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MODELING AND ESTIMATION OF STAGE-SPECIFIC DAILY SURVIVAL PROBABILITIES OF NESTS

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Abstract. In studies of avian nesting success, it is often of interest to estimate stage-specific daily survival probabilities of nests. When data can be partitioned by nesting stage (e.g., incubation stage, nestling stage), piecewise application of the Mayfield method or Johnson's method is appropriate. However, when the data contain nests where the transition from one stage to the next occurred during the interval between visits, piecewise approaches are inappropriate. In this paper, I present a model that allows joint estimation of stage-specific daily survival probabilities even when the time of transition between stages is unknown. The model allows interval lengths between visits to nests to vary, and the exact time of failure of nests does not need to be known. The performance of the model at various sample sizes and interval lengths between visits was investigated using Monte Carlo simulations, and it was found that the model performed quite well: bias was small and confidence-interval coverage was at the nominal 95% rate. A SAS program for obtaining maximum likelihood estimates of parameters, and their standard errors, is provided in the Appendix.

Key words: estimation; maximum likelihood; Mayfield model; modeling survival; nesting success; nest survival; stage-specific survival.

INTRODUCTION

In the study of avian populations it is often of interest to estimate nesting success—the probability a nest survives the nesting period to produce at least one fledgling. In a typical nest-survival study, an area is searched for active nests. When an active nest is found, the stage of the nest is recorded (i.e., egg-laying, incubation, nestling), and often the nest is aged by examining clutch size (egg-laying stage), candling (Weller 1956) or floating (Westerkov 1950) the eggs (incubation stage), or observing feather development in the young (nestling stage). The nest is then rechecked after an interval of one or more days, and the fate and stage of the nest are recorded. Here, "fate" refers to whether the nest survived (i.e., at least one egg or nestling remain in the still-active nest, or at least one fledgling was produced) or failed over the interval (failure is the complement of survival). For nests that survived, the stage of the nest will be evident, whereas for nests that failed, the stage at which it failed may be difficult or impossible to determine. Stage and age information gleaned from the first visit can, however, be used in conjunction with knowledge of the species biology (e.g., average clutch size, average days incubation) to determine the stage of the nest that would be expected had it survived over the interval. Because methods suitable for aging nests depend on the species being studied, and because the focus of this paper is on parameter estimation and not data collection, methods for aging nests will not be discussed further.

If K active nests are found and monitored to either fledging or failure during a study, a naive estimator of nesting success (Mayfield [1961] calls this "apparent success") is s/K, where s is the number of nests producing at least one fledgling (i.e., a successful nest). Mayfield (1961, 1975), recognizing this estimator is positively biased because nests that fail shortly after initiation are underrepresented in the sample, proposed instead that the daily survival probability of a nest, p, be estimated as $1-$ (number of nests that fail)/(number of nest days observed). Nesting success is then estimated as p^J, where J is the average number of days in the nesting period. Johnson (1979), and later Hensler and Nichols (1981), derived the likelihood for the experimental situation considered by Mayfield (1961, 1975) and showed that the Mayfield estimator was the maximum-likelihood estimator.

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As originally formulated, the Mayfield method assumes the day a nest fails is known exactly (Heisey and Nordheim 1995). In practice, this is often not the case because an interval of several days may pass before a nest can be rechecked. To address this issue, Mayfield suggested that exposure days for a nest destroyed during an interval >1 d be calculated as one-half the length of the interval (Mayfield 1961, Johnson 1979:654). Later, Miller and Johnson (1978) recommended exposure days for longer intervals (e.g., >7–10 d) be assigned a value of 40% of the interval between visits, and Johnson (1979) introduced a model that accommodated an unknown date of destruction, without imposing such ad hoc rules.

