On Improving Telemetry-Based Survival Estimation

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Abstract

Survival estimation is an important aspect of population ecology and conservation biology, and radiotelemetry is a major tool for assessing factors influencing survival time in free-ranging birds and mammals. Despite the advantage of telemetry in providing extensive and continuous survival information, telemetry-based survival estimates can be biased or imprecise when methods are misused. Simple cumulative survival estimators like the Heisey and Fuller and Kaplan-Meier methods have underlying assumptions and sampling requirements that commonly remain unverified by researchers. Telemetry studies often limit survival analysis to simple univariate tests that do not consider the range of factors potentially influencing mortality risk in free-ranging animals. Continuous-time modeling approaches like Cox Proportional Hazards or Anderson–Gill methods, or their discrete-time analogues, are superior because they are robust to a range of study design limitations and can handle multiple categorical or continuous covariates including those that vary with time or subject age. Parametric models may be difficult to fit in telemetry studies because the appropriate hazard function in wildlife populations usually is not known. The main assumptions in survival study design are that 1) subjects represent the population of interest, 2) mortality risk is independent between subjects, and 3) subjects are lost to follow-up (i.e., censored) randomly. These assumptions are prone to violation in telemetry research, and their assessment and possible remediation should be prioritized. Telemetry studies often are characterized by small sample size or short duration; both attributes lead to low numbers of mortalities and thus lack of precision in the survival estimate. I conclude that telemetry-based survival estimation will benefit from increased emphasis on modeling approaches designed to elucidate survival determinants in complex systems, combined with more rigorous attention to basic assumptions and study design limitations. (JOURNAL OF WILDLIFE MANAGEMENT 70(6):1530–1543; 2006)

Key words

Survival estimation is an important aspect of wildlife population biology. Survival rates derived from studies on free-ranging animals are crucial for addressing basic questions in ecology and in the development of population models and species conservation and management programs (e.g., Lebreton et al. 1992, Beissinger and Westphal 1998, McCallum 2000, Reid et al. 2002). Over the last decade, wildlife survival estimation has improved in rigor and level of insight, largely through the use of software designed for modeling complex survival functions (Harrell and Goldstein 1997, White and Burnham 1999, Williams et al. 2002). Yet, while the above-mentioned advances have improved the potential for accurate survival estimation, concern remains over bias and lack of precision in survival estimates derived specifically from ecological research (Krebs 1999, McCallum 2000, Fox 2001, Winterstein et al. 2001, Williams et al. 2002, Zens and Peart 2003). Such concern stems from the fact that longitudinal survival data require specialized analytical techniques not commonly encountered in basic statistics courses or textbooks, and constraints in the design and implementation of field studies can limit both analytical options and levels of statistical inference. Thus, conducting robust survival estimation in studies of free-ranging animals often can be challenging.

I reviewed recent (1989–2004) *Journal of Wildlife Management* papers involving survival estimation ($n = 256$) and found that 64.1% of studies used radiotelemetry to assess survival, compared to fewer studies using either population counts (6.6%) or capture–recapture methods (32.3%; includes live encounter, dead recovery, and mixed-recovery

models). While it is conceivable that telemetry-based survival research may be over-represented in the *Journal of Wildlife Management*, telemetry doubtless will remain the principal tool for estimating survival in free-ranging birds and mammals for the foreseeable future. The advantage of telemetry over alternate survival monitoring methods is that 1) death events and their specific cause can be confirmed when transmitters are equipped with mortality sensors, and 2) survival status can be evaluated non-invasively and more intensively via radiomonitoring. Yet, although the availability of telemetry technology has revolutionized survival estimation for many species, constraints like the high cost of transmitters compared to other markers, and the difficulty in deploying non-invasive radios on smaller animals, can limit the use of telemetry in survival studies. An additional consideration is that telemetry-based survival data often include incomplete observations (right-censoring) when subjects are lost to follow-up due to transmitter failure or emigration from the study area; specialized techniques are required to fully utilize survival information derived from such animals.

Violation of basic assumptions and study design limitations in telemetry studies can lead to biased or imprecise survival estimates (White and Garrott 1990, Bunck et al. 1995, Krebs 1999, Tsai et al. 1999*b*, Winterstein et al. 2001, DelGiudice et al. 2002, Williams et al. 2002). Basic principles for reducing bias and increasing precision in survival estimation have been described extensively for human medicine and clinical trials (see Anderson et al. 1980, Pocock 1983, Marubini and Valsecchi 1995, Buyse et al. 1996, Harrell et al. 1996). Yet, accuracy assessment in telemetry-based survival research has received only modest

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attention (Winterstein et al. 2001, Williams et al. 2002), implying that critical review of this topic and development of standardized guidelines is warranted.

Accuracy in Survival Estimation

Survival Function

Individuals in a population have heterogeneous survival or mortality rates (survival = 1 − mortality) that are determined by genetic, demographic, and environmental factors. The aim in modern survival research is to quantify the influence of such factors on baseline survival rates. Telemetry-based survival data consist of repeated observations (radio signals) that reveal whether a subject is alive, dead, or missing (i.e., no signal) during a monitoring session. Collectively, such observations serve to build the survival function, $S(t)$, which represents the cumulative probability of survival of an individual at least until a specified time, t;

$$S(t) = P(T \geq t),$$

where T, the survival time, is a random variable (Collett 2003). T can be considered as continuous or discrete (Lawless 1982), and it follows that the precision by which a subject's time-to-death is estimated is directly related to the frequency by which t is measured; more frequent monitoring leads to shorter time intervals and a more representative survival function (Fig. 1a for several examples of continuous survival functions).

Binomial Estimation

To illustrate potential shortcomings in survival estimation, consider the binomial model where survival is determined simply by the number of subjects (n) and deaths (d) at the end of the study:

$$S = 1 - (d/n)$$

This estimator fails to make full use of telemetry data because it classifies survival status discretely (dead or alive) over an extended time interval and therefore ignores differences in time-to-death among individuals. It follows that the resulting survival estimate will be biased unless the mortality rate is constant through time. The binomial approach also suffers from assumptions that limit its relevance in telemetry studies: 1) all subjects should be recruited to the study at its outset (i.e., no delayed entry) otherwise individuals will differ in their baseline mortality risk, and 2) subjects are not lost to follow-up (i.e., no right-censoring) because animals whose fate is unknown cannot be counted as dead or alive at the end of the study (see Ingram and Kleiman 1989, Doksum and Gasko 1990). Despite these restrictions, the binomial estimator remains in use in telemetry studies (e.g., Whitten et al. 1992, Stuart-Smith and Boutin 1995, Swenson et al. 1999, McCorquodale et al. 2003, Theberge et al. 2006), even though more powerful survival estimators are readily available.

Survival Estimation without Explanatory Variables

The majority of telemetry-based survival studies describe cumulative survival over time using simple estimators that extend the binomial model. These methods differ in their specific design, assumptions, and data requirements, which can lead to differences in their overall performance.

