


10-1986

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Nelson, Michael E. and Mech, L. David, "MORTALITY OF WHITE-TAILED DEER IN NORTHEASTERN MINNESOTA" (1986). *USGS Northern Prairie Wildlife Research Center*. 339.
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MORTALITY OF WHITE-TAILED DEER IN NORTHEASTERN MINNESOTA

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Abstract: Two hundred nine white-tailed deer (*Odocoileus virginianus*) were radiotracked in the central Superior National Forest, Minnesota, from 1973 through winter 1983-84; 85 deaths were recorded. Annual survival was 0.31 for fawns (<1.0 years old), 0.80 for yearling (1.0-2.0 years old) females, 0.41 for yearling males, 0.79 for adult (≥ 2.0 years old) females, and 0.47 for adult males. Monthly survival rates were high from May through December (0.94-1.00), except for yearling (0.60) and adult (0.69) bucks during the November hunting season. Most mortality occurred from January through April when gray wolf (*Canis lupus*) predation was an important mortality source for all cohorts. Yearling males were most vulnerable to hunting and adult males to wolf predation.

J. WILDL. MANAGE. 50(4):691-698

Understanding population dynamics of white-tailed deer depends on the accurate measurement of survival and mortality. However, measuring mortality and its magnitude is difficult. Halls (1984:785) recently concluded that "non-hunting mortality may be the most significant unknown parameter in population modeling and monitoring" of this species. Overexploitation of intensively hunted populations is a possibility without adequate survival and cause-specific mortality data.

Radio telemetry has been used to directly measure survival and detect sources of mortality for whitetails (Logan 1973, Nelson and Mech 1981). However, such data are subject to biases associated with capture periods, representative sampling, and seasonal variation in survival. Heisey and Fuller (1985) addressed such problems and presented new statistical procedures for working with them. We use Heisey and Fuller's (1985) techniques to analyze 10 years of data on survival and cause-specific mortality rates of white-tailed deer that are harvested by man and preyed upon extensively by wolves.

This study was supported by the U.S. Fish and Wildl. Serv., the U.S. For. Serv., North Central For. Exp. Stn., the Mardag Found., and the Minn. Dep. Nat. Resour. We thank J. J. Renneberg, S. T. Knick, R. K. Field, and J. W. Burch for field assistance. P. D. Karns provided data on road-killed does. T. K. Fuller advised

us on data analyses and critiqued an early draft of the manuscript.

STUDY AREA

This study was conducted in a 2,500-km² area in the eastcentral Superior National Forest of northeastern Minnesota (48°N, 92°W). The area is near the northeastern limit of deer range and is cool temperate, with annual snowfall averaging >1.0 m from mid-November through mid-April. Forests of the region are mixed coniferous-deciduous (Nelson and Mech 1981). The deer population varied from 0.2 to 0.4 deer/km² during the study (Floyd et al. 1979, Nelson and Mech 1986).

Wolf predation and firearm hunting are major sources of mortality for deer (Hoskinson and Mech 1976, Nelson and Mech 1981). The firearm season spans the 1st half of November and has been limited to bucks-only hunting since 1974. An archery season for either sex occurs from September through October.

METHODS

Deer were captured on winter ranges from January 1973 through April 1984, primarily by rocket net and clover traps. Most were drug immobilized (Seal et al. 1970), weighed, aged via incisor sectioning (Gilbert 1966), blood sampled (Seal et al. 1978), and radiotagged. Trapping was conducted by a 2-4 person crew working 4-5 days/week. Deer were radiolocated from ground and air 1-3 times/week throughout the year. Deer were examined for cause of mortality as close to death as possible (generally $\leq 1-3$ days). Predation was considered the cause of death when there was evi-

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dence of blood and a struggle. When there were no carcass remains and/or no definite evidence of any other specific mortality cause, wolf predation was considered to be the probable cause of death because all such carcasses were 90–100% consumed, and carcasses resulting from disease or malnutrition were rare. Deer dying ≤ 12 days after capture were excluded from analyses because capture myopathy can occur up to 12 days after capture (Harthoorn 1977).

