

NEST SURVIVAL ESTIMATION: A REVIEW OF ALTERNATIVES TO THE MAYFIELD ESTIMATOR

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Abstract. Reliable estimates of nest survival are essential for assessing strategies for avian conservation. We review the history of modifications and alternatives for estimating nest survival, with a focus on four techniques: apparent nest success, the Mayfield estimator, the Stanley method, and program MARK. The widely used Mayfield method avoids the known positive bias inherent in apparent nest success by estimating daily survival rates using the number of exposure days, eliminating the need to monitor nests from initiation. Concerns that some of Mayfield's assumptions were restrictive stimulated the development of new techniques. Stanley's method allows for calculation of stage-specific daily survival rates when transition and failure dates are unknown, and eliminates Mayfield's assumption that failure occurred midway through the nest-check interval. Program MARK obviates Mayfield's assumption of constant daily survival within nesting stages and evaluates variation in nest survival as a function of biologically relevant factors. These innovative methods facilitate the evaluation of nest survival using an information-theoretic approach. We illustrate use of these methods with Lark Bunting (*Calamospiza melanocorys*) nest data from the Pawnee National Grassland, Colorado. Nest survival estimates calculated using Mayfield, Stanley, and MARK methods were similar, but apparent nest success estimates ranged 1–24% greater than the other estimates. MARK analysis revealed that survival of Lark Bunting nests differed between site-year groups, declined with both nest age and time in season, but did not vary with weather parameters. We encourage researchers to use these approaches to gain reliable and meaningful nest survival estimates.

Key words: *apparent nest success, Lark Bunting, Mayfield method, nest success, nest survival estimation, program MARK, Stanley method.*

Estimación de la Supervivencia de Nidos: Una Revisión de las Alternativas del Estimador Mayfield

Resumen. Es esencial contar con estimaciones confiables de la supervivencia de nidos para evaluar las estrategias de conservación de las aves. Revisamos la historia de modificaciones y las alternativas para estimar la supervivencia de nidos, enfocándonos en cuatro técnicas: éxito aparente del nido, el estimador de Mayfield, el método de Stanley y el programa MARK. El método de Mayfield, ampliamente usado, evita el conocido sesgo positivo inherente al éxito aparente del nido mediante la estimación de tasas de supervivencia diaria usando el número de días de exposición, eliminando así la necesidad de monitorear los nidos desde el inicio. Las preocupaciones de que algunos de los supuestos del método de Mayfield son restrictivos estimularon el desarrollo de nuevas técnicas. El método de Stanley permite el cálculo de tasas de supervivencia diarias específicas para cada etapa cuando las fechas de transición y fracaso son desconocidas, y elimina el supuesto del método de Mayfield que sostiene que el fracaso ocurre en el medio del intervalo de monitoreo del nido. El programa MARK elimina el supuesto del método de Mayfield sobre supervivencia diaria constante dentro de las etapas de nidificación y evalúa la variación en la supervivencia de nidos como función de factores biológicamente relevantes. Estos métodos innovadores facilitan la evaluación de la supervivencia de nidos usando un enfoque teórico-informativo. Ilustramos el uso de estos métodos con datos de nidos de *Calamospiza melanocorys* provenientes de Pawnee National Grassland, Colorado. Las estimaciones de supervivencia de los nidos calculadas usando los métodos de Mayfield, Stanley y MARK fueron similares, pero las estimaciones del éxito aparente de los nidos fueron entre 1–24% mayores que las otras estimaciones. Los análisis con MARK revelaron que la supervivencia de los nidos de *C. melanocorys* difirió entre grupos de sitio-año, disminuyó con la edad del nido y el tiempo de la estación, pero no varió con parámetros climáticos. Estimulamos a los investigadores a usar estos enfoques para obtener estimaciones de supervivencia de nidos confiables y válidas.

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INTRODUCTION

Estimates of nest survival are an essential component of avian demographic modeling and are important for evaluating habitat management strategies. Although annual reproductive success (young produced per female per year) may be a more desirable metric for examining population dynamics (Thompson et al. 2001), nest survival is thought to be a more sensitive indicator of the effects of habitat differences (Armstrong et al. 2002). Because measures of nest survival are our most efficacious way of evaluating avian conservation and management practices, these measures need to be as reliable and informative as possible. Most researchers have used the terms *nest success* or *nesting success* to refer to the probability that a nest will fledge at least one conspecific (i.e., nonparasitic) young over the entire nesting period. Following Dinsmore et al. (2002), we will use the term *nest survival*.

Numerous methods have been developed for estimating nest survival, but only a few have gained wide use among avian ecologists. Over the past three decades, many estimates have been based on the popular Mayfield estimator. When it was introduced, the Mayfield estimator represented an enormous advance in nest survival estimation. Because some assumptions of the Mayfield estimator are restrictive, new approaches that relax the assumptions have been developed. Here, we review the progressive improvements (see Appendix) for estimating nest survival and evaluate the assumptions and utility of the various methods. While we recognize that it is possible to apply methods from survival time analysis models (Kaplan and Meier 1958, Cox 1972, Nur et al. 2004) to estimate nest survival, we restrict our discussion to methods originally developed for estimating nest survival. We discuss two recently proposed approaches in greater detail. Stanley's (2000) method allows for calculation of stage-specific daily survival rates even when the timing of transition between nesting stages and the period in which failure occurred are unknown. Dinsmore et al. (2002) present a new method using program MARK (White and Burnham 1999) to evaluate variation in nest survival as a function of biologically relevant factors (e.g., nest age, time during season, weather). Program MARK eliminates the assumption that daily nest survival rates remain constant within the nesting stage. Both methods

obviate the assumption that failure occurs midway through nest-check intervals. Additionally, these methods facilitate use of Akaike's Information Criterion (AIC) to evaluate models explaining variation in nest survival (Akaike 1973, Burnham and Anderson 2002). We analyze Lark Bunting (*Calamospiza melanocorys*) nest survival data using these two new methods, and compare the results with apparent nest success and Mayfield estimates.