Heisey and Fuller method.—The Heisey–Fuller (HF) method (Trent and Rongstad 1974, Heisey and Fuller 1985) is derived from the Mayfield and other nest survival estimators (Mayfield 1975, Krebs 1999), where survival rate over a discrete time unit (usually a day) is determined from the number of death events (d) per radio-days (r):

$$S = 1 - (d/r),$$

with variance,

$$\text{var}(S) = S(1 - S)/r$$

The HF assumes that survival probability is constant within each defined time interval, which is akin to having a random chance of mortality at any given point within the interval. Therefore, the HF is parametric and analogous to a piecewise exponential model (Trent and Rongstad 1974, see also Hougaard 2000). Because of the constant survival restriction within intervals, daily survival rate easily translates to that for an interval comprised of t days, through exponentiation: $S(t) = S^t$. This estimator can then be extended to populations where survival rates vary over I intervals:

$$S = \prod_{i=1}^{I} S_i$$

The HF provides a simple way of representing a variable survival function, and it may be particularly appropriate for populations where mortality risk is constant for short periods but changes periodically (e.g., Miller et al. 1998, Ballard et al. 1999, Williams et al. 2004). However, even minor variation in survival rate within a time interval can impose bias on this estimator (Tsai et al. 1999*b*), so the assumption of constant survival within an interval needs to be tested explicitly, preferably a priori (Williams et al. 2002). It follows that this constraint can be challenging for populations with unknown survival patterns or when mortality risk is never stationary. Published HF intervals tend to range over biologically meaningful time units such as seasons or years (Ballard et al. 2000, Hayes et al. 2000, Kamler et al. 2002), but only a handful of recent papers (e.g., Clark et al. 1989, Dusek et al. 1992, Pletscher et al. 1997) are explicit about testing for constant survival probability within HF intervals. Most researchers test the assumption by examining survival rates qualitatively across time, but an alternative would be to fit parametric models to the survival data to confirm constant survival probability. The HF survival estimates are easily calculated using program MICROMORT (Heisey and Fuller 1985), but if survival monitoring is conducted at ragged (irregular) intervals, the HF estimator should be substituted with a likelihood-based alternative to correct for bias (Johnson 1979, Bart and Robson 1982; see also Miller and Johnson 1978, Hensler and Nichols 1981).
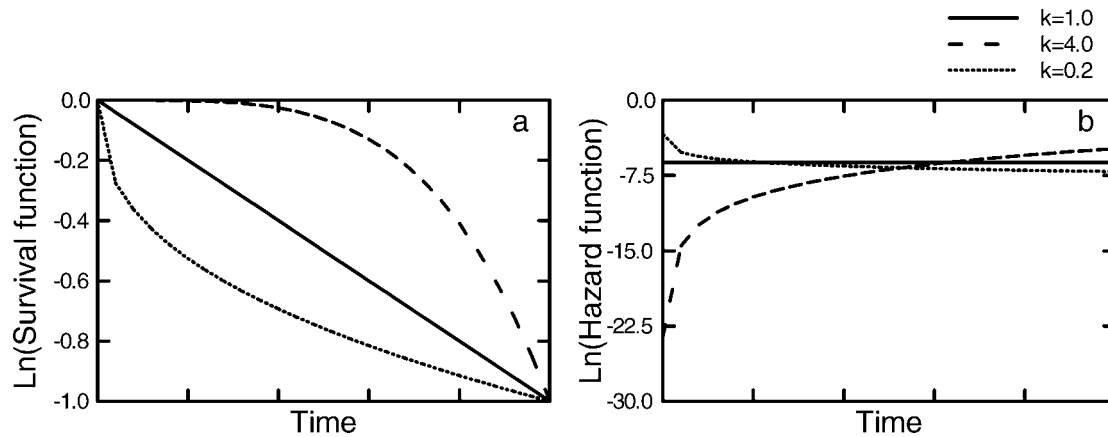
Figure 1. Natural-log transformed survival (a) and hazard (b) functions from a Weibull distribution with a fixed hazard rate (0.002). Three different values of the dimensionless shape parameter, k, are graphed.

Kaplan–Meier method.—The Kaplan–Meier (KM) approach (Pollock et al. 1989a,b) is the survival estimator of choice in most statistical software programs and has gained widespread use in wildlife research (Winterstein et al. 2001). The KM differs from HF estimation by considering the specific timing of death events in defining the survivor function; this is achieved by relaxing the assumption of constant survival within the interval and instead defining interval endpoints by the mortality events themselves. Survival rate for k unique death times is calculated as the product of survival during each of the separate intervals, i:

$$S = \prod_{i=1}^{k}[1 - (di/vi)]$$

where d_i is the number of deaths and v_i is the number of subjects at risk during i. Variance can be calculated using Greenwood's formula (Pollock et al. 1989a):

$$\text{var}(S) = S^2\left[\sum_{i=1}^{n}\left(\frac{d_i}{v_i(v_i - d_i)}\right)\right]$$

Because death events define interval lengths, logically the KM estimator follows a step-function where survival is constant within intervals. For example, KM survival estimates were calculated for 52 moose (*Alces alces*) calves that received radiotransmitters shortly after birth and were monitored for up to 2 years (D. Murray, Trent University, unpublished data; Fig. 2a). The KM estimator leads to a disjunct survival function when mortality patterns are pulsatile, such as during the early (<30 days) neonatal period when calves suffered high mortality (Fig. 2a). One drawback associated with KM estimation is that a new parameter is estimated with each death event, so low precision is a natural consequence of high mortality (Miller 1983). In theory, tied death times are not possible using the KM method and require special consideration (Hosmer and Lemeshow 1999, Collett 2003, but see Pollock et al. 1989a).

The KM method initially was developed for clinical trials where all subjects enter the study at its well-defined time origin (Lee 1992). However, delayed recruitment of subjects is common in telemetry studies (e.g., Carroll 1990, Harmata et al. 1999, Porter et al. 2004), and under such conditions the generalized KM (GKM) estimator should be used because it adjusts conditional probability of survival for late recruits (Cox and Oakes 1984, Pollock et al. 1989a). However, the GKM is sensitive to small sample sizes, specifically if early mortality events occur prior to recruitment of an adequate sample of subjects (Woodroofe 1985). Furthermore, absurd survival estimates may be produced when late recruits enter the study after all individuals from the initial subject group have died or are lost to follow-up. In such cases the counting process analogue of the KM estimator, the Nelson-Aalen estimator, should be adopted because of its superior small sample properties (Pan and Chappell 1998, DelGiudice et al. 2002).

