

# Wildlife Survival Estimation: Recent Advances and Future Directions

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Survival is a major determinant of animal population size and trend, and survival estimation has received considerable attention from population and conservation biologists seeking to understand patterns of abundance and numerical change in ecological systems. Although researchers commonly consider survival to be a population parameter, it is an attribute of individual animals. Because genetic, demographic, ecological, and environmental factors act upon individuals to influence survival, the objective of modern survival analysis is to quantify the role of such factors on mortality risk. In recent years, survival has been a prevalent topic of study in the *Journal of Wildlife Management* compared to other demographic attributes like productivity and dispersal (Fig. 1). However, survival tends to be more difficult to estimate properly than other demographic parameters (McCallum 2000, Fox 2001), especially among free-ranging animals where cryptic behavior patterns and difficulties in marking and monitoring often lead to small sample sizes and a high proportion of subjects succumbing to an unknown fate. These problems can limit the amount and quality of survival data obtained from ecological studies, and the challenge for researchers is to apply robust methodology that will make effective use of survival information obtained under sometimes constraining field conditions.

Survival estimation has its early roots in human medicine and epidemiology (Oakes 2001), but in recent decades, considerable effort has focused on the development of reliable survival methods for application with free-ranging animals (Brownie et al. 1985, Burnham et al. 1987, Pollock et al. 1990, Lereton et al. 1992). In the last 20 years, substantial improvements have been made in this arena, both in terms of capture, marking, and monitoring techniques facilitating comprehensive survival assessment for free-ranging animals (Krebs 1999, Kenward 2001, Millspaugh and Marzluff 2001), and in the development of software programs allowing for the analysis of complex survival functions (Williams et al. 2002). Together, these changes have elicited a flurry of innovative survival research in animal ecology (Lebreton et al. 1992, Cam et al. 2002, DelGiudice et al. 2002, Dinsmore et al. 2002). These recent

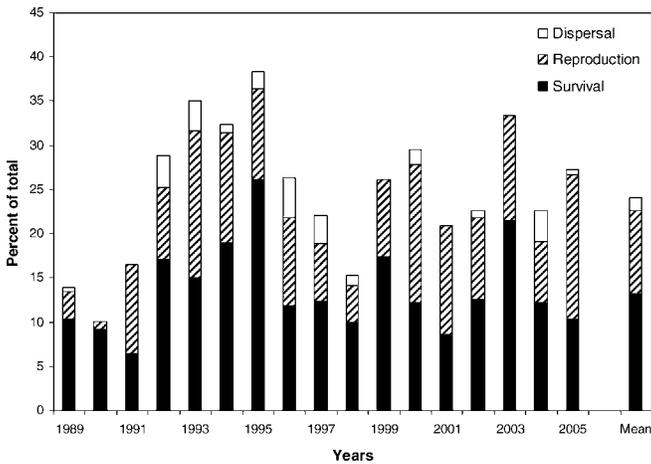
advances notwithstanding, there remains significant interest in the current state of survival estimation in wildlife research, particularly in terms of basic assumptions that may be difficult to meet in many research studies, or in the application of specialized analytical techniques requiring particular specification (Krebs 1999, Williams et al. 2002, Zens and Peart 2003, Rotella et al. 2004). Thus, a general review of current methodology and new developments in wildlife survival estimation should be timely and beneficial.

## Selecting an Appropriate Method

Broadly speaking, the type of organism under study and the specific objectives of the study should guide the method used in survival estimation. Although recent (1989–2005) survival papers in the *Journal of Wildlife Management* have focused exclusively on birds and mammals, survival estimation commonly involves invertebrates (Hwang and Lindroth 1997, Lord and Baylis 1999, Jones and Coulson 2006), fish (Burnham et al. 1987, Gruber et al. 2001), amphibians (Wood et al. 1998, Anholt et al. 2003), and reptiles (Stanford and King 2004, Converse et al. 2005). Other important criteria include whether survival is assessed in discrete increments or on a more-or-less continuous time scale, if subjects are individually marked, the detection probability associated with marked individuals, if the fate of subjects can be determined, and whether the underlying survival pattern follows a known statistical distribution (Fig. 2; McCallum 2000). It follows that the particular species under investigation and the study methods will influence technical considerations such as live-capture protocol (e.g., trapping success, trap heterogeneity), marking method (e.g., type and size of tag, radiotransmitter battery lifespan and signal strength), and monitoring intensity (precision in death-event timing, rates of loss to follow-up).