APPARENT NEST SUCCESS

Early attempts to estimate nest survival rates incorporated a simple calculation of the number of successful nests divided by the total number of nests found. This estimate is usually called *apparent nest success* but has also been referred to as *the traditional method* (Johnson 1979, Hensler and Nichols 1981) and the *naïve estimator* (Heisey and Nordheim 1990, Stanley 2000). Avian ecologists have long recognized that apparent nest success estimates are positively biased because successful nests have a higher probability of being detected than failed nests (Snow 1955, Coulson 1956, Hammond and Forward 1956, Peakall 1960, Mayfield 1961, 1975). The only way to ensure an unbiased estimate using apparent nest success is to find every nest at initiation (Klett and Johnson 1982), which is possible only when nest detectability is high or when destroyed nests may be found with approximately the same probability as active nests, as in some island-nesting or colonial species (Johnson and Shaffer 1990). In field studies of many bird species, especially passerines, it is impossible to meet this assumption. Furthermore, the extent of the positive bias for this estimator is inconsistent, so comparisons of apparent nest success between study areas are not valid. Using Monte Carlo simulations, Hensler and Nichols (1981) demonstrated that positive bias in apparent nest success ranged between 9% and 27%, and that the bias is exacerbated by low daily survival rates but not affected by sample size.

THE MAYFIELD ESTIMATOR

Harold Mayfield was the first to propose a remedy for the recognized difficulty with apparent nest success (Mayfield 1961, 1975). Using data from his study of Kirtland's Warblers (*Dendroica kirtlandii*) in Michigan, he incorporated the time that a nest has been under observation (ex-

posure days) as a factor in calculating daily survival rates (DSR), such that

$$\text{DSR} = 1 - \frac{\text{no. of failed nests}}{\text{no. of exposure days}}.$$

To obtain an estimate of nest survival over the entire nesting period, the daily survival rate is raised to the power equivalent to the average number of days (d) in the nesting period: Nest survival = (DSR) ^{d} .

This method eliminates the need to monitor every nest beginning at initiation and provides a vast improvement over apparent nest success estimates. However, the Mayfield estimator is based on several assumptions, some of which may not be met in many circumstances (Table 1). The Mayfield estimator provided a starting point for evaluating nest survival upon which subsequent investigators have generalized.

EVALUATION AND EXPANSIONS OF THE MAYFIELD ESTIMATOR

Suspected violation of the assumptions of the Mayfield estimator led to early criticism of the method (Green 1977, Dow 1978). In response to these concerns, Johnson (1979) evaluated Mayfield's estimator by formally deriving it and comparing it to another maximum-likelihood estimator that he developed. Johnson's estimator retains the assumption of constant daily survival probability within a nesting stage, but does not require timing of failure to be known. The Mayfield estimator gave results similar to Johnson's estimator, and Johnson ultimately endorsed the Mayfield estimator because it is much easier to compute. Mayfield's estimator performed well unless nest-check intervals were long (>15 days); a slight modification of the midpoint assumption (to 40% of exposure time rather than 50%) was recommended for longer intervals (Miller and Johnson 1978, Johnson 1979). Johnson also determined that the Mayfield estimator is fairly robust to heterogeneity of daily survival rates among nests, and provided a computation of standard error.

Hensler and Nichols (1981) mathematically showed that the Mayfield estimator is a maximum-likelihood estimator and used Monte Carlo simulations to compare apparent nest success to the Mayfield method. Their results demonstrated that the Mayfield estimator outperforms apparent nest success, unless all nests are located at initiation. Hensler and Nichols (1981) provided

guidelines regarding the requisite sample size of nests needed to obtain various levels of precision in nest survival estimates and recommended that estimates should never be calculated using samples smaller than 20 nests.

EVALUATING VISITOR IMPACT

The assumption that finding and monitoring a nest does not influence its outcome (Table 1) has been challenged frequently (Bart 1977, Bart and Robson 1982, Nichols et al. 1984, Rotella et al. 2000; see review in Götmark 1992). Bart and Robson (1982) noted that observers sometimes prolong intervals between nest checks to minimize disturbance and decrease the interval length when failure is suspected so that time of failure can be recorded more accurately. They discouraged this protocol because a more complicated model is required to estimate nest survival when the interval between nest checks changes relative to nest fate (Bart and Robson 1982).