For a basis to examine annual survival rate, we developed a model of annual survival that starts at 1 June when the deer population is at or near its maximum size. To enhance the model's efficiency (Heisey and Fuller 1985), we partitioned the year into 5 periods: June–October; November; December; January–April; and May. June–October is snow free, and deer occupy summer ranges. The breeding and firearm hunting seasons occur in November, and December involves migration to winter range and transition into winter. January–April are the cold and deep-snow months of winter range use, and May is a transition into summer when deer occupy summer ranges and cohort sizes are minimal.

We also computed monthly survival and mortality rates to examine variation in survival within the year. Monthly intervals were considered most desirable and necessary to minimize biases from combining time periods with different rates.

Monthly and annual survival and cause-specific mortality rates were calculated for fawns, yearling females, yearling males, adult females, and adult males using the microcomputer program MICROMORT (Heisey and Fuller 1985). MICROMORT calculates annual (S^*) and monthly (S_i) survival from a daily survival rate, s_i , which is the probability of an animal surviving 1 day. The estimate of s_i is:

$$\frac{x_i - y_i}{x_i}$$

where i is the period being used, x_i is the total number of transmitter days, and y_i is the total number of deaths during the period (Trent and Rongstad 1974, Heisey and Fuller 1985). Daily survival, s_i , is expanded to desired intervals; i.e., weekly, monthly, etc. In addition, MICROMORT computes annual (M_j^*) and monthly (M_{ij}) cause-specific mortality rates from a daily mortality rate, m_{ij} , which is the probability that an animal alive at the beginning of a day in

interval i dies during the day due to source j . The estimate of m_{ij} is: y_{ij}/x_i , where y_{ij} is the number of deaths in interval i due to source j . Desired interval rates then are determined by summing the daily probabilities of mortality (Heisey and Fuller 1985). MICROMORT also computes confidence intervals, variances, and covariances.

Monthly fawn survival was estimated by 2 methods because fawns were only radiotracked starting in January. Fecundity rates of road-killed does were compared with fawn:radioed-doe ratios from November through April, which did not determine causes of mortality. Fawn:doe ratios were adjusted using mortality rates of radioed does to compensate for adult doe mortality occurring during the same period. Telemetry from January to May, as described above, provided both survival data and causes of mortalities. Annual fawn survival was determined from the product of the June–December ratio data and the January–May survival from telemetry. Summer fawn survival was estimated from the June–November difference in fawn:doe ratios.

Male and female fawn data and yearly data for all ages and sexes were combined because of limited sample size. Cohort and consecutive monthly differences in survival and cause-specific mortality were examined by z -tests:

$$Z = \frac{r_1 - r_2}{(V_1 + V_2 + 2 \text{Cov}[r_1, r_2])^{0.5}}$$

where r_1 and r_2 are the rates being compared, V_1 and V_2 are the variances of the rates, and Cov is their covariance (Heisey 1985). We considered rates to be significantly different at $P \leq 0.13$. All significant comparisons are presented with their P values.

RESULTS

Two hundred nine deer were monitored during 1973–84; of those, 52 were followed as they aged through 1–2 cohorts. Considering those, survival data came from a sample equivalent to 273 deer (Table 1).

Collectively the deer were radiolocated approximately 10,000 times yielding 73,164 deer days of data (Table 1). During that time, 85 deaths (49 adults, 19 yearlings, and 17 fawns) were recorded: 44 from wolf predation, 22 from hunting, 12 probably from wolf kills, 2 from poaching, 2 from drowning, 1 from dogs, 1 from malnutrition, and 1 from a vehicle collision. We

Table 1. Annual survival and cause-specific mortality rates of radio-collared white-tailed deer in northeastern Minnesota, 1973–84.

