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MAKING MEANINGFUL ESTIMATES OF NEST SURVIVAL WITH MODEL-BASED METHODS

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Abstract. Model-based methods for analyzing nest survival can be used to investigate effects of continuous and categorical covariates and to produce less biased and more precise estimates of nest survival than design-based methods. Herein, we modeled avian nest survival using the logistic-exposure method, demonstrated how to make meaningful model-based estimates of nest survival, and provided examples using SAS. To produce estimates of nest survival with model-based methods, one first fits a model to the data and then uses that model to produce estimates for specific values of covariates in the model. Covariate values can be based on the sample (e.g., means for continuous covariates and proportions for categorical covariates), however, the sample of nests (and nest-days) is usually non-random and therefore may not be representative of the population of interest. Alternatively, nest-survival estimates can be based on covariate values that the investigator believes are more representative of the population to try and reduce bias resulting from non-random sampling. We discuss a general method that can be used to reduce bias by adjusting estimates for nests that were never observed. We illustrate the method with an example that involves estimating period survival when daily survival varies by date. When the survival model includes interactions among covariates, main effects can be misleading; it is therefore important to present survival estimates as functions of the interacting covariates. When support exists for multiple models, predictions should be generated from each model and then averaged to produce survival and precision estimates that account for model selection uncertainty. We offer some suggestions for presenting model-based results from studies of avian nest survival.

Key Words: design-based, estimation, logistic exposure, Mayfield method, model based, nest survival, population, sample, SAS.

HACIENDO ESTIMACIONES SIGNIFICATIVAS DE SOBREVIVENCIA DE NIDO CON MÉTODOS BASADOS EN MODELOS

Resumen. Métodos basados en modelos para el análisis de sobrevivencia de nido pueden ser utilizados para investigar efectos de covariantes continuas y categóricas, y para producir menos polarizaciones negativas y estimaciones de sobrevivencia de nido más precisas que los métodos basados en diseño. Además, modelamos sobrevivencia de nido utilizando el método de exposición logística, demostramos cómo hacer estimados basados en modelos significativos de sobrevivencia de nido, y proporcionamos ejemplos utilizando SAS. Para producir estimados de sobrevivencia de nido con métodos basados en modelos, primero se tiene que ajustar un modelo a los datos y después utilizar ese modelo para producir estimados para valores específicos de covariantes en el modelo. Los valores covariantes pueden estar basados en la muestra (ej., medias para covariantes contiguas y proporciones de covariantes categóricas), sin embargo, la muestra del nido (y días del nido) usualmente no es al azar, y por ello quizás no sea representativa para la población de interés. Alternativamente, las estimaciones de sobrevivencia de nido pueden ser basadas en valores covariantes los cuales el investigador crea sean más representativos de la población, para así tratar de reducir el sesgo causado por el muestreo de no azar. Discutimos un método general que puede ser utilizado para reducir el sesgo al ajustar estimaciones para nidos que nunca fueron observados. Ilustramos el método con un ejemplo que involucra período de estimación de sobrevivencia cuando la sobrevivencia diaria varía por día. Cuando el modelo de sobrevivencia incluye interacciones entre covariantes, efectos principales pueden ser engañosos; es por ello que es importante presentar estimaciones de sobrevivencia como funciones de covariantes interactuando. Cuando existe un soporte para modelos múltiples, las predicciones deben ser generadas de cada modelo y después ser promediadas para producir estimaciones de sobrevivencia y precisión que cuenten para la incertidumbre de selección del modelo. Ofrecemos algunas sugerencias para presentar resultados, basados en modelo para estudios de aves y sobrevivencia de nido.

Recent advances in techniques for modeling nest survival (Dinsmore et al. 2002, Rotella et al. 2004, Shaffer 2004a) provide new opportunities to examine nest survival in far greater detail than was previously possible with Mayfield's (Mayfield 1975) or similar methods (Johnson 1979). New methods allow daily survival to be rigorously modeled in terms of categorical, continuous, and time-dependent (e.g., nest age) explanatory variables. The new approaches can be used with simple or complex models and they can provide survival

estimates that are comparable to past studies that used Mayfield's method, provided the investigator is willing to make the usual Mayfield assumptions that survival is constant nest to nest and day to day. A major advantage of the new techniques, however, is that they accommodate models in which daily survival rates vary among nests and among nest-days. These model-based estimators of nest survival are more realistic and precise, and less biased than Mayfield's estimator.

We used the logistic-exposure method (Shaffer 2004a) to model avian nest survival as a function of multiple explanatory variables and demonstrate how to make meaningful model-based estimates of survival. We describe various strategies for constructing model-based estimators and discuss circumstances under which one strategy may be more appropriate than another. We used the logistic-exposure method and provide examples using this method in SAS (SAS Institute 2004). However, the principles involved apply to other model-based methods as well (Dinsmore et al. 2002, Nur et al. 2004; Heisey et al., *this volume*). We provide SAS code that streamlines the process of generating model-based estimates when multiple models are involved and model-averaging is necessary. We offer suggestions for presenting model-based results.

EMPIRICAL VERSUS MODEL-BASED ESTIMATION

The properties of a sample are determined by the manner in which data are observed. For instance, if sample units are obtained completely at random then the sample mean provides an unbiased estimate of the population mean. Designs based on some form of random sampling lend themselves to design-based estimation because the design itself justifies the basic inference that results (Morrison et al. 2001). Design-based estimators, also known as empirical estimators, involve few assumptions, aside from the sample being representative of the population as a result of random sampling. A study of cavity nesting in artificial structures provides an example in which design-based inference is possible. In this situation, monitoring takes place on a sample of structures that can reasonably be assumed representative of a larger population of structures. Both successful and unsuccessful nests are easily detected, and therefore, the apparent estimator (number successful/number initiated) is an unbiased, design-based estimator of nest survival. Another situation in which design-based inference might be possible involves the use of radio telemetry to continuously monitor females for evidence of nesting.

