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MODELING AVIAN NEST SURVIVAL IN PROGRAM MARK

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Abstract. Understanding the factors influencing nesting success is a primary goal of many studies. To do this effectively, more advanced tools than Mayfield's ad hoc estimator are needed. The recent development of a nest-survival model in program MARK provides a powerful and flexible tool for the study of avian nest survival that can incorporate seasonal variation in survival and nest-specific covariates. We briefly review the model and its development, illustrate how to include the effects of daily nest age and observer visits to nests, and conclude with an example analysis of Red-winged Blackbird (*Agelaius phoeniceus*) nest survival in Iowa. In this example, we found evidence for stage-specific differences in nest survival, seasonal patterns in nest survival that were best explained by a quadratic-time trend, and that survival differed between years. An exploration of several nest-specific covariates revealed that blackbird nest survival was positively affected by nest height, weakly affected by nest placement (nests placed in living vegetation may have experienced slightly higher survival), and unaffected by clutch size and within- and between-cell nest placement.

Key Words: *Agelaius phoeniceus*, nest survival, program MARK, Red-winged Blackbird.

MODELANDO SOBREVIVENCIA DE NIDO EN PROGRAMA MARK

Resumen. Entender los factores que influyen el éxito de anidación es una meta primordial para muchos estudios. Para lograrlo efectivamente se necesitan más herramientas avanzadas que las estimador ad hoc Mayfield. El reciente desarrollo del modelo de sobrevivencia de nido en el programa MARK es muy poderoso y flexible para el estudio de sobreviviencia de nidos de aves, el cual permite incorporar variación estacional en sobrevivencia y covariantes específicas de nido. Revisamos brevemente el modelo y su desarrollo, ilustramos cómo incluir los efectos de edad diaria de nido y visitas observadas de nidos, y concluimos con un ejemplo de análisis de sobrevivencia de nido de Tordo Sargento (*Agelaius phoeniceus*) en Iowa. En este ejemplo encontramos evidencia de diferencias de estado específicas y patrones estacionales en sobrevivencia de nido, los cuales fueron mejor explicados por una tendencia cuadrática de tiempo, y encontramos que la sobrevivencia difirió entre los años. Una exploración de varias covariantes específicas de nido reveló que la sobrevivencia de nido de tordos estaba positivamente afectada por la altura de nido, débilmente afectada por la colocación de nido (nidos colocados en vegetación viva quizás hayan experimentado una sobrevivencia ligeramente más alta), y no hayan sido afectadas por el tamaño de la nidada y dentro y entre colocación de nidos célula.

Ornithologists have long been interested in studies of avian reproductive success, and nest survival, is the metric most frequently measured. The terms nest success, nesting success, and nest survival are used interchangeably in the literature and refer to the probability that ≥one egg hatches (precocial species) or that ≥one young fledges (altricial species). We prefer the term nest survival because success can be attained on >one nesting attempt in a season. Furthermore, if the species is precocial, nest survival may include the nest building, egg-laying, and incubation stages. If the species is altricial, nest survival will include these three stages plus the nestling stage. Much of the nest-survival literature emphasizes estimating the probability that a nest is successful, although recently the focus has shifted more towards understanding factors that influence nest survival (Dinsmore et al. 2002, Rotella et al. 2004, Rotella 2005).

Approaches to estimating nest survival have until recently been rather simplistic. The early use of traditional estimates of apparent nesting success (the proportion of nesting attempts that are successful) was overshadowed by widespread acceptance of the Mayfield method (Mayfield 1961, 1975) by the 1970s. However, despite recent progress in the development of new approaches (Rotella et al. 2004) to modeling nest survival, the Mayfield estimator and its many variations (e.g., the Mayfield logistic approach; Hoover and Brittingham 1998, Aebischer 1999) are still widely used. The Mayfield approach, while intuitive and easy to compute, has several disadvantages that limit its use in investigating complex questions of avian nest survival: (1) survival is assumed to be constant over time, (2) the model cannot handle covariates in an efficient manner, and (3) the timing of losses must be known exactly. Given these deficiencies, alternate approaches to understanding avian nest survival were needed. This motivated the development of three similar approaches to modeling nest survival in a likelihood-based framework (Dinsmore et al. 2002, Stephens 2003, Shaffer

2004a) and a burgeoning interest in Bayesian approaches (He et al. 2001, He 2003).

Typically, ornithologists are interested in estimating nest survival for one of three primary reasons: (1) a desire to understand the processes that affect avian nest survival, (2) to provide best estimate(s) of nest survival, or (3) to incorporate estimates of nest survival into population-growth models. In this paper, we summarize the general approach to modeling avian nest survival in program MARK, introduce recent computational developments in MARK that will be useful to analyzing nest survival, comment on the application of this model to other types of studies, and provide a detailed example that illustrates our general modeling approach.

NEST-SURVIVAL MODEL

The nest-survival model described below (Dinsmore et al. 2002) is available in program MARK (White and Burnham 1999, Cooch and White 2005). This model is an extension of that described by Johnson (1979) and Bart and Robson (1982) and within the framework of MARK it offers a powerful and flexible tool for modeling nest survival. Many of the recent methods developed to analyze nest-survival data are similar, and the choice of a method probably depends more on the familiarity of the user with the software than with the details of the approach. MARK also offers the advantage of being menu driven, and minimizes the need for a user to be familiar with programming.