While the Mayfield estimator is a significant improvement over the naive estimator (however, see Johnson and Shaffer [1990]), the assumption that daily survival probabilities of nests over the nesting period are constant and homogeneous is restrictive. In an effort to relax this assumption, it has been suggested that the Mayfield estimator be applied in a piecewise fashion. That is, the data are first partitioned into more homogenous units, for example, by nest stage (e.g., incubation vs. nestling) or the experience of the adult (e.g., experienced vs. first-year breeders) (Mayfield, 1961, 1975, Johnson 1979, Bart and Robson 1982, Klett and Johnson 1982, Hensler 1985, Heisey and Nordheim 1990), and then Mayfield estimates are obtained for each partition. Difficulties with this approach arise, however, when it is not clear to which partition an observation belongs (Hensler 1985). To illustrate, consider a nest found during the incubation stage and that candling of the eggs revealed they were close to hatching. Now suppose the nest was rechecked three or more days later, but before the young could possibly have fledged, whereupon it was found the nest had failed. Should this observation be counted as failure during the incubation stage, or survival during the incubation stage and failure during the nestling stage? If the latter, how should exposure days be allocated among the incubation and nestling stages? This situation is problematic because there is insufficient information upon which to make a decision, and arbitrary decisions, such as censoring the data, can introduce bias (Hensler 1985). Generalized nest-survival models that account for age-specificity (Pollock and Cornelius 1988, Heisey and Nordheim 1990) or allow heterogeneity to be modeled using habitat or other covariates (Natarajan and McCulloch 1999) have been developed. Such models, however, often require very large sample sizes, and customized software for applying the models is frequently unavailable. Hence, they are of limited practical value to field biologists.

In this paper, I describe and evaluate using Monte Carlo simulations, a new model for estimating daily survival probabilities of nests that addresses some of the difficulties inherent in applying other methods. In particular, the model allows joint estimation of stage-specific daily survival probabilities even if the exact time of transition from one stage to the next is unknown, it makes no ad hoc assumptions regarding the time of failure of a nest, and it allows time intervals between visits to nests to vary. Moreover, the parameters of the model can be readily estimated using widely available software (e.g., procedure NLIN, SAS Institute 1989).

Data and Model

The data required for each active nest found (nests failing prior to being found are not used) includes the interval of exposure, t, which is the number of time units (herein days will be assumed) between finding and rechecking the nest ($t \in T$: $t = 1,2,\ldots$; T is the set of *observed* exposure intervals); the fate of the nest, y ($y = 1$ for survived, $y = 0$ for failed), over the interval t; and a categorical variable indicating nest type. Nest type reflects the stage of the nest when it was found and again when it was rechecked:

Type A—found and rechecked during egg-laying stage (begins when the first egg is laid and ends at the onset of incubation);

Type B—found during egg-laying stage, rechecked during incubation stage (begins at the onset of incubation and terminates when the first egg hatches);

Type C—found and rechecked during incubation stage;

Type D—found during incubation stage, rechecked during nestling stage (begins upon hatching of first egg and terminates upon fledging of the first young); and

Type E—found and rechecked during nestling stage.

For purposes of developing the model below, it is assumed that t is short enough that an entire stage cannot be skipped, and that fledging date can be accurately determined. The latter assumption is necessary to ensure that too many exposure days are not credited to a nest, thereby biasing parameter estimates (the effect of violating this assumption is reported in *Results*, below). It is important to note that nest type is required for all nests. Hence, in the event a nest fails, sufficient information to determine the stage expected after an interval t must be gathered when the nest is found. Additional stages (hence, more nest types), or stages that are defined differently, may be specified at the discretion of the investigator. The model presented below is easily modified to handle such cases.

For type-A, type-C, and type-E nests, the likelihood for the data can be constructed from a straightforward application of Johnson's (1979) model. We begin by modeling the survival or failure of a nest over an interval t as a Bernoulli trial with parameter p^t: $P(Y =$

$y|p) = (p^t)^y (1 - p^t)^{1-y}$, where y is defined above and p is the daily survival probability of the nest. If we assume that for nests in the ith stage ($i = 0,1,2$ for egg-laying, incubation, and nestling stages, respectively) daily survival probabilities are homogeneous and constant, and let p_i denote this probability, then the full likelihood for a data set consisting only of type-A, type-C, and type-E nests would be proportional to:

$$\prod_{t \in T} [(p_0^t)^{s_{At}}(1 - p_0^t)^{f_{At}}(p_1^t)^{s_{Ct}}(1 - p_1^t)^{f_{Ct}}(p_2^t)^{s_{Et}} \times (1 - p_2^t)^{f_{Et}}] \quad (1)$$

where s_{jt} is the number of type j nests that survive (j = A, C, E) and f_{jt} is the number of type-j nests that fail over an interval t. Using standard maximum-likelihood methods (e.g., Larsen and Marx 1986), we can derive estimators for p_i and standard error $\text{SE}(p_i)$. These estimators are given in Johnson (1979:655).

