UNCERTAIN NEST FATES IN SONGBIRD STUDIES AND VARIATION IN MAYFIELD ESTIMATION

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ABSTRACT.—Determining whether nesting attempts are successful can be difficult. Yet, current protocols for estimating nesting success do not address how uncertain nest fates should be handled. We examined the problem of nest-fate uncertainty as it relates to Mayfield estimation of nesting success and in analyses of factors that influence success. We used data from Minnesota to illustrate the potential effect of uncertain fate; 40% of Ovenbird (Seiurus aurocapillus; n = 127) nests and 30% of Least Flycatcher (Empidonax minimus; n = 144) nests had uncertain fates. How this uncertainty is incorporated into Mayfield estimates of success varied widely among researchers. In a survey of researchers who use the Mayfield method, 9 of 22 respondents (of 40 contacted) excluded nests with uncertain fate. Excluding uncertain fates is counter to how Mayfield first described his estimator and can result in severe downward bias. The remaining respondents (59%) included nests with uncertain fate but varied in how they terminated the exposure period. We developed a simulation model that calculated Mayfield estimates using different approaches and compared them with a known rate of nesting success. Magnitude of bias in Mayfield estimates varied considerably in our simulations. The approach with the least bias terminated exposure with the last observed active date for nests with uncertain fate, and with the midpoint between last observed active and first observed inactive dates for nests with known fate. In addition, information necessary to interpret and compare Mayfield estimates often is not reported. These values, including variance estimates and the period lengths used to estimate survival rates, should be reported with Mayfield estimates. Finally, nest fate is commonly used as a categorical variable in studies of factors affecting nesting success. In this approach, however, nests with uncertain fate must be excluded. An alternative approach is Cox regression, which incorporates nests with uncertain fate. Received 22 October 1998, accepted 23 November 1999.

RECENT CONCERN over declines of Neotropical migratory bird populations has stimulated a sharp increase in studies of nesting success. Information on nesting success is critical for predicting declines in avian populations, understanding causes of declines, and developing management strategies to curb or prevent them (Martin 1992, Martin and Geupel 1993). To understand factors influencing nesting success, comparisons of success estimates across habitat gradients, landscape features, and geographic ranges are necessary. Such comparisons require standardized monitoring and analysis protocols. Martin and Geupel (1993), Ralph et al. (1993), and Martin et al. (1997) provide guidelines for such standardization. Despite these efforts, however, several issues remain

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unresolved and are handled inconsistently among researchers.

First, researchers vary in how they incorporate data from nests with uncertain fate in Mayfield estimation (Mayfield 1961), and how nests with uncertain fate are handled can bias Mayfield success estimates. Second, researchers vary in how they terminate the exposure period used in Mayfield estimation, and choice of termination method can influence estimates of nesting success. These issues are especially problematic when comparing results across studies, and they have not been adequately addressed in the literature. For example, recent attention has focused on identifying source and sink populations of passerines (Donovan et al. 1995, Robinson et al. 1995) by using Mayfield estimates in demographic models. These models are sensitive to slight changes in nesting-success rates, so even a slight bias in Mayfield estimation can lead to errors in source or sink assessments. Finally, although nests with un-

TABLE 1.   Fate evidence criteria. Fates for nests meeting one or more of these criteria were considered known; fates for nests not meeting any of these criteria were considered uncertain.

Evidence for fledging	Evidence for failure
1. Fledglings seen or heard outside of nest.	1. Nest damaged and inactive.
2. Chicks bulging out of nest or stretching wings at last visit.	2. Broken eggs, dead chicks, or scattered feathers.
3. Feather development indicates chicks are ready to fledge at last active visit.	3. Contents of nest gone during egg laying, incubation, or early nestling stages, before fledging is possible.
4. Rim of nest flattened and/or feces on rim and outside nest at first inactive visit.	

certain fate can be used in Mayfield estimation, they must be excluded in some analyses that evaluate factors affecting nesting success (hereafter, "causal analyses"). For example, to examine factors affecting nesting success, Hanski et al. (1996) used nest fate as a dependent variable in logistic regression models. Nests with uncertain fates must be excluded from such models, and classification of ambiguous nest fates can be quite subjective. Solutions to this problem have not been discussed in the literature, and the distinction between nesting-success estimation and causal analysis has not been clear. The goal of causal analysis is distinct from nesting-success estimation, and uncertain nest fates can have different effects on the two types of analyses.

To address these issues, we (1) identify approaches to nest-fate uncertainty and exposure-period termination currently in use for Mayfield estimation, (2) use simulated data and real data to compare methods, (3) suggest which methods are the most appropriate for estimating nesting success, and (4) distinguish nesting-success estimation from causal analysis and identify appropriate causal-analysis methods that can incorporate nests with uncertain fates.