Life-table methods are designed for monitoring survival in discrete stages or intervals, and can involve either a lateral cross-section of the population at discrete times or longitudinal monitoring of a cohort from birth to death. Currently, life-table methods rarely are used in survival studies involving birds and mammals because they do not usually allow for individual variability in mortality risk and they typically require age- (or stage-) structured data (Caughley 1977, Seber 1986, 1992). Lateral reconstruction

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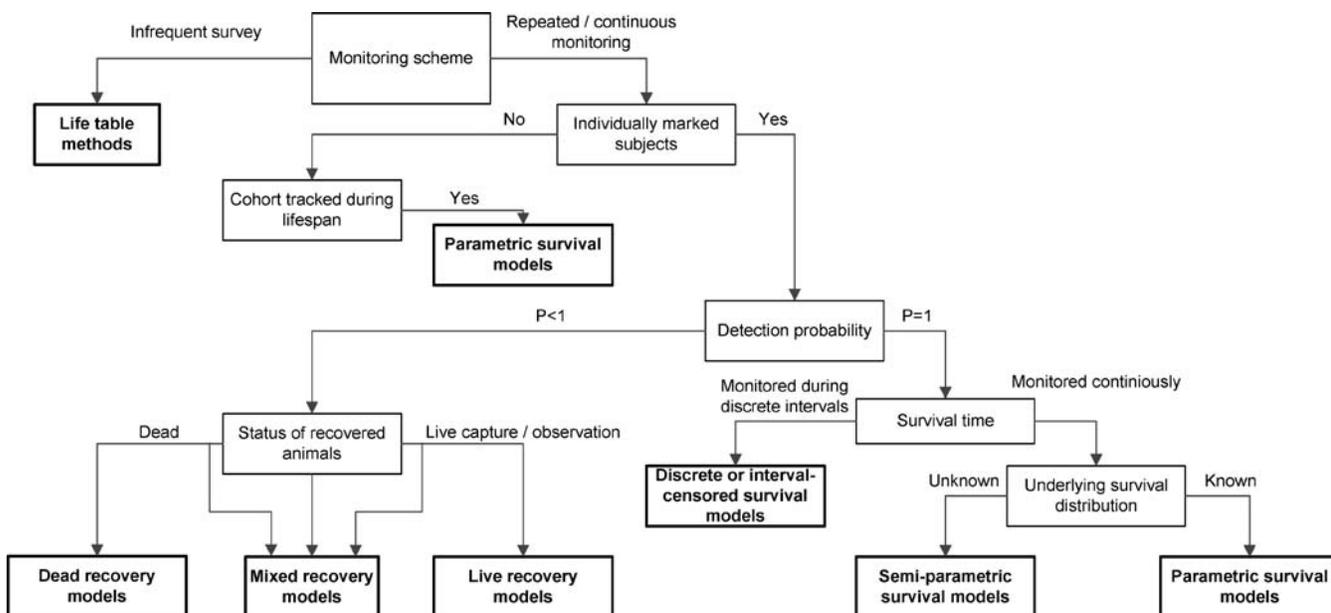
**Figure 1.** Percent of papers published in *Journal of Wildlife Management* addressing survival versus other demographic parameters (1989–2005).

methods are subject to 2 additional constraints that further limit their utility: 1) rate of population change should be known, and 2) the population should be at a stable age distribution (Hairston and Twombly 1985). Comparable survival estimation methods such as key-factor analysis (Newton 1988), age-composition analysis (Fryxell et al. 2001), and change-in-ratio methods (Seber 1982) also tend to make restrictive assumptions and often require destructive sampling. Thus, they are uncommon in current wildlife survival estimation.