Rotella et al. (2000) developed a model to estimate nest survival under circumstances where observing a nest affects nest survival. They used Monte Carlo simulation to evaluate three models: (1) the Mayfield estimator; (2) a maximum-likelihood estimator of daily survival rate (Johnson 1979, Hensler and Nichols 1981, Bart and Robson 1982); and (3) an observer-effects model (a maximum-likelihood estimator of daily survival rate with observer effects). When there were no observer effects, all models produced unbiased estimates of daily survival rate. When observer effects were present, the observer-effects model had minimal bias, whereas models ignoring observer effects underestimated daily survival rates. However, the observer-effects model was less precise. Rotella et al. (2000) encouraged researchers to consider whether minimizing bias or maximizing precision would be more relevant to their research questions. They recommended researchers use simulations to evaluate whether observer effects needed to be incorporated, pointing out that large sample sizes (perhaps greater than 600 nests) are needed to detect subtle observer effects.

THE ASSUMPTION OF CONSTANT DAILY SURVIVAL RATE

Realizing that the assumption of constant daily survival rates can be restrictive, numerous investigators have developed models to account

TABLE 1. Comparison of assumptions of three nest survival estimation methods: Mayfield (1961, 1975), Stanley (2000), and MARK (White and Burnham 1999).

Assumptions ^a	Mayfield	Stanley	MARK	Evaluation and references ^b
Nest fates are known for all nest intervals used in analysis	Yes ^c	Yes ^c	Yes	Mayfield and Stanley methods can use partial data for nests remaining active at completion of field season
Nests found constitute a random sample of the population of nests under consideration	Yes	Yes	Yes	Statistically necessary for making inference. Violating this assumption may bias estimate ^{1,2}
Daily survival probability is constant within nesting stages	Yes	Yes	No	Often biologically restrictive ^{2,3,4,5,6,7,8,9,10,11,12,13}
When nests are followed to completion, hatching/fledging date is known	Yes ^c	Yes	Yes	Achievable for altricial birds (nestling development) and precocial birds (floating or candling eggs) ^{14,15,16}
Failure date is known	Yes	No	No	Often logistically undesirable (daily nest checks may influence survival) ^{9,11,17}
Alternatively, when failure date is unknown, failure occurred midway between last two observations	Yes	No	No	Robust if nest-check intervals are short (<15 days) ¹⁷ . Biologically restrictive when change in nesting stage affects daily survival rate ^{3,17,18}
Finding and monitoring a nest does not influence survival	Yes	Yes	Yes	May be biologically unrealistic depending on field procedures ^{4,8}
Daily nest survival is the same for all nests	Yes	Yes	No	Often biologically unrealistic ^{13,17,19}
Nest age can be determined	No	Yes ^c	Yes ^c	Achievable using behavioral cues, or floating or candling eggs ^{12,13,14,15,16}
For altricial species, timing of transition between nest stages is known	Yes ^c	No	Yes	Necessary for calculation of stage-specific survival rates ⁹
Nest fates are independent	Yes	Yes	Yes	Less critical biologically. Dependent fates will result in underestimated variance ²⁰
Nest survival for any day is independent of the fact that it has survived previous days	Yes	Yes	No	Less critical biologically ¹¹

^a Modified from Aebischer (1999).

^b References: 1. Bromaghin and McDonald (1993); 2. Heisey and Nordheim (1995); 3. Klett and Johnson (1982); 4. Bart and Robson (1982); 5. Pollock and Cornelius (1988); 6. Heisey and Nordheim (1990); 7. Natarajan and McCulloch (1999); 8. Rotella et al. (2000); 9. Stanley (2000); 10. Manly and Schmutz (2001); 11. Dinsmore et al. (2002); 12. Stanley (2004); 13. Nur et al. (2004); 14. Westerskov (1950); 15. Weller (1956); 16. Lokemoen and Koford (1996); 17. Johnson (1979); 18. Miller and Johnson (1978); 19. Green (1977); 20. He et al. (2001).

^c For optimal use of method.

for possible heterogeneity in daily survival rate through the nesting period (Bart and Robson 1982, Klett and Johnson 1982, Pollock and Cornelius 1988, Heisey and Nordheim 1995, Nata-

rajan and McCulloch 1999, Stanley 2000, He et al. 2001, Manly and Schmutz 2001, Dinsmore et al. 2002, Stanley 2004). Klett and Johnson (1982) recommended piecewise application of

the Mayfield method when variation in nest survival was due to an identifiable factor, but the assumption that survival remained constant within nesting stages (i.e., laying, incubation, nestling) was retained. Bart and Robson (1982) developed an iterative generalized likelihood model to account for changes in survival rate within nesting stages. Despite the numerous options for evaluating variation in daily survival rates, these methods have not yet been widely adopted by field biologists. This may be because several of the methods require large sample sizes, specialized software, or complicated mathematical procedures for implementation (e.g., Pollock and Cornelius 1988, Heisey and Nordheim 1995, Natarajan and McCulloch 1999, He et al. 2001). Calculating stage-specific survival rates using the Mayfield method is a simple alternative, but is complicated by the need to assign each exposure day to a nesting stage despite uncertainty associated with the timing of transitions and failures (Hensler 1985, Stanley 2000).

Two relatively new methods, demonstrated in Stanley (2000) and Dinsmore et al. (2002), address the issue of constant daily survival in different ways. Similar to the Mayfield method, the Stanley (2000) method assumes survival within stages to be constant, but eliminates the need to assign each exposure day to a specific stage. Dinsmore et al. (2002) incorporated nest survival models with no assumption of constant daily survival into the readily accessible program MARK (White and Burnham 1999). Because both of these methods provide software to facilitate use, and both eliminate some of the assumptions of the Mayfield estimator, they represent alternatives for researchers to consider when estimating nest survival. We focus on Stanley's (2000) method and program MARK, evaluating the strengths, limitations, and data requirements of these techniques, before comparing these methods to Mayfield's estimator and apparent nest success in a case study.