Nest fate can be difficult to determine. Researchers commonly visit passerine nests at intervals of three to four days (Martin and Geupel 1993), and if the expected fledging time occurs during the last interval between visits, evidence indicating success or failure can be ambiguous. Data that we collected in Minnesota revealed that 40% of Ovenbird (*Seiurus aurocapillus*) nests and 30% of Least Flycatcher (*Empidonax minimus*) nests had uncertain fates (as determined by criteria in Table 1). Nest fate may be relatively easy to determine for some species, but determining nest fate is more dif-

ficult than generally acknowledged. Current protocols do not specify how to handle uncertain nest fates in nesting-success estimation (i.e. Martin and Geupel 1993, Ralph et al. 1993, Martin et al. 1997). These protocols suggest that accurate classification of nest fate is important, but this is misleading because final nest fates do not need to be known when using the Mayfield estimator of nesting success (Mayfield 1961). Excluding nests that have uncertain fate is a common practice, but it causes downward bias in the Mayfield estimator (see below).

Overview of the Mayfield estimator.—Mayfield developed his estimator to correct for the upward bias commonly found with the apparent estimator (successful nests/total nests). This upward bias occurs because successful nests are more likely to be found than nests that fail early in the nesting cycle (Mayfield 1961, Johnson 1979, Hensler and Nichols 1981). The Mayfield estimator minimizes this bias by basing overall survival estimates on the daily survival estimate, which incorporates the amount of time that nests are observed. The daily survival estimate (p) is calculated by:

$$p = 1 - (L/E), \qquad (1)$$

where L is the number of losses occurring in the sample during the time the nests were observed and E is the total number of observation days (exposure days) for all nests in the sample. The daily survival estimate extends to the period survival probability for egg laying, incubation, brood rearing (i.e. nestling period), or all of them combined by $S = p^j$, where j is the average period length for the species in days. For example, the nestling survival rate for a species with a 12-day nestling period is p^{12}. Because daily survival can vary across nesting stages, separate Mayfield estimates are often

calculated for each stage (egg laying, incuba-
tion, brood rearing) and multiplied together to
derive the overall estimate of nesting success
(Mayfield 1961, Johnson 1979).

Uncertain fates in the formula.—It is not im-
mediately apparent how uncertain nest fates
should be handled in the above formula. One
might assume that the number of losses (*L*)
should equal the total number of nests minus
the successful (i.e. at least one young raised to
"fledging") nests. If this is the case, there is no
room for uncertain nest fates, and all data from
nests with uncertain nest fates must be exclud-
ed. However, on careful reading of Mayfield
(1961), one finds that his "*L*" did not equal total
nests minus successful nests. Rather, it repre-
sented known losses, and he did not worry
about determining whether nests actually
fledged young. He was somewhat cryptic on
the issue but had many uncertain nest fates in
his samples from Kirtland's Warblers (*Dendroi-
ca kirtlandii*). Of the 154 Kirtland's Warbler
nests Mayfield (1960:258) observed during the
incubation stage, 41 had unknown fates. Ex-
posure days from these nests formed a large
proportion of his sample. If Mayfield had ex-
cluded nests with uncertain fate, his survival
estimate for the incubation period would have
dropped from $(1 - (35/878))^{14} = 0.56$ to $(1 -
(35/645))^{14} = 0.45$, assuming an average expo-
sure period per nest of 5.7 days.

Current inconsistency in Mayfield estimation.—
At a number of meetings where nesting-suc-
cess methodology was discussed, we observed
that some researchers excluded nests with un-
certain fate from their Mayfield calculations.
They also varied in how they terminated the ex-
posure period, thus leading to variation in the
number of exposure days used. To assess the
extent of this problem, we sent a survey to 40
researchers who use the Mayfield estimator. We
assembled the list of researchers by using an e-
mail list maintained by the USGS Breeding Bi-
ology Research and Monitoring Database
(BBIRD) program and by scanning recent pub-
lished articles that used the Mayfield estimator.
The sample was not exhaustive or random; we
merely used it to document and illustrate po-
tential variation among researchers. The results
were revealing. A large proportion of respon-
dents excluded nests with uncertain fate (9 of
22 respondents), others included them, and
both groups varied in how they terminated the

exposure period. In fact, the 22 respondents
used 9 different approaches to deal with the
combined problems of exposure termination
and nest-fate uncertainty (Table 2). Our sam-
pling method was not rigorous, but the varia-
tion among researchers was disconcerting giv-
en the current interest in comparing rates of
nesting success spatially. Clearly, an evaluation
of this issue is warranted.