Comparison between estimators.—The main distinguishing feature between the HF and KM estimators is the determinant of time interval endpoints, and by extension, the assumption of constant survival probability during the interval (Bunck et al. 1995, Winterstein et al. 2001). However, the basic structural similarity of the 2 approaches causes convergence in survival estimates when HF intervals are radio-days (Pollock et al. 1989a). Although it is not practical or efficient to adjust HF survival timelines to achieve such convergence, the important point is that in most cases the 2 methods should provide comparable results provided that their respective assumptions and sample size needs are met. In general, HF may be preferable over KM when mortality events are particularly common or rare, if mortality occurs in identifiable pulses, or if cause-specific mortality rates are of interest. Alternatively, KM may be superior if mortality rates are never stationary during the study or if intervals with constant survival cannot be identified objectively.

Statistical comparison of survival rates.—To test for differences in HF survival rates between groups, confidence limit overlap can be determined using the z-statistic for 2 groups or using contingency tables for ≥ 2 groups (Heisey and Fuller 1985, Sauer and Williams 1989). Comparison of KM survival curves usually occurs via nonparametric like-
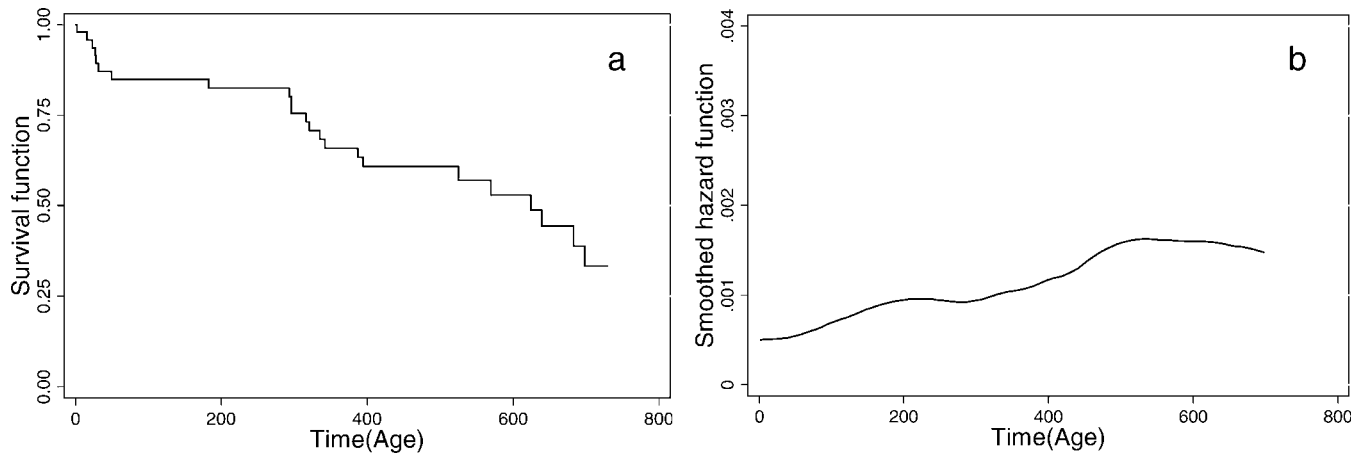
Figure 2. Kaplan–Meier survival function (a) and smoothed instantaneous hazard function (b) for 52 moose calves monitored for survival in northwestern Minnesota, USA. The smoothed hazard function was obtained using the Epanechnikov smoothing function (see Klein and Moeschberger 2003).

lihood ratio tests, log-rank tests, or Wilcoxon tests (Lee 1992, Hosmer and Lemeshow 1999). My review of the literature revealed that the majority of telemetry-based survival studies published in *Journal of Wildlife Management* (1989–2004) restricted survival analysis to the above simple tests, despite their limited value when used with observational data. Indeed, the log-rank and Wilcoxon tests were developed for hypothesis tests in clinical trials (where randomization and balanced designs are the norm), making these methods both sensitive to differential censoring and mortality rates and weak when multiple variables are considered (Hutchings et al. 1991, Bull and Spiegelhalter 1997). Furthermore, they are not amenable to temporal variation in covariate effects, nor to continuous covariates or their interactions. It follows that these simple tests have limited value in the analysis of survival data from complex and uncontrolled field studies, and therefore I recommend that their exclusive use should be scrutinized. My recommendation is analogous to that proposed for estimating avian nest survival rates, where until recently the Mayfield and related estimators were used extensively despite their known restrictive assumptions and limitations (Williams et al. 2002, Rotella et al. 2004).

Survival Estimation with Explanatory Variables

The complexities of survival estimation in observational telemetry studies can be addressed more effectively by fitting multivariate survival models than by using the simple tests I described above. Similarly, nest survival estimation is now commonly modeled using multivariate approaches that are designed to overcome limitations imposed by simpler estimators (Dinsmore et al. 2002, Jelhe et al. 2004, Nur et al. 2004, Rotella et al. 2004, Shaffer 2004). Currently, survival modeling in wildlife telemetry research falls into discrete-time versus continuous-time approaches, with the discrete-time approach considering the number of deaths over distinct, fixed-length time intervals and continuous-time methodology tracking time-to-death across uninterrupted timelines. Each method has its own analytical

approach and philosophy, and to date the 2 have remained surprisingly distinct even though they should provide comparable results under most circumstances (see Holford 1980, Efron 1988, Williams et al. 2002). Documentation supporting the theory and application of discrete-time methods specifically for telemetry studies is scant, but maximum-likelihood methods used in nest-survival analysis (Dinsmore et al. 2002, Jehle et al. 2004, Rotella et al. 2004) are relevant. In contrast, there exists a broad literature on survival estimation using continuous-time methods applicable to telemetry data (see Lawless 1982, Cox and Oakes 1984, Lee 1992, Hosmer and Lemeshow 1999, Kalbfleisch and Prentice 2002, Collett 2003, Klein and Moeschberger 2003). Although I place greater emphasis on continuous-time methods in the following discussion of survival models, it is clear that basic assumptions and study design limitations are applicable to both approaches.

Hazard function.—Although the survival function and survival rate are of primary interest in cumulative survival estimators like HF and KM, statistical modeling of survival data typically involves estimation of the hazard function, $h(t)$, which corresponds to the probability of death at age t, given survival to t (Collett 2003). Conceptually, $h(t)$ represents the instantaneous probability that an individual will die in an infinitesimally small time interval, conditional upon survival to the beginning of the interval;

$$h(t) = \lim_{\Delta t \to 0} \frac{P(t \leq T < t + \Delta\ t | T \geq t)}{\Delta t}$$

$S(t)$ is directly related to $h(t)$ such that a survival function can be determined if the hazard is known, and vice versa (Collett 2003). An analogous relationship between $S(t)$ and $h(t)$ exists for discrete-time models (see Lawless 1982).