Here, the survival of a nest refers to the probability that a nest survives a specified time interval, typically 1 d. Briefly, the assumptions of this model are:

1. Nests are correctly aged when they are discovered.
2. Nest fates are correctly determined.
3. Nest discovery and subsequent nest checks do not influence survival.
4. Nest fates are independent.
5. Homogeneity of daily nest-survival rates.

Assumption 1 is the strongest, but in many studies the nest can be accurately aged using proven techniques such as candling or egg flotation (Westerkov 1956). Meeting assumption 2 is not often a problem if evidence at the nest can be used, e.g., the presence of eggshell fragments in the nest cup to infer hatching (Mabee 1997). Assumption 3 can be relaxed and modeled directly using the approach of Rotella et al. (2000). Assumption 4 can be a problem for analyses of aggregated species (e.g., colonial nesting birds), although violation of this assumption could be minimized by careful selection of nests for inclusion in the sample. Assumption 5 simply implies that estimated survival rates apply equally to all nests.

The nest-survival model in program MARK requires five pieces of information for each nest, and these are indexed by the letters in parentheses:

1. The day the nest was found (*k*).
2. The last day the nest was checked alive (*l*).
3. The last day the nest was checked (*m*).
4. The fate of the nest (0 = successful, 1 = unsuccessful) (*f*).
5. The number of nests with this encounter history. This will normally be 1 as most studies will include nest-specific covariates in the analysis.

Program MARK uses this information to construct an encounter history for each nest in live-dead (LDLD…) format. Examples of rules governing the coding of the triplet involving *k*, *l*, and *m* (where $k \le l \le m$) and the fate (*f*) can be found in the MARK help file.

In the nest-survival model, the encounter history is coded differently than in other models in program MARK. Basic nest information (*k*, *l*, *m*, and *f*) is entered in days by the analyst and then converted in MARK to an encounter history. The first step is for the analyst to convert calendar dates (the format in which field data are usually collected) to numerical days such that day 1 is the first date any nest in the sample was monitored. To illustrate this, suppose that in a 2-yr study the first nest was found on 5 May in year 1 and on 2 May in year 2. To convert dates to days, as required by MARK, 2 May would become day 1, 5 May would be day 4, etc. MARK then uses this information and the fate to construct the appropriate encounter history in LD format. Note that it is not necessary that time intervals between nest visits be equal, nor do they need to follow any consistent pattern between nests.

If appropriate, nests are assigned to groups using the following lines in the input file in program MARK:

```
Nest survival group = 1;
                        /* k  l   m  f number */
/* 1994  33   */    13 15  15 0     1;
/* 1994  15   */    54 57  57 0     1;
/* 1994  39B  */    32 35  35 0     1;
/* 1994  29   */    13 15  15 0     1;
Nest survival group = 2;
/* 1994  33   */    15 24  26 1     1;
/* 1994  15   */    57 68  68 0     1;
/* 1994  16   */    17 20  24 1     1;
/* 1994  21   */    13 20  20 0     1;
   etc.
```

Groups will usually represent discrete subsets of the data such as nests monitored at different sites or in different nest stages. A comment field (the text between /* and */, ignored by MARK) can be used to reference nest-specific information of interest to the analyst, such as a nest identification number or nest stage.

The following illustrates the likelihood (L) function for the daily survival (S_i) from day i to day i+1 for a sample of n nests is:

$$L(S_i \mid k_j, l_j, m_j, f_j) \propto \prod_{j=1}^{n}\left[\left(\prod_{\substack{i=k \\ (k<l)}}^{l-1} S_i\right)\left(1-\prod_{i=l}^{m-1} S_i\right)^{f}\left(\prod_{i=l}^{m-1} S_i\right)^{1-f}\right]$$

To illustrate how the model is parameterized, consider a nest that is found on day 1, is checked and still active on day 6, and is checked again on day 9 and found to be depredated. The fate of this nest is coded as 1 (f = 1, a failure).

Day								
1	2	3	4	5	6	7	8	9
↑					↑			↑
Found					First check			Last check
(k)					(l)			(m)

This nest is known to have survived until day 6. The probability of surviving the first interval (from day 1 to day 6) is then

$$\prod_{\substack{i=k \\ (k<l)}}^{l-1} S_i = S_1 S_2 S_3 S_4 S_5$$

The nest was lost sometime between days 6 and 9. The three possible outcomes explaining this loss are: 1) the nest was lost between days 6 and 7 [$(1-S_6)$], 2) the nest survived until day 7 and was lost between days 7 and 8 [$S_6(1-S_7)$], and 3) the nest survived until day 8 and was lost between days 8 and 9 [$S_6S_7(1-S_8)$]. The probability of being lost any time during the interval between days 6 and 9 is then 1 minus the probability of surviving this interval, which can be written as

$$\left(1-\prod_{i=l}^{m-1} S_i\right)^{f} = 1 - S_6 S_7 S_8$$

The third term in the model likelihood has a value of one. Thus, the overall probability of observing this encounter history is $S_1S_2S_3S_4S_5[1 - S_6S_7S_8]$.

Building models in program MARK is straightforward for those who are familiar with the program, have a basic understanding of generalized linear modeling, and possess an understanding of basic statistical methods. MARK offers a wide array of modeling options including the choice of a link function, the ability to provide initial parameter estimates to aid model convergence, and the ability to include functions in the design matrix (useful for modeling nest-age effects—see below), all of which are particularly useful for nest-survival analyses. Output options include estimates of real parameters (they can be exported to the spreadsheet Excel for easy construction of graphics) and the betas (necessary for generating predictive functions outside MARK), a variance–covariance matrix of the betas, and model averaging. The time needed to run models will vary depending on complexity. Using a fast computer with lots of memory (>512 MB of RAM), most model runs will take <1 min, unless you have a huge dataset with lots of individual covariates, which can take an hour or more to complete a single model run.