ADVANCED ESTIMATORS

STANLEY'S METHOD

Stanley (2000) presented a new nest survival estimation model that calculates stage-specific survival rates even when the exact timing of stage transitions and nest failures are unknown. The SAS code for this model is provided online (Ap-

pendix). For altricial species, the onset of incubation and the timing of hatching may not be known exactly if nests are not visited daily. An advantage of Stanley's model over the Mayfield method is that arbitrary decisions to assign exposure days or failures to nesting stages are not needed, thereby eliminating problems with commonly used decision rules (Manolis et al. 2000) and streamlining analysis of large data sets. For transition periods (onset of incubation and hatching), Stanley's method assumes that the transition occurs with equal probability on each day during the interval (Stanley 2000). Stanley (2000) reviewed the performance of his model through Monte Carlo simulations and demonstrated that the bias of nest survival estimates was small, even when sample sizes are low ($n = 25$), as is often the case in field studies.

This method minimally requires the following information for each nest: (1) duration of each exposure interval; (2) fate of nest during the interval (i.e., successful or unsuccessful); and (3) nesting stage at the beginning and end of each interval. This model does not require knowledge of failure date, and the interval between nest checks may vary.

A practical benefit of the Stanley (2000) method is that the data required correspond closely to data required to meet standardized protocols for monitoring nests (e.g., Martin and Geupel 1993, Martin et al. 1997). Stanley's (2000) method requires classifying nests into one of five categories (laying, transition from laying to incubation, incubation, transition from incubation to nestling, or nestling), based on the nesting stage at the beginning and end of each nest-check interval. Techniques have been developed to assess nest age via egg floating (Welterskov 1950) or egg candling (Weller 1956, Lokemoen and Koford 1996), but these methods may be challenging to implement when nests are difficult to reach or when handling nest contents is prohibited or undesirable. However, precise knowledge of nest age is not needed for this method, so other means of determining approximate nest age (e.g., behavioral cues) may be sufficient (Armstrong et al. 2002). For circumstances in which nest age is unknown, Stanley developed a generalization of his 2000 model (Stanley 2004).

Stanley's method also provides a log-likelihood output for each analysis, which facilitates computation of AIC values. Using the Stanley

TABLE 2. Comparison of nest survival estimates (\pm SE) for New Zealand Robins. Data from Armstrong et al. (2002) were reanalyzed for comparison among methods.

Study area	<i>n</i> (nests)	Stanley nest survival (stage-specific) ^a	Stanley nest survival (constant) ^b	Mayfield nest survival (constant) ^b	Apparent nest success ^c
Tiritiri Matangi	123	0.37 \pm 0.06	0.41 \pm 0.05	0.41 \pm 0.05	0.58
Paengaroa	35	0.28 \pm 0.08	0.29 \pm 0.08	0.28 \pm 0.08	0.43
Boundary Stream	30	0.43 \pm 0.14	0.49 \pm 0.10	0.49 \pm 0.10	0.60
Pureora					
Predator control	51	0.60 \pm 0.07	0.60 \pm 0.08	0.60 \pm 0.07	0.65
No predator control	96	0.25 \pm 0.04	0.28 \pm 0.05	0.27 \pm 0.04	0.26

^a Calculated as the product of stage-specific survival of the incubation and nestling periods: $DSR_{inc}^{d1} \times DSR_{nest}^{d2}$, where $d1$ is the average number of days in the incubation stage (19 days for New Zealand Robins) and $d2$ is the average number of days in the nestling stage (21 days in this case).

^b Calculated assuming a constant daily survival rate across stages.

^c Calculated as (no. of successful nests)/(total nests found).

method and AIC model selection, Armstrong et al. (2002) determined that nest survival rates for New Zealand Robins (*Petroica australis*) varied by time in season, that predator control improved nest survival rates, and that survival rates varied by stage (with a site by stage interaction potentially due to changes in predator communities among sites). This improved understanding of factors affecting nest survival will direct future research and management of New Zealand Robins.

We reanalyzed data from Armstrong et al. (2002) to compare estimates from the Stanley method, the Mayfield estimator, and apparent nest success. Nest monitoring regimes varied among sites, with nest-check intervals ranging from 3 to >7 days (see Armstrong et al. 2002 for details). Mayfield estimates were calculated assuming that failure occurred at the midpoint between the final nest checks. Stage-specific rates were not calculated using the Mayfield method because the timing of transition between stages was not always known.

The reanalyzed data demonstrate how misleading apparent nest success results may be by contrasting them to those obtained using the Mayfield estimator and the Stanley method (Table 2). The New Zealand Robin apparent nest success estimates are inflated in 4 of 5 instances, consistent with simulated results from Hensler and Nichols (1981). Apparent nest success estimates approximated the results from the Mayfield estimator and the Stanley method only at the Pureora study site, which had a more intensive nest-monitoring regime (Armstrong et al.

2002). Because simulations show bias with the Mayfield estimator and the Stanley method to be minimal, one can have greater confidence in these methods than in apparent nest success. The Mayfield and Stanley method estimates are quite similar when a constant daily survival rate within nesting stage is assumed for both. Stanley (2000) points out that his method collapses into Johnson's (1979) method when there are no transitional intervals and collapses into the Mayfield estimator when nests are checked daily.

