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## USE OF SURVIVAL TIME ANALYSIS TO ANALYZE NESTING SUCCESS IN BIRDS: AN EXAMPLE USING LOGGERHEAD SHRIKES

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**Abstract.** Ornithologists commonly estimate nest survival using the Mayfield method, which produces relatively unbiased estimates provided that key assumptions are met. However, this method cannot statistically model nest failure in relation to quantitative variables, nor can it consider the joint effects of two or more independent variables. We demonstrate the use of an alternative method, survival time analysis. Survival time analysis can incorporate nests that are found at different points in the nesting cycle and nests whose ultimate outcome is unknown. The method allows one to examine variation in nest mortality during the course of the nesting period. To demonstrate this method we analyze data on Loggerhead Shrike (*Lanius ludovicianus*) nests, collected as part of a 3-year monitoring program of shrubsteppe habitat in north-central Oregon. We evaluate nesting success with respect to laying date, nest height, and annual variation in failure rate. We demonstrate three types of analyses: Kaplan-Meier estimation (a nonparametric method), Cox proportional hazards model (a semiparametric method), and Weibull parametric regression. Using these maximum-likelihood methods one can carry out likelihood-ratio tests and Akaike's Information Criterion model selection. The best predictive model included the effects of date and year. Nest failure rate changed during the nesting cycle and was heterogeneous among nests, thus violating assumptions of the Mayfield method. We discuss drawbacks to the use of logistic regression (another Mayfield alternative) to analyze nest success. Estimates of the age of a nesting attempt upon discovery are required for survival time analysis; we encourage ornithologists to collect such information.

**Key words:** breeding date, Cox proportional hazards model, Kaplan-Meier function, logistic regression, Mayfield method, nest failure, survival analysis.

### Uso del Análisis de Tiempo de Sobrevivencia para Analizar el Éxito de Nidificación: Un Ejemplo Utilizando *Lanius ludovicianus*

**Resumen.** Los ornitólogos generalmente utilizan el método de Mayfield para estimar la sobrevivencia de los nidos, un método que produce estimaciones relativamente poco sesgadas siempre y cuando se cumplan sus suposiciones claves. Sin embargo, este método no es capaz de modelar estadísticamente los fracasos de nidificación en relación con variables cuantitativas, ni tampoco puede considerar el efecto conjunto de dos o más variables independientes. Aquí, demostramos el uso de un método alternativo, el análisis de tiempo de sobrevivencia, el cual puede incorporar nidos que son encontrados en diferentes tiempos durante el ciclo de nidificación y también nidos cuyo resultado final es desconocido. El método permite examinar la variación en la mortalidad de nidos durante el transcurso del período de nidificación. Con el fin de demostrar este método, analizamos datos de nidos de *Lanius ludovicianus* colectados como parte de un programa de monitoreo del hábitat de estepa arbustiva durante un período de 3 años en Oregon nor-central. Evaluamos el éxito de nidificación con respecto a la fecha de puesta, altura del nido y variación anual en la tasa de fracaso. Demostramos tres tipos de análisis: estimación de Kaplan-Meier (un método no paramétrico), modelos de riesgo proporcional de Cox (un método semi paramétrico) y regresión paramétrica de Weibull. Utilizando estos métodos de máxima verosimilitud uno puede seleccionar modelos realizando pruebas de cocientes de verosimilitudes y utilizando el criterio de información de Akaike. El modelo con mayor capacidad predicativa incluyó los efectos de la fecha y el año. La tasa de fracaso de nidos varió durante el ciclo de nidificación y fue heterogénea entre nidos violando así, las suposiciones del método de Mayfield. Discutimos las desventajas del uso de regresiones logísticas (otra alternativa al método de Mayfield) para el análisis del éxito de los nidos. Para el análisis de tiempo de sobrevivencia se requiere la estimación de la edad de un intento de nidificación en el momento de ser descubierto, por lo que sugerimos a los ornitólogos coleccionar dicha información.

## INTRODUCTION

One of the most important and widely studied population parameters reported on by avian

ecologists is nest survivorship, the probability that a nest, once initiated, will produce at least one surviving young at the end of the nesting period. Nest survivorship, one component of re-

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productive success, is for example the focus of attention for many studies that attempt to determine source-sink status for populations (Robinson et al. 1995, Donovan et al. 1995, Simons et al. 2000, but see Pease and Grzybowski 1995, Thompson et al. 2001). At present, there are numerous monitoring and research programs that focus on this parameter, including the BBIRD program (Martin et al. 1997).

The most common method used to estimate nest survivorship is the Mayfield method (Mayfield 1961, 1975). Apparent nest success, estimated by dividing the number of successful nests (i.e., nests that produce one or more young) by the total number of nests at risk, provides a biased estimate of nest success when nests in the sample are found at different stages. This is because nests found later in the nest cycle will typically have fewer days of observation and thus fewer days at risk of nest failure. The Mayfield method is intended to overcome the bias associated with finding some (or all) nests at different stages. Johnson (1979) and Hensler and Nichols (1981) demonstrated how to calculate standard errors and carry out simple statistical tests. Since then, numerous studies have used this method to estimate nest survivorship (Manolis et al. 2000, Farnsworth et al. 2000, DeSanto et al. 2002, Liebezeit and George 2002, Burhans et al. 2002). Though it is widely used, the Mayfield method has many limitations, which have been enumerated before (Johnson 1979, Hensler and Nichols 1981, Klett and Johnson 1982, Johnson and Shaffer 1990, Dinsmore et al. 2002, Jehle et al. 2004), and which we discuss below.

In this paper we present a valuable alternative to the Mayfield method for the statistical analysis of nest survivorship. This approach is well established in biomedical studies and has various names including "survival time analysis" (Hosmer and Lemeshow 1999), "time-to-failure analysis" (Kalbfleisch and Prentice 1980), "time-to-event analysis" (Hosmer and Lemeshow 1999, Collett 2003), and "survival analysis" (Marubini and Valsecchi 1995, Allison 1997). Whereas the last-mentioned label is commonly used, the terminology is ambiguous and therefore we prefer "survival time analysis."

Specific analytic methods that comprise survival time analysis include the Kaplan-Meier survival function (Marubini and Valsecchi 1995) and Cox proportional hazards model (also referred to as Cox regression; Cox 1972). The former has been commonly used in analyzing ra-

dio-transmitter tracking data (Pollock et al. 1989, White and Garrott 1990, Millspaugh and Marzluff 2001) but not often to study nest survivorship (exceptions include Aldridge and Brigham 2001). The Cox proportional hazards model has not been widely used in avian ecology in general and applications to studies of nest survivorship are rare (but see Renner and Davis 2001). Least often used in avian-ecological studies of any kind are parametric survival-time regression techniques such as the Weibull regression (Hosmer and Lemeshow 1999). In this paper we present examples of the application of all three analytic methods.

We present these alternative methods due to limitations of the Mayfield method. The first limitation is that the Mayfield method makes several restrictive and unrealistic assumptions. The Mayfield method assumes: (1) Probability of nest failure is constant over time, either over the entire nesting period or within a shorter period, such as the incubation period. (2) Homogeneity of failure probability among nests. This assumption is violated if, for example, nests situated in one type of shrub are more likely to fail than other nests. (3) Independence of outcome among nests. This assumption might be violated if nests adjacent to each other are more likely to all survive or all fail compared to other nests (e.g., due to the action of a single nest predator or collapse of a single large tree).

Survival time analysis, in contrast, does not require adherence to these assumptions and, moreover, its statistical methods can accommodate and explicitly test for deviations from these assumptions.

The second limitation is that the Mayfield method allows for only very simple statistical analysis. It does not allow for (1) evaluating the effect of a quantitative variable (covariate); (2) evaluating the effect of one variable while statistically controlling for other variables; (3) evaluating statistical interactions; or (4) analyzing clustered data (e.g., the same nesting tree with multiple nests).

In short, one cannot carry out the type of statistical modeling commonly carried out with linear models (e.g., multiple regression, ANOVA). Yet such statistical modeling is easily implemented with survival time analysis and many statistical packages are available to do so, including SAS (Allison 1997), S-PLUS (MathSoft

1999), STATA (StataCorp. 2001), and EGRET (Cytel Software 2000).