Modeling Considerations in MARK

The nest-survival model in program MARK offers a suite of modeling options, similar to other models in MARK. Once a set of candidate models is built in MARK, Akaike's information criterion (AIC; Akaike 1973) model selection is used to choose a model or models for inference (Burnham and Anderson 2002). Two features in MARK may be especially useful to users of the nest-survival model. First, the product function can be easily used to create non-linear relationships for covariates, as described in the MARK help file. Second, for those interested in incorporating a daily nest-age effect, a simpler approach than that of Dinsmore et al. (2002) can now be used. Consider an example where the nesting season is 10 d long and a nest is found at age 10 on day 1 and hatches (at age 15) on day 6. Under the old approach, a series of covariates, one for each day, was created to specify daily nest ages in the encounter history, as follows:

```
1  6  6  0  1        10 11 12 13 14 15
0  0  0  0;
```

Note that the first 5 numbers refer to k, l, m, f and nest frequency while the last 10 numbers are the daily nest age covariates. In MARK, the daily nest-age effect would be modeled in the design matrix by including a single column with a linear arrangement of daily covariates (Fig. 1a). Constructing the matrix of covariates using this approach can be cumbersome and is unnecessary. Instead, this encounter history could be constructed by replacing the daily

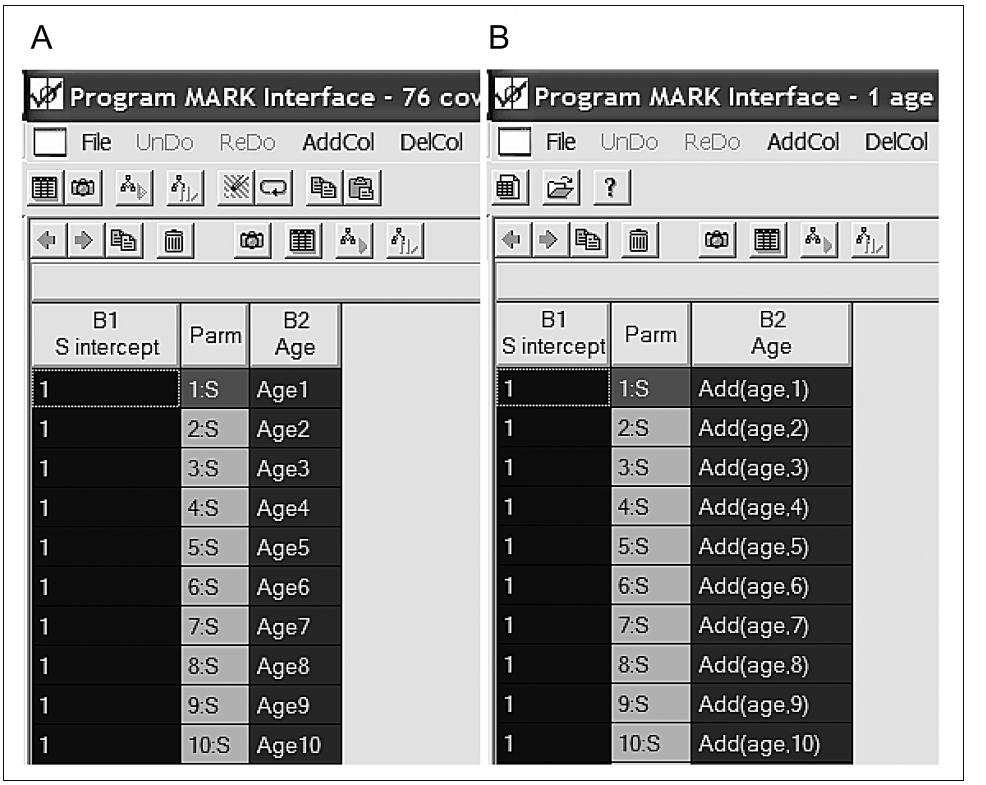

FIGURE 1. The design matrix in program MARK showing how age effects can be coded. In (a) the age effect is entered as a series of day-specific covariates in the input file while in (b) only a single age covariate is entered in the input file.

nest-age covariates with a single covariate for the age of the nest at discovery. The new encounter history would then be:

1 6 6 0 1 10;

Here, the same daily nest-age effect is modeled in MARK using the design matrix and a product function that increments the nest age daily until is succeeds or fails (Fig. 1b).

Some investigators may also be interested in modeling the possible effect on survival of observer visits to the nest (Rotella et al. 2000, Stephens 2003). The idea here is that survival may somehow be affected (usually negatively) for a short time period after the actual nest visit by the researcher. To model this in MARK, create a series of nest-specific covariates, one for each day that is coded as 1 for a nest visit and 0 otherwise. To run this observer-effect model, add a single column in the design matrix and fill it with the day-specific covariates (Fig. 2).