PROGRAM MARK

Dinsmore et al. (2002) present a nest survival model recently added to program MARK that is a generalization of the maximum-likelihood estimator of Bart and Robson (1982). This program is available online (Appendix). Using MARK, nest survival can be modeled as a function of biologically relevant covariates (e.g., age of parent, body condition of parent, year, nest age, time during season, weather, catastrophic events) without needing to partition the data into smaller subsets. Program MARK provides researchers with a powerful tool for assessing factors influencing nest survival when adequate data can be collected. For this method, nests with uncertain fate are not included in analysis. To maximize the utility of this method, nest age should also be determined within 1–2 days (Dinsmore et al. 2002) by floating or candling (as described above). If stage-specific nest survival rates are desired, exact dates of transition must be known.

A minimum of five metrics for data input are needed: (1) the day the nest was found; (2) the last day the nest was known to be present; (3) the last day the nest was checked (for successful altricial nests this should be the day the nest fledges young, whereas for successful precocial nests this should be the day of hatching); (4) fate of the nest (i.e., successful or unsuccessful); and (5) the frequency of nests with the same history. This model does not require knowledge of failure date, and the interval between nest checks may vary. It is not necessary to assume that the daily survival rate is constant, enabling researchers to evaluate temporal variation in daily survival rates.

Dinsmore et al. (2002) provide an excellent example of developing *a priori* hypotheses and predictions about nest survival and evaluating their support using AIC model selection. Using program MARK, the researchers determined that Mountain Plover (*Charadrius montanus*) nest survival was higher in nests tended by males and that daily survival probability increased with nest age and decreased following precipitation (Dinsmore et al. 2002). Models incorporating a quadratic temporal trend had strong support, suggesting that nest survival was higher early and late in the breeding season, with a midseason decline. Their results provide new insight on factors influencing nest survival for Mountain Plovers, and demonstrate the power of MARK for examining complex and biologically meaningful questions.

In contrast, earlier methods have limited ability to evaluate factors influencing nest survival because continuous data must be partitioned into discrete subsets for such analyses. For example, using Stanley's method, Armstrong et al. (2002) had to collapse a time variable into arbitrary categories in order to evaluate a temporal trend within the breeding season. Furthermore, non-interacting effects cannot be modeled using the methods developed by Mayfield or Stanley. Program MARK enables researchers to evaluate continuous variables, temporal trends, and non-interacting effects when modeling nest survival.

The Mountain Plover data also demonstrate how variable apparent nest success estimates may be, even within a single study. In 6 years, apparent nest success ranged from a low of 45% to a high of 72%, but MARK analysis revealed no evidence for yearly differences in nest survival (Dinsmore 2001). In only one of the 6

years was apparent nest success similar to overall nest survival (calculated as a product of daily nest survival estimates from program MARK). In 5 of 6 years, apparent nest success was higher than overall nest survival to a variable degree (Dinsmore 2001).

COMPARISON OF NEST SURVIVAL ESTIMATORS: CASE STUDY

METHODS

We used four methods (apparent nest success, Mayfield, Stanley, and MARK) to analyze Lark Bunting nest survival at three study sites on the Pawnee National Grassland, Weld County, Colorado (40°41'N, 104°29'W) during the breeding seasons of 2000–2002 (Table 3). We located 253 nests (29 in 2000, 141 in 2001, and 83 in 2002) by dragging a rope between two observers 25 m apart and by observing adult behavior. Ages of nests were determined by floating eggs (Westerskov 1950) when nests were first located. We checked nests every 1–4 days until the nest failed or fledged and determined nest fates by watching parent-offspring interactions on the day of fledging.

For each site-year group, we calculated apparent nest success and both stage-specific (with daily survival rates calculated separately for each stage) and constant nest survival (calculated assuming a constant daily survival rate across stages) using Mayfield and Stanley methods. Data from the egg-laying period were sparse (ca. 4% of egg-stage data) and were combined with incubation stage data for Mayfield and Stanley methods. To calculate Mayfield estimates, we assumed that failure occurred at the midpoint between the final nest checks. Because our nest-age data were accurate to within 2 days, we were able to assign exposure days to nesting periods to calculate stage-specific rates using Mayfield. For comparative purposes, we calculated a nest survival estimate using MARK, assuming a constant daily survival rate. This is not the optimal use of MARK; indeed, a primary benefit of this method is that daily survival rate is not assumed to be constant.

We also used program MARK (White and Burnham 1999) to evaluate variation in daily survival probabilities of Lark Bunting nests relative to factors of possible ecological importance. We limited our analyses to a set of 11 *a priori* models that examined the effects of year,

TABLE 3. Comparison of nest survival estimates (\pm SE) for Lark Buntings at three sites on the Pawnee National Grassland, Colorado, 2000–2002. Data were not collected for all sites in all years.