Although design-based inference leads to estimators that are unbiased, those estimators can have large variances in comparison to model-based estimators. As their name implies, model-based estimators arise from the use of a model to exploit relationships between a response variable (Y) and predictor variables (X's), also known as covariates. For example, if Y is observed to vary linearly with X, then that relationship can be utilized in a model-based estimator of Y that will have smaller variance than the design-based estimator of Y, which ignores information about Y that is provided by X.

Non-random sampling is the norm in studies of nest survival because inactive nests do not have the same discovery probability as active nests. Therefore, design-based inference using the apparent estimator as illustrated above is usually not appropriate. Model-based methods can be used to increase precision when sampling is random, and they can help overcome issues resulting from certain types of non-random sampling. Mayfield's method is an example of a model-based estimator that addresses the issue of non-random sampling. Mayfield's model is somewhat simplistic in that it assumes that daily survival rates are constant within each stage of nesting and are the same for all nests. Mayfield's method treats the nest-day, rather than the nest, as the sampling unit. However, the sample of nest-days is itself non-random because nests are found at various ages and the probability of locating a nest is often a function of nest age. For example, newly initiated nests are irregularly attended by parents during laying and therefore are less likely to be found by nest searchers using methods that rely on flushing an adult near the nest; these nests are therefore underrepresented in samples. Mayfield's assumption of constant survival within stage was his way of dealing with this predicament. For instance, that assumption allows one to estimate the daily survival rate of a 1-d-old nest even if no 1-d-old nests are observed. Modern analysis tools, such as Shaffer's (2004a) logistic-exposure method, permit greater flexibility in addressing this and related issues. For example, Grant et al. (2005) used polynomial models to relax the assumption that survival was constant day to day and nest to nest and to generate model-based estimates of nest survival. Further complications resulting from uneven distribution of search effort across the breeding season, habitats, study areas, and years can also be addressed with model-based methods.

DAILY SURVIVAL VERSUS PERIOD SURVIVAL

We use the term daily survival to refer to the probability that a nest survives a given day, conditional on it being active at the beginning of that day. Similarly, we use the term period survival to refer to the probability of surviving a period of several days, conditional on being active at the beginning of that period. Period-survival estimates often are presented for the period beginning with the laying of the first egg through the day of fledging. Although modeling of nest survival is usually done in terms of daily survival rates, period-survival estimates are better-suited for some applications, such as when assessing population growth rates.

Perhaps the most widely used model-based estimator involves the estimation of period survival (P), which is simply the product of daily survival rates for each day in the period:

$$\hat{p} = \hat{s}_1, \hat{s}_2 \ldots \hat{s}_k$$

where the $\hat{s}_i$ are daily survival rate estimates and k is the number of days in the period. If a constant-survival model is used then $\hat{p} = \hat{s}^k$. Approximate lower and upper confidence bounds for P can be obtained by performing the same computations on the lower and upper bounds for the S_i.

FITTING A MODEL

The process of generating model-based estimates begins with development and selection of a nest-survival model (or models). The model expresses nest survival (typically daily survival rate) as some function of covariates, which can be either categorical or continuous and be measured on a group-, nest-, or unit-of-time (e.g., values can change daily) basis. The logistic-exposure method expresses the logit of daily survival rate as a linear combination of the covariates. We used the GENMOD procedure of SAS (SAS Institute 2004) to estimate parameters of our logistic-exposure models. We used the information-theoretic approach to rank models and assess their relative weights (Burnham and Anderson 2002). Model selection is an important topic that is beyond the scope of this paper.

Once a nest-survival model has been chosen and fitted, model-based estimates of survival are derived by substituting specific values for each covariate in the model. If no single model stands out as best, model-based estimates can be produced from each of the top models and the results averaged to arrive at a single estimate that reflects both sampling variability and model-selection uncertainty (Burnham and Anderson 2002).

ESTIMATING SURVIVAL

Model-based estimation differs from design-based estimation in that the investigator must choose values of covariates on which estimates will be based. The appropriate values for covariates will depend on the question being asked and what additional information the investigator may have about the population of interest. Two questions commonly addressed with model-based estimation are: what is the survival rate for a population of interest, and what is the effect of a covariate on nest survival? Categorical covariates often represent treatments, habitats, or years, whereas continuous covariates often reflect environmental factors, like precipitation, or temporal factors, such as nest age. Selection of covariate values to answer the first question could be based on values derived from the sample of nests or on additional knowledge about the population of interest. To answer the second question, values of categorical covariates are usually chosen to isolate a given treatment level or to provide an average across all levels of a treatment. Continuous covariates are usually evaluated at multiple levels that span the range of values in the sample or population of interest. We discuss and illustrate these approaches in detail below.

Covariate Values Based on the Sample

With this approach, covariate values are derived strictly from the data. A major limitation of this approach is that the sample of nests is usually non-random and therefore may not be representative of the population of interest. The sample mean (or median if the distribution is skewed) is the value usually used for a continuous covariate and the proportions of the sample represented by the various levels of a categorical covariate are used for a categorical variable.