A few additional points are worth mentioning. As noted by Dinsmore et al. (2002), currently no method is available for estimating extra-binomial variation (over-dispersion) in typical nest-survival studies, and this is an area where additional research is needed (Rotella et al. 2004; Johnson, *this volume*). Also a formal goodness-of-fit test for nest-survival data is lacking, and the only way to minimize problems with lack of fit is to take care to meet model assumptions in the study design and data collection stages. Care must be given to the selection of nests to be included in a nest-survival analysis. Most studies will seek to infer the results to a larger population of interest, meaning that the sample must be representative of that larger population. This can best be assured by using consistent field methods. Nest searches should be allocated proportionally to available habitat and an effort should be made to avoid finding only easy nests, such as those most accessible to the researcher. And finally, the sample of nests must be sufficiently large to generate survival estimates with good precision. No rules exist for determining sample size because this will depend on the amount of information provided by each nest (number of exposure days) and the level of detail in the

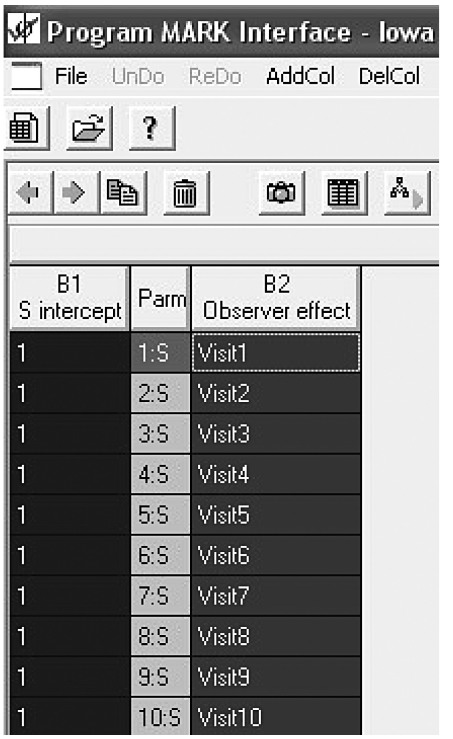

FIGURE 2. The design matrix in program MARK showing how an observer effect on nest checks can be coded. This design matrix codes for a simple model, S_{ObsEff}, where the observer effect in column two (B2) was modeled with a series of day-specific covariates called Visit1, Visit2, etc.

analysis (e.g., how many nest stages are being modeled). A related issue is the independence of nest-fates assumption, which makes studies of colonial birds problematic. In species where nests are aggregated, violation of this assumption could be minimized by study design considerations such as selecting nests from throughout the colony.

EXAMPLE—RED-WINGED BLACKBIRDS

To illustrate the use of program MARK for a nest-survival analysis, we present a detailed example below that includes a general modeling approach and presentation of select MARK output. This example is intended primarily as an illustration of a program MARK nest-survival analysis and not as a thorough biological analysis.

The Red-winged Blackbird (*Agelaius phoeniceus*) is a common and widespread breeding bird throughout much of North America where it breeds in a variety of wetland and upland habitats (Yasukawa and Searcy 1995). Information on its breeding biology is extensive (Beletsky 1996), and it is arguably one of the better studied North American breeding birds. The mating system is polygynous (Searcy and Yasukawa 1995, Beletsky 1996); eggs and young are brooded only by the female, although the male assists with feeding (Yasukawa and Searcy 1995). Apparent nesting success estimates ranged from 40–88% in a large study (Dyer et al. 1977). The causes of nest failure are varied, but most sources indicate that predation is the primary factor (Caccamise 1976, Yasukawa and Searcy 1995). Factors thought to influence nesting success are many and include weather, habitat type, habitat characteristics at the nest site, brood parasitism by Brown-headed Cowbirds (*Molothrus ater*), and age and experience of the tending adults (Yasukawa and Searcy 1995). Collectively, this information suggests several interesting hypotheses regarding the nest survival of the Red-winged Blackbird that can be easily tested in MARK.

METHODS

In 1994, JJD initiated a study of Red-winged Blackbird nest survival at a set of mesocosms on the Hinds Irrigation Farm near Ames, Iowa. The study continued through 2002, except that no data were collected in 2000. Mesocosms were constructed in 1989, and each consisted of a polyethylene tank 3.35 m in diameter and 0.91 m deep. The tanks were arranged in eight rows of six tanks each, spaced at 5.61 m intervals. Tanks were sunk into the ground so that the rims were just above ground surface. Each tank was filled with a three-inch layer of gravel covered with about 53 cm of sediment taken from another wetland. In fall 1989, cattail (*Typha* spp.) rootstocks were planted in the mesocosms (two plants per square meter, or about 15 plants per mesocosm). Cells were capable of holding water, and were seeded from wetland soils and the seed bank it contained. By fall 1991, the number of cattail shoots in the mesocosms ranged from 62–92 shoots per square meter, similar to shoot densities found in natural wetlands in north-central Iowa (Crumpton 1993).

Nests were located by systematically searching mesocosms at 2 or 3 d intervals. An observer walked the perimeter of each cell and carefully checked the vegetation for new nests. Red-winged Blackbirds vigorously defend their nest, making them relatively easy to locate. When a new nest was found the location of that nest within the cell was carefully noted. Because of the ease of locating nests and the frequency of searches, most (N = 162; 88% of total) nests were found during the nest building or egg-

laying stages. Because of the small size of the cells, the contents of most nests could easily be viewed without entering the cell, either directly or with the use of a mirror attached to a pole. Only rarely was it necessary to enter the cell to view the contents of a nest.

