

A REVIEW OF NEST SURVIVAL MODELS

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ABSTRACT

In many nest survival studies nests are not found until after incubation has begun, and nests which fail are of unknown age while nests which succeed can be aged afterward. Originally ornithologists ignored all these problems and just reported the fraction of nests which were successful (Naive Approach). Now, typically, ornithologists consider the survival time to be from first encounter, and they use what has come to be known as the Mayfield method (Mayfield 1961, 1975) or some variation of it. Pollock (1984) and Pollock and Cornelius (in prep.) considered a new approach which allows estimation of the survival distribution from the time of nest initiation, which is the actual time origin. Nests which succeed are used to estimate the proportions of nests being found (encountered) in each time interval. Assuming that these encounter probabilities also apply to the nests which fail, it is possible to estimate a series of discrete failure time probabilities for all the nests. Here we review the models and assumptions for the Naive approach, the Mayfield method and the Pollock method. We compare estimates and their precision. We also explore the differences between the modeling of nest survival and egg survival.

Key Words: Egg survival, Mayfield method, Nest survival, Nesting survival, Pollock method, Survival analysis.

1. INTRODUCTION

Nesting survival studies are those in which an ornithologist chooses a study area and searches for active nests to observe. Nests found are visited regularly until they are either abandoned or destroyed, or until they produce young birds which hatch and later fledge. For any given species, it is generally accepted that the number of days from egg initiation to hatching (incubation) is approximately constant, and the number of days from hatching until fledging is again approximately constant. In these 2 intervals of time, the nest and its young are at risk to such perils as predator pressure, lack of availability of food, bad weather and others.

In many nest survival studies nests are not found until after incubation has begun; and nests which fail are of unknown age, while nests which succeed can be aged afterwards. Three distinct methodologies or models have served to describe this special kind of data and are to be reviewed in this article.

In Section 2 we consider the Naive approach originally considered by ornithologists. With this method all the special aspects of the data are ignored and simply the fraction of nests which are successful is reported.

In Section 3 we consider the the Mayfield method. In Mayfield (1961, 1975) the survival time from first encounter is considered. This enables one to find the total number of nest days of exposure and this together with the number of failures enables one to obtain a daily survival rate. In Section 4 some more recent extensions of the basic Mayfield method are reviewed.

In Section 5 we review a new approach (Pollock 1984; Pollock and Cornelius in prep.) which allows estimation of the survival distributions from the time of nest initiation which is the natural time origin. Nests which succeed are used to estimate the proportions of nests found (encountered) in each time interval. Assuming that these encounter probabilities also apply to the nests which fail it is possible to estimate a series of discrete failure time probabilities for all the nests. In Section 6 a detailed comparison of the three approaches is made using some mourning dove data and then using some Great-Tailed Grackle data.

Nest success is defined as survival of one or more eggs' in a nest until the young have fledged. The paper concludes with a general discussion section.

2. NAIVE SUCCESS ESTIMATES

In the earliest studies of nesting success, it was customary to report one's findings by giving the numbers of nests and eggs in the sample, the number of eggs that hatch, number of young birds fledged and various derived percentages. Mayfield (1961) described this practice, without citing examples of it.

To illustrate, let us consider the data originally analyzed by Nichols et al. (1984). In a study area 59 nests of mourning doves (Zenaida macroura) are discovered by field workers, and then observed periodically until it is determined that 34 of them fail to produce nestlings, and 25 of them produce either 1 or 2 nestlings. (For pedagogical reasons we are ignoring the fact that this was a 2-year study.) The naive result that might be published

from this is that of all dove nests established in the wild, 25/59 or 42.4% will yield new birds, (std. error = 6.4%), in accordance with binomial distribution theory.

The first difficulty with this approach is a kind of sampling bias problem. We make use of a sample of discovered nests to make inference for a population of concealed nests, assuming the sample to be randomly selected from the population. But even when this method was practiced, field workers would find and take data from every nest they possibly could, simply because of the great difficulty of finding a satisfactory number of nests to report on.

Unhatched nests encountered in the wild will be of various unknown ages, 1, 2, ..., J days, where J is the incubation period for the species. Nests near J days of age have a higher probability of survival than nests near 1 day of age. Yet in the procedure just outlined, the average survival observed was taken to be the average survival of all nests initiated in the wild. All nests are initiated at age 1, not at some distribution of ages from 1 through J.