When type-B and type-D nests are present, expression 1 is not an adequate model for the data. This is because type-B nests contain information on daily survival probabilities during both the egg-laying and incubation stages, and type-D nests contain information on daily survival probabilities during both the incubation and nestling stages that is not accounted for in expression 1. To model type-B and type-D nests, we begin by considering the probability such a nest survives an interval t. To illustrate, for a type-B nest the probability of survival can be modeled as:

$$P(\text{survival}) = P(s|h_1)P(h_1) + P(s|h_2)P(h_2) + \ldots + P(s|h_{t-1})P(h_{t-1})$$

where $P(s|h_k)$ is the probability the nest survives the interval t given incubation begins k days after the nest is found ($k = 1, \ldots, t - 1$), and $P(h_k)$ is the probability incubation begins k days after it is found. If we assume the onset of incubation occurs with equal probability over the $t - 1$ days following discovery of the nest, then we can set $P(h_k) = 1/(t - 1)$ ($t > 1$). Thus, $P(\text{survival})$ becomes:

$$P(\text{survival}) = \frac{1}{t-1}(p_0 p_1^{t-1} + p_0^2 p_1^{t-2} + \ldots + p_0^{t-1} p_1)$$

and we get for type-B nests the following expression:

$$\left(\frac{1}{t-1}\sum_{k=1}^{t-1} p_0^k p_1^{t-k}\right)^{s_{Bt}} \left[1 - \left(\frac{1}{t-1}\sum_{k=1}^{t-1} p_0^k p_1^{t-k}\right)\right]^{f_{Bt}}$$

which is proportional to the probability s_{Bt} nests survive and f_{Bt} nests fail the interval t. The corresponding expression for type-D nests is similar. Taking the product over all nest types, the likelihood for the nest-survival data is proportional to:

$$\prod_{t \in T} \left[(p_0^t)^{s_{At}}(1 - p_0^t)^{f_{At}}\left(\frac{1}{t-1}\sum_{k=1}^{t-1} p_0^k p_1^{t-k}\right)^{s_{Bt}} \times \left[1 - \left(\frac{1}{t-1}\sum_{k=1}^{t-1} p_0^k p_1^{t-k}\right)\right]^{f_{Bt}} (p_1^t)^{s_{Ct}}(1 - p_1^t)^{f_{Ct}}\right] \times \prod_{t \in T} \left[\left(\frac{1}{t-1}\sum_{k=1}^{t-1} p_1^k p_2^{t-k}\right)^{s_{Dt}} \left[1 - \left(\frac{1}{t-1}\sum_{k=1}^{t-1} p_1^k p_2^{t-k}\right)\right]^{f_{Dt}} \times (p_2^t)^{s_{Et}}(1 - p_2^t)^{f_{Et}}\right]. \quad (2)$$

When parameters are constrained so as to be equal (i.e., daily survival probabilities are constant across nest stages so $p_0 = p_1 = p_2$), the likelihood in expression 2 collapses to Johnson's (1979) model.

Estimators for the model in expression 2, derived using standard maximum-likelihood methods, are not closed form and do not simplify to a compact, general expression. Nonetheless, maximum-likelihood parameter estimates can be obtained in a straightforward manner using iteratively reweighted least squares (Jennrich and Moore 1975, Green 1984, Burnham 1989). This approach is easily implemented in SAS using procedure NLIN (SAS Institute 1989), and is illustrated in the Appendix. Confidence intervals can be computed after Burnham et al. (1987:214). Once stage-specific daily survival probabilities and their standard errors have been estimated, nesting success over the entire nesting period (P_s) is estimated as $P_s = p_0^{J_0} p_1^{J_1} p_2^{J_2}$ where J_0, J_1, and J_2 are the average number of days in the egg-laying, incubation, and nestling stages, respectively. The variance of P_s can be approximated using the delta method (Seber 1982: 7–9; also Hensler 1985).

Methods

Performance of the model in expression 2 was evaluated by examining the effects on parameter estimates of: (1) number of active nests found (n), (2) interval length (t), and (3) violating the assumption that fledging date is known exactly. Nest survival data were generated using Monte Carlo simulations under a 3 × 3 × 4 × 4 factorial design with $p_1 \in \{0.90, 0.93, 0.96\}$, $p_2 \in \{0.90, 0.93, 0.96\}$, $n \in \{25, 50, 100, 200\}$, and $t \in \{1, 2, 4, 8\}$. One thousand data sets were generated for each of the 144 possible treatment combinations. An incubation stage of 14 d and nestling stage of 11 d were chosen for simulation because these are average values for the Western Meadowlark (*Sturnella neglecta*) (Baicich and Harrison 1997), and it was data collected for this species (by B.W. Baker, USGS, Fort Collins, Colorado, USA) that provided the motivation for this model. Data for the egg-laying stage were not simulated in this study for two reasons: (1) to reduce

TABLE 1. Effects of sample size (n) on bias (i.e., $E[\hat{p} - p]$) and actual 95% confidence-interval coverage for estimates of stage-specific daily survival probabilities under the assumption that fledging dates for nests are known, and for violation of this assumption.