To overcome the Mayfield method's limited capabilities for statistical analysis, it has become increasingly commonplace for ornithologists to use logistic regression to analyze nest success (usually scored 0 = failed or 1 = survived). Logistic regression indeed provides a powerful and flexible means of statistical analysis (Nur et al. 1999, Hosmer and Lemeshow 2000) and its use has become more widespread (e.g., Burhans et al. 2002, Liebezeit and George 2002, Rodewald 2002). However there are important limitations on the use of logistic regression. It may be inefficient (reducing statistical power) and, in some cases, may introduce bias into analyses (Manolis et al. 2000).

Many others have proposed elaborations or alternatives to the Mayfield method; we discuss these alternatives in relation to survival time analysis (Bart and Robson 1982, Pollock and Cornelius 1988, Heisey and Nordheim 1990, Bromaghin and McDonald 1993, Rotella et al. 2000, Manly and Schmutz 2001, Dinsmore et al. 2002).

The objectives of this paper are to (1) familiarize ornithologists with survival time analysis and clarify terminology, (2) give an example of its utility for statistical analysis of nest survivorship, using field data on Loggerhead Shrike (*Lanius ludovicianus*) nests, (3) demonstrate the range of statistical techniques available, (4) consider advantages and limitations of this method compared with other statistical methods (e.g., logistic regression), and (5) provide recommendations for those wishing to implement survival time analysis.

## OVERVIEW OF SURVIVAL TIME ANALYSIS

Survival time analysis (STA) was developed for biomedical applications, and the terminology used still reflects this epidemiological origin, though this type of analysis is equally suitable for ecologists and behaviorists. Recommended texts for nonstatisticians are Collett (2003), Hosmer and Lemeshow (1999), Allison (1997), and Marubini and Valsecchi (1995).

The basic paradigm is as follows: A nesting attempt is discovered at age  $t$  days, where day 0 is considered the day of clutch initiation (laying of first egg). Note that, for the analysis, it is not necessary for nests to be found at day 0. When nests are found and included in the study after day 0, this is referred to as "staggered en-

try" or "left-censoring." One can consider a shorter period, for example just the nestling period, in which case day 0 would refer to the onset of the nestling period (i.e., first day of hatching). Note that "time" in survival time analysis here refers to age of the nesting attempt (henceforth referred to as "age of the nest") in days. Note also that survival time analysis requires that the age of the nest be estimated at the time that it enters the study.

Periodically, the nest is checked, and the field biologist determines at each visit if the nest is active or has failed (Martin and Geupel 1993). Ideally, all nests are checked regularly until the nest fails or succeeds in fledging young. However, it is sometimes not possible to keep checking nests, or the ultimate outcome may be uncertain (Manolis et al. 2000). In this case we have partial information; we might know, for example, that the nest survived until day 10 of the nestling period, but we do not know what happened after that. This situation (unknown outcome and therefore unknown date of failure) is referred to as right-censoring, or sometimes as just "censoring."

Survival time analysis can accommodate both staggered entry (left-censoring) and incomplete information on outcome (right-censoring). However, note that, in the language of survival time analysis, a nest that survives the observation period is considered to be censored. Only nests that are known to fail are not censored, because it is only for those nests that we know time to failure. Successful nests have an undefined time to failure, and are considered censored observations.

In many studies nests may not be checked daily; in this case, exact date of failure may not be known and is usually interpolated (Martin and Geupel 1993). For example, one may establish that the nest failed between day 16 and day 20. Where a nest is known to have failed but the exact date is not known (e.g., between days 16 and 20), this is referred to as "interval censoring," a third type of censoring (Collett 2003, Hosmer and Lemeshow 1999). This form of censoring is not considered in detail in survival time analysis, but we return to this topic.

There are three types of survival time analyses one can carry out:

*Simple descriptive analyses.* An example is the Kaplan-Meier estimate. Simple statistical tests, (e.g., the log-rank test) can be performed to compare survival functions, but the effects of

quantitative variables cannot be analyzed (Hosmer and Lemeshow 1999, Collett 2003).

**Semiparametric analyses.** This refers to the Cox proportional hazards model (Cox model for short) introduced by Cox (1972). This method statistically models the hazard rate, also referred to as the failure rate, which in this case is the daily rate of nest failure. The hazard rate is assumed to be a function of time (here, age of the nest in days), but this method does not attempt to explicitly characterize that function. In the simplest case, one compares two groups, each consisting of a cohort of nests, on the assumption that nests for one group (e.g., treatment group) will, at any time  $t$ , have a hazard rate that is proportionally greater or less than that of another group (e.g., control group). The assumption made in this analysis is that the time-specific ratio of these two hazard rates (e.g., that of the treatment group vs. that of the control group) is a constant. The null hypothesis is that the ratio of hazard rates is 1 (i.e., no difference between groups). The same approach can be used to compare nests with regard to one or more quantitative variables (Marubini and Valsecchi 1995); we give examples of such application below.

**Parametric analyses.** As with the Cox model, the hazard rate at a given time is modeled as a function of categorical or quantitative variables, or a combination of quantitative and categorical variables. The difference between semiparametric and parametric analyses is that, in the latter case, the hazard rate is explicitly modeled as a simple function of time (i.e., one or a few parameters are assumed sufficient to characterize hazard rate as a function of time). In the case of exponential regression, the simplest example of parametric regression, the hazard rate is assumed to be constant with time. This is the same assumption that the Mayfield method makes. In the case of Weibull regression the hazard rate is a monotonic (increasing or decreasing), curvilinear function of time and characterized by a single parameter,  $p$ . The Weibull regression is considered the centerpiece of parametric regression, with many convenient properties (Collett 2003); another type of parametric regression analysis is log-logistic regression (Marubini and Valsecchi 1995, Collett 2003). We emphasize that both semiparametric and parametric analyses allow the hazard rate to depend on a combination of quantitative and qualitative factors; the difference is

in how they treat the relationship of failure to time.

The five key assumptions of survival time analysis with respect to nest survival are (1) at the time of discovery the age of the nesting attempt can be ascertained, (2) nests discovered and monitored are representative of the larger study population of nests of interest, (3) date of failure can be ascertained (i.e., reasonably estimated) where a nest is known to have failed, (4) censoring is "uninformative" (i.e., censored and uncensored nests are otherwise similar), and (5) nest outcomes are independent of each other, once one accounts for the influence of independent variables.

Here we provide an example of each type of analysis, using data from a 3-year study of Loggerhead Shrikes conducted in north-central Oregon. We consider variation in nest survivorship in relation to three variables: date of clutch initiation, height of nest from the ground, and year. The first two are quantitative variables; the last variable is qualitative. Our main goal was to determine whether patterns of nest survivorship could be explained by some combination of these three variables, and whether the effect of any one variable depended on either of the other two (i.e., to identify interactions). A secondary goal was to characterize variation in nest failure rate with time (age of the nest), since such variation is intrinsic to survival time analysis but is not amenable to study with the Mayfield method.

## METHODS

### FIELDWORK

Loggerhead Shrikes were studied on the Naval Weapon Systems Training Facility, Boardman, Morrow County, Oregon (45°50'N, 119°42'W). Dominant shrub habitats on the facility generally were within the big sagebrush/needle-and-thread grass (*Artemisia tridentata*/*Hesperostipa comata*) and big sagebrush/bluebunch wheatgrass (*A. tridentata*/*Agropyron spicatum*) associations (Franklin and Dyrness 1988). However, due to a history of disturbance, shrub communities at the time of the study were patchily distributed and much of the facility had been converted to cheatgrass (*Bromus tectorum*). A 2500-ha study area was established that included nearly all the big sagebrush habitat. Shrub cover varied locally from 10–35%; dominant grasses included cheatgrass, Sandberg's bluegrass (*Poa sandbergii*), and needle-and-thread grass.