We demonstrate how to produce an estimate of daily survival with SAS (SAS Institute 2004) based on a model that includes nest stage (laying, incubation, and nestling) and date as explanatory variables (Fig. 1). The value 172 following date in the ESTIMATE statement is the mean value of date in the sample, and values following stage represent the proportion of observations in the incubation, laying, and nestling stages, respectively. The estimate produced by the ESTIMATE statement is in the logit scale and needs to be back transformed to obtain an estimate of the daily survival rate. To do this

```
SAS code:

  proc genmod data=a descending;
    class stage;
    a=1/t;
    fwdlink link = log((_mean_**a)/(1-_mean_**a));
    invlink ilink = (exp(_xbeta_)/(1+exp(_xbeta_)))**t;
    model success = stage date/ dist=bin ;
    ods output Estimates=preddsr;
    estimate 'sample' intercept 1 stage .43 .07 .50 date 172;
  run;

  /*transform linear prediction to dsr*/
  data preddsr2; set preddsr;
    dsr=(exp(estimate))/(1+exp(estimate));
    dsrlow95 = (exp(lowercl))/(1+exp(lowercl));
    dsrup95 = (exp(uppercl))/(1+exp(uppercl));
  run;

  proc print; run;

  Output from proc print:

 Label Estimate  StdErr  Alpha   LowerCL  UpperCL   dsr   dsrlow95   dsrup95

 Sample  2.8501   0.0875   0.05    2.6786   3.0216  0.945   0.936     0.954
```

FIGURE 1. SAS code and selected output illustrating use of the ESTIMATE statement in PROC GENMOD to estimate daily nest survival using the logistic-exposure method.

we output the estimate using an ODS output statement and do the transformation in a data step to produce the daily survival estimate (Fig. 1). Output from the ESTIMATE statement also includes the estimated standard error and 95% confidence limits for the logit. Although it is not possible to compute a standard error for the daily survival rate estimate from this output, we can produce a confidence interval for daily survival rate by back-transforming the logit confidence limits.

How should we interpret this model-based estimate of daily survival? Clearly it pertains to survival on day 172 (the average date in our sample), but the stage of the nesting cycle that this estimate reflects is less clear. Recall that we used the proportions of observations in the incubation, laying, and nestling stages to weight our estimate of daily survival rate. Because fewer nests are often found during egg-laying, our sample probably under represents the proportion of time spent in the laying stage and over represents the proportion of time spent in the incubation and nestling stages. An estimator that does not account for differences in nest encounter probabilities can give a biased view of the average daily survival rate across all stages of the nesting cycle. We provide a solution to this problem in the next section.

When might estimates based on means or proportions from the sample of nests be useful? Sometimes it may be reasonable to assume that the observed sample of nests is reflective of a larger population of nests. For example, a study examining nest survival of grassland passerines in relation to distance to edge could result in a sample of nests that approximated the unknown distribution of distances for all nests initiated in a field. If nest survival was found to vary with distance to edge, then one might want to base the estimate of survival of all nests on the average distance to an edge. A potential problem exists with using the mean value from the sample because the sample will be biased towards conditions that favor a nest being successful. Thus, if survival increases with distance to edge, the mean distance of sample nests will tend to overestimate the true mean. If the effect of distance on survival is not strong, then the bias may not be a big concern, but how one would objectively make that determination is unclear. We illustrate a procedure that can be used to correct for this type of bias in a later example.

Estimates based on covariate values derived from the sample may be sufficient when assessing treatment effects. Suppose in the above example that we wish to compare survival

between managed and unmanaged grasslands. We must control for effects of distance to edge for this comparison to be meaningful. One way of doing that is to base the survival estimate for each treatment (unmanaged and managed) on the average value of distance calculated from the sample of all nests. This would be appropriate if the effect of distance was the same for both treatments (i.e., no treatment by distance interaction exists). However, no compelling reason exists to base the comparison on the mean value because the estimated treatment effect (i.e., difference in logit survival rates) is the same for all values of distance, unless treatment and distance interact. If treatment and distance are found to interact, then one should estimate treatment effects for a range of distance values (see below).

Covariate Values Based on the Target Population

Returning to our earlier example, suppose we desire an estimate of average daily survival rate that reflects the actual time allocated to each stage of nesting. We can produce such an estimate by specifying values of 0.19 (4/21) for laying, 0.48 (10/21) for incubation, and 0.33 (7/21) for the nestling stage. Here the proportions used for each stage are based on knowledge that laying, incubation, and nestling periods are 4, 10, and 7 d, respectively. This estimator gives equal weight to each day of the nesting cycle and theoretically produces an unbiased estimate of the average daily survival rate across all days of the nesting cycle. We say theoretically because the model must be correct to ensure that the estimator will be unbiased. This estimator utilizes information about the target population of nests (i.e., the length of each nest stage) that is not necessarily derived from the sample, and is an attempt to remove bias that results from the sample of nest-days being non-random. This estimator might be useful for comparing survival among species that had different age-related patterns in daily survival, or different durations in laying, incubation, or nestling periods.

Estimates that reflect the target population of nests are usually more desirable than those based on the sample. The target population might be defined as all nests initiated in a particular habitat block, all nests exposed to a particular treatment, or it can be somewhat nebulous as in the previous example. Consider an example in which the objective is to estimate nest survival in grass buffer strips surrounding wetlands in cropland. The target population is all nests initiated in buffer strips for some large cropland area. Suppose we choose a sample of five buffer strips to survey and that some of those strips are too large to be surveyed completely. Therefore we sample only a portion of the larger strips. Suppose the analysis indicates that survival varied among strips but was otherwise constant. A model-based estimator that gives equal weight to each buffer, regardless of the buffer size, will be a biased estimator of overall survival unless each buffer contained the same number of nests. In contrast, an estimator that weights each buffer by its area would be a reasonable estimator of overall survival if nest densities were similar among buffers. Issues like these require careful consideration on the part of the investigator to ensure that estimators are appropriate for the intended target population.