A key assumption for our analyses is that the transition time between nest stages is known. If these are unknown, then the approach of Stanley (2000) can be used to estimate stage-specific nest survival rates. In our example, we visited nests frequently and were able to accurately assign transition times on the basis of one or more of the following pieces of evidence: (1) known nest-initiation date based on observation of egg-laying, (2) presence of both eggs and young in the nest on a single visit, or (3) presence of young in the nest that could be readily aged based on personal experience (Baicich and Harrison 1997). Based on published information, we assumed that Red-winged Blackbirds laid one egg per day, that incubation began with the laying of the second to last egg and lasted 11 d, and that the nestling period lasted 12 d (Yasukawa and Searcy 1995, Baicich and Harrison 1997). Lastly, we assumed that hatch day was the first day the nest contained ≥one nestling.

In our nest survival analysis, we were interested in understanding the possible influence of several factors on nest survival, many of them suggested in previous studies. These factors illustrate many of the advantages of modeling nest survival in MARK, and included:

1. Nest stage. We collected data during the egg-laying, incubation, and nestling stages for this analysis; some nests were observed during construction, but too few to incorporate into this analysis. We hypothesized that evidence of stage-specific differences in nest survival would be evident with survival being lowest during the nestling stage due to the increased activity at the nest (Caccamise 1978).
2. Nest position in mesocosms. We examined whether nest placement along the edge (E) or in the center (C) of the mesocosm had any influence on nest survival. We defined the edge as a ring that included the outer 1 m of each mesocosm; the remainder of the cell was considered the center. Because most nest losses in this species are thought to result from predation (Caccamise 1976, Beletsky 1996), we hypothesized that survival would be lower near the edge of the mesocosm because those nests were more accessible to nest predators, such as raccoon (*Procyon lotor*), mink (*Mustela vison*) (Knight et al. 1985, Sawin et al. 2003), American Crow (*Corvus brachyrhynchus*), and Common Grackle (*Quiscalus quiscula*).
3. Nest position among mesocosms. Given the arrangement of mesocosms, we investigated whether nests located in the outer (O), middle (M), or interior (I) band (24, 16, and 8 cells, respectively) had different nest-survival probabilities. We hypothesized that there might be slight differences in nest survival within these bands with survival generally being higher in interior nests due to decreased vulnerability to nest predators.
4. Nest height. We measured height of the nest above water (in centimeters) and hypothesized that higher nests would have increased survival because they were less accessible to raccoons and minks. For nests where height was not measured (N = 8), we assigned them the mean height (75 cm) of the entire nest sample.
5. Nest placement. Here, we were interested in the placement of the nest in live or dead vegetation. We hypothesized that nests in live vegetation were higher and offered better nest concealment, and would thus result in greater survival. Conversely, nests placed in dead vegetation were lower and more conspicuous and were expected to be more vulnerable to predation and experience lower survival. These hypotheses are generally consistent with other information suggesting that nests placed in live material are more successful (Yasukawa and Searcy 1995). We also note that seasonal variation in vegetation growth meant that a greater percentage of dead material occurred early in the nesting season while live material predominated later in the season.
6. Clutch size. We included clutch size as a covariate for all stages and for the nestling stage only, and reasoned that nests with larger clutches might be more vulnerable to predators because of increased activity at the nest (especially true during the nestling stage; Yasukawa and Searcy 1995). Caccamise (1976) reported that apparent nest success was lowest for small clutches, although this may have been the result of partial depredations and nest abandonment. That study also found that nests with a clutch of three eggs were the most successful while nests with four or five eggs experienced lower success.
7. Temporal patterns in survival within years. Other studies of avian nest survival (Klett and Johnson 1982) have found

evidence for within-year differences in nest survival. These patterns arise from a variety of factors including differences in nest timing between more and less experienced adults, temporal shifts in predator communities, weather patterns, and changes in the behavior of adults and young. For Red-winged Blackbirds, Caccamise (1976) showed that survival initially declined during the first 4 d of the incubation period, leveled off through the early nestling stage, and then dropped again until the young fledged.

8. Temporal patterns in survival between years. Others (Beletsky 1996) have noted that Red-winged Blackbird nest survival varied greatly from year to year with some years of almost total failure and other years with high nest survival. In some years, most nests were lost to predation, perhaps due to one or a few predators, while in other years most nests were successful.

We divided nests into three groups to correspond to different nest stages (egg-laying, incubation, and nestling). Thus, it was possible that a single nest could be a member of 1, 2, or 3 groups. For nests that were members of >one group, we censored the nest on the last day of observation for the first stage, and then initiated it on that day for the second stage. As an example, consider a nest from a two-stage (incubation and nestling periods) analysis that is found on day one and is in the incubation stage when it is discovered. Furthermore, suppose the nest is known to hatch on day 10, but then fails sometime between days 15 and 17 (before the young successfully fledge). This nest would be split into two encounter histories, one corresponding to each nest stage, and nest stages would be considered groups in the analysis. The encounter history for the incubation stage would be:

```
Nest survival group = 1;
     1     10     10     0      1;
```

The first three numbers are *k*, *l*, and *m*, the next number is fate, and the last column corresponds to the number of nests with this encounter history. Note that this stage is coded as a success (fate = 0) because it successfully transitioned into the nestling stage. The second encounter history for this nest would be:

```
Nest survival group = 2;
     10     15     17     1      1;
```

Notation is as above, except that this nest belongs in a different group (group 2 = nestling stage) and was unsuccessful (fate = 1, meaning the young did not fledge).

