

A Long-Term Age-Specific Survival Analysis of Female White-Tailed Deer

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Abstract

We conducted a 13-year survival (i.e., time survived since birth) and cause-specific mortality study, divided into 2 phases (Phase I = years 1–6; Phase II = years 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 [WSI] of 45–195) and hunting pressure. Most studies of survival and cause-specific mortality of northern deer have assumed constant survival rates for adults of each sex (≥ 1.0 yr old pooled) 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 that 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 instantaneous risk of death began to increase at age 6 years. This difference likely reflected differences in winter severities, associated changes in 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 we included 76 neonates (i.e., ≤ 0.6 yr old) 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 year of life. We compared cumulative survival estimates for these data using the generalized Kaplan–Meier (GKM) and the iterative Nelson estimator (INE), and we illustrate the potential for bias when applying the GKM to left-truncated data. Median age of survival for females was 0.83 years old (90% CI = 0.79–1.45 yr old) using the INE and 0.43 years old (90% CI = 0.17–0.78 yr old) using the GKM. Lastly, we used a simulation approach to examine the potential for bias resulting from pooling adults. These simulations suggest that models using the constructed discrete time variable give nearly unbiased survival estimates and provide support for researchers and managers applying age-specific hazards derived during study periods to determine the reliability of adult age-pooled survival estimates. As indicated by our data, it is important to consider environmental variation and its interactions with natural mortality forces (e.g., predation) and age distribution of the population when setting harvest goals. (JOURNAL OF WILDLIFE MANAGEMENT 70(6):1556–1568; 2006)

Key words

Canis lupus, cause-specific mortality, hazard, iterative Nelson estimator, Kaplan–Meier, *Odocoileus virginianus*, survival, white-tailed deer, winter severity, wolf predation.

Studies that focused on the influences of environmental (e.g., location, season, predation, and human activities) and demographic (e.g., age, sex, deer density) factors on survival and cause-specific mortality rates have enhanced our understanding of the population dynamics of northern deer (*Odocoileus* spp.) and other herbivores (Nelson and Mech 1986, Fuller 1990, Bartmann et al. 1992, Van Deelen et al. 1997, Gaillard et al. 2000). For white-tailed deer, the most common analytical approach has involved separate examinations of fawn ($0.6 < x < 1$ yr old) and adult survival of a sex (≥ 1 yr old pooled). Consequently, researchers have reported little on continuous or near continuous age-specific survival of adults of this species (e.g., classic life table models such as those described in Caughley [1977] and Southwood [1978]). In contrast, for a number of other ungulates, survival over the life cycle of adult females has been shown to have a strong relationship with age (Caughley 1966,

Loison et al. 1999, Gaillard et al. 2000, Festa-Bianchet et al. 2003).

In an effort to expand our knowledge of these aspects of population dynamics, DelGiudice et al. (2002) examined age-specific survival and cause-specific mortality of 153 female white-tailed deer, 0.6–17.5 years old, over a 6-year period in north-central Minnesota. This relatively long-term study provided the time to accumulate a study cohort representative of a local target population and permitted assessment of the impact of competing mortality forces (e.g., wolf predation, hunter harvest) relative to widely varying winter conditions.

Wolves and hunter harvest were the primary sources of natural and human-mediated mortality, respectively, but the cause-specific hazard curves differed from one another over the lifetimes of deer. These findings, and a nonlinear association of the cumulative winter severity index (WSI) with the relative risk of death of deer as winters progressed, suggested that stratifying on 2 or 3 age classes and estimating time survived from the initiation of the study,

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rather than stratifying by year or phase, could obscure important patterns, associations, and sources of variation in the underlying survival and hazard functions. Ultimately, this could lead to erroneous interpretations and difficulties in making comparisons to studies whose 2- or 3-level age strata might actually represent widely disparate underlying survival distributions on the continuous age scale.

DelGiudice et al. (2002) also raised a number of analytical issues relevant to traditional approaches (e.g., life table) of estimating survival of deer and other species (Eberhardt 1985). In DelGiudice et al. (2002), they defined survival time as age, with birth date (i.e., 6 Jun of each deer's birth year) serving as the origin. However, because recruitment of deer into the study was conditional upon deer surviving long enough to allow winter capture and radiocollaring, the youngest recruits were 0.6 years old. Further, they accumulated sample sizes by live-capture during 6 winters of the study. Thus, as with many other deer survival analyses (Nelson and Mech 1986, White et al. 1987, McNay and Voller 1995, Van Deelen et al. 1997, Ballard et al. 1999), data of DelGiudice et al. (2002) were left-truncated and estimates of survival were conditional on each deer surviving long enough to be winter-captured and radiocollared. Moreover, small to moderate sample sizes in the left tail of the age distribution (i.e., younger ages) yielded generalized Kaplan-Meier (GKM) estimates of survival that were biased low (Woodroffe 1985, Tsai 1988, Pan and Chappell 1998, Winterstein et al. 2001). Consequently, DelGiudice et al. (2002) employed the iterative Nelson estimator (INE) of survival, which is more robust to left-truncation (Pan and Chappell 1998), and compared curves generated from the 2 approaches. Whereas, the GKM-derived median age of survival of our study cohort was only 1.5 years old, the INE estimate was 3.6 years old.

Long-term studies are essential to understanding natural processes and phenomena that develop slowly or are rare, highly variable, subtle, or complex, as well as to testing ecological concepts and theoretical constructs (Lutz 1945, Strayer et al. 1986, Franklin 1989, Tilman 1989, Gaillard et al. 2000). All of these considerations apply to deer survival and its putative associations with ecological and environmental factors and other sources of variation that influence populations over time and space (Eberhardt 1985, Gaillard et al. 1998). Long-term studies maximize the captured variation of conditions associated with these factors and with the often time-dependent process of accumulating large sample sizes, which affords analytical advantages (DelGiudice and Riggs 1996, Gaillard et al. 1998, Morrison et al. 2001). Seventy to eighty percent of experimental and observational studies in ecology and wildlife science last ≤ 3 years, and most last ≤ 2 years (Tilman 1989, Millsaugh and Marzluff 2001). Many long-term efforts have demonstrated the misleading nature of such short-term studies (Lutz 1945, Wickman 1980, Brown et al. 1986, Peterson 1987, Franklin 1989).

"This begs the question, how long is long-term?" (Morrison et al. 2001:101). Or, how long is long enough?

Certainly it will depend on the species being studied, the ecosystem in which they live, and the "dynamic speed of that system" (Strayer et al. 1986). But, it also may depend on logistic factors (e.g., funding) influencing a study's progress. Since reporting our interim findings (DelGiudice et al. 2002), the continuation of our long-term study has provided an additional 7 years of follow-up, during which our study cohort of females has more than doubled. We have also captured and monitored the survival and cause-specific mortality of white-tailed neonates (Carstensen et al. 2003, Carstensen Powell 2004, Carstensen Powell and DelGiudice 2005).

Our primary objectives were to 1) examine the potential effects of changes in sample size and inclusion of neonates monitored from birth (i.e., survival estimates were no longer conditioned on all subjects surviving to age 0.6 yr) on the age-specific survival and hazard estimates for female white-tailed deer, 2) examine the effect of pooling adults (≥ 1 yr old) on survival analyses and population projections, and 3) demonstrate the value of long-term research to understanding survival and the hazards of northern deer.