Survival and hazard functions can follow a variety of shapes fitting to a range of statistical distributions (Fig. 1). In the simplest case, $h(t)$ is constant and the corresponding survival function follows an exponential decay (i.e., if $h(t) = \theta$ then $S(t) = \exp^{-\theta t}$, see Fig. 1). Survival trends in a population sometimes can be described by a monotonically

Table 1. Cox proportional hazard (CPH), Weibull, and Exponential regression models of survival in 52 juvenile moose in northwestern Minnesota, USA, 1995–2000. Transmitters were deployed on calves in the first week following birth and survival was monitored for up to 2 years. Female calves were coded as 1.

Model	Covariate	Hazard ratio	SE	z	P	Model P	AIC[a]
CPH	Gender	0.279	0.130	2.74	0.006	0.006	150.280
Weibull	Gender	0.407	0.169	2.17	0.030	0.035	124.566
Exponential	Gender	0.383	0.157	2.34	0.019	0.019	123.318

[a] Akaike's Information Criterion.

increasing or decreasing mortality risk fitting a Weibull distribution (McCallum 2000, Fox 2001), but if temporal variability in mortality risk is pronounced, more complex functions may better capture trends in hazards (Heisey and Fuller 1985, White and Garrott 1990, Tsai et al. 1999a). In human medicine, hazard functions tend to use subject age or time since study initiation as the time variable (Collett 2003, Klein and Moeschberger 2003), but many wildlife studies consider calendar time as the temporal variable especially when subject ages are not known or if seasonal fluctuations in mortality risk are pronounced and repeatable (see Tsai et al. 1999a).

Practically speaking, a hazard function can be fit to survival data by first estimating the cumulative hazard function for the dataset, $H(t)$, which represents the cumulative number of deaths per individuals at risk and is associated to the KM survival function by $H(t) = -\ln[S(t)]$ (Klein and Moeschberger 2003). An alternate method for estimating cumulative hazard, which has better small-sample properties, is the Nelson–Aalen (NA) estimator:

$$H(t) = \sum_{t_i < t} d_i / v_i$$

with variance,

$$\mathrm{var}[H(t)] = \sum_{t_i < t} d_i / v_i$$

where d_i and v_i are as described above. The derivative (slope) of the NA function provides a crude estimate of $h(t)$, and the continuous hazard function can be approximated by non-parametric smoothing or by parametric splines (Klein and Moeschberger 2003; see Fig. 2b). However, the particular choice of a smoothing function and bandwidth can have substantive influence on the shape of the function and thus should be based on both statistical cross-validation and biological plausibility (Mueller and Wang 1994, Joly et al. 1998, Hess et al. 1999, Tsai et al. 1999a). Qualitatively, the hazard function for the moose calf dataset (Fig. 2b) illustrates a gradual increase in mortality risk up to about day 500, followed by a shallow decline in hazards thereafter.

Cox proportional hazards.—The Cox proportional hazards (CPH) model is based on partial likelihood analysis and is the most widely used multivariate survival analysis procedure in the medical and social sciences (Singer and Willett 1991, Allison 1995). If $h_i(t)$ is the hazard function for individual i at time t, and the ith individual is associated with a covariate vector $x_I = (x_{i1}, x_{i2}, \dots, x_{ip})$, then the CPH model is

$$h_i(t) = h_0(t)\exp(\beta_1 x_{i1} + \beta_2 x_{i2} + \dots + \beta_p x_{ip})$$

where $h_0(t)$ represents the baseline hazard corresponding to the hazard function of an individual with covariate vector $x_I = (0,0,\dots.0)$, and β is an unknown parameter (Hosmer and Lemeshow 1999, Collett 2003). The CPH model is considered to be semiparametric because the parametric form of the hazard is not actually specified, but $h_i(t)$ and $h_j(t)$ differ only such that the hazard ratio, $h_i(t)/h_j(t) = \exp(\beta)$, is not time-dependent. In other words, $h_i(t)$ and $h_j(t)$ are proportional through time and differ multiplicatively by the exponential term involving the covariates. Thus, the CPH model is equivalent to a piecewise exponential model with constant hazards. Because the CPH model does not assume a specific hazard function, it is robust to the range and variability of hazards typically encountered among wildlife populations.

Hazard ratios are generated for each variable in CPH models and allow for rigorous interpretation of covariate effects (Riggs and Pollock 1992, Hosmer and Lemeshow 1999, Collett 2003). Referring to the moose calf dataset, CPH analysis revealed that the overall mortality risk of female calves was ~0.28 that for males (Table 1). However, because CPH models lack an underlying parametric form, the tendency may be to restrict model interpretation to covariate effects without exploring important information contained in the hazard function and its survival distribution (Singer and Willett 1991, Hosmer and Lemeshow 1999). For example, all that was revealed by the moose calf model output was that females had lower mortality risk than males, but closer examination of the survival function by gender (Fig. 3a) shows coincident pulses in mortality risk when calves were aged 1–30 and 320–400 days. Qualitatively, male yearlings experienced an overall steeper increase in late hazards (up to about day 500) compared to females (Fig. 3b).

Covariates influencing survival may be fixed or vary temporally, and the CPH model is easily extended to accommodate time-dependent covariates (Hosmer and Lemeshow 1999, Collett 2003). In the wildlife literature, time-dependent covariates include environmental conditions, location, age, and time itself (Cox et al. 1998, Krapu et al. 2000, Pietz et al. 2003, Johnson et al. 2004) but could also include factors like body condition, behavior patterns, breeding or dispersal status or habitat. With the advent of Global Positioning System and satellite telemetry, it is now possible to merge explicit spatial information with survival data at a fine temporal scale. This should lead to improved survival analysis for individuals occupying a variety of areas
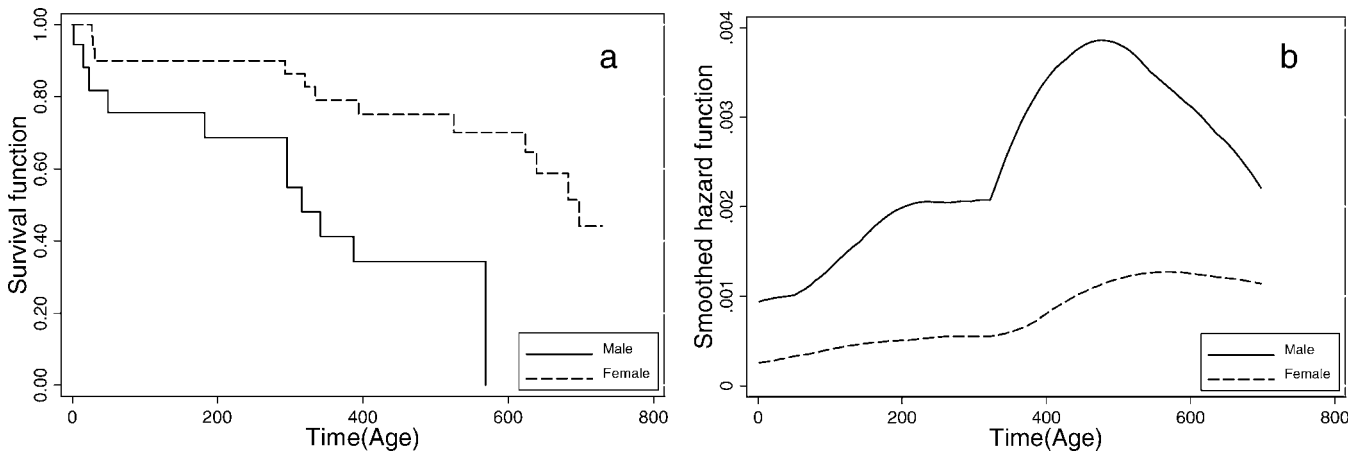
Figure 3. Gender-specific Kaplan–Meier survival function (a) and smoothed instantaneous hazard function (b) for 52 moose calves monitored for survival in northwestern Minnesota, USA. The smoothed hazard function was obtained using the Epanechnikov smoothing function (Klein and Moeschberger 2003).