	Cohorts					Total
	Fawns (Jan–May)	Yearlings		Adults		
		Females	Males	Females	Males	
<i>N</i> deer	78	40	39	78	38	273
Deer days	5,829	6,930	7,459	39,415	13,531	73,164
<i>N</i> deaths	17	4	15	24	25	85
Annual survival (S^*) ^a		0.80 ⁺	0.41 ⁺	0.79 ⁺	0.47 ⁺	
95% CI	0.31 ^b	0.65–1.00	0.26–0.65	0.72–0.87	0.34–0.63	
Mortality rates (M_j , relative importance %)						
Wolves	0.21 (57)	0.05 ⁺ (25)	0.16 ⁺⁺ (27)	0.17 ⁺ (81)	0.19 ⁺ (35)	
Hunting	0.00	0.00 ⁺	0.34 ⁺ (58)	0.01 ⁺ (5)	0.28 ⁺ (53)	
Poaching	0.00	0.05 ⁺ (25)	0.04 ⁺ (7)	0.00	0.00	
Malnutrition	0.02 (5)	0.00	0.00	0.00	0.00	
Dogs	0.02 (5)	0.00	0.00	0.00	0.00	
Drowning	0.00	0.00	0.05 ⁺ (8)	0.00	0.02 ⁺ (4)	
Road kill	0.00	0.05 (25)	0.00	0.00	0.00	
Probable wolf kills	0.12 (32)	0.05 ⁺ (25)	0.00	0.03 ⁺ (14)	0.04 ⁺ (8)	

^a Rates, confidence intervals, and significance testing computed according to Heisey and Fuller (1985). Rates followed by the same superscript symbols are not significantly different from each other ($P > 0.10$, all significant comparisons were $P < 0.06$). Annual survival and mortality was compared statistically only among yearling and adult cohorts.

^b Product of summer survival (from ratios) and Jan–May survival based on radio telemetry (Table 2).

lost radio contact with 9 deer (4 adult females, 3 yearling females, 1 adult male, and 1 yearling male) possibly from radio failures or unreported hunting mortality.

Annual Survival and Cause-specific Mortality

Annual fawn survival was 0.31 (Table 2). Annual yearling survival was 0.80 for females and 0.41 for males, and adult survival was 0.79 for females and 0.47 for males (Table 1).

The annual mortality rates from wolf predation were similar for both male cohorts and for adult females (0.16–0.19), but less for yearling females (0.05) (Table 1). Wolf predation and human hunting were the primary sources of mortality and varied in importance between cohorts (Table 1).

Monthly Survival and Cause-specific Mortality

Monthly fawn survival generally was lower than that of yearlings and adults (Fig. 1). Yearling and adult survival was high from May through October, decreased for males and adult females during November, and was generally lowest from December through April.

June–October.—Fawns had the lowest survival rate of all cohorts during this period. Al-

though we had no direct measure of fawn survival through October, our data comparing numbers of fawns/radioed doe in November against doe fecundity rate indicated a June through November survival of 0.66 (Table 2).

Monthly yearling and adult deer survival ranged from 0.94 to 1.00 ($\bar{x} = 0.99$) during this period; mortality was due to poaching, archery hunting, and wolf predation.

November.—November fawn survival could not be measured. Yearling and adult survival remained high for females in November (0.94 and 1.00) but decreased for males ($P < 0.001$) as a result of the buck-only firearm hunting (Fig. 1). Also, adult female survival in November was less than in October because of wolf predation ($P = 0.01$). Wolf predation on yearlings and adults, while previously low or absent, suddenly increased with adult females experiencing more predation than yearling females (Table 3).

December.—Fawn survival in December decreased; monthly mortality more than doubled that of summer and fall (Table 2). December yearling and adult survival resumed the high rate of summer and fall ($P < 0.03$) although wolf predation on adult males appeared to increase (Table 3).

January–April.—Except for males during the

Table 2. Monthly and annual fawn survival in northeastern Minnesota based on fecundity rate of 265 road-killed does, number of fawns observed with radioed does ≥ 2 years old, and calculations from telemetry data 1973–84.