The entire area was surveyed systematically for breeding shrikes between 15 April and 23 May 1995–1997. Observers typically covered 250 ha per day by walking slowly with frequent stops to scan the surrounding vegetation until a predetermined site boundary was met. All sightings of shrikes were mapped and repeat visits were made when necessary to determine nest location. Once discovered, nests were monitored every 1 to 4 days until they succeeded or failed (Martin and Geupel 1993). Where exact failure date was unknown, we used the midpoint practice of estimating failure date, assuming that failure occurred halfway between the penultimate nest check (when the nest was active) and ultimate nest check (when the nest had failed; Martin and Geupel 1993). Additional territories and nests were located throughout each season as the entire study area was covered on a regular basis during the course of nest checks.

A total of 146 nests were discovered and monitored over a 3-year period. For 137 of these nests, we obtained what we considered to be moderately precise estimates of the age of the nest (i.e., within 2 days of the true age); the analysis presented here used these 137 nests. A majority of the 137 nests ( $n = 75$ ) were discovered before or during egg laying; for nests found later, nest age was calculated on the assumption that the female laid one egg per day until clutch completion and the onset of incubation. Age was also estimated for nests discovered during or after hatching, on the basis of size and appearance of nestlings. The nine nests for which we had poor estimates of nest age (and which were excluded from the analyses presented here) were found during egg laying ( $n = 1$ ; nest contents unknown), incubation ( $n = 4$ ), or during the nestling period ( $n = 4$ ).

For the purposes of Mayfield estimation, and based on average values compiled from nests with complete information on timing for the respective period (rounded to the closest integer), we calculated an average of 6 days for the laying phase ( $n = 38$  nests), 16 days of incubation ( $n = 38$  nests), and a 17-day nestling period ( $n = 48$  nests). Thus the total nesting period was 39 days.

Date of clutch initiation was calculated on the basis of date of discovery of the nest and the estimated age of the nest at discovery. For analysis, dates were standardized to a mean of zero for the sample (= 4 May; median clutch initiation date = 1 May). Nest height was measured

to the closest cm; statistical analysis was conducted on height measured in m.

#### STATISTICAL ANALYSIS

All analyses were done using STATA 7.0 (StataCorp 2001). Note that in addition to the commercial statistical packages listed in the Introduction, public-domain programs are available such as KMSURV (for Kaplan-Meier estimation) and COXSRV (for Cox proportional hazards regression), available from several websites, including <<http://www.mcgill.ca/cancerepi/links/software/>>.

For the Kaplan-Meier survival functions, we tested for differences among groups using the log-rank test. For the Cox proportional hazards model and Weibull regression we estimated the hazard rate ratio,  $h$ . Where we compared two groups (e.g., late nesters vs. early nesters),  $h$  is the ratio of the hazard rate for one group to the hazard rate of the other. Where the independent variable is quantitative,  $h$  estimates the relative increase in the daily nest failure rate with an increase of one unit in the independent variable (Marubini and Valsecchi 1995). Under the null hypothesis,  $h = 1$  (i.e., no increase in the nest failure rate with a change in the independent variable). For the Weibull regression analysis, we also estimated the parameter  $p$ , which reflects the change in the hazard rate over time. A constant hazard rate (as assumed by the Mayfield method and in exponential regression) necessarily implies that  $p = 1$ . In contrast,  $p > 1$  implies that the hazard rate increases with time;  $p < 1$  implies that the hazard rate decreases with time. The Cox model makes no assumptions about how the hazard rate varies with time, and so allows the greatest flexibility. We illustrate the Cox model treating "date" as both a categorical variable (early vs. late) and as a quantitative variable (date of clutch completion).

We used a hierarchical approach in model selection to identify the optimal predictive model given the three independent variables of interest. First, we considered all models with zero, one, two, or all three of the independent variables; there were eight such models. To select a model of maximal parsimony we used Akaike's Information Criterion (AIC; defined as AIC = deviance of the model +  $2k$ , where deviance of the model =  $-2\log$  likelihood and  $k$  = number of parameters in the model; Lebreton et al. 1992). To compare AIC among models, we used AIC<sub>c</sub>,

TABLE 1. Comparison of measures of nesting success for Loggerhead Shrikes in north-central Oregon for 1995–1997. Shown are estimates of apparent success  $\pm$  SE, Mayfield estimates (with 95% CI), and Kaplan-Meier estimates (with 95% CI).

Year	<i>n</i> (nests)	Apparent nest success	Mayfield estimate (95% CI)	Kaplan-Meier estimate (95% CI)
1995	37	0.432 $\pm$ 0.083	0.293 (0.171–0.498)	0.298 (0.155–0.456)
1996	42	0.524 $\pm$ 0.078	0.477 (0.342–0.662)	0.446 (0.281–0.598)
1997	58	0.483 $\pm$ 0.066	0.418 (0.304–0.575)	0.417 (0.285–0.544)
All years	137	0.482 $\pm$ 0.043	0.405 (0.326–0.502)	0.398 (0.311–0.484)

the AIC value corrected for small sample size (Burnham and Anderson 2002). To identify the optimally parsimonious model, we ranked models according to AIC<sub>c</sub> and calculated  $\Delta$ AIC<sub>c</sub> for each, defined as the difference in AIC<sub>c</sub> between a given model and the model with lowest AIC<sub>c</sub>; we also calculated AIC<sub>c</sub> weights, which estimate the probability a specified model is the true model, given that one of the models being considered is indeed the true model (Burnham and Anderson 2002).

Where there was support for inclusion of one or both of the quantitative variables (date, nest height) in the preferred explanatory model, we next examined functional relationships for that variable, to establish whether the relationship was linear or nonlinear. To do so we examined a nested series of models, in which the specified independent variable was linear, quadratic, or cubic (Link and Sauer 1998, Burnham and Anderson 2002); additional explanatory variables were also included if they were selected in the first stage. We selected among the three functional relationships of the quantitative variable (comparing also the assumption of constant hazard rate with respect to the variable) using AIC<sub>c</sub> and comparing AIC<sub>c</sub> weights.

The third stage in the analysis was to consider pairwise interactions among the three variables. Here we examined *a priori* hypotheses of interest using likelihood-ratio tests (Lebreton et al. 1992, Link and Sauer 1998). To examine the interaction of variable  $x_1$  and  $x_2$  we compared a model with the interaction (plus main effects  $x_1$  and  $x_2$ ) to a model with only main effects ( $x_1$  and  $x_2$ ); whether or not a third variable was included in these comparisons was determined by the model-selection results in the first stage. We report *P*-values associated with the likelihood-ratio tests comparing models with and without interactions. We present both AIC<sub>c</sub> and likeli-

hood-ratio statistics; note that the likelihood-ratio statistic is a function of the deviance, just as is AIC<sub>c</sub> (Hosmer and Lemeshow 1999).

To evaluate the assumption of proportional hazard rates, we followed the test of Grambsch and Therneau (1994) as implemented in STATA (StataCorp 2001). To evaluate goodness of fit in the Weibull regression we used the *streg* procedure in STATA (StataCorp 2001), which estimates the degree of excess heterogeneity due to overdispersion. We did this for all models with low (preferred) AIC<sub>c</sub> values. This goodness of fit test is not available for the Cox model. We report parameter estimates (including means)  $\pm$  SE, unless otherwise indicated.

RESULTS

KAPLAN-MEIER SURVIVAL FUNCTION:  
BETWEEN-YEAR AND WITHIN-SEASON  
EFFECTS

Apparent nest success (i.e., fraction of nests surviving to fledging), Mayfield estimates, and Kaplan-Meier estimates are presented for each year of the study and for the 3 years pooled (Table 1). As expected, apparent nest success was higher in every year and for all years pooled than were the comparable Mayfield and Kaplan-Meier estimates. In turn, Kaplan-Meier and Mayfield estimates were similar to each other in each year and overall. For all years pooled, the Kaplan-Meier estimate of survival to day 39 was  $0.398 \pm 0.044$ .