during their lifespan, each with a specific mortality risk. However, the choice of the particular form of the time-dependent covariate (discrete vs. continuous, current-time vs. time-lagged, etc.) can exact substantive influence on the outcome of the analysis and therefore requires careful consideration (Andersen 1991, Harrell 2001, Pollock 2002); if time-dependent covariates follow complex patterns or are interactive with other covariates, then model interpretation will be difficult (Fisher and Lin 1999).

The assumption of proportional hazards is critical to CPH model fit and requires verification through model re-estimation, analysis of residuals, or a variety of graphical methods (Therneau et al. 1990, Gail 1991, Lin et al. 1992, Grambsch and Therneau 1994). For example, hazards between genders in the moose dataset were proportional using a test of the distribution of Schoenfeld residuals ($\chi^2_1 = 0.77$, $P = 0.38$), and KM survival curves were largely parallel across genders when plotted on a log-scale (Fig. 4). However, because hazards are not considered explicitly in the CPH modeling procedure, it may be tempting to assume that hazard proportionality is upheld without conducting the appropriate tests (Singer and Willett 1991). My review of *Journal of Wildlife Management* survival papers indicated that a minority of telemetry studies where CPH model structure could be inferred from the text ($n = 17$) actually provided evidence that the assumption of proportional hazards had been tested. This apparent lack of model checking is alarming but consistent with my overall finding that statistical reporting of survival analysis methodology in the wildlife literature is deficient (see also Andersen 1991).

When the proportional hazards assumption fails to be satisfied, a stratified CPH model should be estimated where different baseline hazard functions are assumed across strata. This modification implies that the relationship between survival and the variable used to define the stratum cannot be estimated directly, but rather that interstrata comparisons need to be conducted by comparing differences between survival rates (Hosmer and Lemeshow 1999, Therneau and Grambsch 2000, Collett 2003). Alternatively, in the absence

of proportional hazards, the time axis can be partitioned to accommodate shorter time periods, time-dependent covariates can be used to model nonproportionality, or alternative models such as accelerated failure time or additive hazards can be used (Therneau and Grambsch 2000).

Andersen–Gill models.—When subject timelines are punctuated by monitoring gaps, hazards become discontinuous and therefore not amenable to standard CPH analysis. In wildlife research, such gaps can be common when animals are periodically absent from the study area and radio contact is temporarily lost or if transmitters fail and subjects only receive new units at a later time. Although it may be tempting to infer continuous survival time for subjects experiencing temporary monitoring gaps, such interpolation is biased in favor of individuals whose fate ultimately is known, and thus it should be avoided (Bart and Robson 1982, Bunck et al. 1995, Winterstein et al. 2001). Instead, the Andersen–Gill (AG) model constitutes a counting process analogue to the standard CPH model that handles discontinuous time intervals (Andersen and Gill 1982,
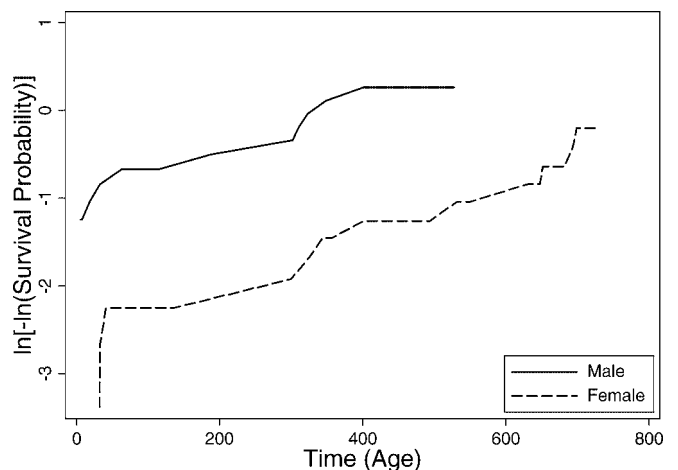

Figure 4. Natural-log transformed smoothed hazard estimates for 52 moose calves monitored for survival in northwestern Minnesota, USA.

Fleming and Harrington 1991, Andersen et al. 1993). The AG model has yet to receive widespread application in the wildlife literature, although 2 recent exceptions are worthy of mention: DelGiudice et al. (2002) used AG models to evaluate factors associated with mortality in a white-tailed deer (*Odocoileus virginianus*) population, and Johnson et al. (2004) used AG models to examine spatial influences on grizzly bear (*Ursus arctos*) mortality risk. In both studies, AG models allowed researchers to include survival data from animals with monitoring gaps and delayed entry into the study. Thus, AG models hold promise for telemetry-based studies especially where subjects are long-lived or widely ranging and disjunct monitoring timelines are prevalent.

Parametric models.—Although nonparametric continuous-time models probably serve most wildlife survival analysis needs, sometimes a fully parametrized hazard function might be preferred either to test hypotheses about the shape of the hazard function, to fit parsimonious survival estimates based on specific hazards, or to produce age-specific survival rates when such rates cannot be calculated directly from the data (Allison 1995, McCallum 2000, Collett 2003). However, for many wildlife populations, our knowledge of the shape of the hazard function is inadequate to select a parameteric relationship a priori (White and Garrott 1990, Williams et al. 2002), leaving analysts with the need to determine $h(t)$ through post hoc diagnostic tests. Also, if delayed entry into the study is extensive, or if age-specific survival rates differ and age information is incomplete for the population, determining the precise baseline hazard function will be problematic. Thus, parametric survival models are especially useful in cases where specific cohorts are monitored through time and the underlying hazard function follows a simple trajectory.