Study Area

Our study area (791 km²) for winter capture of deer ≥ 0.6 years old, described by DelGiudice et al. (2002), was located along the southeastern boundary of the Chippewa National Forest in north-central Minnesota, USA (46°52'–47°15'N and 93°45'–94°07'W). Spring–summer–autumn ranges (including fawning areas) enlarged this area to 1,865 km² (46°49'–47°11'N and 93°35'–94°20'W; Carstensen Powell et al. 2005). Elevations were 400–475 m above sea level. Trembling aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), paper birch (*Betula papyrifera*), black ash (*Fraxinus nigra*), balsam fir (*Abies balsamea*), red pine (*Pinus resinosa*), and jack pine (*Pinus banksiana*) dominated the uplands in deciduous and mixed deciduous–coniferous stands, whereas northern white cedar (*Thuja occidentalis*), black spruce (*Picea mariana*), balsam fir, and tamarack larch (*Larix laricina*) were predominant on the lowlands (Doenier et al. 1997). Logging of aspen and conifer species was common throughout the study in areas near the sites used for trapping deer. Common browse species included beaked hazel (*Corylus cornuta*), mountain maple (*Acer spicatum*), sugar maple (*Acer saccharum*), red-osier dogwood (*Cornus stolonifera*), and ironwood (*Ostrya virginiana*). Most (66–89%) of the female deer were seasonal migrators, moving mean distances of 11–16 km between ranges, and exhibiting high fidelities for their winter and spring–summer–autumn home ranges (DelGiudice 1997). Spring migration end-dates have ranged from early March to early June.

We calculated a Minnesota Department of Natural Resources (MNDNR) WSI by accumulating one point for each day with a snow depth ≥ 38.0 cm and one point for each day with an ambient temperature $\leq -17.7^\circ\text{C}$ during November–May. During 1990–2003, maximum WSIs ranged from 45 (1999–2000 and 2001–2002) to 195

(1995–1996), with maximum mean weekly snow depths ranging from 0–88 cm and monthly mean daily minimum temperatures dropping down to -28°C (National Oceanic and Atmospheric Administration 1990–2003, DelGiudice 2004). Winters 1995–1996 and 1996–1997 were severe (WSIs of 195 and 159), with prolonged deep snow cover up to 100 cm. Conversely, 3 consecutive mild winters occurred during 1997–1998 to 1999–2000 with WSIs of 45–50. During June–October 1991–2003, monthly mean daily maximum temperatures ranged from 6 to 28°C (National Oceanic and Atmospheric Administration 1991–2003).

Wolves were the dominant predator of white-tailed deer ≥ 0.6 years old; pack sizes (winter) and territories ranged from 2–8 members and from 62–186 km^2 , respectively (DelGiudice 1998, 2004, DelGiudice et al. 2002). Black bears (*Ursus americanus*), red foxes (*Vulpes vulpes*), bobcats (*Felis rufus*), and fishers (*Martes pennanti*) were also abundant on the study area (Dexter 1992–2004, Garshelis 1994). Coyotes (*Canis latrans*) were not common.

Methods

Winter Capture and Handling of Deer

We provide only a general description of winter capture, handling, and monitoring of deer (see DelGiudice et al. 2005 for greater detail). During January–March 1991–2003, we captured $>90\%$ of the female deer by Clover trap (Clover 1956) but sporadically augmented these efforts with rocket netting (Hawkins et al. 1968) and net-gunning from helicopter (Wildlife Capture Services, Marysville, Utah). We blindfolded physically restrained deer and immediately injected them intramuscularly (IM) with 100 mg of xylazine HCl and 300–400 mg of ketamine HCl. Once induced, handling included ear-tagging, monitoring rectal temperature, weighing to the nearest 0.5 kg, blood and urine sampling, fitting very high frequency (VHF; Telonics, Mesa, Arizona; Advanced Telemetry Systems, Isanti, Minnesota) or Global Positioning System (GPS; Advanced Telemetry Systems) radiocollars, physical examination, morphological measurements, and determination of pregnancy status via dop-tone ultrasound (Pocket-Dop, Imex Medical Systems, Golden, Colorado) or portable real-time ultrasound (Sonovet 600 Veterinary Ultrasound System, Universal Medical Systems, Bedford Hills, New York). We extracted a last incisor for age determination by cementum annuli (Gilbert 1966). During 5 winters (1996–1997, 1998–1999 to 2001–2002), we assessed the condition of some deer using the deuterium-dilution technique (Carstensen 2002, Carstensen Powell 2004), and during 3 winters (1999–2000 to 2001–2002), we inserted vaginal implant transmitters (Model M3940, Advanced Telemetry Systems) into 3, 25, and 25 captured deer, respectively (Carstensen 2002, Carstensen et al. 2003, Carstensen Powell 2004).

Before release, each deer received 1,500,000 international units of a broad-spectrum antibiotic IM, followed by reversal of anesthesia by an intravenous injection of 15 mg of yohimbine (Mech et al. 1985). All radiocollars included a mortality switch, and we investigated cause of death for all

mortalities as described by DelGiudice et al. (2001). Postrelease capture-related mortality (i.e., death from any proximate cause within 14 d of release) was about 2.5% (DelGiudice et al. 2005).

Spring Capture and Handling of Newborn Deer

Carstensen et al. (2003) and Carstensen Powell et al. (2005) have reported doe monitoring protocols and techniques used to locate neonates. Handling of physically restrained neonates included monitoring rectal temperature, ear-tagging, weighing to the nearest 0.2 kg, measuring new hoof growth (for aging, Sams et al. 1996) and other morphological characteristics, blood sampling from the external jugular vein, fitting an expandable radiocollar (designed to detach within 5–6 months), and release (Carstensen Powell and DelGiudice 2005, Carstensen Powell et al. 2005). There was no evidence of marking-induced abandonment or mortality (Carstensen Powell et al. 2005). Animal handling followed protocols approved by the University of Minnesota's Institutional Animal Care and Use Committee under Animal Subjects Code Numbers 9701A00007, 9911A25961, and 0208A29962.

We monitored neonate survival daily for about 12 weeks, followed by 2–3 times per week, via a mortality switch (with a 4-hr threshold) in the radiocollar (Carstensen Powell et al. 2005). We investigated deaths for cause within 24 hours of signal detection and we evaluated evidence (e.g., puncture marks, caching).

Survival and Statistical Analyses

Estimation of $S(t)$ and $h(t)$.—We considered 4 different datasets constructed from radiocollared individuals we followed on the study area: 1) 152 females ≥ 0.6 years of age followed from 1 January 1991 to 8 July 1996 (Phase I), 2) 191 females ≥ 0.6 years of age followed from 9 July 1996 to 31 December 2003 (Phase II), 3) a cohort of 302 females ≥ 0.6 years of age followed from 1 January 1991–31 December 2003 (resulting from combining Phases I and II; note that some individuals are in both data sets), and 4) 302 females ≥ 0.6 years of age (from [3]) and 76 neonates (36 F, 40 M) followed from 28 May 1997–31 December 2003. The 2 phases represent 2 independent examinations of the data (rather than well-defined biological periods), with Phase I corresponding to the time period considered by DelGiudice et al. (2002). We found no significant differences in neonate survival related to gender in a Cox proportional hazards model fit to these data ($P=0.16$, 95% confidence interval on the risk ratio of M:F = [0.83, 2.96]), but we censored males at age 0.5 years under the assumption that risk of death for males and females may diverge during their first winter.

