn vulnerability; however, some patterns are apparent. Mass appears to be the primary factor affecting fawn vulnerability to bears, since all the fawns killed by bears were below the mean birth mass (3 of 4 of these were from young mothers). This fits with the pattern we observed of older and heavier fawns being able to escape bear predation (no fawns were killed by bears after June). Mass appeared less important than home range location in fawn vulnerability to wolves. Two of 5 fawns killed by wolves were above the mean birth mass, but only one fawn living outside wolf territories was killed by wolves.

When fawn mass, doe mass, doe age, fawn birth date, and fawn SUN level were tested together and singly in a multiple-factor test, only fawn SUN level was significant. This may indicate that although the other variables we examined are related to fawn SUN, it is SUN itself that is the most basic factor in determining which fawns survive. Because SUN level is an important nutritional indicator (DelGiudice et al. 1987, 1990, 1994), this finding might seem reasonable. However, it is hard to understand how nutritional condition could make much difference in whether fawns sufficiently young to hide rather than run from predators are killed. Thus, it is possible that the link between young, and thus inexperienced, does and low SUN levels in their fawns might be important in terms of where the does choose to keep their fawns (Ozoga and Verme 1986) or to some other behavioral trait of the doe or fawn. Our fawn sample, then, may not have been large enough to truly distinguish among all these factors despite the statistical significance of SUN levels.

Management implications

We agree with Ozoga and Verme (1986) that maximum fawn-rearing success is attained when mature does predominate in the breeding population. Management of harvest to produce such an age structure may be an important strategy where predation on neonates markedly reduces deer recruitment, particularly in areas where other options (e.g., predator control) are limited and predators and hunters compete significantly.

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