	Jun	Nov	Dec	Jan	Feb	Mar	Apr	May	Annual survival
Fawns/does		61/53	42/42	35/39	30/36	21/32	20/36		
<i>N</i> does ^a	100	91	89	88	85	83	79		
<i>N</i> fawns ^b	160	105	89	79	71	55	44		
Fawn survival	(0.94) ^c	(0.94) ^c	0.85	0.89	0.90	0.77	0.80		
Fawn survival ^d				0.78	0.91	0.88	0.90	0.98	0.31 ^e

^a Hypothetical *N* surviving based on calculations from telemetry data.

^b Observed fawns/radioed doe \times *N* does surviving each month (Jun estimated from fecundity).

^c Estimated from Jun–Nov survival.

^d Based on telemetry data (S_i).

^e Annual survival based on Jun–Dec ratio (0.56) \times product of Jan–May (0.55) telemetry data.

November hunting season, monthly survival rates decreased to annual lows for yearlings and adults during January–April ($\bar{x} = 0.95$, range 0.89–1.00) although the consecutive monthly differences were not significant. Survival in January appeared to be less for fawns than for male and female yearlings ($P = 0.11$) and adult females ($P = 0.13$). March survival also was higher for adult females ($P = 0.04$) and adult males ($P = 0.008$) than for fawns.

Wolf predation constituted the primary mortality factor for all cohorts during January–April (Table 3) and caused a reduction in yearling and adult survival. Mortality rates from wolf predation were similar among yearling and adults but generally higher for fawns.

May.—Survival for each cohort, including fawns, increased to an annual high in May ($\bar{x} = 0.99$, range 0.98–1.00). Fawns were the only cohort that experienced mortality from wolf predation at this time, albeit low (0.02).

Monthly Confidence Intervals

Monthly 95% confidence intervals on survival rates were generally $< \pm 0.15$ but ranged from ± 0.03 – 0.22 for fawns, ± 0.07 – 0.17 for male and female yearlings, ± 0.02 – 0.04 for adult females, and ± 0.04 – 0.13 for adult males. Confidence intervals were inversely related to radioed-deer days/death (Fig. 2).

DISCUSSION

Fawn Survival

We measured only the magnitude of summer and fall fawn survival. However, wolf scat analyses from our study area and others indicate that fawns were the major summer prey and that predation was the primary cause of early

fawn mortality (Pimlott et al. 1969, Frenzel 1974, Voigt et al. 1976, Fritts and Mech 1981). Severe winter weather and its influence on fetal development can substantially reduce neonatal survival (Verme 1977), and that relationship may have applied to our deer population, which was subject to several severe winters (Nelson and Mech 1981). The relative importance of those and other sources of summer fawn mortality, and how they are related, remains to be examined.

Most winter fawn mortality was from wolf predation, but there was also a large amount classified as probable wolf kills. Considering that only 1 of 85 deaths for all deer was from malnutrition, it is likely that most, if not all, winter mortality in our study was from wolf predation. If so, winter predation rates of fawns might be 1.3–2.0 \times those of yearling and adult males. However, fawns killed by wolves may have been predisposed because of a combination of inadequate nutrition and severe weather and would have died even without predation. Blood assays at the time of capture suggested that wolf-killed deer (adults included) had marginal fat reserves when compared to surviving deer (Seal et al. 1978). Trainer et al. (1981) found that fawns killed by coyotes (*Canis latrans*) in winter weighed less at capture than surviving fawns. However, those authors believed that many of the fawns killed would have survived in the absence of coyotes. It remains conjecture whether our wolf-killed fawns would have survived without wolf predation. The present deer population is well below the levels imposed by habitat and winter weather alone (Mech and Karns 1977). This implies that wolf predation was limiting yearling recruitment to the population.