This sampling was not unknown or as unappreciated by field workers as our discussion might imply. Presumably, training and experience gained by field workers can help them become better able to find many nests in the first few days of incubation. This will result in samples that are more nearly representative of the population. Bias in the estimator can also be reduced in this case by consideration of the data. Once nest eggs hatch, the age of the nest becomes known; those nests not found early in the incubation period can be discarded from the analysis. If all eggs in a nest fail, the exact age

of the nest when first found remains unknown, but a well-trained field worker can estimate it fairly accurately anyway, so that failing nests too old when first found can also be eliminated from the analysis.

Some problems remain unsolved here. No matter how well trained the field worker, it is always difficult to find concealed nests at or near the time of initiation, limiting the amount of useful data available. Some nests will initiate and fail before they are ever found. And nests which produce no hatchling can be aged only approximately at best, lending uncertainty to the determination of data to omit from analysis. It is also possible to collect data which cannot even be used in the analysis, e.g., by finding new nests in the waning days of a field study and being unable to continue observing them long enough to determine whether they will hatch or fail.

3. THE MAYFIELD METHOD

Mayfield (1961, 1975) was apparently the first to consciously model nest survival in a sophisticated way and in a manner that could effectively remove some of the difficulties associated with the earlier practiced Naive estimation methods.

Mayfield's approach was to formulate the survival problem in terms of daily survival during the incubation period, in contrast to the Naive method of determining total survival only. He advocated that data should be used to ascertain the number of nest-days of "exposure" or risk. From this and the number of nest failures, a daily failure and daily survival rate can be determined, using the additional assumption that the daily survival rate is a

constant for all days in the incubation cycle. If the daily survival rate is P_{DAILY} , then the interval survival rate (corresponding to the Naive p) is P_{DAILY}^J , where J is the number of days in the incubation period.

A great advantage gained by Mayfield's method is the ability to make use of almost all the data collected in the field. Any viable nest that is observed on 2 different days can be included in the calculations. Another advantage is that there is less demand for inclusion of nests found near the beginning of the incubation cycle; all days in the cycle are equally valuable.

To illustrate the Mayfield method, let us again consider the dataset analyzed by Nichols et al. (1984). There were 59 nests, with 25 hatching and 34 failing, but now we will note that the hatching nests were observed to occur 11 after 1 to 8 days, 8 more after 9 to 16 days, and 6 after 17 or more days; while the failing nests failed 16 within the first 8 days, 9 within the next 8, and 9 within the final 10 of 26 days (some of these may be nestling deaths rather than all egg deaths). Thus the nests which hatched account for $11 \times 8 + 8 \times 16 + 6 \times 26 = 372$ nest-days, and the nests which failed account for $16 \times 8 \times 0.5 + 9 \times (8 + 8 \times 0.5) + 9 \times 10 \times (16 + 10 \times 0.5) = 361$ nest-days. In such a study, where nests are not observed every day, the exact day a nest failed would not be known, so Mayfield suggested that the midpoint between the observations be used, hence the "0.5" values given here. In fact the nests in this example were observed daily, so the number of nest-days is known exactly, without recourse to estimating that all successful nests hatched at the endpoints of 8 or 10 day intervals and that all failing nests failed at their midpoints; successful nests and failing nests

accounted for 386 and 324 nest-days, respectively. There were 34 failing nests in 710 nest-days of data, whence $q_{\text{DAILY}} = 34 / 710 = 0.04789$, $p_{\text{DAILY}} = 0.9521$ (std. error = 0.008014); $p = p_{\text{DAILY}}^{**} = 0.2792$ (std. error = 0.0610).

Mayfield (1975) argued the case that survival rate is unlikely to be constant from day to day, though he continued to advocate assuming this on the grounds that the usual nesting study failed to obtain sufficient data to make differing daily estimates, and the daily rate might not vary so seriously as to require differing rates. He did suggest attempting to determine different rates for hatching and fledging, and he proposed applying a Chi-Square test of the difference between these.

4. EXTENSIONS TO THE MAYFIELD METHOD

If nests are not observed on a daily basis, Mayfield proposed that nests found to fail be assumed to have failed in the center of the unobserved period. This actually is in defiance of the constant daily survival rate assumption: it is a linear rather than a geometric decrease.

Miller and Johnson (1978) gave apparently the first published critique of this assumption. They proposed that when days are skipped between nest visits and failure is subsequently observed, then not the mid-point, but the 40% point should be assigned as the day of failure.