Kaplan-Meier survival functions for each year are depicted in Figure 1A. There was no overall significant difference among the 3 years (log-rank test, likelihood-ratio statistic = 3.5, *df* = 2, *P* = 0.17). Examining the Kaplan-Meier year-specific survival curves revealed that in the first half of the nesting period, day 1 to day 19, the survival curves for each year were quite similar and generally overlapped. However, beginning at about

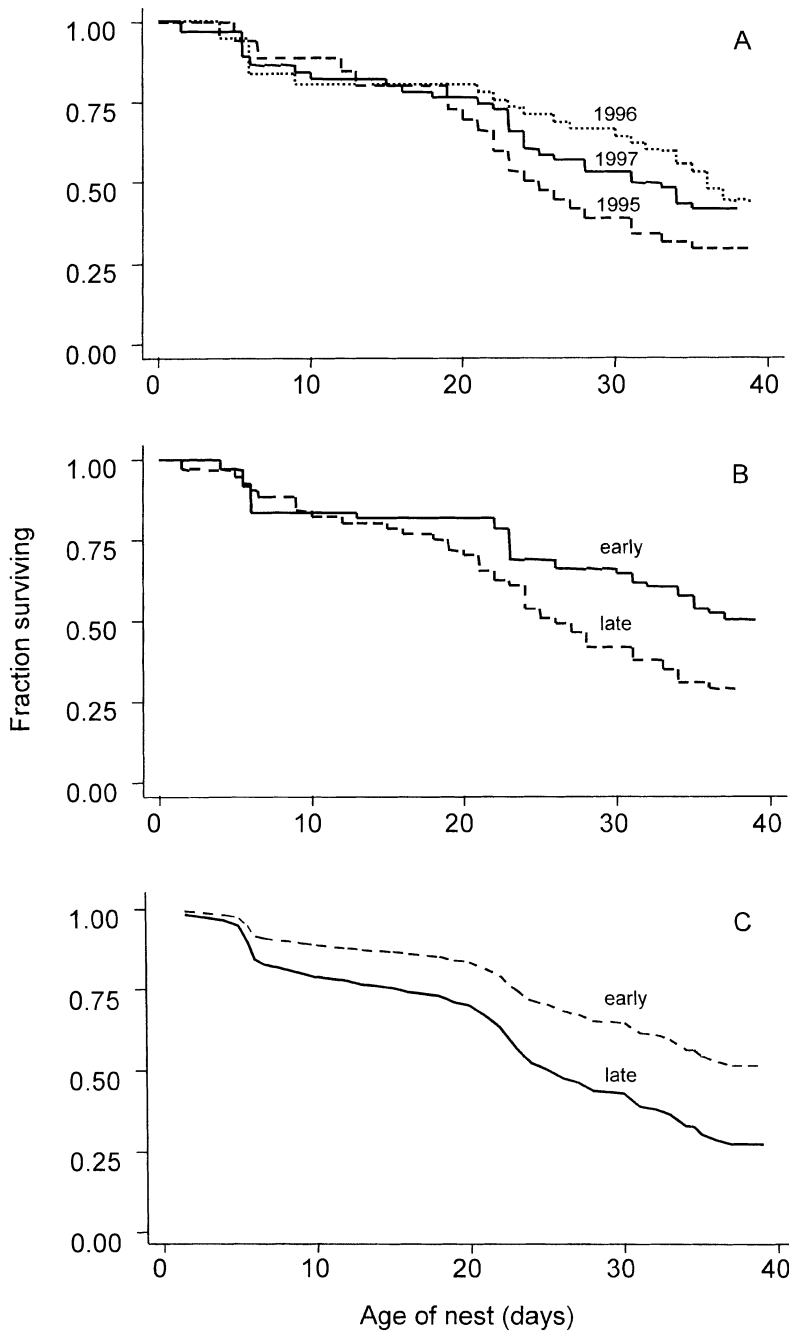


FIGURE 1. Cumulative survival functions for Loggerhead Shrike nests, showing the fraction surviving in relation to nest age. (A) Kaplan-Meier survival functions for 1995, 1996, and 1997. Differences among years are not significant (see text). (B) Kaplan-Meier survival functions for "early" nests (initiated before 1 May) and "late" nests (initiated 1 May or later). Cumulative survival for the two groups differed ( $P = 0.010$ ). (C) Cox proportional hazards model survival functions for early and late nests. Cumulative survival for the two groups differed ( $P = 0.006$ ).



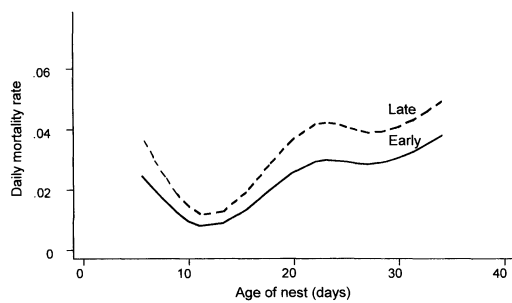


FIGURE 2. Daily mortality rate (hazard rate) of Loggerhead Shrike nests in relation to nest age, as estimated by Cox proportional hazards model for early and late nests (defined as in Fig. 1).

day 19 (3 days before hatching), the survival curves for the three years separated and remained distinct, though as noted the overall differences among the years were not significant.

The Kaplan-Meier survival functions for early vs. late breeders (clutch initiation before 1 May vs. 1 May or later; Fig. 1B) were significantly different (log-rank test, likelihood-ratio statistic = 7.8,  $df = 1$ ,  $P = 0.005$ ). Early in the nesting period (during egg laying and the first week of incubation) there was very little difference between the two survival curves, but after the first week of incubation (after day 13) the two curves diverged, especially so after hatching (about day 22; Fig. 1B).

COX PROPORTIONAL HAZARDS MODEL

*Date as a qualitative variable.* The results of Cox proportional hazards regression for the effect of early vs. late nests was an estimated failure rate ratio of  $h = 1.94 \pm 0.48$  (likelihood-ratio statistic = 7.5,  $df = 1$ ,  $P = 0.006$ ; Fig. 1C). That is, late breeders were almost twice as likely to fail per day (over the course of the nesting cycle) as were early breeders. The cumulative survival curves gradually diverge (Fig. 1C), in contrast to the Kaplan-Meier survival curves (Fig. 1B). The difference between the two graphs is due to the assumption of the Cox model that the ratio of the hazard rates for the two groups is a constant over time. We therefore tested for the validity of the assumption of proportional hazards rate (Grambsch and Therneau 1994); in this case the assumption of proportionality was confirmed ( $\chi^2_1 = 0.3$ ,  $P > 0.6$ ).

The change in the hazard rate with age of the nest is shown in Figure 2 for early and late nests. Daily mortality rate was high at about day 5 and again after about day 22, and lowest at days 10 to 12.

*Model selection and analysis using Cox model.* Treating date as a quantitative variable, the preferred model included date and year, but not nest height (Table 2). The model with date only was similar in  $AIC_c$  to that of the model with date and year, and  $AIC_c$  weights were also similar (0.36 vs. 0.28, respectively). Thus, date was

TABLE 2. Analysis of Loggerhead Shrike nest success using Cox proportional hazard models evaluated using Akaike's Information Criterion adjusted for small sample sizes ( $AIC_c$ ). The number of parameters in each model is given by  $k$ .

Model	$k$	Log likelihood	$\Delta AIC_c$	$AIC_c$ weight
Effects of Date, Year, and Nest Height				
Date + Year <sup>a</sup>	4	-305.82	0.00	0.36
Date	2	-308.15	0.45	0.28
Date + Nest Height + Year	5	-305.72	1.96	0.13
Date + Nest Height	3	-308.05	2.34	0.11
Null	1	-311.04	4.18	0.04
Year	3	-309.43	5.10	0.03
Nest Height	2	-310.51	5.18	0.03
Nest Height + Year	4	-308.76	5.88	0.02
Effects of Year and Date (linear and nonlinear effects)				
Date <sup>2</sup> + Year <sup>b</sup>	5	-304.56	0.00	0.45
Date + Year	4	-305.82	0.37	0.37
Date <sup>3</sup> + Year	6	-304.55	2.18	0.15
Year	3	-309.43	5.47	0.03

<sup>a</sup>  $AIC_c = 619.94$ .  
<sup>b</sup>  $AIC_c = 619.57$ .