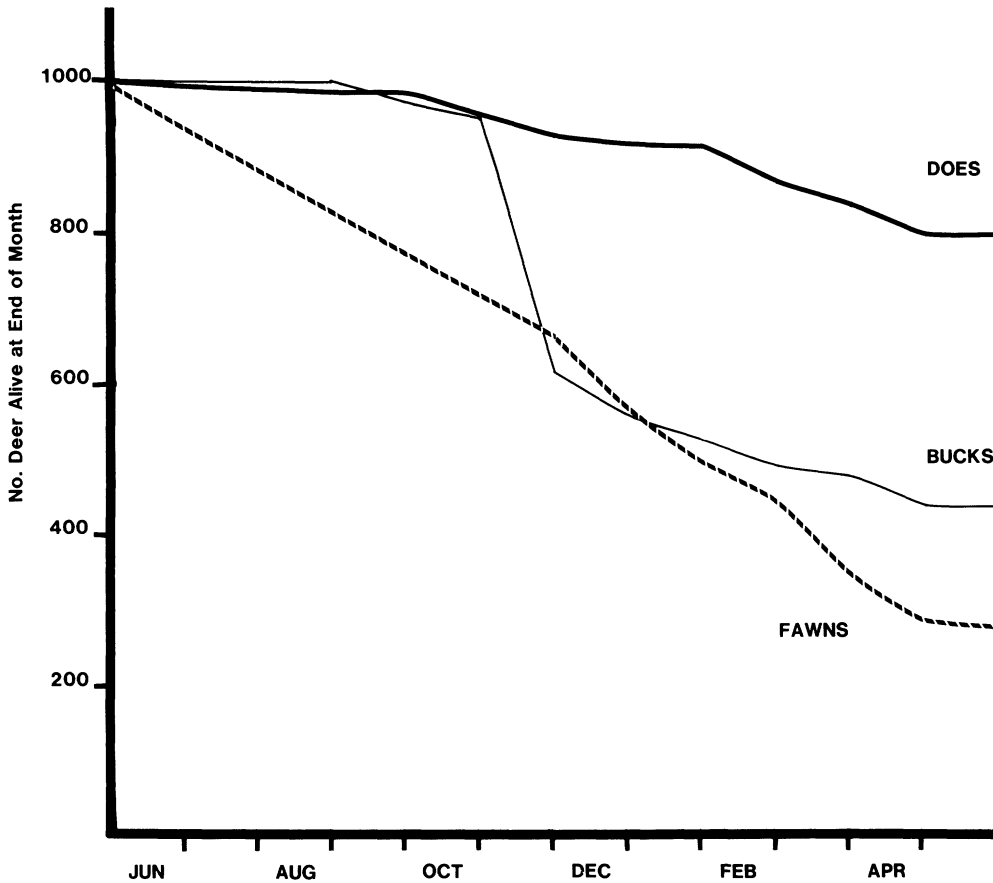


Fig. 1. Seasonal survivorship curves for radio-collared deer in northeastern Minnesota. June–October fawn survival rates are average monthly values, based on number of fawns observed with radioed does in November compared with assumed fecundity rates for the does. Yearling and adult survival was similar and was combined for graphical clarity.

Fawn survival only reached yearling and adult levels in May when fawns were 11 months old. The annual fawn survival of 0.31 was approximately 40% that of older females and 66–76% that of males.

Sex and Age Differences in Survival

Annual survival of yearling and adult females was approximately 2× that of males, resulting both from bucks-only hunting and from less wolf predation on yearling females. Higher wolf predation on adult males from December to February suggested that adult males were more vulnerable to predation than although differences were not significant.

Adult mortality was higher for male than for female un hunted Columbian white-tailed deer (*O. v. columbianus*) (Gavin et al. 1984). Male

deer killed by predators generally were younger than females, also indicating lower male survival. Furthermore, male white-tailed deer generally comprise a greater percentage of kills by wolves, relative to their availability, indicating a sex-related vulnerability to wolf predation (Pimlott et al. 1969, Mech and Frenzel 1971, Kolenosky 1972, Mech and Karns 1977). Lower male survival appears to be a major cost of natural selection that has favored sexual dimorphism and polygyny in ungulates (Clutton-Brock et al. 1982).