Interactions among Covariates

Model-based methods can be used to demonstrate the effect of a covariate while holding the effects of other covariates in the model constant, or to demonstrate interactions involving two (or more) covariates. To demonstrate this we fit a logistic-exposure model with covariates nest height and habitat (field or forest) and their interaction to data from Peak et al. (2004) on Indigo Buntings (*Passerina cyanea*). For ease of illustration we did not consider effects of nest stage or nest age. We held the effect of nest height constant by using the mean value of nest height from the sample (0.5 m) while producing an estimate for field and forest habitats (Figs. 2, 3a).

We also estimated daily survival across a range of nest heights for a population of nests split equally between field and forest habitats (Fig. 2, 3b). However, strong evidence indicated an interaction between nest height and habitat in these data. Thus, it was necessary to allow nest height and habitat to co-vary in order to obtain a clear understanding of the effect of each variable on survival (Fig. 2, 3c). This example clearly shows how main effects can be misleading when interactions are present.

Estimating Period Survival when Survival Varies with Date

Generating estimates that apply to the target population can be challenging because often we lack necessary information about that population. Earlier we discussed the desire to base the survival estimate on the mean covariate value (distance to edge) in the target population when the sample mean is a biased estimator. A similar situation occurs when daily survival varies with date and the objective is to estimate period

```
proc genmod data=indigo ;
    class hab;
    a=1/t;
    fwdlink link = log((_mean_**a)/(1-_mean_**a));
    invlink ilink = (exp(_xbeta_)/(1+exp(_xbeta_)))**t;
    model success = hab nestht*hab/ dist=bin ;

  /* estimate DSR by habtype while holding nestht = 0.5 */
    estimate 'field' intercept 1 hab 1 0 nestht .5 nestht*hab .5 0;
    estimate 'forest' intercept 1 hab 0 1 nestht .5 nestht*hab 0 .5;

  /* estimate DSR for 3 values of  nestht  giving equal weight to each habtype */
  estimate 'nesth0' intercept 1 hab .5 .5 nestht 0 nestht*hab 0 0;
  estimate 'nesth1' intercept 1 hab .5 .5 nestht 1 nestht*hab .5 .5;
  estimate 'nesth2' intercept 1 hab .5 .5 nestht 2 nestht*hab 1 1;

    /* estimate DSR by nestht and habtype to examine interaction */
    estimate 'field 0' intercept 1 hab 1 0 nestht 0 nestht*hab 0 0;
    estimate 'field 1' intercept 1 hab 1 0 nestht 1 nestht*hab 1 0;
    estimate 'field 2' intercept 1 hab 1 0 nestht 2 nestht*hab 2 0;
    estimate 'forest 0' intercept 1 hab 0 1 nestht 0 nestht*hab 0 0;
    estimate 'forest 1' intercept 1 hab 0 1 nestht 1 nestht*hab 0 1;
    estimate 'forest 2' intercept 1 hab 0 1 nestht 2 nestht*hab 0 2;
run;
```

FIGURE 2. SAS code to estimate daily survival rates by habitat type and nest height using the logistic-exposure method.

survival of all nests (P). The problem is easily seen when one considers the situation in which nests are classified as either early or late on the basis of nest initiation date. Let N_1 and N_2 be the numbers of initiated nests, and n_1 and n_2 the numbers of sample nests from the early and late periods. Let $N = N_1 + N_2$ and $n = n_1 + n_2$. Denote period-survival estimates for the two groups by $\hat{p}_1$ and $\hat{p}_2$. An intuitively reasonable estimator for P is $(N_1/N)\ \hat{p}_1 + (N_2/N)\ \hat{p}_2$. Because N_1 and N_2 are unknown, it is tempting to substitute n_1/n for N_1/N and n_2/n for N_2/N. However, if, for example, $P_1 > P_2$, then the expected value of n_1/n will be greater than N_1/N, and the estimator of P will be biased toward early nests.

Miller and Johnson (1978) proposed a solution to this problem in which they estimated N_i by dividing the number of successful nests by $\hat{p}_i$. Dinsmore et al. (2002) and Grant et al. (2005) used a related approach that is based on methods of Horvitz and Thompson (1952) and that incorporates information on both successful and unsuccessful nests. We provide an example (and SAS code; Shaffer 2004b) by considering the second-best model for Clay-colored Sparrow (*Spizella pallida*) from Grant et al. (2005). That model included cubic polynomial age effects and linear date effects:

$$\text{logit}(\hat{s}) = 2.054 + 0.812 \times \text{age} - 0.086 \times \text{age}^2 + 0.003 \times \text{age}^3 - 0.006 \times \text{date} \quad (1)$$

We begin by asking the simple question, what is the period survival rate (from initiation to fledge) of a nest initiated on day j? To be successful, the nest must first survive day j as a 1-d-old nest, then survive day $(j + 1)$ as a 2-d-old nest, and so on until it survives day $(j + k - 1)$ as a k-d-old nest. Note that for ease of notation, we are considering a nest to be 1 d old during its first day of exposure. We can express this relation as follows:

$$P_j = S_{j1}\, S_{(j+1)\,2} \cdots S_{(j+k-1)\,k} \quad (2)$$

It is clear from (1) and (2) that estimates of P_j will be different for each value of j. Period survival of all nests is a weighted average of the individual period survival rates: $P = \sum(N_j/N)P_j$, where N_j is the number of nests initiated on day j and $N = \sum N_j$. Thus to estimate P, we require estimates of the N_j (or estimates of N_j/N) for all j. Grant et al. (2005) estimated the N_j by scaling the number of observed initiations on day j upward to account for nests that failed before they could be discovered. For example, if they discovered a 2-d-old nest that was initiated on day j, they considered that nest to represent $1 \div \hat{s}_{j1}$ initiated nests. Similarly, a nest found at 3 d of age was considered to represent