TABLE 3. Results of Cox and Weibull regression analyses for effects of clutch initiation date (measured in days) and year on nesting failure rate in Loggerhead Shrike nests of north-central Oregon, 1995–1997. Both models estimated the hazard ratio as  $h = \text{Year} + \text{Date} + \text{Date}^2$ . Clutch initiation date was standardized so that 0 = 4 May (the sample mean). The model for each analysis (Cox, Weibull, respectively) is the best-approximating model as determined by Akaike's Information Criterion adjusted for small sample size ( $AIC_c$ ; Table 2, 4).

Independent variable	Hazard ratio ( $h \pm \text{SE}$ )
Cox proportional hazards model <sup>a</sup>	
1995 vs. 1997	1.536 $\pm$ 0.441
1996 vs. 1997	0.810 $\pm$ 0.235
Date	1.021 $\pm$ 0.0072
Date <sup>2</sup>	0.9996 $\pm$ 0.0023
Weibull regression model <sup>b</sup>	
1995 vs. 1997	1.502 $\pm$ 0.430
1996 vs. 1997	0.796 $\pm$ 0.231
Date	1.0209 $\pm$ 0.0072
Date <sup>2</sup>	0.9996 $\pm$ 0.0023

<sup>a</sup>  $n = 137$  nests, log likelihood = -304.56.

<sup>b</sup>  $n = 137$  nests, log likelihood = -115.51.

clearly an important variable, while year was to a lesser extent.

We then compared linear, quadratic, and cubic relationships for date, while including year effects. The  $AIC_c$ -preferred model treated the hazard rate as a second-order function of date (Table 2). The coefficient of the linear term was positive while the coefficient of the quadratic term was negative (Table 3); thus the relation-

ship was positive but decelerating (concave down). However, the difference in  $AIC_c$  between the quadratic and linear models for date (plus year) was only 0.37. The  $AIC_c$  weights for quadratic and linear relationships for the effect of date were also similar (0.46 vs. 0.37, respectively); thus, both relationships were well supported. None of the three pairwise interactions involving date, nest height, and year were significant (all likelihood ratios  $< 2.5$ , all  $P > 0.3$ ).

The estimated increase in the hazard ratio with each 1-day delay in clutch initiation, assuming a linear relationship with date, was  $h = 1.012 \pm 0.0050$ . In other words, the daily probability of nest failure was estimated to increase by 1.2% as the clutch initiation date increased by 1 day. Since the failure rate ratio is measured on a multiplicative scale, the estimated ratio of failure rates for two nests initiated, say, 10 days apart is  $(1.012)^{10} = 1.127$ , or a difference of 12.7%. This coefficient was similar whether or not one included adjustment for year.

#### WEIBULL REGRESSION

Treating laying date as a quantitative variable in a Weibull regression analysis, we obtained an optimal predictive model, one that included date and year but not nest height (Table 4). This model passed the goodness-of-fit test (overdispersion parameter  $\theta < 0.01$ ,  $P = 0.5$ ). Neither the model with a linear date term nor the model with a quadratic date term demonstrated overdispersion.  $AIC_c$  and  $AIC_c$  weights were very similar

TABLE 4. Analysis of Loggerhead Shrike nest success using Weibull regression models evaluated using Akaike's Information Criterion adjusted for small sample size ( $AIC_c$ ). The number of parameters in each model is given by  $k$ .

Model	$k$	Log likelihood	$\Delta AIC_c$	$AIC_c$ weight
Effects of Date, Year, and Nest Height				
Date + Year <sup>a</sup>	4	-116.77	0.00	0.36
Date	2	-119.08	0.40	0.30
Date + Nest Height + Year	5	-116.71	2.03	0.13
Date + Nest Height	3	-118.99	2.31	0.11
Null	1	-122.23	4.63	0.04
Year	3	-120.63	5.60	0.02
Nest Height	2	-121.69	5.62	0.02
Nest Height + Year	4	-120.01	6.47	0.01
Effects of Year and Date (linear and nonlinear effects)				
Date <sup>2</sup> + Year <sup>b</sup>	5	-115.51	0.00	0.45
Date + Year	4	-116.77	0.36	0.38
Date <sup>3</sup> + Year	6	-115.51	2.18	0.15
Year	3	-120.63	5.96	0.02

<sup>a</sup>  $AIC_c = 241.85$ .

<sup>b</sup>  $AIC_c = 241.48$ .

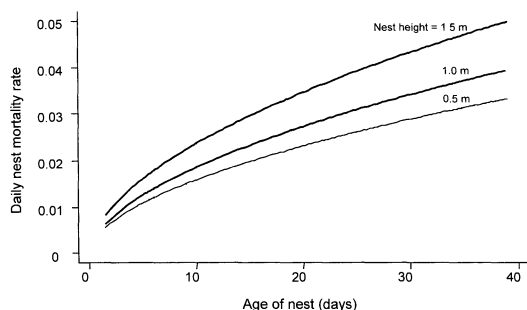


FIGURE 3. Daily mortality rate (hazard rate) of Loggerhead Shrike nests as a function of nest age and nest height. Shown are estimated hazard rate functions (as predicted by the Weibull regression model) for nests at 0.5 m, 1 m, and 1.5 m. Although hazard rates appeared to vary by nest height, this variable was not included in the most parsimonious model as determined by  $AIC_c$  (Table 4).

to those obtained for the Cox model. In addition, the  $AIC_c$  preferred functional relationship of daily mortality rate to date (controlling for year) was quadratic, but, as with the Cox model, this was only slightly preferred over a linear relationship ( $AIC_c$  weights were 0.45 and 0.38, respectively; Table 4). For the quadratic-date plus year model, the quadratic coefficient was negative but the linear term was positive, just as it was with Cox model (Table 3). None of the three pairwise interactions involving date, nest height, and year were significant (all likelihood ratios  $< 2.3$ , all  $P > 0.3$ ).

The hazard rate ratio in relation to date (treated as a linear variable), controlling for year, was  $h = 1.013 \pm 0.0049$ . In other words, the daily failure rate increased by 1.3% per day as the season progressed, very similar to the estimate obtained from the Cox model. The hazard rate also increased with age of the nest:  $p = 1.57 \pm 0.20$  (95% CI 1.23–2.01;  $P < 0.004$ ). Thus, an exponential regression analysis cannot be justified since  $p$  is clearly and significantly greater than 1.

For nest height, the estimated hazard ratio was  $1.54 \pm 0.64$  ( $P = 0.3$ ), suggesting that the failure rate increased by 54% with each 1-m increase in nest height. However, the standard error of this estimate was large. Figure 3 demonstrates results of the Weibull regression analysis and shows the predicted hazard rate (as a function of age of the nest) for nests at heights of 0.5 m, 1 m, and 1.5 m. We use this to graphically illustrate Weibull regression results, but

note that nest height was not included in the  $AIC_c$  preferred model.

## DISCUSSION

### FACTORS INFLUENCING NEST SUCCESS IN LOGGERHEAD SHRIKES

We used survival time analysis to statistically describe and analyze daily nest mortality of Loggerhead Shrike nests in relation to several factors: date of laying, differences among years, and nest height. We found evidence of an effect of laying date, such that later nests were at greater mortality risk, a result that has been reported for other species (Newton 1973, Nolan 1978, Price et al. 1988, Hochachka 1990, Schaub et al. 1992, Anderson et al. 2001). Burhans et al. (2002), in contrast, reported a peak in nest mortality in midsummer, followed by a drop in late summer. Zimmerman (1984) detected a significant quadratic trend in nest mortality of Dickcissels (*Spiza americana*), such that nest mortality increased throughout most of the breeding season, but then leveled off in the latter part of the season. Our study also supports a nonlinear relationship of nest mortality and laying date.

There was moderate support for the importance of annual differences in nest mortality rates. Model selection using  $AIC_c$  favored a model including date and year effects. However, statistical tests of annual differences in mortality rates alone were not significant. Once differences in laying date were accounted for, annual differences did appear to be important. Examining the Kaplan-Meier survival functions for the 3 years suggests that any differences among years were manifest in the nestling period, and perhaps late incubation period, rather than in the laying and early to mid-incubation stages. This apparent difference in temporal patterns leads us to speculate that the causes of nest failure differ for the two stages of the nesting cycle (e.g., different nest predators or different search behavior by predators during the early part of the nesting period compared to late in the nesting period).