Johnson (1979) compared the performance of the original Mayfield estimator (50%), his and Miller's "Mayfield-40%" method, and a third method in which the failure assignment is made by maximizing the likelihood of the Mayfield model. Johnson (1979) also first published variance estimates for the estimator, by deriving the estimator as a maximum likelihood estimate instead of a heuristic quantity, and then mathematically deriving its large

sample variance (from the maximum likelihood information matrix). He then compared the 3 interpolation methods on some datasets and concluded that the differences in results were not substantial, and therefore in many cases the original Mayfield method is acceptable and the easiest one to use; one of the other methods may be significantly better if the interval between nest visits is very long.

Using Mayfield's nesting model, Hensler and Nichols (1981) again showed that his proposed estimator is a maximum likelihood estimator. They calculated its asymptotic distribution and proposed an estimator of the asymptotic variance. From this they derived confidence intervals and tests of significance for daily survival. They performed extensive Monte Carlo simulation to determine the performance of the estimators and tests under many different sets of conditions. They showed the Naive estimator of nesting success to be quite inferior to the Mayfield estimator. They gave sample size requirements to achieve set levels of accuracy for their tests.

Bart and Robson (1982) did a thorough job of characterizing the sampling distribution of the Mayfield method(s), showing, for example, that its normality could be improved by means of a square root transformation. They obtained a sampling distribution close to that of Johnson. They also developed distributions of differences between 2 rates and products of 2 rates (say an early rate and a late rate are thought to be different and being tested, but the net over-all rate remains the focus of the researcher's interest ($p = PEARLY^J \times PLATE^* = PDAILY^J$)). Hensler (1985) proposed applying the Mayfield method "piecewise" to this type of problem and showed how to generalize the Mayfield estimation procedure for it.

Mayfield's implicit assumption that all nests have the same daily rate(s) of survival was challenged by Green (1977). The argument was essentially that density-dependent mortality rates are sometimes observed, and if so, they are a manifestation of heterogeneity; in particular, "novice" nesters are less successful than "experienced" nesters. Johnson (1979) presented a modification of the method to expose heterogeneity and adjust for it. The procedure employed was to age the nests and compute daily mortality rates by age of nest, compute a regression line through these data and accept the intercept of this line as the success rate, instead of the rate that comes from the standard Mayfield method with the pooled data. Based on some data, Johnson declared that Mayfield's method seems to be quite robust to heterogeneity.

An assumption acknowledged by Mayfield (1975) is that the sampling process does not perturb the success rates. Mayfield preferred a daily observation period, but noted that some observers believe that visiting a nest too frequently imparts greater mortality to it. His method does not require daily visits. Some field workers have adopted the custom of being in the field every day, but visiting a nest only, say, once a week so long as distant observation of the nest suggests it is still succeeding; if the distant observation casts doubt on successfulness of the nest they may make an unscheduled visit in order to document accurately the time of failure. If the act of visiting increases the probability of failure, this is certainly a biasing procedure. Bart and Robson (1982) also proposed extensions of the model for varying survival rates and for visitor-induced depression of survival, describing briefly the techniques required to develop them. They pointed

out that it is not necessary to visit nests daily, nor at any certain fixed interval. Visiting intervals may vary systematically or randomly. It is, however, necessary to avoid using the field worker's belief about the current fate of the nest to decide when to visit.

5. THE POLLOCK METHOD

Pollock (1984) and Pollock and Cornelius (in prep.) offered a new discrete survival model allowing estimation of the survival distribution from the time of nest initiation, a more natural time origin, rather than from time of first encounter as used by all the earlier models. They also abandoned the assumption that survival events (nest days) need have constant probability.

Pollock's method was the first to model nesting survival intentionally from the first day of the nest. This is done by using the observed age distribution of successful nests to infer the unobservable age distribution of failing nests. Survival probabilities can be conditioned on this distribution. (Earlier models could roughly accomplish the same result only if their failing nests were found on the first day with very high probability, and on later days with close to zero probability.) There is no constant probability assumption in this model because each day-or-event probability is estimated separately, without constraint, independently of the others.

Model Structure

This model uses a discrete distribution free approach. We denote the age at death or successful termination of the i th nest as T_i . This random variable can take on the integer values 1, 2, ..., J because J is the fixed known number of units of time for incubation and fledging.