$$1 \div \left(\hat{s}_{j1}\, \hat{s}_{(j+1)^2}\right)$$

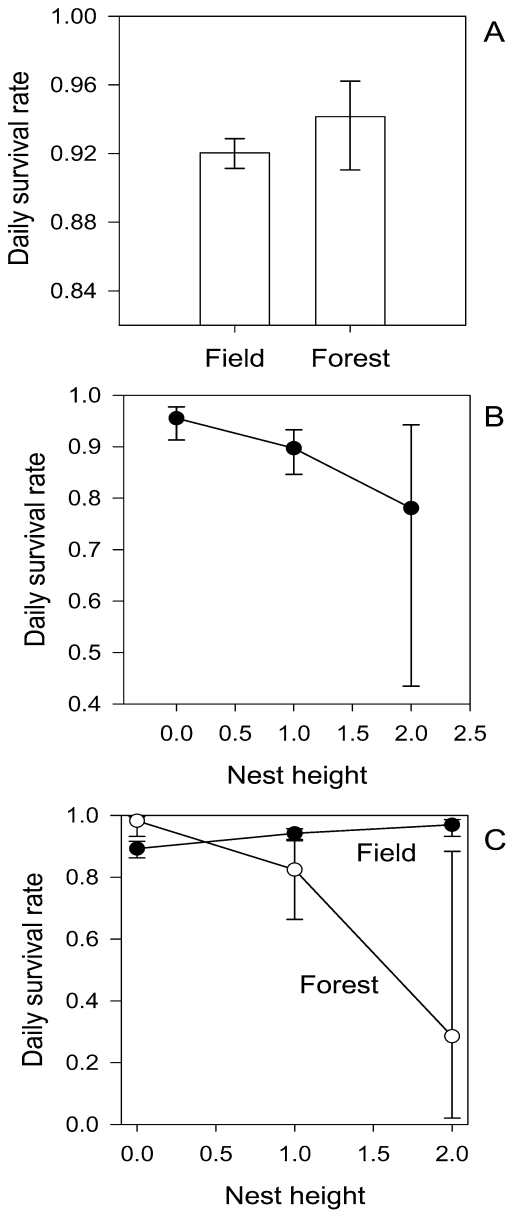

FIGURE 3. Effects of two covariates and their interaction from a logistic-exposure model of daily nest survival of Indigo Buntings (*Passerina cyanea*) in northeast Missouri. Data are from Peak et al. (2004).

initiated nests. These values were then summed by date of initiation to produce estimates of the N_j (Fig. 4).

This type of model-based estimator has received relatively little use, but appears to have potential for improving estimates of nest survival and nest density. However, properties of the estimator and situations under which it performs adequately have not been thoroughly investigated, and Grand et al. (2006) suggested caution in the use of the estimator because it is sensitive to errors in survival estimates. In addition, no straightforward method currently exists for computing estimates of precision. We expect the estimator to provide reasonable results when samples are large (N >100), when daily survival rates are not excessively low (>0.90), when nest searches are frequent and span the entire nesting season, and when the model fits the data and is not over-parameterized. The importance of a well-fitting model in model-based estimation can not be overstated, especially in this situation because the survival model is used to estimate both the daily survival rates and numbers of initiated nests. Thus errors in prediction from the survival model have the potential to be compounded. We consider the issue of model fit in greater detail later.

MODEL-AVERAGED ESTIMATES

We extend the above strategies for model-based estimation based on a single model to the multiple-model situation in which model averaging is necessary. In general, we produce a prediction based on a given set of covariate values from each model and then average the predictions using equations 4.1 (mean) and 4.9 (unconditional variance) from Burnham and Anderson (2002). We illustrate this with the Clay-colored Sparrow data from Grant et al. (2005). We consider four models for describing age-related patterns in survival (Fig. 5). The first is the cubic-age model reported by Grant et al. (2005) The estimated logit for a 10-d-old nest was 3.096 ± 0.144 (SE). The second model allowed for linear effects of age within laying, incubation, and nestling stages. The estimated logit from this model was 2.916 ± 0.126. The third model allowed survival to vary among stages but assumed that it was constant within a stage. The estimated logit from this model was 2.940 ± 0.125. The final model was based on the assumption of constant survival from initiation to fledging. The estimated logit from this model was 2.862 ± 0.087.

Model weights for the four models were 0.99, 0.01, <0.01, and <0.01, respectively, which indicates that the cubic-age model was vastly superior to the other models and that model averaging was unnecessary. For sake of illustration, however, the model-averaged prediction for a 10-d-old nest would be (0.99)(3.096) + (0.01)(2.916) + (0)(2.940) + (0)(2.862) = 3.093.