We also examined the influence of nest height on nest mortality and found little evidence of an effect. In contrast, several previous studies have found evidence of an effect of nest height, or, more generally, of nest placement (Best and Stauffer 1980, Conner et al. 1986, Li and Martin 1991, Kelly 1993, Misenhelter and Rotenberry 2000, DeSanto et al. 2002) but some have not (Braden 1999). For example, both Wilson and

Cooper (1998) and Burhans et al. (2002) found that nest height and nest mortality were negatively correlated.

#### COMPARISON OF SURVIVAL TIME ANALYSIS WITH THE MAYFIELD METHOD

One of the principal advantages of survival time analysis in comparison with the Mayfield method is the ability to analyze nest data in a statistically sophisticated fashion, using readily available software. For example, survival time analysis allowed us to analyze a linear effect of nest height on nest survivorship, as well as investigate deviations from linearity. The Mayfield method would only allow group comparisons (e.g., low nesters vs. high nesters). In addition, with survival time analysis one can examine the effect of one variable while statistically controlling for another. Wilson and Cooper (1998) found that nest height was correlated with nest success, but they also reported that late nests were more successful and that late nests were higher up, which suggests confounding, a possibility they did not examine. With survival time analysis it is easy to control for such confounding.

A second advantage of survival time analysis is the ability to describe and identify patterns of age-specific variation in nest mortality. In contrast, the Mayfield method assumes constancy within the period in question. Mayfield estimates can be used to compare nest survivorship for periods within the nesting cycle, but these periods need to be identified *a priori*. If a change in nest survivorship occurred in the middle of a Mayfield period it would be hard to detect. Kaplan-Meier survival curves can provide a potent tool for assessing potential differences in nest survivorship, while parametric regression analyses can be used to statistically evaluate whether daily nest mortality varies with the age of the nesting attempt.

Even more sophisticated analyses can be carried out using survival time analysis, including analysis of time-varying covariates. These can either be subject-specific (the covariate for each subject [in this case, nest] changes over time) or subject-independent (the covariate changes over time for all subjects in the study). An example of the former might be examination of the effect of parental feeding frequency, which varies during the course of the nesting period (Evans Ogden and Stutchbury 1997), on nest survivorship. An example of the latter might be a weather variable which varies on a daily basis (e.g., Dins-

more et al. 2002). Furthermore, one can analyze nest survivorship incorporating clustering (e.g., several nests produced by the same pair; Hosmer and Lemeshow 1999). Survival time analysis provides a convenient and rigorous means of examining heterogeneity of mortality rates due to unknown (i.e., random) effects (Andersen et al. 1997, Natarajan and McCulloch 1999).

The final reason for preferring survival time analysis to the Mayfield method is the likelihood of violations of assumptions made by the Mayfield method. The first is the assumption of constancy of nest failure rate over time (age of the nest). This assumption was not upheld in our study and is probably commonly violated (Nolan 1978, Schaub et al. 1992, Morton et al. 1993). The second assumption is of homogeneity of nest failure rates among nests. This assumption was not upheld (i.e., failure rates differed with respect to date of clutch initiation). We maintain that heterogeneity of nest failure rates is commonplace. Other studies have demonstrated that nest survivorship varies with, for example, age of parent (Grant and Grant 1989, Geupel and DeSante 1990, Lozano et al. 1996), and nest placement (Moorman et al. 2002). With survival time analysis one can statistically test for or control for whichever variable or covariate one suspects may be related to nest failure rates and one can do this for several variables at once.

#### OTHER MAYFIELD ALTERNATIVES

Many authors have provided alternatives to the Mayfield method (Johnson 1979, Bart and Robson 1982, Pollock and Cornelius 1988, Heisey and Nordheim 1990, Bromaghin and McDonald 1993, Rotella et al. 2000, Manly and Schmutz 2001). What distinguishes survival time analysis from nearly all of these Mayfield alternatives is the combination of readily available software and the power and flexibility to develop sophisticated statistical models, models that include statistically controlling for several variables at once, examining trends (including polynomial trends), and testing for interactions, time-varying covariates, individual-nest covariates, clustering of outcomes, etc. The exception to this generalization is the program MARK (Dinsmore et al. 2002) which we discuss separately.

Just as with survival time analysis, some alternative methods allow nest survival to be time dependent (i.e., age dependent), in which case the age of the nest upon discovery needs to be esti-

mated (Klett and Johnson 1982, Pollock and Cornelius 1988, Bromaghin and McDonald 1993, Natarajan and McCulloch 1999, Manly and Schmutz 2001). Other methods follow Mayfield and do not explicitly allow for variation in survival with age of the nesting attempt (Bart and Robson 1982, Rotella et al. 2000). Many of the methods assume the outcome of the nesting attempt is known (Bromaghin and McDonald 1993, Manly and Schmutz 2001, Dinsmore et al. 2002); that is, they do not allow for right-censoring.

Recently, Dinsmore et al. (2002) demonstrated the value of using the “nest survival model” in MARK (White and Burnham 1999), especially because this program allows for evaluating individual and group- and time-specific covariates coupled with a flexible interface. Indeed, program MARK provides the ornithologist a very useful tool for studying patterns influencing nest survivorship. We note that survival time analysis, too, provides the same advantages. In addition, unlike the nest survival model in MARK, survival time analysis does not require that nest fate be known. Survival time analysis also allows for semiparametric analysis, while in MARK only parametric analysis is possible (i.e., time-specific survival must be explicitly modeled). Survival time analysis can be carried out with a wide variety of statistical packages that are generally very easy to learn. Implementation of nest survival analysis with MARK is described by Dinsmore et al., but is not yet included in the user guide by Cooch and White (2003). One of the strengths of survival time analysis is well-developed theory and practical applications, with many graphical procedures available (Hosmer and Lemeshow 1999). In particular, extensive diagnostic tests, including assessment of model fit, identification of influential observations, and tests of the assumption of proportional hazards, are available (Collett 2003, Chapters 4 and 7).

#### COMPARISON WITH LOGISTIC REGRESSION

Logistic regression is another widely used analytic method (Burhans et al. 2002, DeSanto et al. 2002, Liebezeit and George 2002, and Rodewald 2002). However, there are serious drawbacks to the use of logistic regression that do not apply to survival time analysis:

First, logistic regression does not take into account the number of days that a nest survives. Thus this method throws away information

about nest-survival rates. Second, logistic regression does not allow for nests to be discovered at different ages. A nest discovered late in the nesting period, is (all else being equal) more likely to survive to fledging than a nest discovered at initiation. Thus, logistic regression can confound nest discovery with nest survival. If nests with attribute  $x$  are discovered later in the nesting period than other nests, then, all else being equal, their survival will appear to be higher. Third, logistic regression assumes the outcome of a nest is known. Consider that we might know a particular nest survived to day 10, but we may not know whether it ultimately fledged young or not. What do we do with that nest in the analysis? We would be introducing a bias in the analysis if we said this nest fledged young, but we also bias the analysis if we omit the nest altogether (Manolis et al. 2000). In some studies, the number of nests dropped from a logistic regression analysis due to unknown outcome can be quite large (e.g., DeSanto 2002). Fourth, logistic regression can provide no insight into variation in nest mortality with respect to age of the nest. Survival time analysis, in contrast, provides graphical and statistical estimation for age-dependent variation in nest mortality.

#### ASSUMPTIONS OF SURVIVAL TIME ANALYSIS

The validity and utility of survival time analysis depend on conformity with its assumptions. The first assumption is that the age of the nesting attempt can be determined. This may be the most serious limitation for ornithologists and is discussed in detail below. The second assumption is that nests included in the study are representative of the entire population of nests. The difficulty is that the higher the mortality rate the more likely a nest will fail before it is discovered (and thus before it can be included in the study sample). Conclusions are restricted to the sample of nests discovered before they fail, even though this may not represent the entire population of nests. This drawback is common to survival time analysis, the Mayfield method, and most other alternatives. In contrast, several investigators have developed methods that take into account the probability of nest discovery (Hensler and Nichols 1981, Pollock and Cornelius 1988, Bromaghin and McDonald 1993, Dinsmore et al. 2002). Further work in this area should be encouraged.