Survival estimation in birds and mammals usually involves monitoring the fates of individually marked subjects through repeated measurements or in continuous time (Fig. 2). Survival of individuals can be estimated using capture–

recapture methods (e.g., live-recapture, mark–resight, dead-recovery, and mixed-recovery models) or radiotelemetry. The advantage of these approaches over the life table and related alternatives is that researchers can characterize individual variation in survival probability over a given timeline and can associate it to relevant covariates in a rigorous statistical framework. In cases where researchers infer survival time without relocating all subjects during a given sampling event (i.e., detection probability < 1), as is the case in capture–recapture or band–recovery studies, the state (live or dead) of subjects when they are recovered determines the family of survival models available for use (Fig. 2). These families of models include nuisance parameters related to detection probability because the actual fates of most subjects usually remain in question. In contrast, researchers can use more straightforward methods to estimate survival time if the fates of the large majority of subjects are determined during periodic relocations (e.g., radiotelemetry or nest–survival studies). Under such circumstances, whether researchers measure the subject survival status within discrete time intervals (e.g., ‘known fate,’ nest survival, or interval-censored approaches) or continuously until each subject dies or is censored from the study, will determine the applicable estimation models (Fig. 2). However, this distinction is largely philosophical and both discrete-time and continuous-time approaches tend to provide comparable results in most situations. When researchers monitor survival time continuously and the survival function follows a known statistical distribution, parametric approaches can be used to model survival (Fig. 2).

Many software options exist for conducting wildlife survival estimation, and although an exhaustive review of



**Figure 2.** Conceptual framework for selecting an appropriate family of survival estimation methods. Individually marked subjects include animals with distinct natural markings or those marked with tags, bands, or radiotransmitters. Detection probability refers to encountering subjects during a relocation session, where  $P < 1$  for individuals monitored through live capture or dead recovery. When  $P = 1$  monitoring can be considered in the context of survival status during a discrete time interval or continuous monitoring of survival until time-to-death. Bolded boxes refer to the family of survival estimation models that are available given the data structure.

survival analysis packages is beyond the purview of this introductory paper, a few summary comments are appropriate; detailed reviews are available elsewhere (Harrell and Goldstein 1997, Williams et al. 2002). Life-table analysis can be conducted using most general statistical software programs or using specialized packages that allow for more complex life-table structures (e.g., Tiemeyer and Ulmer 1991, Smith 1998). Researchers can estimate survival for live-recovery studies using program RELEASE (Burnham et al. 1987) or programs JOLLY and JOLLYAGE (Pollock et al. 1990) and can estimate survival for dead-recovery studies using programs BROWNIE and ESTIMATE (Brownie et al. 1985). Each of the above programs is subsumed by program MARK (White and Burnham 1999), which is the industry standard for wildlife survival estimation from capture–recapture and band-recovery studies. Program MARK is particularly powerful because it allows for construction and evaluation of a variety of survival models based on a large number of independent variables. Discrete or interval-censored survival data also can be analyzed using program MARK, whereas most general statistical programs can accommodate parametric and semi-parametric continuous-time survival models. A more detailed listing of survival estimation and other software programs available for the wildlife sciences is available through the Patuxent Software Archive ([www.mbr-pwrc.usgs.gov/software.html](http://www.mbr-pwrc.usgs.gov/software.html)). One point, however, is that the correct application of these various methods can be challenging and requires careful attention to data structure, model specification, and assumption checking (Williams et al. 2002).

## Special Section

This Special Section follows a symposium on survival estimation at the 2004 Wildlife Society (TWS) annual meeting in Calgary, Alberta. In response to our own questions about the current state of survival estimation, we sought to assemble a series of papers that would review the primary methods in modern survival analysis in wildlife research, highlight potential pitfalls and limitations, and describe new applications and recent developments. The special section begins with Brett Sandercock's assessment of the 7 major classes of mark–recapture models that researchers commonly use to estimate apparent survival and other parameters from live-encounter data. Sandercock discusses the fundamental parameters that contribute to observed return rates and explains how progressively more complicated mark–recapture models build on this basic framework. He discusses the trade-off with advanced mark–recapture models; they estimate apparent survival with greater precision and less bias but require additional sampling effort. Finally, in a theme common to this special section, he emphasizes that given the range of alternative models and software tools now available, new studies in wildlife ecology should be designed to take advantage of the best possible statistical procedures.