We combined year and nest stage effects into groups, resulting in $3 \times 8 = 24$ groups for our analysis. Note that in MARK it is possible to run the same analysis by coding the groups as covariates, although we prefer the use of groups. Other nest-specific covariates included nest height (continuous), clutch size (discrete), nest support (binary), nest placement within a mesocosm (binary), and nest position among mesocosms (discrete, three categories).

We used a hierarchical-modeling approach to build models to explain variation in the nest survival of Red-winged Blackbirds, mainly to keep the model set small with such a large number of covariates. Model building occurred in three steps:

1. We began by fitting five models to explain within and between year variation in nest survival. These models included constant survival, linear (T) and quadratic (TT) time trends, and year effects (year). We also chose to combine year effects with the best source of within-season temporal variation (constant, T, or TT) into an additive model. In our notation, a T denotes a linear temporal pattern, which can occur within a season or specific nest stage.
2. We next explored possible stage-specific differences by adding three sources of variation: (a) constant survival within each stage, (b) a linear time trend in survival within each stage, and (c) a quadratic time trend within each stage. For time trends, we considered models with separate trends for each stage and with a common trend across stages.
3. Finally, to the best model from step 2 we added the nest specific covariates singly. If >one individual covariate was represented in competing models (ΔAIC < 2), we then combined them in an additive fashion in a single model.

After the modeling was complete, we followed the general approach of Burnham and Anderson (2002) for making inference from our model set. Our results emphasized (1) understanding the factors influencing nest survival in Red-winged Blackbirds, and (2) using models to predict the influence of various factors on nest survival under a range of scenarios.

RESULTS AND DISCUSSION

Across the 8-yr study, we monitored a total of 184 nests (Table 1; 2,775 effective samples due to some nests being in >one group) during the period 8 May–20 August. Clutch size

TABLE 1. TOTAL NUMBER OF RED-WINGED BLACKBIRD (*AGELAIUS PHOENICEUS*) NESTS AND THE NUMBER BY NEST STAGE MONITORED NEAR AMES, IOWA, 1994–2002.

		No. by nest stage		
Year	No. nests	Egg-laying	Incubation	Nestling
1994	23	11	23	13
1995	26	26	26	15
1996	17	16	17	16
1997	53	48	50	28
1998	20	20	18	3
1999	14	14	14	10
2001	8	5	8	3
2002	23	22	23	14
TOTAL	184	162	179	102

ranged from two–five eggs, and the percent of the total for each clutch size was 2% (two eggs), 23% (three eggs), 69% (four eggs), and 6% (five eggs). We considered a total of 17 models in our analysis. Our results suggest that the nest survival of Red-winged Blackbirds was influenced by year, temporal variation within nest stage, nest height and support, clutch size, and between-cell placement of nests in the mesocosms (Table 2). All of the top models contained the effect of temporal variation within nest stage, with a separate quadratic trend for each stage. The quadratic trend performed slightly better than a linear trend within nest stage (ΔAIC difference of 1.04), and both of these were substantially better than other trend models (Table 2). Evidence for year effects on survival was strong. Compared to 2002, nest survival in 1996 was substantially greater (β_{1996} = 2.97 on a logit scale, SE = 1.09, 95% CI was 0.84, 5.11) while survival in 1998 was lower (β_{1998} = –1.72 on a logit scale, SE = 0.56, 95% CI was –2.81, –0.63). Survival in all other years did not differ from 2002.

The top model had weak evidence for an effect of nest height (β_{Height} = 0.23 on a logit scale, SE = 0.16, 95% CI was –0.08, 0.55), and it suggested that nests placed at a greater height experienced higher survival. The effect of nest support in the third best model was also weakly positive ($\beta_{Support}$ = 0.13 on a logit scale, SE = 0.15, 95% CI was –0.17, 0.43), hinting that nests placed in live material survived better. The effects of clutch size and within- and between-cell nest placement were weak, and the confidence intervals for those effects were nearly symmetrical around zero.

One of the advantages of the modeling approach used in program MARK lies in the predictive nature of the models. Given a model, meaningful values of the variables (e.g., a nest-specific covariate) can be input to illustrate how they influence nest survival. In this example, we were especially interested

TABLE 2. MODEL SELECTION RESULTS FOR RED-WINGED BLACKBIRD (*AGELAIUS PHOENICEUS*) NEST SURVIVAL NEAR AMES, IOWA, 1994–2002.

Model	AIC_c	ΔAIC_c	w_i	K	Deviance
Year+*TT* by stage+height	786.21	0.00	0.23	17	751.99
Year+*TT* by stage	786.26	0.05	0.22	16	754.07
Year+*TT* by stage+support	787.56	1.35	0.11	17	753.34
Year+*TT* by stage+height+support	787.87	1.66	0.10	18	751.62
Year+*TT* by stage+clutch	788.04	1.83	0.09	17	753.82
Year+*TT* by stage+between cell	788.16	1.95	0.08	17	753.94
Year+*TT* by stage+within cell	788.22	2.01	0.08	17	754.00
Year+*TT* by stage+clutch (nestlings only)	788.29	2.08	0.08	17	754.06
Year	830.82	43.01	0.00	8	813.97
TT by stage	834.90	48.69	0.00	9	816.83
T by stage	835.94	49.73	0.00	6	823.91
TT across stages	842.16	55.95	0.00	3	836.15
TT within stages	842.96	56.75	0.00	3	836.95
Nest stage	844.28	58.07	0.00	3	838.27
T within stages	855.68	69.47	0.00	2	851.67
T across stages	857.65	71.44	0.00	2	853.64
Constant survival	859.12	72.91	0.00	1	857.12