The third assumption is that date of nest failure can be ascertained. In our study, this could

be approximated due to regular nest checks at 1 to 4 day intervals. For studies which check nests at 1 to 2 day intervals this assumption should not present a problem, but infrequent nest checks (e.g., every 10 days) may present difficulty, and survival time analysis may not be the most appropriate method.

The fourth assumption is that censoring is as likely for one nest as any other. The investigator can directly compare properties of censored and uncensored nests to determine if there are any systematic differences. The final assumption is independence of outcome once all independent variables have been accounted for. Goodness-of-fit tests will help the investigator confirm this assumption.

#### AGEING NESTS: A REQUIREMENT OF SURVIVAL TIME ANALYSIS

The first assumption in applying survival time analysis to avian nesting studies is the ability to age nests at discovery. Note that many of the methods suggested as alternatives to the Mayfield method also require ageing of nests (Pollock and Cornelius 1988, Bromaghin and McDonald 1993, Manly and Schmutz 2001, Dinsmore et al. 2002). For nests discovered before or during egg laying, ageing is not a major difficulty since females will lay eggs at regular intervals (e.g., for passerines, one egg per day), thus allowing one to calculate date of clutch initiation.

For nests discovered during incubation, ageing will usually be more difficult. Whereas one can backdate a successfully hatched clutch (if hatching date is known), one cannot do so for a clutch which fails during incubation. The sample would be biased if clutches which fail to hatch are excluded, while those that hatch are included. To age nests discovered during incubation, there are two commonly used approaches: (1) candle the eggs (Hanson and Kossack 1957, Lokemoen and Koford 1996) or (2) "float" the eggs (fresh eggs sink, partly incubated eggs are neutrally buoyant, and fully incubated eggs float; Walter and Rusch 1997, Brua and Machin 2000, Dinsmore et al. 2002). We recommend that investigators adopt one of these two approaches, if feasible. However, care should always be practiced in handling small and delicate eggs.

For nests discovered during hatching, ageing should not present a problem, if nest contents can be examined. Ageing nests discovered later in the nestling period can pose some difficulties,

though. In this case one can rely on nestling mass, wing length, feather development, and total nestling length. Use of these methods, or a combination of them, has been shown to be reliable in several studies (Holcomb and Twiest 1971, Carlsson and Hoernfeldt 1994). Use of photographs of nestlings of known age helps improve accuracy of ageing (Hanson and Kossack 1957, Podlesak and Blem 2001).

Even if it is not possible to use the methods described to estimate the age of nests discovered during incubation, it will usually be possible to use survival time analysis to analyze nest survivorship specifically during the nestling or chick-rearing period. Those nests discovered before hatching and which survive to hatching will not be left-censored for such an analysis; for those nests discovered after hatching, their age can usually be determined as discussed above. The exception is nests whose contents cannot be examined.

We conclude by noting that survival time analysis requires information on age of nests because it allows for the possibility that nest mortality varies with age of the nest, and allows one to graphically and statistically evaluate this possibility. The Mayfield method does not require information on the age of nests because it assumes that nest mortality is independent of age (and time), either for the entire nesting period or for *a priori* identified subperiods. However, the assumption of a constant mortality risk is not widely upheld, as attested to by this study and others (Nolan 1978:403, Schaub et al. 1992, Renner and Davis 2001, Manly and Schmutz 2001, Dinsmore et al. 2002). We therefore encourage field biologists to design their studies so that age of nests at discovery can be ascertained.

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#### LITERATURE CITED

ALDRIDGE, C. L., AND R. M. BRIGHAM. 2001. Nesting and reproductive activities of Greater Sage-

- Grouse in a declining northern fringe population. *Condor* 103:537–543.
- ALLISON, P. D. 1997. Survival analysis using the SAS system: a practical guide. SAS Institute Inc., Cary, NC.
- ANDERSEN, P. K., J. P. KLEIN, K. M. KNUDSEN, AND R. T. PALACIOS. 1997. Estimation of variance in Cox's regression model with shared gamma frailties. *Biometrics* 53:1475–1484.
- ANDERSON, M. G., M. S. LINDBERG, AND R. B. EMERY. 2001. Probability of survival and breeding for juvenile female Canvasbacks. *Journal of Wildlife Management* 65:385–397.
- BART, J., AND D. S. ROBSON. 1982. Estimating survivorship when the subjects are visited periodically. *Ecology* 63:1078–1090.
- BEST, L. B., AND D. F. STAUFFER. 1980. Factors affecting nesting success in riparian bird communities. *Condor* 82:149–158.
- BRADEN, G. T. 1999. Does nest placement affect the fate or productivity of California Gnatcatcher nests? *Auk* 116:984–993.
- BROMAGHIN, J. F., AND L. L. McDONALD. 1993. A systematic-encounter-sampling design for nesting studies. *Auk* 110:646–651.
- BRUA, R. B., AND K. L. MACHIN. 2000. Determining and testing the accuracy of incubation stage of Ruddy Duck eggs by floatation. *Wildfowl* 51:181–189.
- BURHANS, D. E., D. DEARBORN, F. R. THOMPSON III, AND J. FAABORG. 2002. Factors affecting predation at songbird nests in old fields. *Journal of Wildlife Management* 66:240–249.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and inference: a practical information-theoretic approach. 2nd ed. Springer Verlag, New York.
- CARLSSON, B.-G., AND B. HOERNFELDT. 1994. Determination of nestling age and laying date in Tengmalm's Owl: use of wing length and body mass. *Condor* 96:555–559.
- COLLETT, D. 2003. Modelling survival data in medical research. 2nd ed. Chapman & Hall/CRC, Boca Raton, FL.
- CONNER, R. N., M. E. ANDERSON, AND J. G. DICKSON. 1986. Relationships among territory size, habitat, song, and nesting success of Northern Cardinals. *Auk* 103:23–31.
- COOCH, E., AND G. C. WHITE [online]. 2003. Program MARK—a gentle introduction. 2nd ed. <<http://www.phidot.org/software/mark/docs/book/>> (28 April 2004).
- COX, D. R. 1972. Regression models and life tables (with discussion). *Journal of the Royal Statistical Society Series B* 34:187–220.
- CYTEL SOFTWARE. 2000. EGRET Statistical Software. Cytel Software Corp., Cambridge, MA.
- DESANTO, T. L., M. F. WILLSON, K. E. SIEVING, AND J. J. ARMESTO. 2002. Nesting biology of tapaculos (Rhinocryptidae) in fragmented south-temperate rainforests of Chile. *Condor* 104:482–495.
- DINSMORE, S. J., G. C. WHITE, AND F. L. KNOPF. 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83:3476–3488.
- DONOVAN, T. M., F. R. THOMPSON III, J. FAABORG, AND J. R. PROBST. 1995. Reproductive success of migratory birds in habitat sources and sinks. *Conservation Biology* 9:1380–1395.
- EVANS OGDEN, L. J., AND B. J. STUTCHBURY. 1997. Fledgling care and male parental effort in the Hooded Warbler (*Wilsonia citrina*). *Canadian Journal of Zoology* 75:576–581.
- FARNSWORTH, G. L., K. C. WEEKS, AND T. R. SIMONS. 2000. Validating the assumptions of the Mayfield method. *Journal of Field Ornithology* 74:658–664.
- FRANKLIN, J. F., AND C. T. DYRNES. 1988. Natural vegetation of Oregon and Washington. Oregon University Press, Eugene, OR.
- GEUPEL, G. R., AND D. F. DESANTE. 1990. Incidence and determinants of double brooding in Wrentits. *Condor* 92:67–75.
- GRAMBSCH, P. M., AND T. M. THERNEAU. 1994. Proportional hazards test and diagnostics based on weighted residuals. *Biometrika* 81:515–526.
- GRANT, B. R., AND P. R. GRANT. 1989. Evolutionary dynamics of a natural population. University of Chicago Press, Chicago.
- HANSON, H. C., AND C. W. KOSSACK. 1957. Methods and criteria for aging incubated eggs and nestlings of the Mourning Dove. *Wilson Bulletin* 69:91–101.
- HEISEY, D. M., AND E. V. NORDHEIM. 1990. Biases in the Pollock and Cornelius method of estimating nest survival. *Biometrics* 46:855–862.
- HENSLER, G. L., AND J. D. NICHOLS. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. *Wilson Bulletin* 93:42–53.
- HOCHACHKA, W. 1990. Seasonal decline in reproductive performance of Song Sparrows. *Ecology* 71:1279–1288.
- HOLCOMB, L. C., AND G. TWIST. 1971. Growth and calculation of age for Red-winged Blackbird nestlings. *Bird Banding* 42:1–17.
- HOSMER, D. W., AND S. LEMESHOW. 1999. Applied survival analysis: regression modeling of time to event data. John Wiley, New York.
- HOSMER, D. W., AND S. LEMESHOW. 2000. Applied logistic regression, 2nd ed. John Wiley, New York.
- JEHLE, G., A. A. YACKEL ADAMS, J. A. SAVIDGE, AND S. K. SKAGEN. 2004. Nest survival estimation: a review of alternatives to the Mayfield estimator. *Condor* 106:472–484.
- JOHNSON, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk* 96:651–661.
- JOHNSON, D. H., AND T. L. SHAFFER. 1990. Estimating nest success: when Mayfield wins. *Auk* 107:595–600.
- KALBFLEISCH, J. D., AND R. L. PRENTICE. 1980. The statistical analysis of failure time data. John Wiley, New York.
- KELLY, J. P. 1993. The effect of nest predation on habitat selection by Dusky Flycatchers in limber pine-juniper woodland. *Condor* 95:83–93.
- KLETT, A. T., AND D. H. JOHNSON. 1982. Variability in nest survival rates and implications to nesting studies. *Auk* 99:77–87.
- LIEBEZEIT, J. R., AND T. L. GEORGE. 2002. Nest predators, nest-site selection, and nesting success of the Dusky Flycatcher in a managed ponderosa pine forest. *Condor* 104:507–517.