Annual and seasonal survival generally were similar between yearlings and adults of the same sex. However, more wolf predation on adult females than on yearling females during November, and possibly at other times, indicated that there may be subtle age-related differences in mortality. A slightly higher hunting mortal-

Table 3. Monthly wolf predation rates of radio-collared white-tailed deer in northeastern Minnesota 1973–83.^{ab}

Month	Fawns (both sexes)	Yearlings		Adults	
		Female	Male	Female	Male
Jun		0	0	0.01	0
Jul		0	0	0.01	0
Aug		0	0	0.01	0
Sep		0	0	0	0
Oct		0	0	0	0.04
Nov		0	0.04	0.05	0.02
Dec		0	0	0.02	0.07
Jan	0.22	0	0	0.01	0.10
Feb	0.09	0	0.06	0.04	0.09
Mar	0.10	0.05	0.06	0.02	0
Apr	0.08	0.04	0.11	0.05	0.06
May	0.02	0	0	0	0

^a Monthly mortality rates (M_{ij}) after Heisey and Fuller (1985).

^b Significant statistical comparisons from Z tests:

1. For Nov, yrl females < ad females ($P = 0.04$).
2. For Jan, fawns > yrl ($P = 0.11$) and ad females ($P = 0.13$). P values judged significant.
3. For Mar, fawns > ad females ($P = 0.07$) and ad males ($P = 0.02$). When probable wolf kills were excluded from predation, P values changed to $P = 0.03$ and $P = 0.07$ for females and males, respectively.

ity for yearling than adult males in November, less predation on yearlings in December, and increased predation on adult males in December suggested that this phenomenon may also occur for males.

Age-related survival differences are well documented for both male and female ungulates. Yearling and 2-year-old male white-tailed deer are more vulnerable to hunting than are older adult males (Maguire and Severinghaus 1954, Roseberry and Klimstra 1974, McCullough 1979). Dasmann and Taber (1956) argued that greater hunting vulnerability was related to a lack of experience. However, greater hunting vulnerability of younger cohorts also was observed in a refuge population with no prior hunting. Roseberry and Klimstra (1974) maintained that higher vulnerability of yearling and 2-year-old males resulted from dispersal, which exposed them to unfamiliar areas during the hunting seasons. At least 50% of our yearling male dispersal occurred in fall and may result in a similar survival disadvantage related to hunting.

However, vulnerability of maturing deer to hunting does not carry over to wolf predation. Yearling and middle-aged deer are less vulnerable to wolves than are older adults (Pimlott et al. 1969, Mech and Frenzel 1971, Mech and Karns 1977, Fritts and Mech 1981). For youn-

ger males decreased vulnerability probably resulted from lower social rank and less breeding activity, resulting in decreased energy expenditure. In addition, the incidence of leg arthritis is greater in older male deer, which probably influences their ability to escape predation (Wobeser and Runge 1975).

For females survival appears related to the burden of lactation imposed on maternal does. One would predict that nonmaternal yearlings, in particular, would have higher survival than adults since lactation is a costly metabolic process (Verme 1967, Moen 1978, Bahnak et al. 1981, Clutton-Brock et al. 1983). Maternal does have only a short time between cessation of lactation and winter to replenish fat reserves that influence winter survival. Because fawns in our area rarely breed, yearlings probably build greater fat stores.

In summary, the probability of overall survival for each cohort in our study area can be ranked. Fawns have the lowest survival, which probably is directly related to the effect of prenatal nutrition on body size and condition. Survival in male yearlings and adults is lower than in females, probably because of the costs of breeding competition and sexual dimorphism. Thus male survival is higher only than that of fawns. Yearling males are more vulnerable to hunting, probably because of their dispersal tendencies, but adult males deplete their fat reserves early because of rutting and are more predisposed to predation. Survival is highest for females probably because they lack the body size and physiological and behavioral constraints of the other cohorts.