As the above example demonstrates, the process of generating model-averaged predictions is straightforward. In practice, however,

```
SAS code:

  data found;
  input initdate findage @@;
  cards;
  120 7 120 3 120 1 130 11 130 6 130 13 130 3
  run;

  data inits;
    retain b0 2.054 b1 0.812 b2 -0.086 b3 0.003 b4 -0.006; /* coeff. in logistic-
      exposure model */
    set found;
    f=1;
    do age = 1 to (findage-1);
      s = exp(b0 + b1*age + b2*age**2 + b3*age**3 + b4*(initdate
      + age - 1))/(1 + exp(b0 + b1*age + b2*age**2 + b3*age**3
      + b4*(initdate + age - 1)));
       f = f*s;
    end;
    found = 1;
    init = found / f;
    drop b0-b4 age s;
run;

  /* sum to determine no. nests found and to estimate no. nests initiated by date */
  proc means sum;
    class initdate;
    var found init;
  run;

  Output from proc means:

    Initdate    Nobs    Variable        Sum
       120       3       found      3.0000000
                          init      3.5839180

       130       4       found      4.0000000
                          init      5.7407344
```

FIGURE 4. SAS code for estimating numbers of initiated nests with a Horvitz-Thompson estimator that corrects for nests that failed before they could be discovered.

the coding of ESTIMATE statements in SAS can be very tedious and prone to error. The process quickly becomes unwieldy as the number and complexity of models or ESTIMATE statements increase. We developed SAS macro code (Shaffer 2004b) that greatly streamlines the process and reduces opportunities for error. The ESTIMATE statements are created by the macro at the time the model is run. The user controls the process by specifying the desired covariate values in a spreadsheet. Columns in the spreadsheet correspond to effects in the model, with column 1 being reserved for the label that identifies each ESTIMATE statement. Rows correspond to individual ESTIMATE statements, with row 1 containing the names of each effect in the model. Categorical covariates have a column for each category.

MODEL-BASED ESTIMATES OF PRECISION

A critical but sometimes overlooked aspect of estimating nest survival is deriving meaningful estimates of precision. Recall in our previous example that our sample under represents newly initiated nests, resulting in relatively few nest days corresponding to very young ages on which to base inferences. This is reflected in the cubic age and stage-specific linear models by the general narrowing of confidence intervals with increasing age (Figs. 5a, b). Less noticeable is the tendency for the confidence intervals to widen as survival decreases, reflecting the fact that the variance of the binomial distribution approaches its maximum value as the survival probability approaches 0.5. Our main point is that the precision estimates from these two

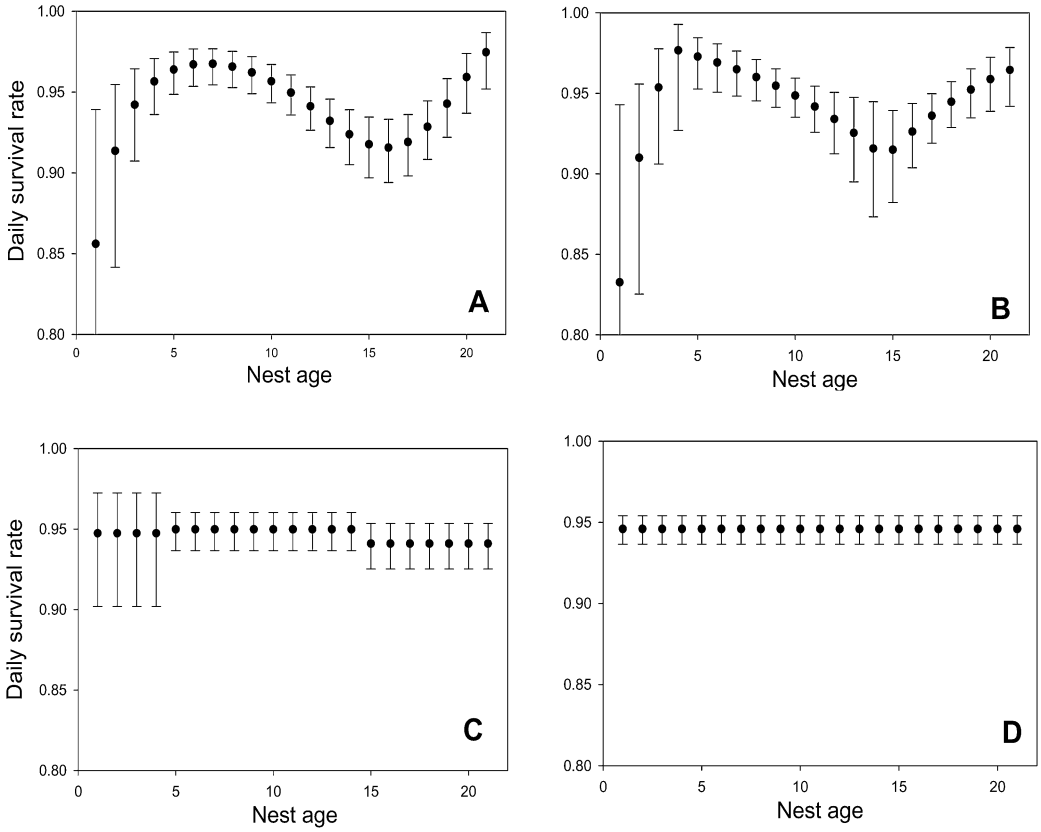

FIGURE 5. Four models of the effect of nest age on daily survival of Clay-colored Sparrow (*Spizella pallida*) nests: (A) cubic-age, (B) stage-specific linear, (C) stage-specific constant, and (D) constant survival. Data are from Grant et al. (2005).

models are intuitively reasonable given what we know about the distribution of nest ages from our sample.

In contrast, the stage-specific constant-survival model and especially the constant-survival model lead to precision estimates that seem unrealistic (Figs. 5c, d). For example, the number of intervals corresponding to 1-, 2-, 3-, and 4-d-old nests were 10, 17, 28, and 43, respectively. Yet, the stage-specific constant-survival model resulted in identical precision estimates for 1-, 2-, 3-, and 4-d-old nests. This is a consequence of the constant-survival assumption, and therefore the appropriateness of the precision estimates is highly dependent on the validity of that assumption.