We compared GKM and INE estimates of $S(t)$ for these 4 data sets. Both GKM and INE estimates of $S(t)$ are step functions, with drops in estimated survival occurring only at observed event times (i.e., ages where deaths are observed). Thus, in both cases we can present $\hat{S}(t)$ as the product of n parameters, where n = the number of unique event times:

$$\hat{S}(t) = \prod_{t_i < t} \hat{\theta}_{t_i}, \quad (1)$$

with t_i ($i = 1, 2, \dots, n$) corresponding to these times and $\hat{\theta}_{t_i} < 1$. Large drops early in time (i.e., small $\hat{\theta}_{t_i}$ for early observation times) will influence $\hat{S}(t)$ for all subsequent t . For the GKM:

$$\hat{\theta}_{t_i} = 1 - \frac{d_i}{n_i}, \quad (2)$$

where d_i = the number of observed events occurring at time t_i and n_i = the size of the risk set at time t_i (i.e., the no. of individuals observed at time t_i). With data that are left-truncated, small values of $\hat{\theta}_{t_i}$ can occur for early event times if 1 or 2 individuals die (because the number of individuals at risk for early event times is small). At the extreme, if all individuals at risk die at time t_i , $\hat{\theta}_{t_i} = 0$ and $\hat{S}(t)$ will be 0 for all values of $t > t_i$. By contrast, the INE estimates θ_{t_i} by an iterative procedure that considers the full data set, including individuals that are not yet at risk at time t_i (Pan and Chappell 1998):

1. Begin with an initial estimate of $S(t) = S^o(t)$.
2. Using the current estimate of $S(t) = S^j(t)$, compute \tilde{d}_i = the expected number of deaths at each observed event time in the original data set. Let $\tilde{n}_i = \sum_{j \geq i} \tilde{d}_j$; $\hat{\theta}_{t_i} = \exp(-\tilde{d}_i/\tilde{n}_i)$.
3. Update the estimate of $S(t)$ using \tilde{d}_i and \tilde{n}_i from step 2: $S^{j+1}(t) = \exp(-\sum_{i: t_i \leq t} [\tilde{d}_i/\tilde{n}_i])$ (like the Nelson Estimator, this update step is based on the cumulative hazard).
4. Repeat steps 2 and 3 until convergence.

We estimated the GKM using functions in the survival package for the R programming language (R Core Development Team 2004) and the INE using SPlus/R functions written by Wei Pan (available from <http://www.biostat.umn.edu/~weiprog.html>).

We also compare penalized likelihood estimates (PLE) of $h(t)$ for these same data sets (Joly et al. 1998, Gu 2002). The hazard function at time t gives the probability of death in a small interval around time t , given that the individual has survived until time t . Thus, the hazard function measures the instantaneous risk of death over an animal's lifetime and is related to $S(t)$ as follows (Cox and Oakes 1984, Kalbfleisch and Prentice 2002):

$$h(t) = \frac{\partial \log S(t)}{\partial t}$$

or

$$S(t) = \exp\left(-\int_0^t h(v)dv\right) \quad (3)$$

The PLE of the hazard is determined by maximizing a penalized likelihood function:

$$pl(\theta) = l(\theta) - \lambda \frac{J(\theta)}{2} \quad (4)$$

where l is the usual log-likelihood, λ is a smoothing parameter, and $J(\theta)$ is a quadratic roughness functional

(most often taken to be the integral of the squared second derivative of θ ; Joly et al. 1998, Gu 2002). Researchers typically approximate the solution to (4) using a set of spline basis functions (Joly et al. 1998, Gu 2002), with λ prespecified by the user or chosen via cross-validation. The choice of λ represents a bias-variance tradeoff, with larger values of λ resulting in smoother estimates with less variance but more bias.

As in DelGiudice et al. (2002), we estimated separate hazards for wolf predation and miscellaneous causes for the ≥ 0.6 -year-old deer data sets (Phases I, II, and combined), as well as an all-causes hazard (accounting for all mortality sources) for all 4 data sets. In the former analyses, we treated deaths from other causes as censored observations. We calculated 90% Bayesian confidence bands (Joly et al. 1998, Du and Gu 2005) to characterize the uncertainty in the estimated hazards. Studies have shown these intervals to have good Frequentist coverage probabilities, although the coverage may be less than nominal (i.e., less than 90% for a 90% CI) near areas of high curvature (Wahba 1983, Nychka 1988, Gu 1992, Du and Gu 2005). We obtained estimates of the hazard using functions written in the R programming language (R Core Development Team 2004) by Chong Gu (gss package; Gu 2002). We used the default smoothing parameter (chosen using an approximate cross-validation score, Gu 2002) in all but 2 cases. We chose a smaller smoothing parameter (less smoothing) for the wolf hazard (Fig. 1d), as it produced an estimate more consistent with DelGiudice et al. (2002, fig. 8b). We chose a larger smoothing parameter (more smoothing) for the miscellaneous hazard (Fig. 1f) because the default choice gave a highly variable estimate (with large uncertainty bounds) for ages > 10 years. We did not estimate the harvest hazard because age-specific sample sizes were small and temporal variation (due to annual issuance of antlerless permits) was great; consequently, this analysis would be less informative.

Population projections: comparing INE and GKM estimates of $S(t)$ and effect of pooling adults.—We constructed 2 postbreeding Leslie matrix models (Leslie 1945, Caswell 2001) based on the GKM and INE estimates of $S(t)$ from the data set that included all adults (1 Jan 1991–31 Dec 2003) and neonates (28 May 1997–31 Dec 2003). We used fecundity rates of 0.84, 1.40, and 1.85 fawns per doe for ages 2, 3, and 4–8 years (prime age adults), respectively, as suggested by Verme (1967; table 15, Verme and Ullrey 1984) for individuals experiencing a “moderate nutritional plane” (note, Verme and Ullrey [1984] list ages at breeding rather than during spring fawning). We assumed that fawns do not give birth as yearlings, which our data support with an extremely low pregnancy rate for fawns in the study cohort (1.8%, $n = 55$). Although we do not have data on the incidence of twinning for older aged does, observations of near 100% pregnancy rates for deer ages 11–16 years in the study cohort (G. D. DelGiudice, MNDNR, unpublished data) suggest that fecundity rates are unlikely to drop much below one even for the oldest individuals. Here, we assumed that fecundity rates drop linearly from a value of