Radio Telemetry Research

The primary benefit of using radio telemetry to study survival and cause-specific mortality is that survival data are obtained directly and causes of mortality are determined in a relatively unbiased manner. A major problem, however, is the need for estimation of mortality on a yearly and seasonal basis so differences in other variables (i.e., weather, population density, and reproduction) can be analyzed relative to survival.

Our results indicated that a minimum of 600 deer days/death must be sampled to consistently obtain 95% confidence intervals of no more than ± 0.10 on monthly survival estimates (Fig. 2). Survival measured on a cohort basis

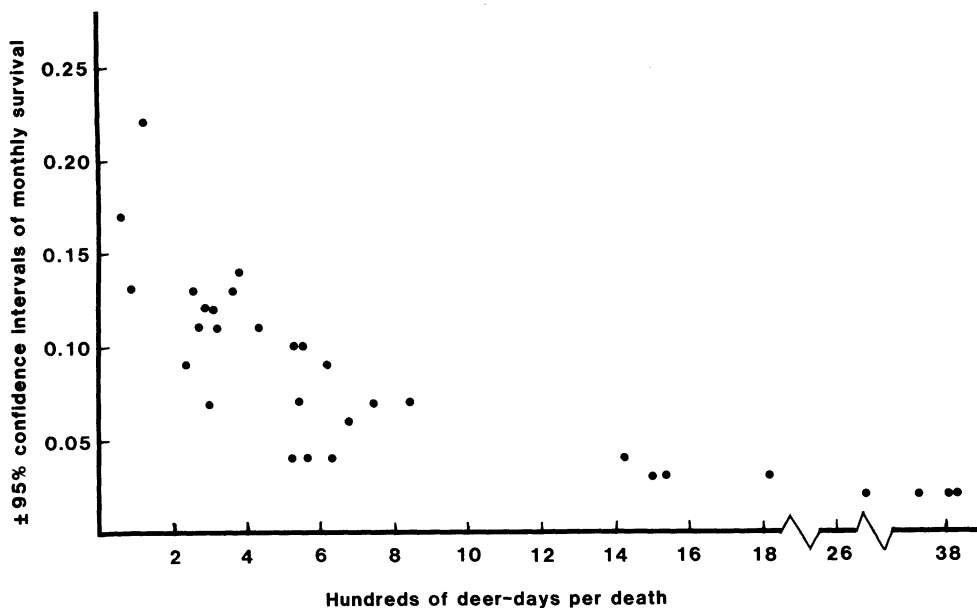


Fig. 2. Relationship between 95% confidence intervals on survival rate of white-tailed deer in northeastern Minnesota and deer days/death.

would require that a minimum of 20 deer/cohort/month be monitored, and even that sample requires nearly 100% survival to minimize confidence intervals. Given the survival rates that we measured, we would have to radiocollar 207 deer to obtain confidence intervals of no more than ± 0.10 on monthly survival in any given year. Accepting wider intervals of up to ± 0.15 would require that only 73 deer be radiocollared. These levels of precision would require 3–8 \times our yearly effort.

If budget constraints dictated the total level of effort and yearly analyses were desired, then it would be best to invest heavily in an intensive, short-term effort (3–5 years) as opposed to a reduced, longer one and accept a lower level of precision in survival estimates. Such a study, however, probably would fail to cover all pertinent environmental variation.

A further consideration in analyzing telemetered survival is the importance of the assumption that daily survival be constant during the period being measured. Simulations of various monthly sampling schemes and survival rates indicate that violations of this assumption can generate deviations of $\geq 27\%$ for survival rates of ≤ 0.50 . Measuring survival rates over smaller intervals (e.g., ≤ 30 days) will minimize

biases associated with variations in daily survival.

It still seems to be a current view that cohort survival rates and causes of mortality are nearly impossible to measure (Hayne 1984:204). While it is true that budgets and human resources may determine what data are obtainable, our study demonstrated that it is possible to determine these variables by means of radio telemetry. Such research should become an integral part of deer population management.

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Received 14 May 1985.

Accepted 29 March 1986.