Parameter values			Fledging date known				Fledging date not known			
			Estimated bias		95% CI coverage		Estimated bias		95% CI coverage	
p_1	p_2	n	p_1	p_2	p_1	p_2	p_1	p_2	p_1	p_2
0.90	0.90	25	−0.0023	−0.0114	0.954	0.950	−0.0030	−0.0038	0.953	0.958
		50	−0.0000	−0.0030	0.960	0.963	−0.0007	0.0048	0.957	0.969
		100	−0.0005	−0.0013	0.958	0.962	−0.0011	0.0061	0.956	0.957
	0.96	25	−0.0024	−0.0039	0.951	0.942	−0.0030	0.0007	0.952	0.956
		50	−0.0015	−0.0019	0.955	0.951	−0.0019	0.0024	0.953	0.963
		100	−0.0009	−0.0009	0.956	0.963	−0.0014	0.0033	0.954	0.973
0.96	0.90	25	−0.0000	−0.0051	0.965	0.961	−0.0005	0.0022	0.960	0.967
		50	−0.0011	−0.0018	0.956	0.962	−0.0016	0.0057	0.953	0.961
		100	−0.0005	−0.0002	0.956	0.960	−0.0011	0.0069	0.952	0.947
	0.96	25	−0.0008	−0.0010	0.954	0.956	−0.0013	0.0031	0.952	0.967
		50	−0.0006	0.0000	0.958	0.961	−0.0011	0.0039	0.956	0.973
		100	−0.0003	−0.0002	0.966	0.963	−0.0008	0.0038	0.964	0.960

Notes: Data in each row are means and are pooled over the four time intervals simulated (hence, results in each row are based on 4000 simulated data sets). The parameters p_1 and p_2 are the daily survival probabilities for the incubation and nestling stages, respectively, under which the data were simulated.

the dimensionality of the simulations, and (2) because terms in the model for the egg-laying stage are mathematically equivalent to those for the nestling stage. Hence, simulations for the egg-laying stage would be redundant.

Nest data were simulated by generating a uniform random variable, u ($u = 1, \ldots, 25$), representing the day a nest was found, then performing a Bernoulli trial with parameter ($p_1^{j_1} p_2^{j_2}$) to determine whether the nest was still active on day u. Here, j_1 ($j_1 = 1, \ldots, 14$) and j_2 ($j_2 = 0, \ldots, 11$) are the number of days the nest was in the incubation and nestling stages, respectively, at the time it was found ($j_1 + j_2 = u$). Given that a nest was active, nest fate was determined by performing a Bernoulli trial with parameter ($p_1^{k_1} p_2^{k_2}$), where k_1 ($k_1 = 0, \ldots, t$) and k_2 ($k_2 = 0, \ldots, t$) are the number of days the nest was in the incubation and nestling stages, respectively, during the interval t ($k_1 + k_2 = t$). Nest type was determined by considering the stages in which u and $u + t$ fell. For example, for $u > 14$ and $u + t > 14$ we would get nest type E. For nests with $u + t > 26$, the number of pre- and post-fledging days in the interval were recorded so the effect of violating the assumption that fledging date is known could be evaluated. The above steps were repeated until data for n active nests were generated. To simplify simulations, nests were checked only once (after t days) following discovery on day u.

Estimates of p_1 and p_2, and their standard errors, were obtained using SAS procedure NLIN (SAS Institute 1989) (see Appendix). Ninety-five percent confidence intervals were computed after Burnham et al. (1987: 214). Model performance was evaluated by estimating bias (i.e., $E[\hat{p} - p]$) of the parameter estimates, and 95% confidence interval coverage.

RESULTS

A total of 144 000 data sets were generated to evaluate the properties of the model in expression 2. Below, a subset of the results are presented that illustrate the dominant patterns observed.

Under the assumption that fledging date is known, absolute bias (i.e., $|E[\hat{p} - p]|$) of estimates for p_1 and p_2 decreased as sample size (n) increased, and was small for $n \geq 100$. When fledging dates were not known, absolute bias for estimates of p_1 likewise decreased as n increased, whereas bias for estimates of p_2 increased (Table 1). In spite of these increases, the ratio of absolute bias to standard error was generally <0.10 irrespective of n. This suggests the effect of bias on the accuracy of the estimates was relatively small (Cochran 1977:12–14). Confidence-interval coverage for p_1 and p_2, for all levels of n, was close to the nominal rate of 95%.