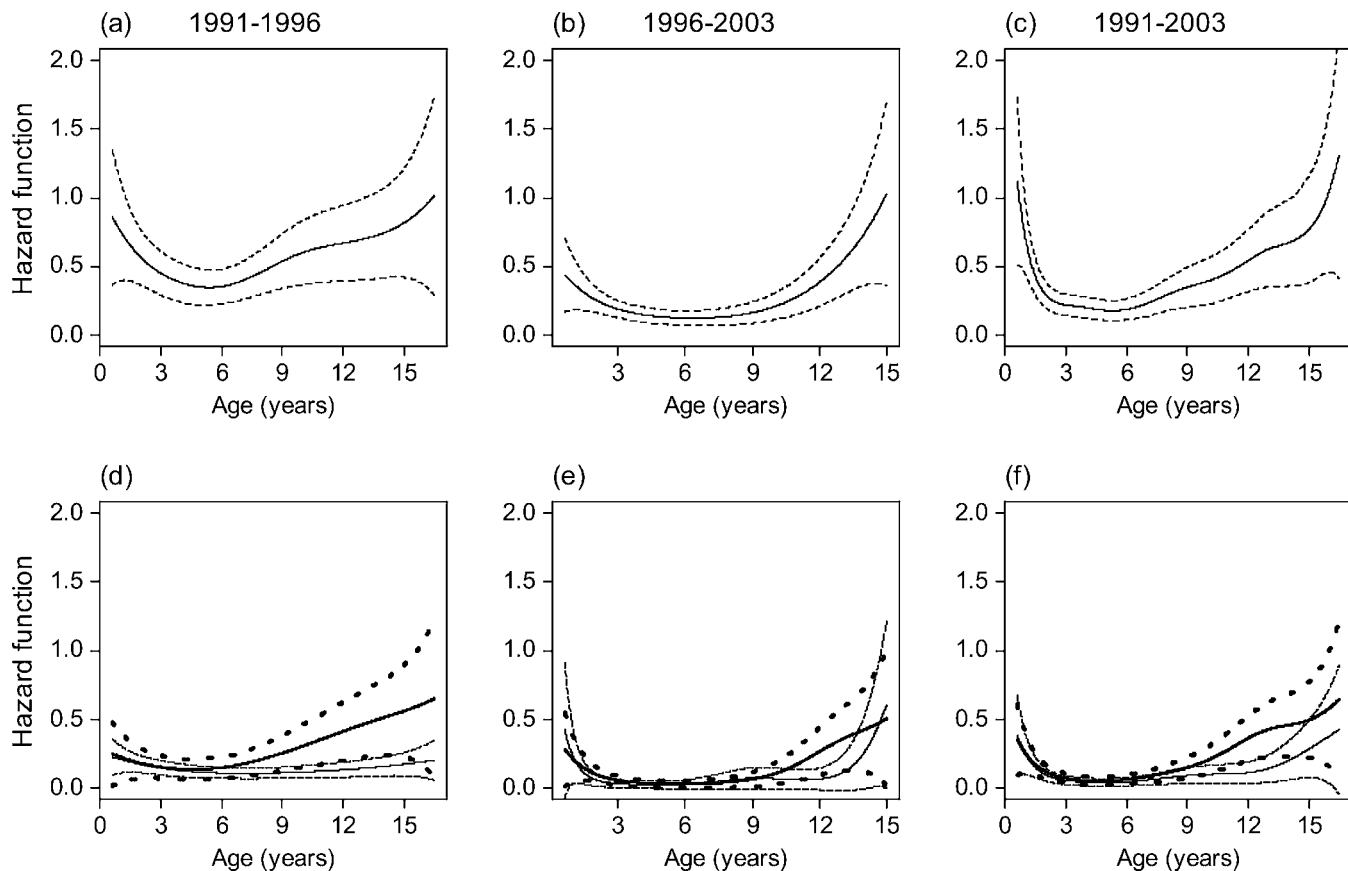


Figure 1. Penalized likelihood estimate (PLE) of the “all-causes” hazard (with Bayesian 90% confidence bands) for radiocollared, female white-tailed deer (≥ 0.6 yr old), north-central Minnesota, USA for time periods: (a) 1 Jan 1991–8 Jul 1996, (b) 9 Jul 1996–31 Dec 2003, and (c) 1 Jan 1991–31 Dec 2003. PLE of wolf (bold line) and miscellaneous-caused hazards for these same deer for time periods (d) 1 Jan 1991–8 Jul 1996, (e) 9 Jul 1996–31 Dec 2003, and (f) 1 Jan 1991–31 Dec 2003.

1.85 fawns per doe at age 9 years to 1 fawn per doe at age 14 years and then remain stable. Finally, we assumed a 50:50 sex ratio at birth. Under the assumption that population dynamics are deterministic (i.e., survival and fecundity rates are constant), the model projects that the population will eventually grow or decline at a rate given by the dominant eigenvalue of the matrix, λ (Caswell 2001). Thus, the models provide a means of comparing the projected growth rates under the assumption of constant survival using GKM and INE estimates of $S(t)$ obtained from the data set that included does ≥ 0.6 years old (1 Jan 1991–31 Dec 2003) and neonates (28 May 1997–31 Dec 2003).

Most wildlife survival studies follow only a limited number of individuals and therefore provide estimates of survival for juveniles (e.g., fawns) and then adults (pooled across ages). To investigate the potential bias resulting from pooling adults, we simulated capture and survival estimation using a sample size of 150 individuals from the age-at-capture distribution observed at our study site. We followed individuals for 1 year (with no censoring) and simulated survival (Y/N) using a binomial random number generator with probability of success determined using age-at-capture and the yearly estimates of survival from the INE estimates of $S(t)$ (from the data set that includes all adults [1 Jan

1991–31 Dec 2003] and neonates [28 May 1997–31 Dec 2003]). The estimates obtained from this analysis are analogous to GKM estimates; censoring (e.g., radiocollar failure) will decrease the precision of the survival estimates but should not appreciably alter the conclusions regarding the bias resulting from pooling adults when estimating survival. We constructed Leslie matrix models using the same fecundity rates as assumed above but under the following assumptions: 1) constant adult survival for does ≥ 1 year old (Model 1), and 2) constant adult survival for ages 1–7 years and then constant survival for ages ≥ 8 years (Model 2). For each simulated data set, we estimated λ under Model 1 and Model 2 (λ_1 and λ_2 , respectively), setting $\lambda_2 = \lambda_1$ if we did not capture any adult deer > 7 years old. We constructed boxplots of the estimates of adult survival rates and histograms of the resulting estimates of λ to illustrate the range of simulation results. Finally, we estimated the bias and mean-squared error (MSE) of the estimates of λ for Model 1 and Model 2 from the 5,000 simulations (with the true λ defined using the INE estimates of $S(t)$); in order to assess the performance of these simplified models and therefore, the effect of pooling adult survival rates on population projections.

Table 1. Winter severity, crude mortality rate, wolf predation, and hunting hazard for female white-tailed deer (≥ 0.6 yr old), north-central Minnesota, USA, 1 Jan 1991–Dec 2003.

Phase interval	Year	Winter statistics ^a						Hunting statistics ^b		
		Final WSI ^c	No. of deer at risk	No. of winter deaths	No. of winter deaths by wolves	Crude mortality rate	Winter deaths by wolf predation (%)	No. of deer at risk	No. of deaths due to hunting	Hunting crude mortality rate
Phase I:	1990–1991	59	22	4	2	0.18	50	14	2	0.14
Jan 1991–	1991–1992	86	32	4	3	0.13	75	27	11	0.41
8 Jul 1996	1992–1993	124	49	4	2	0.08	50	36	3	0.08
	1993–1994	126	62	10	8	0.16	80	43	5	0.12
	1994–1995	61	47	3	2	0.06	67	37	6	0.16
	1995–1996	195	65	24	15	0.37	63	36	0	0.00 ^d
Phase II:	1996–1997	159	69	5	3	0.07	60	41	0	0.00 ^d
9 Jul 1996–	1997–1998	50	43	3	0	0.07	0	23	1	0.04
Dec 2003	1998–1999	46	45	2	1	0.04	50	36	5	0.14
	1999–2000	45	33	2	2	0.06	100	22	1	0.05
	2000–2001	153	77	15	8	0.19	53	50	2	0.04
	2001–2002	45	75	10	5	0.13	50	63	4	0.06
	2002–2003	58	64	5	3	0.08	60	53	7	0.13

^a Winter statistics correspond to 1 Dec–31 May of the current Year (column 2) listed in the table.

^b Hunting statistics refer to early Nov firearms seasons during the second Year (column 2) listed in the table.

^c Winter severity index (WSI) is calculated by accumulating one point for each day with an ambient temperature $\leq 17.7^{\circ}\text{C}$ and one point for each day with a snow depth ≥ 38 cm during 1 Nov–31 May.

^d No antlerless permits were issued in Nov of 1996 and 1997.

Results

Winter and Spring Recruitment of Study Deer

We radiocollared 342 female deer, 0.6–15.7 years old at capture, during January–March 1991–2003; we included 302 deer, aged and surviving ≥ 7 days postrelease, in age-specific survival and hazard analyses. Our sample size since the 1991–1996 analyses (153 F, DelGiudice et al. 2002) almost doubled. Overall mean biweekly and mean total winter sample sizes of radiocollared deer increased from 33 (range = 15–44 deer) and 52 (range = 22–74 deer) during Phase I, to 44 (30–59 deer) and 61 (38–79 deer) during Phase II of the study. Our study cohort represented the segment of the target population ≥ 0.6 years old, which included 27 birth cohorts and deer up to 17.4 years old. After the study's first year, the age distribution of the collared deer was stable through winter 1995–1996 (annual median ages of 5.8–6.7 yr); it is noteworthy that following the high mortality (crude mortality rate of 0.37) of severe winter 1995–1996 (Table 1), median age decreased by winter 1996–1997 (3.7 yr), then rebounded and remained stable (annual median ages of 3.7–5.4 yr) for the remainder of Phase II.