- LEBRETON, J.-D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- LI, P., AND T. E. MARTIN. 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. *Auk* 108:405–418.
- LINK, W., AND J. R. SAUER. 1998. Estimating population change from count data: applications to the North American Breeding Bird Survey. *Ecological Applications* 8:258–268.
- LOKEMOEN, J., AND R. KOFORD. 1996. Using candlers to determine the incubation stage of passerine eggs. *Journal of Field Ornithology* 67:660–668.
- LOZANO, G. A., S. PERREAULT, AND R. E. LEMON. 1996. Age, arrival date, and reproductive success of male American Redstarts *Setophaga ruticilla*. *Journal of Avian Biology* 27:164–170.
- MANLY, B. F., AND J. A. SCHMUTZ. 2001. Estimation of brood and nest survival: comparative methods in the presence of heterogeneity. *Journal of Wildlife Management* 65:258–270.
- MANOLIS, J. C., D. E. ANDERSEN, AND F. J. CUTHBERT. 2000. Uncertain nest fates in songbird studies and variation in Mayfield estimation. *Auk* 117:615–626.
- MARTIN, T. E., AND G. R. GEUPEL. 1993. Nest monitoring plots: methods for locating nests and monitoring success. *Journal of Field Ornithology* 64:507–519.
- MARTIN, T. E., C. R. PAINE, C. J. CONWAY, W. M. HOCHACHKA, P. ALLEN, AND W. JENKINS. 1997. BIRD field protocols. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT.
- MARUBINI, E., AND M. G. VALSECCHI. 1995. Analysing survival data from clinical trials and observational studies. John Wiley, Chichester, UK.
- MATHSOFT. 1999. S-PLUS 2000. MathSoft Inc., Cambridge, MA.
- MAYFIELD, H. 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73:255–261.
- MAYFIELD, H. 1975. Suggestions for calculating nest success. *Wilson Bulletin* 87:456–466.
- MILLSPAUGH, J., AND J. MARZLUFF. 2001. Radiotelemetry and animal populations. Academic Press, San Diego, CA.
- MISENHELTER, M. D., AND J. T. ROTENBERRY. 2000. Choices and consequences of habitat occupancy and nest site selection in Sage Sparrows. *Ecology* 81:2892–2901.
- MOORMAN, C. E., D. C. GUINN JR., AND J. C. KILGO. 2002. Hooded Warbler nesting success adjacent to group selection and clearcut edges in a Southeastern bottomland forest. *Condor* 104:366–377.
- MORTON, M. L., K. W. SOCKMAN, AND L. E. PETERSON. 1993. Nest predation in the Mountain White-crowned Sparrow. *Condor* 95:72–82.
- NATARAJAN, R., AND C. E. MCCULLOCH. 1999. Modeling heterogeneity in nest survival data. *Biometrics* 55:553–559.
- NEWTON, I. 1973. *Finches*. Taplinger, New York.
- NOLAN, V., JR. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. *Ornithological Monograph* 26.
- NUR, N., S. L. JONES, AND G. R. GEUPEL. 1999. Statistical guide to data analysis of avian monitoring programs. USDI Fish and Wildlife Service Biological Technical Publication BTP-R6001–1999, Washington, DC.
- PEASE, C. M., AND J. A. GRZYBOWSKI. 1995. Assessing the consequences of brood parasitism and nest predation on seasonal fecundity in passerine birds. *Auk* 112:343–363.
- PODLESAK, D. W., AND C. R. BLEM. 2001. Factors associated with growth of nestling Prothonotary Warblers. *Wilson Bulletin* 113:263–272.
- POLLOCK, K. H., AND W. L. CORNELIUS. 1988. A distribution-free nest survival model. *Biometrics* 44:397–404.
- POLLOCK, K. H., S. R. WINTERSTEIN, AND M. J. CONROY. 1989. Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management* 53:7–15.
- PRICE, T., M. KIRKPATRICK, AND S. J. ARNOLD. 1988. Directional selection and the evolution of breeding date in birds. *Science* 240:798–799.
- RENNER, M., AND L. S. DAVIS. 2001. Survival analysis of Little Penguins *Eudyptula minor* chicks on Motuara Island, New Zealand. *Ibis* 143:369–379.
- ROBINSON, S. K., F. R. THOMPSON III, T. E. DONOVAN, D. R. WHITEHEAD, AND J. FAABORG. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267:1987–1990.
- RODEWALD, A. D. 2002. Nest predation in forested regions: landscape and edge effects. *Journal of Wildlife Management* 66:634–660.
- ROTELLA, J. J., M. L. TAPER, AND A. J. HANSEN. 2000. Correcting nest-success estimates for observer effects: maximum-likelihood estimates of daily survival rates with reduced bias. *Auk* 117:92–109.
- SCHAUB, R., R. L. MUMME, AND G. E. WOOLFENDEN. 1992. Predation on the eggs and nestlings of Florida Scrub Jays. *Auk* 109:585–593.
- SIMONS, T. R., G. L. FARNSWORTH, AND S. A. SHRINER. 2000. Evaluating Great Smoky Mountains National Park as a population source for the Wood Thrush. *Conservation Biology* 14:1133–1144.
- STATACORP. 2001. Stata statistical software: release 7.0. Stata Corporation, College Station, TX.
- THOMPSON, B. C., G. E. KNADLE, D. L. BRUBAKER, AND K. S. BRUBAKER. 2001. Nest success is not an adequate comparative estimate of avian reproduction. *Journal of Field Ornithology* 72:527–536.
- WALTER, S. E., AND D. H. RUSCH. 1997. Accuracy of egg flotation in determining age of Canada Goose nests. *Wildlife Society Bulletin* 25:854–857.
- WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46(Suppl.):120–138.
- WHITE, G., AND GARROTT, R. A. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, CA.
- WILSON, R. R., AND R. J. COOPER. 1998. Acadian Flycatcher nest placement: does placement influence reproductive success? *Condor* 100:673–679.
- ZIMMERMAN, J. L. 1984. Nest predation and its relationship to habitat and nest density in Dickcissels. *Condor* 86:68–72.