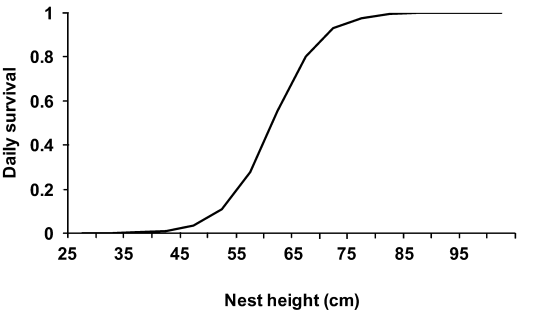

FIGURE 3. Predicted daily survival of Red-winged Blackbird (*Agelaius phoeniceus*) nests of differing heights during the 1995 incubation period. For illustrative purposes, survival is shown only for day one of the nesting season (2 May) across a range of nest height that approximates that seen during this study.

in understanding the influence of nest-specific covariates and nest stage on daily nest survival. To illustrate this, we first predicted the influence of nest height on the daily survival of 1995 nests in the incubation stage (Fig. 3). In this simple example, nest survival is predicted only for nests on day one of the study (2 May), although this could easily be extended to other days. Next, we predicted daily survival rates for each nest stage in what we considered a representative year (1995; Figs. 4–6), and further illustrated the influence of differing nest heights on survival. We chose to use values for the mean, 0.5 SD below the mean, and 1 SD above the mean to show that the influence of height was non-linear. Last, we show the predicted influence of nest support on Red-winged Blackbird nest survival (Fig. 7).

Our results confirm and add to what is known about patterns of Red-winged Blackbird nest survival. Our finding of stage-specific differences in survival is consistent with other literature on this species (Caccamise 1976, 1978), as are our within-stage temporal patterns except for the apparent increase at the end of the nestling stage. This result was unexpected and inconsistent with mechanisms explaining nest survival in altricial species, and we are at a loss to explain why we saw this pattern in our study. Strong year-specific differences in survival have been noted in other studies of this species (Beletsky 1996). Caccamise (1977) found that hatching success decreased with nest height whereas fledging success was not related to nest height. Among the habitat covariates we investigated, both nest height and support appeared to influence nest survival in ways consistent with other studies and published literature. We did not uncover any clear influence of nest placement within or among mesocosms, suggesting that either nest placement at this scale is unimportant or that we were unable to detect such an effect in our study. Clutch size did not appear to influence nest survival, even in the nestling stage, perhaps because our sample of nests included relatively few of extreme clutch sizes (one, two, or five eggs).

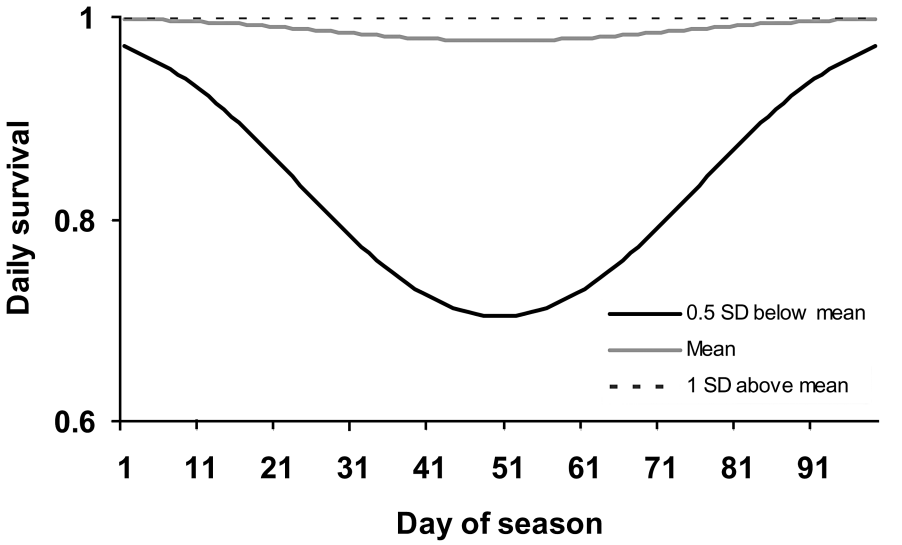

FIGURE 4. Predicted daily survival of Red-winged Blackbird (*Agelaius phoeniceus*) nests during the 1995 egg-laying period. Daily survival is illustrated for three scenarios of nest height: below average (0.5 SD below the mean), average (at the mean), and above average (1 SD above the mean).