	2000		2001		2002	
	Site 2	Site 1	Site 2	Site 3	Site 1	Site 2
Number of nests	29	42	53	46	53	30
Single-stage estimates ^a						
Incubation (Mayfield)	0.49 \pm 0.12	0.40 \pm 0.09	0.66 \pm 0.08	0.55 \pm 0.09	0.51 \pm 0.10	0.53 \pm 0.13
Nestling (Mayfield)	0.56 \pm 0.12	0.27 \pm 0.08	0.68 \pm 0.07	0.50 \pm 0.09	0.39 \pm 0.08	0.35 \pm 0.10
Incubation (Stanley)	0.52 \pm 0.13	0.41 \pm 0.10	0.61 \pm 0.09	0.60 \pm 0.09	0.50 \pm 0.11	0.50 \pm 0.14
Nestling (Stanley)	0.53 \pm 0.12	0.29 \pm 0.09	0.73 \pm 0.07	0.46 \pm 0.09	0.43 \pm 0.09	0.39 \pm 0.10
Stage-specific estimates ^b						
Mayfield	0.27 \pm 0.09	0.11 \pm 0.04	0.44 \pm 0.07	0.27 \pm 0.07	0.20 \pm 0.06	0.19 \pm 0.07
Stanley	0.28 \pm 0.09	0.12 \pm 0.04	0.45 \pm 0.08	0.28 \pm 0.07	0.21 \pm 0.06	0.19 \pm 0.07
Constant survival estimates ^c						
Mayfield	0.27 \pm 0.09	0.12 \pm 0.04	0.44 \pm 0.07	0.28 \pm 0.07	0.19 \pm 0.06	0.17 \pm 0.07
Stanley	0.28 \pm 0.09	0.13 \pm 0.04	0.45 \pm 0.08	0.28 \pm 0.07	0.20 \pm 0.06	0.18 \pm 0.07
MARK ^d	0.30 \pm 0.09	0.13 \pm 0.05	0.45 \pm 0.07	0.29 \pm 0.07	0.20 \pm 0.06	0.17 \pm 0.07
Apparent nest success ^e	0.48	0.14	0.55	0.35	0.43	0.30

^a Survival for a single stage (incubation or nestling) = (DSR)^d, where *d* is the average duration of the stage, measured in days.
^b Calculated as the product of stage-specific survival of the incubation and nestling periods: DSR_{inc}^{d1} × DSR_{nest}^{d2}, where *d1* is the average number of days in the incubation stage (11 days for Lark Buntings at these sites) and *d2* is the average number of days in the nestling stage (8 days in this case).
^c Calculated assuming a constant daily survival rate across stages.
^d Calculated assuming constant survival during the nesting period (including egg laying). This analysis is not commonly done in MARK because it is possible to calculate variation in daily survival through time.
^e Calculated as (no. of successful nests)/(total nests found).

site, nest age, weather parameters, and a temporal trend (*T*) within breeding seasons. We used weather data collected near Nunn, Colorado, within 35 km of all study sites (Shortgrass Steppe Long Term Ecological Research Group 2002). The median maximum daily temperature was 31.7°C (range 10.4–38.7°C), and median daily precipitation was 0 mm (range 0.0 to 30.2 mm). Our 3 years of data were collected during a drought of varying severity; the first two years (2000–2001) were mild compared to the final year (2002), which was a severe drought (National Drought and Mitigation Center 2003).

We expected nest survival to differ among years due to annual variation in several factors including weather, predator numbers, and food availability. We included site in our models to evaluate whether nest survival differed among sites due to variation in microclimatic condi-

tions, predator communities, or resource availability, even though we had attempted to minimize these differences by selecting sites with similar vegetation structure and grazing regime. We hypothesized that survival would decrease with the age of the nest because nest activity increases at Lark Bunting nests during the nestling phase. For altricial species, older nests are thought to have lower survival due to increased activity including parental feeding and spontaneous begging of young. For precocial species, in contrast, older nests would be expected to have higher survival because vulnerable nests would be more likely to fail early in the nesting period (Klett and Johnson 1982, Dinsmore et al. 2002).

We modeled survival as a function of maximum daily temperature and daily precipitation. We believed that extreme temperatures would

TABLE 4. Summary of model selection results for nest survival of Lark Buntings, Pawnee National Grassland, Weld County, Colorado, 2000–2002. Analysis performed in program MARK. Models are listed beginning with the best-fitting model and sorted by ΔAIC_c , the difference between the AIC_c value for the current model and the model with the lowest AIC_c . The AIC_c weight indicates the relative likelihood of each model given the model set and sums to 1.

Nest survival models	Deviance ^a	No. of parameters	ΔAIC_c^b	AIC_c weight
Site*Year + Age + T^c	909.26	8	0.00	0.32
Site*Year + Age	911.34	7	0.01	0.32
Site*Year + Age + T^c + Max. temperature	909.00	9	1.82	0.13
Site*Year + Age + T^c + Precipitation	909.04	9	1.86	0.13
Site*Year + T^c	914.98	7	3.65	0.05
Site*Year	918.18	6	4.79	0.03
Site	925.90	3	6.37	0.01
Age	928.06	2	6.51	0.01
Drought	930.81	2	9.26	0.00
Constant	933.58	1	10.02	0.00
Year	930.79	3	11.26	0.00

^a A measure of model fit. Deviance is the difference in -2 log-likelihood of the current model and -2 log-likelihood of the saturated model.

^b The lowest AIC_c score in the analysis was 925.58.

^c Temporal trend, representing a linear change in nest survival over time.

reduce daily nest survival through heat stress to eggs and young; we hypothesized that precipitation would decrease daily nest survival if Lark Bunting nest predators use olfactory cues that are enhanced by precipitation. To assess a potential drought effect, we also modeled nest survival as a function of severe and mild drought conditions. To evaluate temporal variation, we fit a simple constant survival model to our data. We then added a linear temporal trend model (T) because we hypothesized that nest survival would decrease across the breeding season as food availability decreased. Density trends for grasshoppers (the main prey fed to nestlings) in northern Colorado typically decrease throughout the summer, after peaking in June or mid-July (Przybyszewski and Capinera 1990). Nestlings from early nests would be expected to have greater food availability and subsequently better body condition, thereby reducing begging calls that may attract predators.