Model Parameters

The model encompasses a set of nest failure probability parameters and a set of encounter probability parameters. The failure parameters are

$$q_1 = P(T = 1); q_2 = P(T = 2); \dots; q_J = P(T = J)$$

where q_j is the probability a nest is found failed at age j although it was successful to age $j-1$. The q_j 's are unconditional probabilities of failure, and therefore the probability of a nest succeeding is

$P = 1 - q_1 - q_2 - \dots - q_J$. There are J distinct failure parameters in the model. The age units could be days, two days, weeks or whatever is most appropriate. In fact, it is not even necessary that the age intervals be equal.

The encounter parameters are a set of J nuisance parameters

$\delta_1, \delta_2, \dots, \delta_J$ where δ_j is the probability of an intact nest being first encountered at age j (similar to $\theta_1, \theta_2, \dots, \theta_J$ of Hensler and Nichols (1981)).

A critical assumption of the Pollock model is that these encounter probabilities are independent of the survival probabilities given above. In other words, nests encountered early or late in the cycle are not more or less likely to survive future time units.

Data Available

Application of the Pollock model entails tabulating the number of successful nests first encountered at each possible age, and the number of nests that fail after they are first observed. Successful nests are denoted

$n_{1H}, n_{2H}, \dots, n_{jH}$, where

n_{jH} is the number of nests found of age j which later succeed, and

$n_H = \sum_{j=1}^J n_{jH}$ is the total number of successful nests encountered.

Failed nests are denoted

$n_{1F}, n_{2F}, \dots, n_{jF}$, where

n_{jF} is the number of nests of unknown age which are observed for j units of time and then fail.

$n_F = \sum_{j=1}^J n_{jF}$ is the total number of unsuccessful nests encountered.

Pollock and Cornelius (in prep.) analyzed the likelihood as the product of three conditional multinomial distributions

(i) $P(n_{1H}, n_{2H}, \dots, n_{jH} | n_H)$ the conditional distribution of the numbers of successful nests of each age at encounter (n_{jH} $j = 1, 2, \dots, J$) given the total number of successful nests (n_H);

(ii) $P(n_{1F}, n_{2F}, \dots, n_{jF} | n_F)$ the conditional distribution of the numbers of nests of unknown age which fail after i units of time (n_{jF} $j = 1, 2, \dots, J$) given the total number of nests which fail (n_F);
and

(iii) $P(n_H | n_H + n_F)$ the conditional distribution of the number of successful nests encountered at any time (n_H) given the total number of nests encountered ($n_H + n_F$).

The encounter parameters are estimated by maximizing the likelihood of

(i). The resulting estimators are

$$\hat{\delta}_1 = n_{1H}/n_H, \hat{\delta}_2 = n_{2H}/n_H, \dots, \hat{\delta}_J = n_{jH}/n_H.$$

They are simply the proportions of nests found first in the indicated intervals. Failure parameters are estimated by maximizing the likelihood of (ii) and (iii) and substituting the $\hat{\delta}_j$ estimates found from (i) for the δ_j factors here. These equations are

$$\left\{ \begin{array}{l} (\hat{\delta}_1 \hat{q}_1 + \hat{\delta}_2 \hat{q}_2 + \dots + \hat{\delta}_J \hat{q}_J) / D = n_{1F} / n_F \\ (\hat{\delta}_1 \hat{q}_2 + \hat{\delta}_2 \hat{q}_3 + \dots + \hat{\delta}_{J-1} \hat{q}_J) / D = n_{2F} / n_F \\ \vdots \\ \hat{\delta}_1 \hat{q}_J / D = n_{JF} / n_F \end{array} \right.$$

and $(1 - \sum_{j=1}^J \hat{q}_j) / [(1 - \sum_{j=1}^J \hat{q}_j) + D] = n_H / (n_H + n_F)$

where $D = \hat{\delta}_1 \hat{q}_1 + (\hat{\delta}_1 + \hat{\delta}_2) \hat{q}_2 + \dots + (\hat{\delta}_1 + \hat{\delta}_2 + \dots + \hat{\delta}_J) \hat{q}_J$.

Of these $J + 1$ linear equations only J are independent. Any 1 of the 1st J equations may be eliminated and the rest simultaneously solved for $\hat{q}_1, \hat{q}_2, \dots, \hat{q}_J$.