I detected only rare instances where parametric models were fit to wildlife survival data (e.g., Sievert and Keith 1985, Krementz et al. 1994, Murray et al. 1997, Gregg et al. 2001). Gregg et al. (2001) used Weibull survival models to analyze factors influencing survival of pronghorn (*Antilocapra americana*) fawns up to ~60 days from birth. Weibull models were selected after diagnostic plots revealed that mortality risk declined with age, and this observation was supported statistically by the fitted models. Fitting the moose calf dataset to a Weibull distribution reveals that hazard differs across genders (Table 1). Notably, the dimensionless parameter affecting the shape of the Weibull function does not differ from 1 ($\theta = 0.822 \pm 0.200$, $z_1 = 0.81$, $P = 0.42$), implying that from a statistical perspective moose hazard rate was constant through the 2 years of monitoring. Fitting an exponential model to the same data provides a comparable gender-based hazard ratio but with higher precision (Table 1) and a more parsimonious explanation of mortality risk with comparable statistical inference ($\Delta AIC = 1.248$).

Discrete-time models.—Discrete-time methods designed to estimate survival in nest surveys or live encounter studies can be expanded to accommodate telemetry survival data by assuming that recapture probability (i.e., probability

of determining the subject's survival status during monitoring) is equal to 1 (White and Garrott 1990, Williams et al. 2002). This approach uses information on the number of subjects that die within discrete time intervals, conditional upon the sample of animals at risk at the beginning of the interval, to estimate the probability of survival from t to $t+1$ (White and Burnham 1999). The probability of death is expressed using binomial likelihoods, and survival can be modeled as a nonlinear function of individual covariates or group effects. A link function is necessary to characterize the relationship between the survival rate and covariates, and the logit is the standard because it is bounded by 0 and 1 and is logically related to the binomial distribution (White and Burnham 1999, Williams et al. 2002). For example, using the logit as the function linking survival time to a dichotomous (0,1) group effect, x, the following survival model can be generated;

$$\ln\{s(x)/[1 - s(x)]\} = b_0 + b_x$$

It follows that $\ln\{s(0)/[1 - s(0)]\} = b_0$, and $\ln\{s(1)/[1 - s(1)]\} = b_0 + b$, so that b is actually the log odds-ratio for the group. An analogous model can be generated using the log-log function, where the hazard is assumed to be proportional and follows an exponential model. Again under the simple scenario of a dichotomous group effect the predictive relationship between the baseline survival rate and survival for group 1 would be:

$$\ln\{-\ln[s_1(t)]\} = -\ln[s_0(t)] - b$$

Owing largely to the recent availability of software such as program MARK (White and Burnham 1999, Cooch and White 2001), complex survival models can be developed using the discrete-time approaches I described above. However, as was discussed previously in the context of continuous-time models, successful discrete-time modeling requires appropriate stratification, covariate specification, and link function choice; in cases where these needs deviate from default settings, correct model structure may be difficult to achieve. Also, when using discrete-time approaches models should be fit using time-varying covariates that have a commensurate time scale with survival monitoring intervals (Jelhe et al. 2004, Rotella et al. 2004).

Prevalence of survival modeling.—In recent years, continuous-time survival models have been used in telemetry-based studies on waterfowl (Conroy et al. 1989, Cox et al. 1998, Kirby and Sargeant 1999, Longcore et al. 2000, Davis et al. 2001, Pietz et al. 2003), gamebirds (Carroll 1990, Niewoonder et al. 1998, Smith and Willebrand 1999, Warner et al. 2000, Williams et al. 2004), small mammals (Sievert and Keith 1985, Hasbrouck et al. 1992, Murray et al. 1997, Calvette et al. 2004), raptors (Todd et al. 2003), and large mammals (Beringer et al. 1996, 1998, DelGiudice et al. 2002, Johnson et al. 2004). Similarly, discrete-time methods have been applied to survival studies with waterfowl (Esler et al. 2000a, Fleskes et al. 2002, Devries et al. 2003), gamebirds (Bro et al. 1999), small mammals (Griffin et al. 2005), raptors (Reynolds et al. 2004), and large

mammals (White and Bartmann 1998, Lopez et al. 2003). This extensive taxonomic representation notwithstanding, telemetry studies using either continuous- or discrete-time models tend to be in a minority in the recently published wildlife literature (i.e., <25% [$n = 164$] of papers in my review of *Journal of Wildlife Management*). Furthermore, few survival modeling studies actually employ standard model selection and multimodel inferencing approaches when assessing covariate effects, even though software programs like MARK (White and Burnham 1999, Cooch and White 2001) are readily equipped to deal with such needs. Researchers also rarely apply standard model diagnostic and validation procedures to avoid poorly fitting or overfitting survival models (Harrell et al. 1996). Thus, I suggest that modeling approaches be used more extensively to analyze wildlife survival data and that the veracity of selected models and associated variables be scrutinized carefully.

Assumptions and Accuracy in Survival Data

Selection of Subjects

Subject heterogeneity.—Survival studies assume that subjects comprise a random sample of the population (Krebs 1999, Winterstein et al. 2001), with deviations from this assumption reducing mortality risk variability and thereby increasing bias and perceived precision. Timing the start of the study to ensure that sampling is representative (e.g., during seasons when all groups are available for capture or prior to an anticipated increase in mortality risk) will affect sample heterogeneity (Pollock et al. 1989a, Winterstein et al. 2001). However, unless subjects experience a constant hazard during a study, the choice of a particular study initiation time inevitably will influence the resulting survival estimate. In some cases using the baseline hazard function rather than the mortality rate averaged over an arbitrary interval will provide more representative mortality patterns (Zens and Peart 2003).

A problem receiving limited attention in wildlife research is that of progressive sampling heterogeneity. As a study progresses and individuals experience differential mortality risk, composition of the sample becomes increasingly skewed towards the surviving group. In the moose calf example, males had higher mortality risk than females, and over time females became more prominent in the sample, thus the averaged hazard rate (Fig. 2b) was biased low (see Kowald and Kirkwood 1993, Vaupel and Carey 1993). This bias was not fully revealed by simply examining corresponding survivor functions for the 2 groups (Fig. 3a). Thus, an implicit problem with all survival research is that progressive sample heterogeneity is to be expected as part of normal study progression. The level of bias will be increased by high initial heterogeneity between subjects, high mortality rates, or prolonged study duration (Aalen 1988, Zens and Peart 2003). Progressive sample heterogeneity may be assessed by plotting the baseline hazard function and determining if hazard declines over time, whereas further tests involve comparing hazard functions across relevant covariates where sample heterogeneity is suspected if hazard rates fail to follow similar trends (Vaupel and Yashin 1985). For the moose dataset, the decline in late hazards (Fig. 2b) was apparently due to the loss of males in the sample towards the end of the 2-year period (Fig. 3a). If sample heterogeneity is suspected, survival estimation should be stratified according to the relevant covariate. If such a variable has not been measured, both the basic hazard function and the relative hazard rates will be biased (Gail et al. 1984, Allison 1995). Delayed recruitment of new subjects into the study may alleviate progressive sample heterogeneity provided that late recruits also constitute a random sample of the population; this assumption can be verified by using study entry time as a covariate in survival models. Subject heterogeneity may also be remedied by fitting survival models with heterogeneity included as a nuisance parameter (Service et al. 1998, Fox 2001), although this approach leads to the problem of choosing a functional form for the model and the appropriate distribution for the error term (Allison 1995, Collett 2003).