IMPORTANCE OF A WELL-FITTING MODEL

Model-based estimates are only as good as the models on which they are based. Poorly constructed survival models can result in biased estimates of survival and precision. Unfortunately, no easy method exists to determine how well a model fits the data or to determine if overdispersion (extra-binomial variation) is present. Ideally we would like to have some sort of goodness-of-fit criterion that would allow us to assess model fit and adjust variance estimates for overdispersion. However, the usual goodness-of-fit tests based on the model deviance are not appropriate because the chi-square distribution provides a poor approximation to the sampling distribution of the deviance when sample sizes are small (McCullagh and Nelder 1989, Dinsmore et al. 2002). Small sample sizes are common when continuous covariates are present (i.e., N = 1 for many levels of the covariate). Model-selection results can indicate the relative support for a model compared to other models, and likelihood ratio tests can examine whether a particular model offers significant improvements over another model, but neither assesses how well a model fits the data. Instead, one must rely on ad hoc methods to assess model fit.

We use data from the previous example to illustrate a simple graphical method useful for investigating model fit. The method is analogous to comparing plots of observed and predicted values in ordinary linear regression. The method involves grouping observation intervals into discrete categories on the basis of the average age of the nest during the interval. For example, the first category might consist of intervals in which nests were 1- or 2-d old, the second category would include nests that were 3- or 4-d old, etc. One then estimates daily survival for each age category (treating age category as a CLASS variable) and visually compares the predictions from the best model to those estimates.

We grouped the Clay-colored Sparrow data into 11 age categories that included anywhere from 10 (age = 1−2 d) to 167 (age = 20−21 d) visitation intervals. Predicted values from the cubic age model showed close agreement with observed values of daily survival, except for the first age category (Fig. 6). This is not surprising given the small sample of very young nests. In fact, this situation might be a reasonable candidate for some sort of a weakly structured modeling approach (Heisey et al., *this volume*), such as a piecewise-polynomial spline. This approach would blend together a simple model, fit to the younger nests (where data are sparse), with a more complex model that applied to older nests. Regardless, the cubic age model seems to provide an adequate fit to these data.

Cross-validation (Snee 1977) is another method that can be used to judge the adequacy of a model. Sample sizes must be large enough to develop models first from a portion of the data and then evaluate those models by applying them to the remainder of the data. If cross validation does not reveal serious inadequacies with the structure of the model, then the model parameters can be re-estimated from the entire data set and model-based estimation can proceed from there.

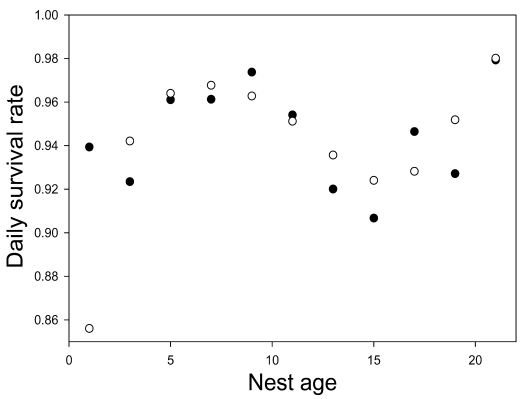

FIGURE 6. Observed (filled symbols) and predicted values (open symbols) of daily-survival rates of Clay-colored Sparrow nests (*Spizella pallida*). Observed values are logistic-exposure estimates based on grouping the data into intervals of age (i.e., 1−2 d, 3−4 d, etc.). Predicted values are based on the cubic-age model from Grant et al. (2005).

Neither of the above methods can guarantee that model-based estimates of survival will be unbiased. However, situations in which a model is clearly inadequate for making meaningful estimates of nest survival should become obvious. Models should also have some biological basis and not be derived purely from curve fitting. For example, Grant et al. (2005) argued that the cubic-age model was biologically reasonable because survival may vary among laying, incubation and/or nestling stages either in response to changes in predator numbers during the nesting season or by changes in cues that may allow predators to locate the nest. They offered several biologically based hypotheses that might explain patterns they observed.

PRESENTING RESULTS

We offer some suggestions for presenting results from studies of nest survival. We assume that through some process the investigator has arrived at a final model that has acceptable fit; other papers offer guidelines for presenting results from model selection or hypothesis testing (Anderson et al. 2001). We focus on presentation of model parameter estimates and estimates of nest survival derived from the model. The final model could be either a single best-fitting model or, in the case of multi-model inference, an average model. In addition to estimates discussed below we recommend reporting descriptive statistics for covariates because the range of variation observed provides the context for inferences that are made. We also suggest reporting descriptive information on visitation intervals and age when found, as that information can provide a gauge to the degree of interval-censoring and left-truncation (Heisey et al. *this volume*), and may be useful in comparisons with other studies.

Model Parameter Estimates

Parameter estimates, which include the intercept (or constant term) and coefficients for each covariate, should be presented along with their standard errors in text or a table. In addition the number of nests and effective sample size (Rotella et al. 2004) should be reported. The coefficients can be difficult to interpret directly

so we also recommend presenting odds ratios and their confidence intervals for covariates of particular interest. Odds ratios offer a more intuitive interpretation than the coefficients themselves (Allison 1999), and by simultaneously considering their magnitude and confidence interval, one can evaluate the strength of support for the effect.

Model-Based Estimates of Nest Survival

We assume that the investigator has generated some model-based survival estimates (and standard errors or confidence intervals) that are appropriate for the objectives. Estimates can be presented in tables or figures but figures often provide more insight, especially for continuous covariates or categorical covariates with several levels. Survival estimates should generally be calculated for the range of observed values of the covariate of interest while holding the values of other covariates in the model constant (see earlier sections on appropriate values for covariates), and provide the reader with specific values for variables that were held constant (as opposed to saying that the variable was held at its mean value). If interactions are present in the model, they should show the effects of one variable for a range of values of the other variable. Survival estimates should not be provided without estimates of precision. If figures are cluttered when estimates of precision are included, the analysis must clearly demonstrate that effects are real and properly documented in the text.