We captured a total of 76 neonates (36 F, 40 M) of radiocollared does during springs 1997 (5), 1999 (8), 2000 (11), 2001 (27), and 2002 (25); estimated age at capture ranged from 0–13 days old (Carstensen Powell et al. 2005). Estimated mean birth dates ranged from 20–28 May during these 5 years (Carstensen 2002, Carstensen Powell 2004).

Hazard, Age-Specific Survival, and Sample Size

Hazard estimates.—The PLE of the all-causes hazard was U-shaped for both phases of the study, indicating elevated risk of death for younger and older aged individuals

(Fig. 1a,b). However, the PLE of the all-causes hazard for Phase II was generally lower and relatively constant for adults between ages 2 and 10 years. By contrast, the PLE of the hazard from Phase I dropped more markedly, and thereafter increased. The hazards associated with wolf predation and miscellaneous causes also appeared U-shaped for the 2 study phases (Fig. 1d,e). Similar to the all-causes hazard estimates, the wolf hazard for Phase II appeared lower and more stable across ages 2–10 years than during Phase I. As expected, the pattern and variation associated with the all-causes and cause-specific hazard curves for the entire study (1991–2003) were intermediate to those of the 2 phases. Mean age of females harvested by hunters (5.5 yr, 95% CI = 4.46–6.54, range = 1.4–17.4 yr old, $n = 48$) was younger than of females preyed upon by wolves (8.1 yr, 95% CI = 6.94–9.26, range = 0.8–17.0 yr old, $n = 74$); those killed by miscellaneous causes (e.g., bobcat-kill, vehicle-kill, accidental death; see DelGiudice et al. 2002) were intermediate in age (6.7 yr, 95% CI = 5.22–8.18, range = 0.7–16.4 yr old, $n = 47$).

When we added data from the capture of neonates, the increase in the hazard for early ages became more pronounced (Fig. 2). We captured these individuals during Phase II; therefore, we cannot determine how the hazard may have changed for individuals < 0.6 years of age between phases of the study. However, these data suggest that the risk of death changes most dramatically for individuals from birth to 2 years old, then remains relatively stable for many years before exhibiting an increasing trend beginning at about 7 years old. The crude mortality rate for the neonates was 0.39 by 12 weeks and 0.51 by 6 months of age. Primary causes of mortality in ascending order of importance were wolf-kill (3.9%), hunter-kill (7.9%), unknown cause

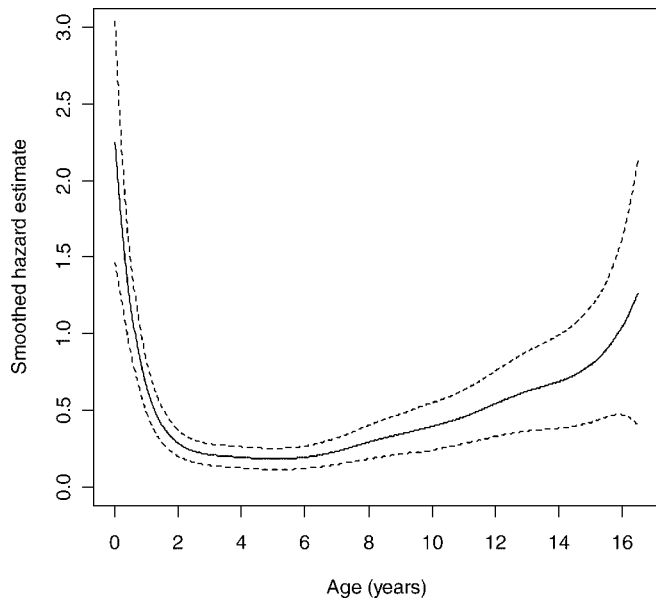


Figure 2. Penalized likelihood estimate (PLE) of the “all-causes” hazard (with Bayesian 90% confidence bands) for radiocollared, female white-tailed deer (including neonates), north-central Minnesota, USA. The data include 302 females ≥ 0.6 years old, monitored from 1 Jan to 31 Dec 2003, and 76 neonates (36 F, 40 M). We monitored female neonates from 28 May 1997 to 31 Dec 2003, whereas we censored males at 0.5 years old.

(10.3%), bobcat-kill (17.9%), bear-kill (20.5%), and unknown predator (23.1%)

GKM and INE estimates of $S(t)$.—The INE-estimate of $S(t)$ for our at-risk cohort (≥ 0.6 yr old) changed little from Phase I to Phase II of the study (Fig. 3a,b), despite increased sample sizes in the younger age classes (Fig. 3d,e) and lower overall estimated hazards during Phase II (Fig. 1a,b). By contrast, the GKM-estimated survival curve of the same cohort exhibited greater apparent sensitivity to sample size (and time), exhibiting precipitous declines in survival between ages 0.6 and 3.0 years during Phase I of the study, but shifting notably to the right during Phase II (Fig. 3a,b).

As expected, including newborn fawns in age-specific survival analyses markedly depressed the median ages of survival of our study cohort. The GKM and INE age-specific survival analyses generated median ages of survival of 0.43 (90% CI = 0.17–0.78 yr old) and 0.83 (90% CI = 0.79–1.45 yr old) years old, respectively, with the most precipitous declines in survival occurring between birth and 1 year old (Fig. 4).

Close inspection of the INE and GKM estimates of $S(t)$ suggests that the differences between the 2 estimators result largely from a few event times with small n_i . The GKM and INE estimates of $\hat{\theta}_{t_i}$ (equation [1]) differ most for t_i with small n_i and for t_i where $d_i > 1$ (i.e., for times where we observed multiple events). For our Phase I data, $n_i \leq 30$ for all t_i , and there are several observed deaths occurring before age 5.5 years, where $n_i \leq 15$, resulting in large drops in the GKM estimate of $S(t)$ (Fig. 3a,d). Two of these drops correspond to times with $d_i > 1$ ($d_i = 2$ at age 1.43 yr and 4 at age 2.45 yr). For our Phase II data, the size of the risk sets

are much larger and the 2 estimates are much more similar, with the INE giving slightly higher estimates of survival (Fig. 3b). The estimates diverge somewhat after the first event (at age 0.71 yr), where $n_i = 11$, and continue to slowly diverge as a result of slightly lower GKM values of θ_{t_i} for ages ≤ 2.43 years (2 deaths occur at age 2.43 yr). The size of the risk set ranges from 23 to 51 during this time. Somewhat surprisingly, the INE and GKM estimates for the combined adult data set are less similar than the corresponding estimates for Phase II (Fig. 3c compared to 3b), despite an overall increase in sample size (Fig. 3f). Again, the differences between the 2 estimators largely result from small GKM estimates of θ_{t_i} corresponding to event times with relatively small risk set sizes ($n_i < 40$) and a few t_i with multiple deaths. Differences between the 2 estimates become more pronounced after adding neonates (Fig. 4). In this case, $n_i < 40$ for ages 0.30–0.71 years and ages 1.22–1.46 years, and there are 6 occurrences with $d_i > 1$ for $t_i \leq 0.78$ years.

Population Projections: Comparing INE and GKM Estimates of $S(t)$ and Effect of Pooling Adults

Estimates of yearly survival from the data set that included all females ≥ 0.6 years old (1 Jan 1991–31 Dec 2003) and neonates (28 May 1997–31 Dec 2003) were similar for the GKM and INE, although INE-based estimates were notably higher for fawns. The projected long-term growth rate (λ) using the GKM estimates of yearly survival was 0.96, indicating that a population with these survival rates and assumed fecundity rates would decrease at a rate of 4% per year. By contrast, λ using the INE estimates of survival was 1.07, suggesting an increasing population.