If the aim of the study is to describe survival rates in the population then a representative sample of subjects is needed, but if the objective is to assess responses to a specific treatment (e.g., habitat manipulation, hunting), then precision may be increased by intentionally reducing sample variance. This approach is encountered in clinical trials where sample sizes are small, heterogeneity in the population is high, or high precision is important for hypothesis testing (Anderson et al. 1980, Gail 1991, Buyse et al. 1996). However, composition of the subject population affects the ability to generalize the results, and in most wildlife studies the need for unbiased survival estimates will override any benefits from selecting homogenous subjects.

Subject independence.—Subject survival times should be distributed independently, because if mortality risk is correlated between individuals then the hazard function will be biased and precision will be inflated (Winterstein et al. 2001, Collett 2003). This assumption may be difficult to uphold in many wildlife studies because free-living animals often experience correlated survival times due to exposure to shared mortality agents. In contrast, sample independence may be more easily achieved in human survival research because of lower correlation in human mortality risk, and the ease by which subjects known to share specific predispositions can be identified and treated accordingly. Simple solutions designed to achieve sample independence, such as using mean survival time for a group or subsampling within groups (e.g., Fox 2001), waste relevant information on individual variability. Instead, survival time can be estimated appropriately for clustered data through robust variance estimation (Prentice et al. 1981, Lin and Wei 1989, Binder 1992, Lee et al. 1992, Lin 1994, Flint et al. 1995). Although such adjustments have been used to correct survival time correlations in wildlife research not involving telemetry (see Grand and Flynt 1996, Guyn and Clark 1999), application in telemetry-based survival modeling is

rare (but see DelGiudice et al. 2002, Pietz et al. 2003) and seemingly poorly understood (e.g., Krapu et al. 2004). Alternatively, frailty models can be used to parameterize the association between mortality events (Hosmer and Lemeshow 1999), but this approach requires selecting an appropriate distribution for the frailty that may be problematic where the underlying pattern of clustering is unclear. Given the likely prevalence of correlated survival times in animal populations, the lack of robust variance estimation in telemetry-based research warrants further attention.

Random censoring.—Although censored individuals provide useful information on minimum survival time, and thus should always be included in survival datasets, their utility in calculating hazards is limited to influencing precision (Vangilder and Sheriff 1990, Fox 2001). The general assumption with censoring is that it is random and noninformative and therefore independent of survival probability. This assumption may be restrictive in wildlife research, where loss to follow-up often is nonrandom (Heisey and Fuller 1985, Tsai et al. 1999b, Winterstein et al. 2001, Williams et al. 2002). For example, survival estimates for some wolf (*Canis lupus*) populations in the western United States may be biased if radiocollared animals are killed illegally by landowners and their transmitters are subsequently destroyed to conceal the mortality event (E. Bangs, U.S. Fish and Wildlife Service, personal communication). Wolves succumbing to such mortality would be censored at a higher rate than other subjects, thereby inflating the survival estimate for the population.

Potential bias from informative censoring has received little attention in wildlife research (see Esler et al. 2000b, DelGiudice et al. 2002, Williams et al. 2002). In contrast, censoring issues have been prominent in the medical literature (Allison 1995, Marubini and Valsecchi 1995, Bull and Spiegelhalter 1997, Collett 2003). Simple adjustments to study design, such as conducting survival monitoring outside the immediate study area to detect emigrants or deploying transmitters with adequate signal strength and battery lifespan, can help alleviate informative censoring rates (Garton et al. 2001, Withey et al. 2001). Alternatively, study duration can be extended to include a minimum number of mortalities if most subjects are expected to live beyond the study termination date. It is important that wildlife survival papers always report censoring rates (e.g., Bender et al. 2004, Lubow and Smith 2004).

Most diagnostic tests for assessing informative censoring require that covariates relevant to censoring status have been measured (Gail et al. 1984, Gail 1991, Oakes 2001). In the above wolf example, proximity of the subject's home range to human development, or the percentage of time that a wolf spends on protected versus private land, could constitute covariates relevant to censoring status. Informative censoring can be tested by plotting subject survival time against censoring covariates, where censored and non-censored individuals are distinguished. If censored animals have different minimum survival times for a particular covariate, then informative censoring is suggested (Collett 2003). Censoring bias also may be revealed where censoring status is identified using a binary variable in logistic regression and covariates are deemed significant (Collett 2003). For example, Herring and Collazo (2004) confirmed that censoring loss was consistent between genders among lesser scaup (*Aythya affinis*), and Esler et al. (2000b) revealed that recapture rates were similar between known-fate versus right-censored harlequin ducks (*Histrionicus histrionicus*). Informative censoring also can be evaluated using a sensitivity analysis where censored animals are assumed to be either at high mortality risk (i.e., dead at the time of censoring) versus low risk (surviving beyond the longest survival time of all subjects). If the survival estimate obtained from properly censored data differs from either modified datasets, censoring is likely to be informative (Allison 1995). Millstap et al. (2004) addressed concern over potential nonrandom censoring in a radiomarked sample of bald eagles (*Haliaeetus leucocephalus*) by providing a range of survival estimates where cases of apparent transmitter failure were considered as either a censoring or death event.

Although none of the above prescriptions is assured of detecting informative censoring if present, they at least offer a measure of confidence that no egregious patterns of bias underlie the data. When informative censoring is detected, options to mitigate its effects are limited to using the aforementioned sensitivity analysis to obtain confidence limits on the survival estimate (Allison 1995), estimating survival separately according to the censoring variable (Collett 2003), or developing survival models where censoring status is parameterized explicitly (see Wu and Carroll 1988, Schlucter 1992, Satten et al. 2001, Scharfstein and Robins 2002). However, this latter approach is complex and may involve making assumptions that are not testable about the distribution of subject survival times (Lagakos 1979, Marubini and Valsecchi 1995).

Explicit time origin.—The time origin in survival studies needs to be explicit and preferably selected a priori (Pollock et al. 1989b, Winterstein et al. 2001, Williams et al. 2002). This point is especially relevant given the prevalence of delayed recruitment of subjects into wildlife telemetry studies and the potential that survival monitoring will begin before an adequate sample size is monitored. Because low initial sample size can affect precision of the survival estimate, it may be preferable to truncate initial survival data up to the point where sample size becomes adequate, even if this means excluding from the analysis subjects who die early in the study.

No transmitter effects.—Transmitters are assumed not to impact subject survival either directly or indirectly through other causes of death (White and Garrott 1990, Winterstein et al. 2001). Numerous studies have revealed transmitter effects in birds and mammals (see Murray and Fuller 2000, Withey et al. 2001), but a common assumption in telemetry research is that transmitter effects are only temporary, which leads to truncation of initial survival timelines at arbitrary times following transmitter deployment (e.g., 2–14 days; Miller et al. 1995, Roberts et al.