Example

The following analysis is of mourning dove (Zenaida macroura) nest data recorded in 1979 and 1980 at Patuxent Wildlife Research Station, Laurel, Maryland by James D. Nichols. These data have also been analyzed by Nichols et al (1984) and Hensler (1985) and were used to illustrate the Naive and Mayfield approaches earlier.

Field workers located 59 ($n = n_H + n_F$) nests containing 1 or 2 eggs each; 34 (n_F) of the nests failed to produce fledglings, 16 (n_{1F}) of those within 8 days of discovery, 9 (n_{2F}) within 9 to 16 days after discovery, and 9 (n_{3F}) after the 16th day. The remaining 25 (n_H) nests did produce nestlings, and

of these, 11 (n_{1H}) were nests first found no more than 8 days after the eggs were laid, 8 (n_{2H}) were found when eggs were 9 to 16 days old, and the remaining 6 (n_{3H}) were found in the nesting stage (at least 17 days old).

The Pollock Model Estimates

Encounter probability estimates for this example are

$$\hat{\delta}_1 = n_{1H}/n_H = 11/25 = 0.44 \text{ (s.e. = 0.0993)}$$

$$\hat{\delta}_2 = n_{2H}/n_H = 8/25 = 0.32 \text{ (s.e. = 0.0938)}$$

$$\hat{\delta}_3 = n_{3H}/n_H = 6/25 = 0.24 \text{ (s.e. = 0.0854)}$$

Associated failure probabilities are

$$\hat{q}_1 = 0.29 \text{ (s.e. = 0.1382)}$$

$$\hat{q}_2 = 0.08 \text{ (s.e. = 0.1442)}$$

$$\hat{q}_3 = 0.28 \text{ (s.e. = 0.1104)}$$

The asymptotic variance-covariance matrix of the \hat{g} and \hat{q} vectors is given in Table 1. Notice that while the standard errors are large, there is some evidence that the failure probabilities are not constant over the nesting period. In the first 8 days of incubation the failure probability is high ($\hat{q}_1 = 0.29$). This might be attributed to predators finding it easy to locate nests and nests of inexperienced breeders being abandoned. In the second 8 days of incubation the failure probability is much lower ($\hat{q}_2 = 0.08$). In the 10 days of nestlings the failure probability appears to rise again ($\hat{q}_3 = 0.28$). This might be attributed to predators being attracted to the nests by the parents feeding the nestlings.

Program SURVIV (White 1983) is useful for this estimation problem, if input specifications are properly made, and especially if the parameter J is small. The 3 likelihood component systems of equations are expressed for SURVIV as 3 "cohorts" in the PROC MODEL specification of program SURVIV.

For our example, the input to SURVIV should appear as in Figure 1.

(Only $2J - 1$ equations need to be specified, because the COHORT cell probabilities always sum to 1, and SURVIV by default creates an additional cell in each cohort whose probability is assigned the difference between 1 and the sum of the other, explicit cell probabilities. This means that one of the J equations in each of the last 2 COHORTs can be dropped from the specification. We omitted the equation defining δ_3 ; we introduced it once in the 2nd COHORT as the expression $1 - \delta_1 - \delta_2$.)

The probability of a nest succeeding is given by $\hat{p} = 1 - \hat{q}_1 - \hat{q}_2 - \hat{q}_3 = 0.35$ with a standard error of 0.0660. This estimate is much more precise than the individual q estimates because of the negative covariances between the \hat{q}_i 's (Table 1).

The flexibility of Program SURVIV is extremely useful. In Figure 2, this second set of code demonstrates imposition of a constant survivorship assumption ($q_1 = q$, $q_2 = (1-q)q$, $q_3 = (1-q)(1-q)q$). The result obtained is that the constant (conditional) probability of failure at each stage is 0.29 with standard error 0.0428. The probability of a nest succeeding is given by $\hat{p} = (1-\hat{q})^3 = 0.35$ with a standard error of 0.0642. A likelihood ratio test of the reduced versus the full model is easily obtained ($\chi^2_2 = 2.8$) and is not significant (p value = 0.25).

Another computer program to solve this estimation problem, NESTING, is available from the authors. Our program can handle larger failure vectors than SURVIV. NESTING solves the likelihood equations explicitly for point estimates and uses simulation for variance estimates, while SURVIV uses a quasi-Newton numerical optimization algorithm (Kennedy and Gentle 1980, pp. 451-460) to obtain all estimates.