Following this general review, Gary White and colleagues

explain how program MARK provides a wide range of models for the estimation of population parameters from mark-encounter data. From this introduction, they focus on multistate models that allow animals to move between states with a probability of transition. Multistate models provide a valuable framework to evaluate important ecological questions such as estimating state-specific survival and transition rates between breeders and nonbreeders to assess the cost of reproduction. After explaining the simplest multistate model, an extension of the Cormack-Jolly-Seber live-recapture model, they present more complicated extensions included in MARK. They conclude by discussing the advantages of using MARK to estimate parameters of the various multistate models, including flexibility of model specification to include group, time, and individual covariates, estimation of variance components, model averaging of parameter estimates, and Bayesian parameter estimation.

In the next paper, Dennis Murray examines methods applicable to, and assumptions required for, analysis of survival using radiotelemetry. After reviewing the variety of methods for estimating telemetry-based survival information, Murray discusses how their statistical assumptions may be commonly overlooked or violated in telemetry research. He then outlines methods of assessing, and sometimes remediating, potential violation of these assumptions. After discussing options for increasing accuracy and precision of telemetry-based survival estimates, such as including appropriate monitoring schedules, subject-recruitment schemes, and sample sizes, he outlines how telemetry-based survival estimation will benefit from increased emphasis on modeling approaches combined with more rigorous attention to basic assumptions and study design limitations.

Dennis Heisey and Brent Patterson then focus on the estimation of cause-specific mortality from a modern biostatistical perspective. They define what is meant by “cause-specific mortality,” and provide a hazard-based representation as a competing risks problem. This leads to the general solution of cause-specific mortality as the cumulative incidence function (CIF). After presenting an easy-to-implement estimator of the nonparametric CIF, they compare this model to the still-popular Heisey-Fuller estimator and another popular, but erroneous, method based on the Kaplan-Meier estimator of  $S(t)$ . They then expand their approach to demonstrate how covariates can be assessed and compared using standard software for Cox proportional hazards models and close by demonstrating the applicability of these methods using a dataset from radio-collared coyotes.

In the concluding paper, Glenn DeGiudice and colleagues report on how they used state-of-the-art survival analysis techniques to assess survival of white-tailed deer (*Odocoileus virginianus*) in Minnesota, USA. Their 13-year study spanned a period of extreme variability in winter severity and hunting pressure, allowing for the quantification of the impact of these important determinants of deer survival. By also monitoring survival of 76 neonates, they were able to fully document the age-specific hazard curve for

female deer and demonstrate that the greatest risk of mortality occurred in the first year of life. Coupled with the finding of greater risk of mortality among older deer, they demonstrated that the lifetime hazard (i.e., instantaneous risk of death) for deer follows a U-shaped curve when plotted against time. This is a significant, if not surprising finding because most studies of survival have assumed constant survival rates for adult deer of a given sex. To build on this point, they simulate potential for bias resulting from pooling adults of all ages.

Overall, these papers provide a review of the current state of wildlife survival estimation, offer insight on how to conduct effective and accurate survival analysis, and hint at where such analyses may lead to in the future. Some readers will find some of the material complex, which emphasizes the point made in several of the papers in this section that wildlife researchers working with survival data should consider seeking the assistance of a biostatistician. In

addition, given that many of the methods discussed in this section have arisen largely as adaptation of methods used in human biomedical applications, wildlife graduate students should be encouraged to pursue biostatistical survival analysis coursework even if the focus is on human applications. We hope that readers of this special section will gain an appreciation for both the numerous options available for modern survival analysis and the points that need consideration when choosing the appropriate methodology for any given study.

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