Our Leslie matrix simulation results suggest that models that pool adults will result in biased estimates of λ , but this bias may be relatively small when compared to the variance of the estimates (Fig. 5a,b). The mean estimates of λ using Model 1 (pooling all adults) and Model 2 (pooling adults 1–7 yr and ≥ 8 yr old) were 1.03 and 1.06, respectively (compared to a true λ of 1.07). The observed age at capture distribution used in simulations was skewed towards younger individuals (Fig. 6a). Estimates of λ from Model 2 had smaller MSE than the corresponding estimates from Model 1 (0.0031 vs. 0.0041), even though estimates of survival for individuals ≥ 8 years old were quite imprecise compared to estimates of fawn survival and survival of all adults (Fig. 6c). On average, Model 2 appears to offer a good approximation to the true survival history (Fig. 6b). Thus, for these data, there is an advantage to estimating 2 separate adult survival rates (for ages 1–7 yr and ≥ 8 yr) when enough older individuals are present in the study cohort.

Discussion

Because our goal was to examine age-specific survival of female deer, the long-term study period was essential to accumulation of sample sizes representative of the female segment of the population. Recruiting females randomly over 13 winters (i.e., staggered entry design) contributed to a

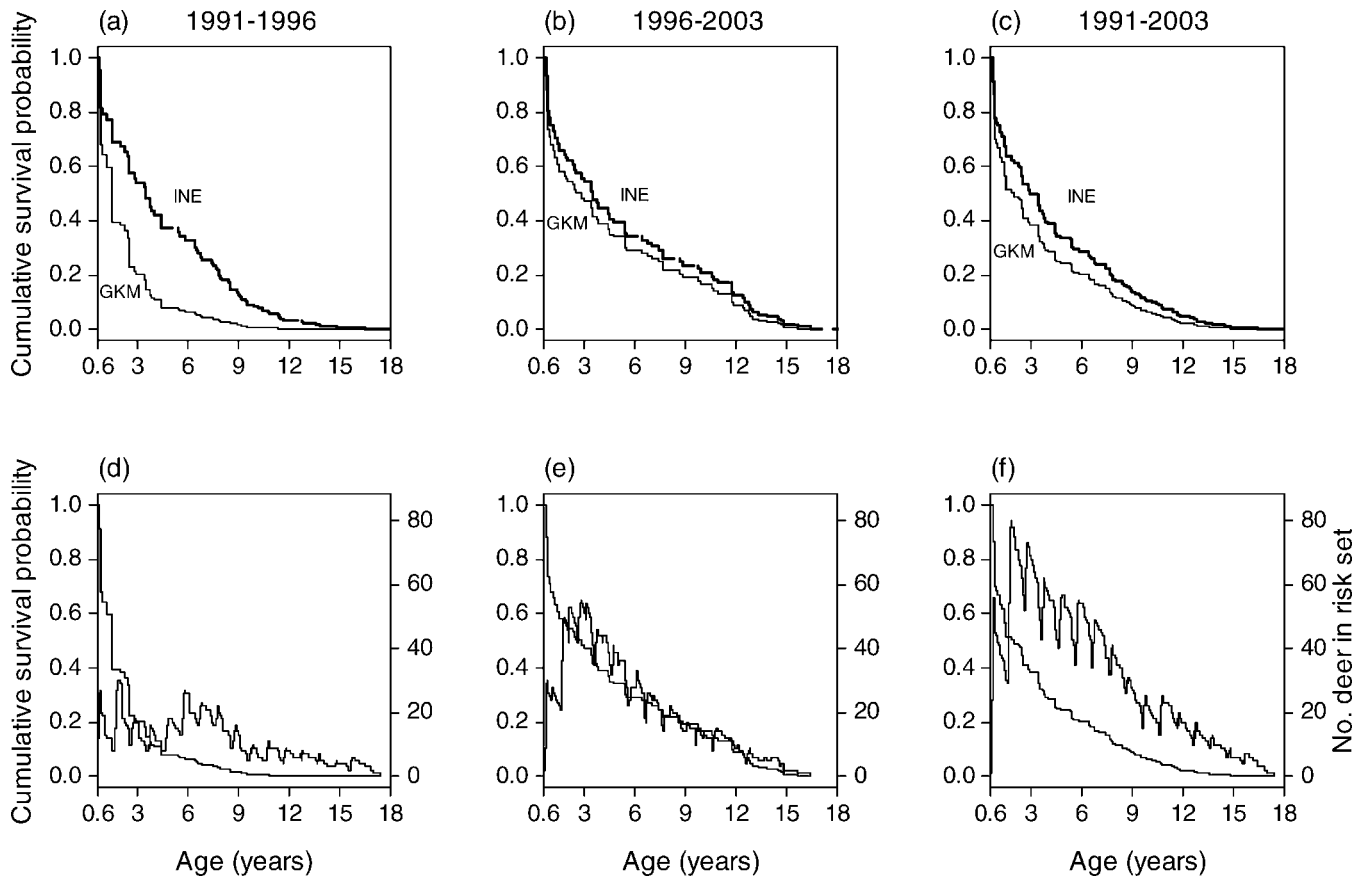


Figure 3. Comparison of generalized Kaplan-Meier (GKM) and iterative Nelson estimators (INE) of cumulative survival, $S(t)$, for radiocollared, female white-tailed deer (≥ 0.6 yr old), north-central Minnesota, USA for time periods: (a) 1 Jan 1991–8 Jul 1996, (b) 9 Jul 1996–31 Dec 2003, and (c) 1 Jan 1991–31 Dec 2003. Sample sizes associated with the GKM estimate of $S(t)$ are presented in (d) 1 Jan 1991–8 Jul 1996, (e) 9 Jul 1996–31 Dec 2003, and (f) 1 Jan 1991–31 Dec 2003.

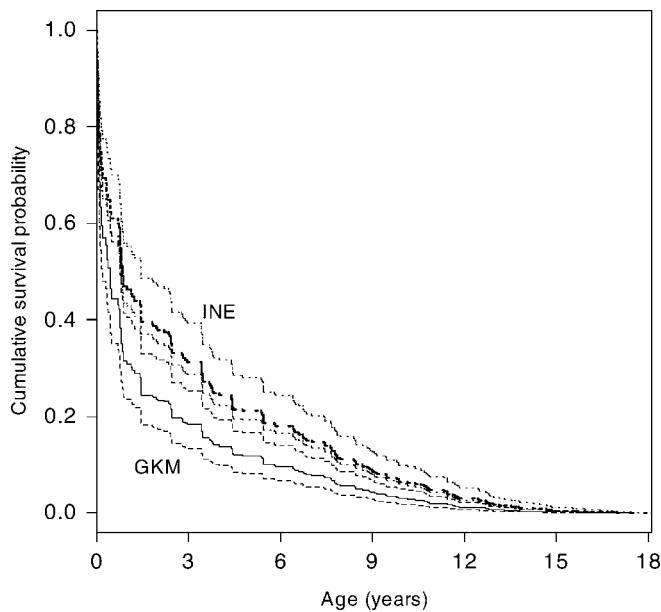


Figure 4. Generalized Kaplan-Meier (GKM) and iterative Nelson estimates (INE) of cumulative survival (with 90% confidence bands) using data collected on 302 radiocollared female white-tailed deer (≥ 0.6 yr old), north-central Minnesota, USA, from 1 Jan 1991 to 31 Dec 2003 and on 76 radiocollared neonates (36 F, 40 M) from 28 May 1997 to 31 Dec 2003. We censored males at 0.5 years old.

generally stable age distribution of our study cohort, which we believe allowed us to accurately track the target population. Consequently, this also minimized potential confounding (by changing age) of our interpretation of annual responses to weather conditions and cause-specific hazards. Further, our long-term data not only facilitated the description of age-specific survival and hazard patterns, they also provided the context for interpreting the importance of such factors to survival within the life cycle of the deer, thus contributing to our knowledge of the causes of such patterns (Eberhardt 1985, Franklin 1989, Tilman 1989, Gaillard et al. 1998). Long-term studies have also been useful for elucidating density-dependent responses (Festa-Bianchet et al. 2003) and senescence relative to survival (Eberhardt 1985). As our study progressed, we were able to incorporate additional objectives into its design. The most relevant example was the inclusion of neonate capture and radio-collaring during Phase II, facilitated by vaginal implant transmitters (Bowman and Jacobson 1998, Carstensen et al. 2003, Carstensen Powell 2004), which allowed us to address survival and cause-specific hazards from birth.