Model Assumptions

The first assumption of the Pollock model is that the nests observed constitute a random sample with respect to survival. This same assumption is required of all sampling procedures to estimate survival rates (radio-tagging method, capture-recapture method). If the nests which are easier to find also have higher predation rates it could be violated.

There is no seasonal component in this model. All nests are treated as a cohort from time of initiation. If the sample were large enough one could stratify the sample into early, medium and late nests and compare the survival distributions. Another possibility is to treat calendar time as a covariate and build a relationship directly into the model. This needs further investigation.

This model requires the assumption that visiting the nest does not influence its survival. Bart and Robson (1982) state that, "In some cases, visiting the subject may temporarily depress its chance of survival. — observers may lead predators to the nest or cause nest abandonment". They present an extension of the Mayfield type model to allow a temporary visitor induced increase in mortality just after the visit. Bart and Robson (1982)

also emphasized the importance of a regular schedule of visits (daily, weekly). Sometimes biologists are tempted to change the schedule if they think a nest is just about to fail.

The model assumptions mentioned above are also required by the traditional Mayfield Method. In addition the Mayfield Method requires the assumption of constant survival per time unit; however in some cases the Mayfield is applied separately to segments of the nesting period to weaken this assumption.

A very critical assumption to this model is that encounter probabilities are not related to the subsequent success of nests. For example, nests encountered close to the beginning of the nesting cycle may happen to be highly visible and accordingly more likely to suffer predation than older nests. This assumption will need to be investigated in more detail using simulation.

6. A COMPARISON OF THE MODELS

Mourning Dove Example

In Table 2 we compare the probability of nest success estimates and their standard errors for the Naive Model (n_H/n), the Pollock Full Model, the Pollock Constant Survival Model, the Mayfield Model and the Mayfield Model calculated for each period separately as we have applied them to the Nichols et al. (1984) data. Both Mayfield estimates are calculated on a daily basis. We find the results on precision somewhat surprising. Intuition suggests that the more parameters that must be estimated, the poorer the precision that will result; Pollock estimates should be rather imprecise. But the realized precisions of both Pollock estimates are almost identical to the Mayfield estimate and are superior to the piecewise Mayfield estimate.

Although the Pollock model estimates more parameter values, it makes use of more information than the Mayfield Model. The Pollock estimates are about midway between the Naive estimate (0.42), which is known to be positively biased, and the Mayfield estimate (0.28). If the standard errors are considered, neither Pollock estimate is significantly different from either Mayfield estimate.

Great-Tailed Grackle Example

We now compare the models using some Great-Tailed Grackle (Quiscalus mexicanus) data collected by Scott Winterstein near Los Cruces, New Mexico in the spring of 1979. Nests were only observed for the incubation period of 14 days ($J = 14$) so that nest success here was defined as having one or more eggs in a nest survive from laying to hatching.

There were 29 nests observed for a total of 281 days and there were 6 nest failures so that there were 275 successful nest days. This means the naive estimate of nest success is $23/29 = 0.79$ ($SE = 0.0752$). The Mayfield daily estimate of nest survival is $275/281 = 0.978648$ which translates into a 0.74 probability of nest success (0.978648^{14}) with standard error of 0.0912.

First we fitted the Pollock model with two periods of 7 days each and obtained failure probabilities of $\hat{q}_1 = 0.2052$ ($SE = 0.0885$) and $\hat{q}_2 = 0.0442$ ($SE = 0.0439$). \hat{q}_1 and \hat{q}_2 are negatively correlated and the difference $\hat{q}_1 - \hat{q}_2 = 0.1610$ has standard error = 0.1082 which is almost significant ($p = 0.07$). For this data and the Mourning Dove data there is evidence of the failure probability dropping from early to late in the incubation period. We calculated the probability of nest success and found it to be 0.75 ($SE = 0.0882$). We also fitted a two-period constant survival model

and compared it to the above model with a likelihood ratio test. We found the likelihood ratio test was significant ($\chi_1^2 = 13.6$; $p < 0.001$) indicating strong evidence against the constant survival model.