To evaluate the extent of the problem, the ap-
proaches in Table 2 must be clearly distin-
guished and terms must be clarified. *Fate* is the
outcome of a nesting attempt (fail or produce
young), which is distinguished from *interval
status* (whether an attempt failed or was viable
at the end of an observation interval). An *obser-
vation interval* is the time between two nest vis-
its. Nest-fate uncertainty may arise at any time
during the nesting cycle. One type of fate un-
certainty, which was addressed by Mayfield
(1961, 1975), occurs when the researcher must
terminate observation before a nest fails or
fledges young. Another type of uncertainty
was not addressed by Mayfield (1961, 1975)
and occurs only with nests that survive to the
potential fledging interval (interval when fledg-
ing is possible; Fig. 1), and evidence is insuffi-
cient to determine fate. We restrict our discus-
sion to the latter type of fate uncertainty.

Survey respondents varied in their approach
to nest-fate uncertainty and exposure-period
termination and in exposure-period termina-
tion approaches within the Methods (Table 2).
In the "Exclusion" method, all exposure days
from nests with uncertain fate were excluded
from analysis. Subgroups within the Exclusion
method differed in exposure-period termina-
tion methods. Exclusion-A terminated expo-
sure at the midpoint between the last two visits
for both failed and successful nests ("Mid-
point" approach; Fig. 1). For failed nests, this
approach is well supported in the literature
(Miller and Johnson 1978, Johnson 1979), and
not surprisingly most survey respondents used
it for failed nests. However, for successful nests
or nests with uncertain fate, the literature is not
clear about how exposure should be terminat-
ed. Survey respondents varied in how they ter-
minated exposure for successful and uncertain
nests. Respondents using Exclusion-B termi-
nated the exposure period at an assumed fledg-
ing date for successful nests, extrapolated from

TABLE 2. Variation in approaches to Mayfield estimation based on a survey of 40 researchers (22 respondents) who use the Mayfield estimate of nesting success. Additional approaches identified through discussions with researchers.

Sub-group	Exposure-period termination method			% of respondents
	Failed nests	Successful nests	Fate uncertain	
		Exclusion[a]		
A	Midpoint	Midpoint	—	27
B	Midpoint	Extrapolation	—	14
		Early termination[b]		
A	Midpoint[c]	Early termination	Early termination	5
B		Whole interval (maximum likelihood)		5
		Last active[d]		
A	Midpoint	Last active	Last active	19
B	Midpoint	Midpoint	Last active	9
C	Midpoint	Extrapolation	Last active	5
		Midpoint[e]		
A	Midpoint	Midpoint	Midpoint	14
B	Midpoint	Extrapolation	Midpoint	5
		Decision rule[f]		
—	Midpoint	Midpoint	—	—

[a] All exposure days excluded for nests with uncertain fates.

[b] Last visit set to occur on an "early termination date" before potential fledging interval begins. Nest may be monitored after this date for other purposes, but exposure days after this interval are not used for Mayfield estimation.

[c] If nest fails before early termination date, midpoint method is used, otherwise early termination date is used as ending point.

[d] Last observed active date is used as termination point for nests within uncertain fate. Exposure days may extend into the potential fledging interval.

[e] Midpoint method is used to terminate exposure days for nests with uncertain fate. Exposure days previous to midpoint of last observation interval are included in analysis.

[f] Decision rule used to determine fate based on how long the nest was active. No nests are considered uncertain.

an earlier known transition date in the nesting cycle ("Extrapolation" approach).

The "Early Termination" method avoided nest-fate uncertainty that occurred during the potential fledging interval by terminating the exposure period before fledging was possible (scenario 4 in Fig. 1). Although fate could be determined for other purposes, exposure days beyond the early termination date were not used for Mayfield estimation. For nests that failed before onset of the potential fledging interval, Early Termination-A terminated exposure with the Midpoint approach. Early Termination-B did not use the Midpoint or other termination method between intervals. Instead, all exposure days were used from each observation interval that had known status (failed or alive), and daily survival was estimated with the maximum-likelihood approach described by Johnson (1979). Researchers who used the Early Termination method excluded the entire potential fledging interval (even if fate was known) because they believed that determining fate was too difficult and subjective. Further,

the probability of fate uncertainty may differ between nests that actually produce young versus those that fail, leading to bias. Excluding the entire potential fledging interval eliminates this potential bias (J. Nichols pers. comm.).