Ecological Interpretation of Hazard Curves

To date, most studies examining the survival of northern deer pooled adults (≥ 1.0 yr or 2.0 yr old) and reported on

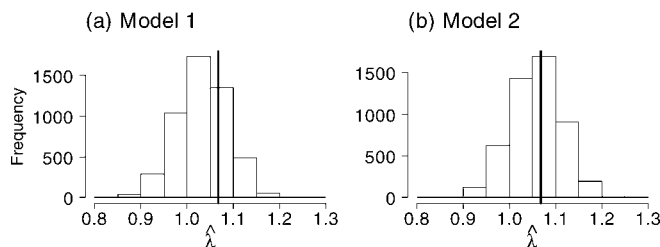


Figure 5. Sampling distribution of $\hat{\lambda}$, the long-term population growth rate from Leslie matrix models, obtained from 5,000 simulated data sets of yearly survival of female white-tailed deer. We formulated Model 1 (a) using a single estimate of adult survival (ages ≥ 1 yr pooled). We formulated Model 2 (b) using 2 adult survival estimates (ages 1–7 yr pooled and ages ≥ 8 yr). We determined survival rates using a binomial random number generator with probability of success determined using the age-specific yearly survival estimates obtained from the iterative Nelson (INE) estimate of cumulative survival, $S(t)$, applied to the data set that included all females ≥ 0.6 years old (1 Jan 1991–31 Dec 2003) and neonates (28 May 1997–31 Dec 2003).

the varying effects of winter severity on fawn or adult survival (Nelson and Mech 1986, White et al. 1987, Fuller 1990, McNay and Voller 1995, Van Deelen et al. 1997). Most of these studies reported higher survival rates for does than for fawns over a range of winter severities. A common assumption is that differences in survival among variously aged adults of each sex are minimal, but to our knowledge, a deer telemetry study has never specifically addressed this assumption. The U-shaped, all-causes, age-specific hazard curve reported by DelGiudice et al. (2002) indicates that the risk of death decreased for ages 1–5 years, then steadily increased for older ages. Others have discussed a typical hazard curve for animals that decreases with age for the immature individuals, is relatively constant for the mature prime ages, and increases with senescence (Siler 1979, Eberhardt 1985). Importantly, we observed that this U- or J-shaped curve persisted in Phase II (9 Jul 1996–31 Dec 2003) of our study; however, the lower, relatively stable risk of death for deer up to age 10 years during Phase II likely reflected differences in natural and human-related influences

compared to Phase I (1 Jan 1991–8 Jul 1996, Table 1). Specifically, following the historically severe winter of 1995–1996, with its crude mortality rate of 0.37 for females ≥ 0.6 years old, antlerless permits were suspended for the next 2 firearm seasons, and only a minimum number were issued during the 1998 season (Dexter 1996–1998), resulting in just one hunter-killed collared doe. Our findings that wolf predation had a greater impact on older does, whereas hunter pressure tends to be greatest on younger females is consistent with other studies (Mech et al. 1971, Mech and Frenzel 1971, DelGiudice et al. 2002). Interestingly, however, our wolf-caused, age-specific hazard curve closely mimics the respective all-causes curves in Phases I and II and shows that the risk of death by wolves began increasing after age 5 years during Phase I, whereas, during Phase II, when winter (i.e., snow) conditions were less severe, the risk of death by wolves was lower and stable through 10 years old. This lower hazard is consistent with the older mean age of females killed by wolves on our study area (8.1 ± 0.58 yr old, $n = 74$), where winters are less severe, compared to females killed by wolves in northeastern Minnesota (approx. 4.6 ± 0.49 yr old, Mech and Frenzel 1971; approx. 5.6 ± 0.84 yr old, M. E. Nelson and L. D. Mech, United States Geological Survey, unpublished data). Collectively, our data and the findings of DelGiudice et al. (2002) indicate that the consequences of assuming constant adult survival rates will likely depend on winter severity and its interaction with wolf predation, variation in annual hunting pressure, and age distribution of the study cohort. Researchers implicated winter severity and hunter harvest in survival differences of mule deer does between studies in northwestern Colorado (White and Bartmann 1983, White et al. 1987). Still others have emphasized the relevancy of age-specific survival to population change under varying natural and human-related circumstances, and of age-structure to determination of density-dependent survival for a number of ungulate species (Gaillard et al. 2000, Festa-Bianchet et al. 2003).

Monitoring of the survival of neonates captured during Phase II provided a more complete understanding of the

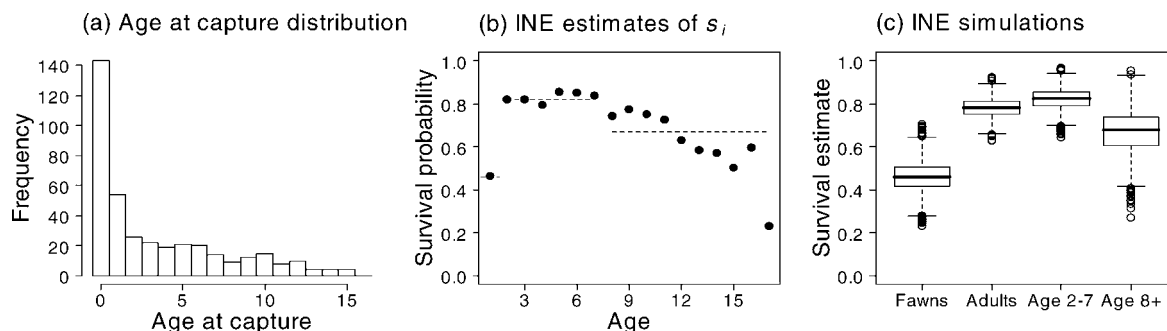


Figure 6. Results of 5,000 simulated data sets of yearly survival of 150 female white-tailed deer sampled from the study cohort's observed age-at-capture distribution (a). We determined survival rates using a binomial random number generator with probability of success determined using the age-specific yearly survival estimates obtained from the iterative Nelson (INE) estimate of $S(t)$, applied to the data set that included all females ≥ 0.6 years old (1 Jan 1991–31 Dec 2003) and neonates (28 May 1997–31 Dec 2003). In (b), the dotted line illustrates Model 2 (with fawn and adult survival parameters determined by the mean across the 5,000 simulated data sets). Panel (c) gives the distribution of survival estimates across simulated data sets, with fawn = survival from birth to age 1 year, adults = survival pooled across all adults (age ≥ 1 yr). Boxes bound the 25th and 75th percentiles, solid line within the box indicates the median, and the whiskers extend to 1.5 times the interquartile range of the observations.