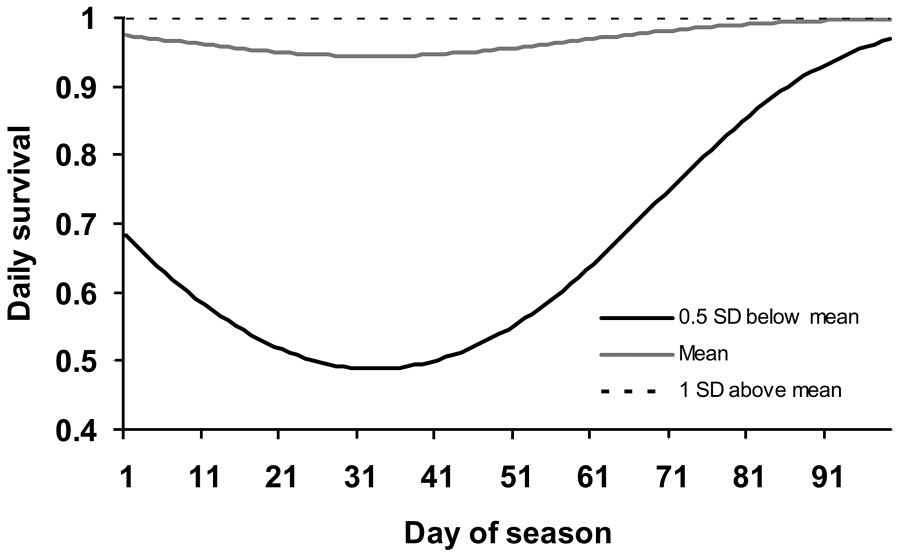

FIGURE 5. Predicted daily survival of Red-winged Blackbird (*Agelaius phoeniceus*) nests during the 1995 incubation period. Daily survival is illustrated for three scenarios of nest height: below average (0.5 SD below the mean), average (at the mean), and above average (1 SD above the mean).

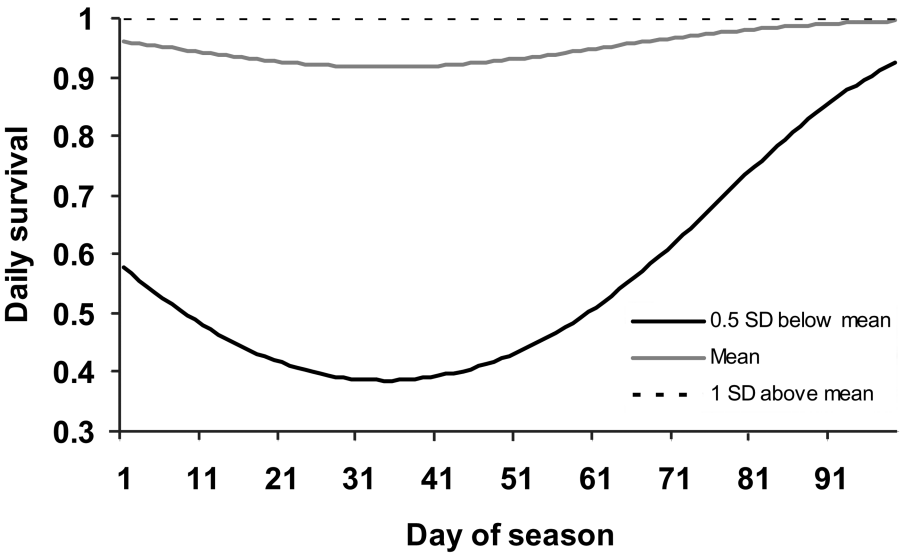

FIGURE 6. Predicted daily survival of Red-winged Blackbird (*Agelaius phoeniceus*) nests during the 1995 nestling period. Daily survival is illustrated for three scenarios of nest height: below average (0.5 SD below the mean), average (at the mean), and above average (1 SD above the mean).

RECOMMENDATIONS

Interest in studies of avian nest survival remains high, and researchers increasingly ask complicated questions in an attempt to better understand the processes affecting nest survival. This demand has promoted several recent developments which are rapidly gaining widespread use in the ornithological community. The long-standing Mayfield method and variations thereof are no longer accepted as the best approach for answering questions of avian nest survival.

The nest-survival model implemented in program MARK is one of these recent advances. Complete documentation for the model can be

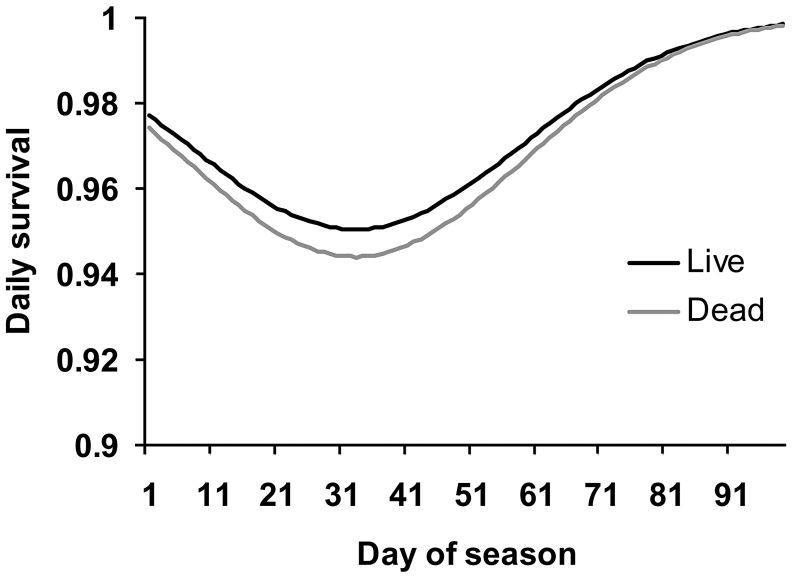

FIGURE 7. Predicted influence of nest support (live or dead material) on the daily survival of Red-winged Blackbird (*Agelaius phoeniceus*) nests during the 1995 incubation period.

found in Dinsmore et al. (2002). Additional support for program MARK is available through a detailed user's guide (Cooch and White 2005) and an on-line discussion group (http://www.phidot.org/forum/index.php). We hope that researchers conducting future studies of avian nest survival will find the nest-survival model implemented in MARK (or a similar model such as those mentioned in the introduction) appealing, and will recognize its many advantages.

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