We evaluated models using AIC corrected for small sample size (AIC_c ; Akaike 1973, Burnham and Anderson 2002). The differences (ΔAIC_c) between each model and the model with the minimum AIC_c value allow for a quick comparison and ranking. The model with the smallest ΔAIC_c is the best-approximating model of the candidate models, given the data. AIC_c weights (w_i) are useful in assessing the weight of evi-

dence in favor of a model (Burnham and Anderson 2002).

RESULTS

For our analysis, the point estimates for single-stage survival rates of Mayfield and Stanley methods (for incubation or nesting periods) differed more than did the stage-specific nest survival (calculated as the product of incubation and nestling periods) or constant nest survival estimates of these methods (Table 3). Apparent nest success varied between 1% and 24% more than the other estimates of nest survival (Table 3). Assuming constant daily survival rates, the nest survival estimates and the standard errors of the Mayfield, Stanley, and MARK methods were similar (Table 3).

MARK analysis revealed that survival of Lark Bunting nests was a function of site and year, daily nest age, and seasonal trend (Table 4). Consistent with our hypotheses, we found daily survival rate declining with both nest age and time in the season. This trend was consistent among sites and years; therefore we illustrate the pattern with one site–year combination (Fig. 1). Models incorporating nest age had substantial support (Table 4); slope estimates for age effect were always negative with confidence intervals that did not include zero (top model: $\beta_{\text{age}} = -0.04$, SE = 0.02, 95% CI = -0.07 , -0.01 on

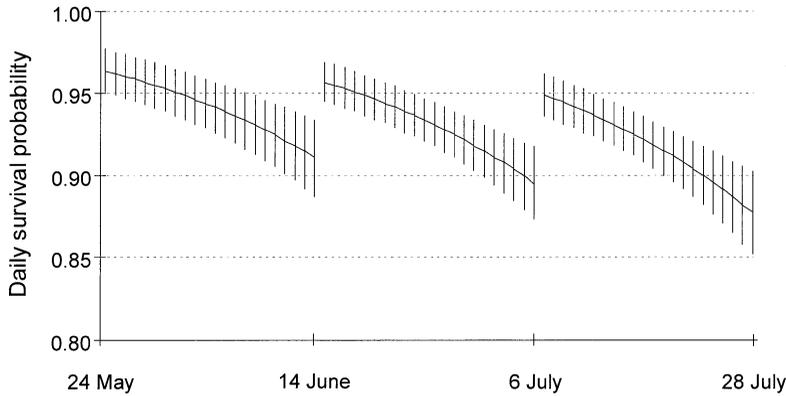


FIGURE 1. Predicted daily survival rates \pm SE for Lark Bunting nests at site 1 in year 2002 on the Pawnee National Grassland, Colorado (other sites and years showed similar pattern). Using the logistic regression equation from the best-approximating model, estimates \pm SE of three example nests were generated beginning with day 0 (laying of first egg) and continuing to day 21 (the day of fledging). Example nests span the breeding season with an early-season nest (24 May–14 June), mid-season nest (15 June–6 July), and late-season nest (7 July–28 July). Analysis performed in program MARK.

a logit scale). Similarly, models with seasonal trend had negative slope estimates with confidence intervals barely including zero (top model: $\hat{\beta}_T = -0.01$, SE = 0.01, 95% CI = -0.02 , 0.00 on a logit scale). Addition of weather parameters did not improve the best model (Table 4); slope estimates for temperature and precipitation had confidence intervals that largely overlapped zero.

DISCUSSION

We evaluated four methods of analyzing nest survival and found results for the Mayfield, Stanley, and MARK methods to be similar. Apparent nest success is positively biased to a variable degree, and thus should not be used as a comparative measure across time or space. We speculate that the similarity among results from the other three methods may be explained by the short duration of our nest-check intervals and our ability to determine nest age within 1–2 days. For certain other data sets, particularly those with small sample sizes, long nest-check intervals, or substantial heterogeneity among stage-specific survival rates, the differences would likely be greater, and they would be greater to an unknown degree.

The Mayfield estimator and its various modifications provide an improved means for estimating nest survival, eliminating the need to find every nest at initiation. However, the original Mayfield estimator assumes constant survival throughout a nesting stage and requires sub-

jective decisions when stage-specific survival estimates are desired, unless transition and failure dates are known.

Mayfield's estimator has gained widespread use among avian ecologists because it is generally superior to apparent nest success and simple to calculate. It took decades to achieve this status, as evidenced by endorsements that appeared in the literature around 1980 (e.g., Johnson 1979, Hensler and Nichols 1981). Recently developed methods generalize upon the Mayfield estimator and its earlier modifications by obviating some of its restrictive assumptions.

These new methods allow researchers to extract more information from nest survival data. More information is extracted because nest survival may now be modeled as a function of biologically relevant covariates, including temporal trends and noninteracting effects, in ways that were previously not possible. The additional information is also more reliable because instead of making restrictive assumptions (e.g., constant survival rate, failure occurred at midpoint of interval), newer techniques account for sources of variation explicitly, thereby reducing bias.