The effect of increasing interval length, t, was to increase absolute bias for both p_1 and p_2 regardless of whether fledging date was known (Table 2). In spite of this increase, the ratio of absolute bias to standard error was generally <0.10, indicating the effect of bias on estimates was relatively small. For $t = 8$, confidence-interval coverage for p_1 and p_2, when fledging date is not known, was less than the nominal rate of 95%.

DISCUSSION

The model presented in this paper is a generalization of Johnson's (1979) model for estimating daily survival

TABLE 2. Effects of time interval length (t) on bias (i.e., $E[\hat{p} - p]$) and actual 95% confidence-interval coverage for estimates of stage-specific daily survival probabilities under the assumption that fledging dates for nests are known, and for violation of this assumption.

Parameter values			Fledging date known				Fledging date not known			
			Estimated bias		95% CI coverage		Estimated bias		95% CI coverage	
p_1	p_2	t	p_1	p_2	p_1	p_2	p_1	p_2	p_1	p_2
0.90	0.90	1	0.0000	−0.0002	0.965	0.965	0.0001	−0.0002	0.965	0.965
		4	−0.0013	−0.0049	0.955	0.959	−0.0016	0.0031	0.955	0.967
		8	−0.0013	−0.0060	0.949	0.954	−0.0036	0.0139	0.941	0.927
	0.96	1	−0.0001	−0.0005	0.964	0.956	−0.0001	−0.0005	0.964	0.956
		4	−0.0017	−0.0021	0.949	0.958	−0.0019	0.0024	0.947	0.969
		8	−0.0030	−0.0026	0.942	0.941	−0.0049	0.0086	0.936	0.952
0.96	0.90	1	−0.0007	0.0008	0.960	0.959	−0.0007	0.0008	0.960	0.959
		4	−0.0005	−0.0033	0.958	0.957	−0.0007	0.0042	0.956	0.961
		8	−0.0004	−0.0021	0.955	0.956	−0.0023	0.0169	0.940	0.890
	0.96	1	−0.0001	−0.0005	0.965	0.963	−0.0001	−0.0005	0.965	0.963
		4	−0.0003	−0.0003	0.958	0.953	−0.0005	0.0040	0.958	0.966
		8	−0.0008	−0.0003	0.954	0.955	−0.0026	0.0099	0.945	0.925

Notes: Data in each row are means, and are pooled over the four sample sizes simulated (hence, results in each row are based on 4000 simulated data sets). The parameters p_1 and p_2 are the daily survival probabilities for the incubation and nestling stages, respectively, under which the data were simulated.

probabilities of nests and, when there are no type-B or type-D nests in the data, it collapses to a piecewise application of Johnson's model. Similarly, when nests are visited daily, the model collapses to a piecewise application of the Mayfield method.

Under the assumption that fledging dates are known the proposed model performed well, even at small sample sizes (n) and large interval lengths (t). Bias (i.e., $E[\hat{p} - p]$) of estimated daily survival probabilities was usually negative but small, and confidence-interval coverage was close to the nominal 95% level for the treatment combinations investigated. It should be noted that, because simulation results were based on only a two-parameter model, larger sample sizes will be required to get comparable levels of accuracy and precision under the three-parameter model in expression 2. When fledging date was not assumed to be known, absolute bias increased and confidence-interval coverage decreased for large t. Nevertheless, for $t \leq 4$, these effects were minor and the model does quite well. A general recommendation would be that, for studies with $t > 4$, an emphasis be placed on determining (and checking nests on) the fledging date.

During model development it was assumed that the onset of incubation (or hatching) occurs with equal probability over the $t - 1$ days following discovery of the nest. Under this assumption $P(h_k) = 1/(t - 1)$. However, if different probability structures can be justified, these can be employed in the model. The only constraint is that the $t - 1$ probabilities sum to 1.

In field studies it is not unusual to find data are sparse for one or more stages. In such cases, the investigator may wish to consider a submodel that constrains daily survival probabilities across stages to be equal, so that data for those stages can be pooled. For example, one might be willing to assume daily survival probabilities during the egg-laying and incubation stages are equal (i.e., $p_0 = p_1$). Parameters under these models, as well as likelihoods for use in model selection, can be estimated by making slight modifications to the SAS program in the Appendix.

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APPENDIX

An SAS program for inputting data and estimating parameters under the model presented in Expression 2, and an interpretation of the output of the program, is available in ESA's Electronic Data Archive: *Ecological Archives* E081-021.