We also fitted the Pollock model with three periods of 5 days 5 days and 4 days. We obtained $\hat{q}_1 = 0.1121$ (SE = 0.0739), $\hat{q}_2 = 0.0817$ (SE = 0.0620) and $\hat{q}_3 = 0.0448$ (SE = 0.0445). Again there appears to be a decline in the failure rates over time but it is not significant. The overall probability of nest success was given by 0.76 (SE = 0.0843). We also fitted a three-period constant survival model and in this case it could not be rejected using the likelihood ratio test. The overall probability of nest success was 0.76 (SE = 0.0834).

In Table 3 we present the overall probabilities of nest success for several models for ease of comparison. Notice that again all of the Pollock model estimates have similar precision to the Mayfield estimate. Notice also that the Naive estimate which we know to be positively biased is higher than all the other estimates but not by very much. The Naive estimate also has similar precision to the other estimates although it is a little bit better (smaller standard error).

7. DISCUSSION

In this paper we have compared the Naive and Mayfield methods with a new method developed by Pollock (Pollock 1984, Pollock and Cornelius in prep.). This method enables the biologist to look at periods of high or low survival during the whole nesting period. Computer programs are available to calculate the estimates. Program SURVIV is very useful for computing

estimates and for comparing models with different numbers of parameters. For example, we compared the full model with a constant survival model.

We believe that our model is a serious competitor to the Mayfield Model. In both examples precision of the estimate of overall probability of nest success is very similar. Further comparisons between the two approaches need to be done using simulation. While the Mayfield approach has the advantage of simplicity and calculation on a hand calculator, our approach has the advantage of using more of the information in the data. In this age of computers computation ease should not be a major consideration. Computer costs will still be much smaller than the costs of collecting the field data.

In our Great-Tailed Grackle example a sample of 29 nests gave a proportional standard error of about 12% for the overall probability of nest success using the Pollock model. In the Mourning Dove example the corresponding proportional standard error based on 59 nests was about 20% which is reasonable for a field study. However, we acknowledge that the individual failure probability estimates were less precise with proportional standard errors up to about one-hundred percent. Further investigation of sample size requirements is necessary.

In this paper we have only considered the probability of nest success. The question of looking at individual egg survival was not considered. One possibility would be to consider the models presented here but using the egg (rather than the nest) as the sampling unit. The problem with this approach would be that the fate of eggs in the same nest are not independent. Often all of the eggs will fail at the same instant. This means any standard errors

calculated will appear smaller than they truly are. A suggestion made by James D. Nichols is to calculate nest success probabilities and also to calculate the number of young fledged per successful nest. Another problem with considering individual eggs is that often the biologist may not know when they fail unless the whole nest is destroyed. The biologist may not want to flush the incubating bird just to count remaining eggs.

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LITERATURE CITED

- Bart, J. and Robson, D. S. (1982). Estimating survivorship when the subjects are visited periodically. Ecology 63, 1078-1090.
- Green, R. H. (1977). Do more birds produce fewer young? A comment on Mayfield's measure of nest success. Wilson Bulletin 89:173-175.
- Hensler, G. L. (1985). Estimation and comparison of functions of daily nest survival probabilities using the Mayfield Method. Statistics in Ornithology, B. J. T. Morgan and P. M. North, eds. Springer-Verlag, pp. 289-301.
- Hensler, G. L. and Nichols, J. S. (1981). The Mayfield method of estimating nesting success: a model, estimators and simulation results. Wilson Bulletin 93, 42-53.
- Johnson, D. H. (1979). Estimating nest success: the Mayfield method and an alternative. Auk 96, 651-661.
- Mayfield, H. (1961). Nesting success calculated from exposure. Wilson Bulletin 73, 255-261.

- Mayfield, H. (1975). Suggestions for calculating nest success. Wilson Bulletin 87, 456-466.
- Miller, H. W. and Johnson, D. H. (1978). Interpreting the results of nesting studies. J. Wildl. Manage. 42, 471-476.
- Nichols, J. D., Percival, H. F., Coon, R. A., Conroy, M. J., Hensler, G. L., and Hines, J. E. (1984). Observer visitation frequency and success of mourning dove nests: a field experiment. Auk 101, 398-402.
- Pollock, K. H. (1984). Estimation of survival distributions in ecology. Proceedings of 12th International Biometrics Conference. Tokyo, Japan.
- White, G. C. (1983). Numerical estimation of survival rates from band-recovery and biotelemetry data. J. Wildl. Manage. 47, 716-728.

Table 1. Variance-Covariance Matrix for $(\hat{\delta}_1, \hat{\delta}_2, \hat{\delta}_3, \hat{q}_1, \hat{q}_2, \hat{q}_3)$
for the Mourning Dove example.