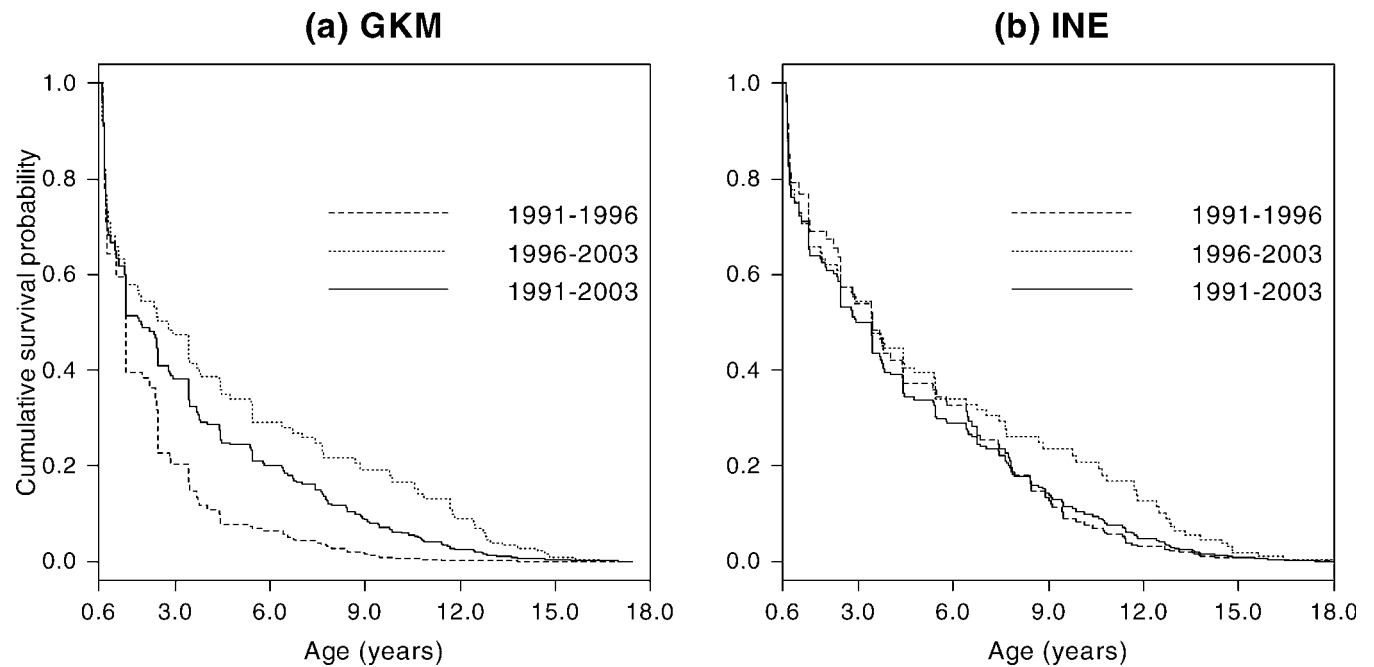


Figure 7. Comparison of (a) generalized Kaplan–Meier (GKM) and (b) iterative Nelson estimators (INE) of cumulative survival (with 90% confidence bands) for radiocollared, female white-tailed deer (≥ 0.6 yr old), north-central Minnesota, USA, during 1 Jan 1991–8 Jul 1996 (Phase I), 9 Jul 1996–31 Dec 2003 (Phase II), and 1 Jan 1991–31 Dec 2003 (combined data from Phases I and II).

age-specific all-causes hazard and survival of the female segment of the population. Clearly, the greatest risk of death for these deer occurred in the first 1–2 years of life, as has been indicated for other ungulates (Eberhardt 1985; Gaillard et al. 1998, 2000). The high mortality rate (0.39) by 12 weeks postpartum was similar to that reported by Carstensen Powell (0.45, 2004) for an expanded data set of neonates captured in 2001 and 2002, as was the importance of predation as the major source of mortality. Other studies have reported mortality rates of northern white-tailed neonates of 0.34–0.51 by 8–12 weeks postpartum (Kunkel and Mech 1994, Long et al. 1998, Ballard et al. 1999).

Comparison of GKM and INE Estimates of Survival

Staggered entry designs often result in small sample sizes in the left tail of the survival distribution (i.e., for early ages when using birth as the time origin or early times when using “start of the study” as the time origin). Our comparison of GKM and INE estimates of cumulative survival for Phase I clearly illustrates the potential bias that may result from applying the GKM to such data sets. With small sample sizes, 1 or 2 deaths can lead to substantial drops in estimated survival. The INE is more robust to problems of small sample sizes in the left tail of the distribution and may offer a viable alternative for survival estimation in studies employing staggered entry. The INE is closely related to the Nelson estimator (NE, also sometimes referred to as the Nelson–Aalen or Breslow estimator) of $S(t)$, which typically differs little from the GKM, except in the tail of the survival distribution (i.e., for large t) or when the size of the risk set is small (Therneau and Grambsch 2000, Winterstein et al. 2001). Fleming and Harrington (1984) suggest, based on theoretical grounds and simulation

work, that the NE of $S(t)$ has smaller variance than the GKM but has an upwards bias. Given the low variability of the INE across phases (Fig. 7), the lower INE estimate of survival in Phase II than Phase I for ages 0.8–2.2, and the close connection between the NE and the INE, we expect the INE may be biased slightly high for the Phase II data. Thus, when starting with a large n (e.g., Phase II and combined data sets), it is less clear which estimate is preferable. All 4 of the data sets considered, although relatively large compared to many wildlife survival studies, result in small n_i for early survival times. Therefore, we have a slight preference for the INE of $S(t)$ for these data. We argue this topic deserves more attention since little theoretical or simulation work has been done to compare the INE and GKM, and we know of no other applications of the INE in the literature.

To our knowledge, no other deer study has integrated neonate and adult survival analyses to estimate median age of survival for the female segment of a population. Although initially a median age of survival from the INE of 0.8 years old seemed low, our Leslie matrix model constructed using these survival estimates and what we feel are reasonable fecundity rates gave $\lambda > 1$, suggesting an increasing population. Indeed, according to independent population models applied to the region of our study area, this population has been increasing (M. Lenarz, MNDNR, personal communication). In truth, the assumptions of the deterministic model are not realistic; survival rates and population size were not constant over the course of the study, and there is considerable uncertainty regarding the assumed fecundity rates, as well as uncertainty in the estimated survival rates. Small uncertainties in demographic

parameters translate into large uncertainties in population projections, making it difficult to reliably predict the true status of the population (Fieberg and Ellner 2000, 2001). The actual value of these calculations is that they indicate the GKM and INE estimates of survival are reasonable and that population stability is possible despite the high mortality rates estimated during the first year of life. Thus, although we were initially surprised that a population with such a low median age of survival could sustain itself, it appears that the relatively high survival rates for prime age deer, combined with high pregnancy rates and a tendency for does to produce twins, is sufficient for population stability.

Management Implications

Managers often set population and harvest goals using deer models that follow a small number of age classes (e.g., <1 yr, ≥1 yr). We've demonstrated that hazard functions may be used to determine appropriate age boundaries for pooling deer into age classes prior to estimating survival inputs for these management models, particularly when sample sizes are limited in portions of the age distribution. Further, our study's findings indicate that managers should consider the impact of environmental variation (e.g., winter severity) and

its interactions with predation and age distribution of the population when setting harvest goals.

Acknowledgments

The MNDNR supported our study, with supplemental funding provided by the Minnesota Environmental and Natural Resources Trust Fund, as recommended by the Legislative Commission on Minnesota Resources, Minnesota Deer Hunters Association, and the Special Projects Foundation of the Minneapolis Big Game Club. D. E. Pierce of the MNDNR, the Cass County Land Department, the United States Forest Service, Potlatch Corporation, and the Blandin Paper Company provided invaluable cooperation and logistical support. We gratefully acknowledge B. A. Sampson and D. W. Kuehn for their efforts in all aspects of the study. R. Nelles, R. Schloesser, and more than 120 field biology interns provided invaluable assistance with animal capture, care, and handling. Finally, we thank fixed-wing pilot, R. Wheaton, for his assistance in monitoring the survival of radiocollared deer, and J. Olson and the crew of Helicopter Capture Services, Inc., for their expert performance in net-gunning deer. B. Patterson, J. M. Gaillard, and K. H. Pollock provided useful comments that helped improve the manuscript.

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Associate Editor: Patterson.