Although modeling is usually done in terms of daily survival rates (actually the logit of daily survival rates), we believe period-survival estimates are more intuitive and are therefore better suited for presentation in some cases. For example, in situations where daily survival is non-constant, period-survival rates can appropriately integrate effects of nest age or stage across the entire nesting cycle and simplify the presentation of other effects by reducing the number of variables in a biologically meaningful way (Fig. 2 in Grant et al. 2005). One must be sure to include information on the length of nest period or nest stages used to generate period-survival estimates. Daily survival estimates make sense when survival is constant (but so do period-survival rates) or when survival is non-constant and the goal is to illustrate effects of age (Fig. 5).

A question we often get is should I report Mayfield estimates too? The motivation behind this question is usually the desire for comparability with past studies that used Mayfield's method. Generally speaking, the answer to this question is no. Mayfield's estimator (including Mayfield logistic regression; Hazler 2004) is based on an approximate likelihood as a result of the midpoint assumption (Heisey et al., *this volume*). This results in a bias that can be either positive or negative depending on the lengths of the intervals between visits (and to a lesser degree on the survival rates themselves [Johnson 1979]). Although the bias is often small enough to be of little concern, it is nevertheless a bias that is unpredictable and inconsistent among data sets.

Johnson (1979) developed an alternative to Mayfield's estimator that was based on an exact likelihood and log link. Johnson's (1979) estimator did not receive much use because software was not readily available and because Mayfield's estimator generally performed well. The logistic-exposure model is also based on an exact likelihood, but uses a different link function than Johnson's (1979) estimator. However, a logistic-exposure model that assumes constant survival (day to day and nest to nest) will give results that are essentially identical to Johnson's estimator (Shaffer 2004a). We compared logistic-exposure and Mayfield estimates using data from several duck nesting studies on file at Northern Prairie Wildlife Research Center. We selected data sets to obtain a wide range in visitation intervals (6–25 d), numbers of nests (33–972), and 34-d-period survival rates (0.10–0.89). Under the assumption of constant-survival, logistic-exposure and Mayfield estimates were nearly identical (Table 1). Confidence intervals were similar when sample sizes were small ($N \leq 44$) or modest ($108 \leq N \leq 180$), and nearly identical when sample sizes were large ($N \geq 547$). We see no reason to report Mayfield estimates along with logistic-exposure estimates.

A more important issue is whether the constant-survival assumption can be justified. Further analysis of the above data sets revealed significant effects of age, date, or both age and date in data sets with $N \geq 132$. Thus, estimates based on the constant-survival assumption are likely biased to some unknown degree. An even bigger issue is how the sample of nests relates to the target population. To be meaningful, estimates of nest survival must be properly weighted to reflect the distribution of nests in the target population. Often practitioners new to modern nest survival methods develop a model and then fail to use that model to estimate nest survival. For example, the analysis might show that survival varied by X1, X2, and X3, but the method used to estimate overall nest survival is to pool all nests without regard to how the population of nests was distributed with respect to X1, X2, and X3. This mistake can lead to serious biases.

TABLE 1. COMPARISON OF LOGISTIC-EXPOSURE AND MAYFIELD PERIOD-SURVIVAL ESTIMATES (34 D) UNDER THE ASSUMPTION OF CONSTANT SURVIVAL FOR NINE DATA SETS

Species	N nests	Visitation interval (days)	Mayfield	Logistic-exposure
Mallard (*Anas platyrhynchos*)	33	6	0.27 (0.14–0.50) [a]	0.28 (0.12–0.45)
Blue-winged Teal (*A. discors*)	44	14	0.84 (0.72–0.98)	0.84 (0.66–0.93)
Gadwall (*A. strepera*)	35	23	0.71 (0.55–0.92)	0.71 (0.49–0.85)
Blue-winged Teal	108	9	0.27 (0.19–0.38)	0.27 (0.21–0.34)
Gadwall	132	19	0.89 (0.82–0.97)	0.89 (0.79–0.94)
Mallard	180	25	0.63 (0.54–0.74)	0.64 (0.54–0.73)
Mallard	547	7	0.10 (0.08–0.13)	0.11 (0.08–0.13)
Blue-winged Teal	553	9	0.39 (0.34–0.44)	0.39 (0.34–0.44)
Gadwall	972	21	0.32 (0.29–0.36)	0.33 (0.30–0.37)

[a] 95% confidence interval.

Therefore, we recommend that when reporting results of model-based estimation, practitioners be explicit about the assumptions they made and the evidence supporting those assumptions. If bias is likely, then potential sources should be reported and discussed.

Recent studies (Dinsmore et al. 2002, Nur et al. 2004, Grant et al. 2005) have demonstrated the importance of age as a covariate in nest-survival models. In most cases, effects of age could not be adequately represented by surrogates such as nest stage (laying, incubation, and brood rearing or, alternatively, egg and nestling). Yet, nest age is often not recorded in many nesting studies. We recommend that investigators whenever possible measure nest age, in addition to recording nest stage and date.

A goal of many nest-survival studies is to obtain an unbiased estimate of nest survival for some population of interest. One way of achieving this would be to base the survival estimate on a random sample of nests from the population. As we have discussed, random sampling of nests is seldom possible. Model-based methods described here offer a practical alternative, and when used properly provide meaningful estimates of nest survival.

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