When the exact time of transition between nesting stages is unknown, Stanley's method provides a means for calculating stage-specific nest survival rates without arbitrary assignment of nest days to nesting stages (Stanley 2000). Program MARK eliminates the assumption of constant daily survival rate and enables investigators to explore correlates of nest survival

(Dinsmore et al. 2002). These methods also facilitate analysis in a contemporary, information-theoretic framework. Software to implement these methods is readily available, enabling researchers to begin using these improved techniques immediately. The recent proliferation of new techniques for estimating nest survival includes several other methods that provide such software (e.g., Rotella et al. 2000, Manly and Schmutz 2001, Nur et al. 2004, Stanley 2004). These various methods give researchers a suite of tools for asking more meaningful questions. The development of additional methods for estimating nest survival is likely to continue and the emphasis for the future should be on selecting the optimal method to achieve desired goals rather than focusing on a single technique.

Because the Mayfield estimator, Stanley's method, and program MARK all calculate daily survival probabilities, results from all three of these methods may reasonably be compared across studies and across time (although for evaluating population dynamics, consistent use of a single method is best). As such, researchers familiar with the Mayfield estimator may switch to Stanley or MARK without losing the advantage of comparison. Indeed, Stanley's method may minimize the variation in the use of decision rules currently prevalent in using the Mayfield estimator (see discussion in Manolis et al. 2000). Program MARK provides researchers with increased flexibility and power for analyzing factors influencing nest survival, including continuous and noninteracting variables. Because apparent nest success is positively biased to a variable degree, it cannot be compared across studies or with estimates generated by other methods.

Given the urgency of avian conservation concerns, we need to decrease the lag time between *development* and *adoption* of improved methods. Also, we need to progress toward investigating factors influencing the process of nest survival in addition to describing existing patterns. We encourage researchers to use these improved models to gain reliable and informative nest survival estimates.

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APPENDIX. Chronological review of nest survival estimators.

Reference	Comments
Anonymous	Proposed apparent nest success (naïve estimator), which requires that all nests are found at initiation; otherwise this estimator has a known positive bias (Hensler and Nichols 1981).
Mayfield 1961, 1975	Developed an estimator allowing for nests found at various stages; observation time incorporated as exposure days to calculate a daily survival rate. Survival rate is assumed to be constant within nesting stage. Date of transition between stages must be known for calculation of stage-specific rates.
Johnson 1979	Demonstrated that biases associated with Mayfield estimator are not large unless nest-check intervals are long (>15 days). Developed a model to account for unknown failure time using a maximum-likelihood estimator. Developed SE for Mayfield estimator. Recommended Mayfield or Mayfield-40% (for long nest-check intervals).
Bart and Robson 1982	Developed an iterative generalized likelihood estimator to allow for variable daily survival rates. Evaluated visitor impact on nest survival.
Pollock and Cornelius 1988	Developed a model to calculate age-specific daily nest survival probability even when nest age is unknown. Grouping of data may be arbitrary and lead to bias (Heisey and Nordheim 1990). Large sample size needed.
Green 1989	Provided a formula to transform apparent nest success estimates into Mayfield estimates. Method assumes that number of nests available to be found is independent of nests already located (untrue for intensively monitored populations, Armstrong et al. 2002).
Heisey and Nordheim 1990	Developed a model to calculate age-specific daily nest survival probability; requires additional restrictive assumptions about encounter probabilities and survival rates within intervals (Bromaghin and McDonald 1993). Large sample size needed.
Bromaghin and McDonald 1993	Developed a model to estimate encounter probabilities of nests. This is a generalization of the Pollock and Cornelius (1988) model.
Heisey and Nordheim 1995	Developed a likelihood-based model to estimate variable survival rates for nests which have been sampled nonrandomly.
Natarajan and McCulloch 1999	Developed a model to calculate variable survival rates and incorporate random individual nest effects. Large sample size needed.
Aebischer 1999	Extended the Mayfield estimator to deal with multiple simultaneous comparisons using generalized linear modeling.
Rotella et al. 2000	Evaluated effect of visiting nests on daily survival. Developed an observer-effects model for use when nest visitation effects are unknown. If observer effect is small, less complex model may be used. SAS code provided.
Stanley 2000	Developed model for calculation of stage-specific survival rates when time of failure and exact transition date between periods are unknown. SAS code provided online at http://www.esapubs.org/archive/ecol/E081/021/default.htm
He et al. 2001	Developed Bayesian model for estimating age-specific daily nest survival.
Manly and Schmutz 2001	Developed and evaluated models allowing for variation in daily survival rates including an iterative Mayfield method and a maximum-likelihood approach. Software available online at http://www.west-inc.com/computer.php
Armstrong et al. 2002	Provided a slight modification to Stanley (2000) SAS code and elucidated formula for calculating confidence intervals when using Stanley method.
Dinsmore et al. 2002	Developed a nest survival model in program MARK that incorporates variable daily survival rates. Allows for evaluation of biologically relevant covariates affecting nest survival. Program MARK is available online at http://www.cnr.colostate.edu/~gwhite/mark/mark.htm
Stanley 2004	Developed a model to calculate stage-specific survival rates when time of failure, exact transition date between periods, and age of nest are unknown. SAS code provided.
Nur et al. 2004	Demonstrated use of several survival time analysis methods for estimating nest survival.