.009856	-.005632	-.004224	-.002967	0.006819	-.005225
-.005632	.008704	-.003072	.006363	-.007553	.002531
-.004224	-.003072	.007296	-.003397	.007346	.002694
-.002967	.006363	-.003397	.019093	-.012361	-.001795
.006819	-.007553	.007346	-.012361	.020808	-.009715
-.005225	.002531	.002694	-.001795	-.009715	.012193

Table 2. Comparison of estimates of nest success probability
and their standard errors for the Mourning Dove example.

<u>Model</u>	<u>Probability of Success</u>	<u>Standard Error</u>
Naive	0.42	0.0643
Pollock Full Model	0.35	0.0660
Pollock Constant Survival	0.35	0.0642
Mayfield	0.28	0.0610
Mayfield Piecewise	0.29	0.0962

Table 3. Comparison of estimates of nest success probability and their standard errors for the Great-Tailed Grackle example.

<u>Model</u>	<u>Probability of Success</u>	<u>Standard Error</u>
Naive	0.79	0.0752
Mayfield	0.74	0.0912
Pollock Two Period	0.75	0.0882
Pollock Three Period	0.76	0.0848
Pollock Three Period Constant Survival	0.76	0.0834

FIGURE 1. Input specification for Nesting survival example analysis by SURVIV (White 1983). Full Pollock Model.

PROC TITLE NESTING SURVIVAL (pooled data example). (PC:nestex.gcw);

PROC MODEL npar=5;

```
COHORT = 25                                /* total successful nests */;
  11: s(1)                                  /* seen period 1 */;
  8: s(2)                                  /* seen period 2 */;
COHORT = 34                                /* failed nests */;
  16: (s(1)*s(3)+s(2)*s(4)+(1-s(1)-s(2))*s(5))
      /(s(1)*s(3)+(s(1)+s(2))*s(4)+s(5))
      /* fail after 1 pd */;
  9: (s(1)*s(4) + s(2)*s(5))
      /(s(1)*s(3)+(s(1)+s(2))*s(4)+s(5))
      /* fail after 2 pd */;
COHORT = 59                                /* total nests */;
  25: (1 - s(3)-s(4)-s(5))
      / (1 - s(3)-s(4) + s(1)*s(3) + (s(1)+s(2))*s(4))
      /* total successful nests */;
```

LABELS;

```
s(1) = first encounter in period 1 [delta (1)];
s(2) = first encounter in period 2 [delta (2)];
s(3) = prob failure at age 1 [q(1)];
s(4) = prob failure at age 2 [q(2)];
s(5) = prob failure at age 3 [q(3)];
```

FIGURE 2. Input specification for nesting survival example by SURVIV (White 1983). Constant survival model.

```
PROC TITLE NESTING SURVIVAL (pooled data example). (PC:nestex1.gcw);

PROC MODEL npar=3;

  COHORT = 25          /* total successful nests */;
    11: s(1)           /* seen period 1 */;
    8: s(2)            /* seen period 2 */;

  COHORT = 34          /* fail nests */;
    16: s(1)*s(3)+s(2)*s(3)*(1.-s(3))+(1.-s(1)-s(2))*s(3)*(1.-s(3))
      *(1.-s(3)) / (s(1)*s(3)+(s(1)+s(2))*
      s(3)*(1.-s(3))+s(3)*(1.-s(3)) *(1.-s(3))) /* fail after 1 pd */;
    9: (s(1)*s(3)*(1.-s(3)) + s(2)*s(3)*(1.-s(3))*(1.-s(3))) / (s(1)
      *s(3)+(s(1)+s(2))*s(3)*(1.-s(3))+s(3)
      *(1.-s(3))*(1.-s(3))) /* fail after 2 pd */;

  COHORT = 59          /* total nests */;
    25: (1 -s(3)-s(3)*(1.-s(3))-s(3)*(1.-s(3))*(1.-s(3))) /
      (1 - s(3)-s(3)*(1.-s(3)) + s(1)*s(3) +
      (s(1)+s(2))*s(3) *(1.-s(3)) ) /*total successful nests */;

LABELS;
  s(1) = first encounter in period 1 [delta (1)];
  s(2) = first encounter in period 2 [delta (2)];
  s(3) = constant prob failure;
```