Table 2. Sample size requirements for differences in survival between 2 groups, according to relative mortality risk and baseline survival rate. The analysis followed Lachin and Foulkes (1986) and Lachin (2000) and compared adequate (0.8) and low (0.5) power scenarios using a 2-tailed test at P = 0.05, assuming infinite study length and an exponential hazard function without any censoring or truncation.

	Baseline survival rate					
	0.80		0.50		0.20	
Power	0.80	0.50	0.80	0.50	0.80	0.50
Relative risk						
1.10	16,573	8,111	6,697	3,227	4,247	2,078
1.25	2,866	1,402	1,176	575	763	373
1.50	808	395	341	166	229	111
1.75	401	196	174	85	121	58
2.0	250	122	112	54	80	38

1995). In some cases, postmarking truncation times may be determined a priori from trials specifically designed to assess transmitter effects, although currently such research often is fraught with experimental design flaws (Murray and Fuller 2000, Withey et al. 2001). Survival curves can help guide objective truncation time selection, provided that mortality events due to natural causes can be distinguished from those associated with transmitters. The high mortality rate among telemetered moose calves following tagging (Fig. 2a) is consistent with elevated mortality risk in unmanipulated neonatal ungulates (see Linnell et al. 1995) and therefore no truncation is necessary. However, quantifying the indirect effects of transmitters on mortality risk will always be challenging using field data, especially if such effects extend beyond the immediate postmarking period or if negative effects actually are related to repeated handling events rather than specifically to transmitters.

Additional Study Design Considerations

Death times and monitoring intensity.—Telemetry offers user-defined flexibility in the frequency and consistency of monitoring observations, and infrequent monitoring can lead to uncertainty in the timing of the death event. My review of the *Journal of Wildlife Management* suggested that most telemetry-based survival studies use either daily or biweekly monitoring schedules, which should be adequate for unbiased survival estimation. However, when survival monitoring occurs as infrequently as monthly (e.g., Harmata et al. 1999, Ballard et al. 2000, Hayes et al. 2000, Kamler et al. 2002), estimated death times will be suspect. Both the HF and KM survival estimators can be modified to account for potential bias due to relocation uncertainty (Bunck et al. 1995, Pollock et al. 1995). However, the estimate will be biased and its variance underestimated if the timing of death events is uncertain and is assumed to occur at a specific point (usually the midpoint) during the monitoring gap (Lindsey and Ryan 1998). Survival model likelihood functions can be adjusted to accommodate the tied death times that inevitably result from infrequent monitoring (Kalbfleisch and Prentice 2002, Collett 2003). However, where survival timelines are characterized by extensive monitoring gaps and uncertain death times, researchers should consider discrete-time (Lebreton et al. 1992, Sandercock 2006) or interval censoring (Finkelstein 1986, Lindsey and Ryan 1998) approaches.

Sample size and power.—Sample size requirements in survival estimation are inversely related to mortality risk differences between groups, and thus they are dependent upon factors such as hazard and censoring rates. Because these are not known a priori for most telemetry studies, conducting robust statistical power analysis for survival research often is challenging. Sample size requirements in survival studies have been distinguished between hypothesis tests for controlled trials versus predictive models for observational studies. In the former case, a variety of statistical power tests are available (e.g., Makush and Simon 1982, Schoenfeld and Richter 1982, Lakatos and Lan 1992). Using a basic approach (Lachin and Foulkes 1986, Lachin 2000), I conducted power analyses for a hypothetical wildlife population (Table 2) and found that sample size needs for adequate statistical power (0.80) differed substantially depending on mortality risk differences between groups. Mortality risk differences <0.50 lead to prohibitive sample sizes (Table 2), even among many low power (0.50) scenarios. Note that my approach was conservative (see Table 2) and thus probably underestimated sample size requirements in most field studies. To put these results into context, I calculated sample sizes in telemetry-based survival studies from the *Journal of Wildlife Management*; on average 189.6 ± 22.5 (n = 153) subjects were included, with the number of uncensored individuals actually succumbing to mortality tending to range between 60–90% of the study population. It follows that most published wildlife survival studies likely have low power except for testing large differences in relative mortality risk.

The second point is that sampling needs are heavily influenced by baseline mortality rates, with populations subject to low risk needing larger sample sizes (or longer studies) for comparable power (Table 2, see also Pletcher 1999). Yet, wildlife biologists rarely consider survival study duration in terms of baseline mortality rates of subjects, and the variability in duration of published survival studies on large mammals (64.6 ± 7.1 months, n = 62), small mammals (42.6 ± 10.2 months, n = 17), and birds (26.4 ± 3.7 months n = 76) likely does not reflect actual survival time differences between taxa. Rather, wildlife study

duration tends to be defined by external factors such as funding cycles or the length of graduate degrees, neither of which is likely to promote adequate sample sizes especially for longer-lived species.

The majority of telemetry studies seek to elucidate relationships between variables rather than test specific hypotheses (Garton et al. 2001). Suggested sampling needs for model-based survival estimation in human research are 10–15 death events per variable under consideration, above a minimum of 30 mortalities (Harrell et al. 1984, Smith et al. 1992, Harrell 2001). My review of the literature revealed that wildlife survival studies typically consider 3–5 covariates in survival models, implying that 60–105 mortalities should be needed to achieve adequate statistical power, using the above rule of thumb. However, sampling needs in wildlife studies may be considerably higher than in human studies because of the potentially greater number of confounding variables in animal field research. Because survival models derived from small datasets tend to be overfit, researchers should be cautious in telemetry-based survival analysis and consider applying appropriate model diagnostics and validation procedures (Harrell et al. 1996).

Management Implications

I recommend improvements in the testing and reporting of basic assumptions related to subject heterogeneity, subject independence, and random censoring, in wildlife survival studies. When assumptions are not upheld, specialized analytical techniques are required. Sample size and study duration should be commensurate with acceptable statistical inference and therefore be sensitive to patterns of mortality and censoring in the study population. Wildlife researchers should recognize the need to complement HF or KM

survival estimation with continuous- or discrete-time survival modeling with multiple variables, and use standard model selection and validation procedures. More broadly, potential differences between different survival modeling approaches need to be elucidated under a range of conditions via analyses of simulated datasets. Whenever possible, researchers should examine changes in mortality risk through an individual's lifespan by including time-dependent covariates among the candidate variables in survival models. The above recommendations can be achieved if comprehensive and user-friendly software is developed that can perform a range of survival analysis procedures, including fitting and testing hazard functions, fitting a range of survival models, assessing model fit and assumptions related to data, determining sample size requirements, and generating publishable graphics. Finally, reviewers and editors should hold wildlife survival manuscripts to high standards of scientific content and rigor. Collectively, these developments will ensure that telemetry-based research continues to play a critical role in answering relevant questions in wildlife management and conservation biology.

Acknowledgments

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