The "Last Active" method terminated exposure for nests with uncertain fate on the last day nests were observed to be active. The last active day could occur after the potential fledging interval began (scenarios 2 and 3 in Fig. 1). Users of this method assumed that nest fates could be determined accurately for some nests, and they did not worry about potential bias that could arise if nest fates were uncertain more often for failed versus successful nests (or vice versa). Last Active subgroups A, B, and C varied in the termination points used for successful nests.

The "Midpoint" method included exposure days from nests with uncertain fate and used the Midpoint approach to terminate the exposure period for uncertain nests. Midpoint subgroups A and B varied in the termination method used for successful nests. The "Decision
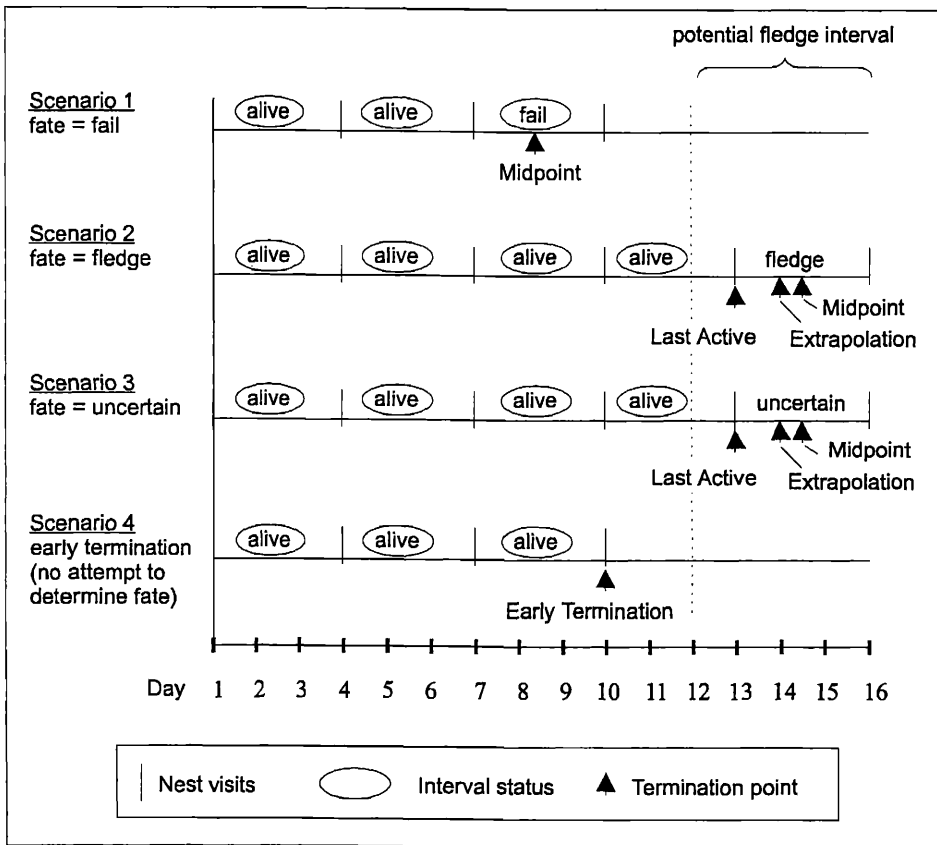
FIG. 1. Exposure-period termination methods used for estimation of nesting success based on a survey of 22 researchers who use the Mayfield estimate. Scenarios depict exposure termination points for nests that fail, fledge young, or have uncertain fates, assuming nests were found on day 1 and predicted fledging date was day 14. *Fate* is the final outcome of a nesting attempt. The *potential fledging interval* is the time period in which fledging can occur, based on knowledge of nesting-cycle length. *Interval status* is the status (alive or failed) at the end of an observation interval. The *Midpoint* approach terminates the exposure period at the midpoint between the date the nest was last observed active and the date the nest was first observed inactive. The *Last Active* approach terminates the exposure period at the date the nest was last observed active. The *Extrapolation* approach terminates the exposure period at a predicted fledging date, extrapolated from an earlier known transition date. The *Early Termination* approach terminates the exposure period before the potential fledging interval begins.

Rule" method assumed that fate needs to be known, but used a decision rule, based on how long young were observed in the nest, to determine fate. Although survey respondents did not mention using decision rules, one protocol suggested their use (Martin et al. 1997).

METHODS

To date, many of the approaches to Mayfield estimation described in Table 2 have not been identified or evaluated in the literature. To evaluate these methods, we developed a model that simulated nesting-

success data with known properties. Each simulation run determined survival length and fate for 100 nests. Nests could survive up to a maximum of 22 days, and exposure began on the same day for all nests (as if they were found on the same day). Daily mortality probability was set separately for each of the possible 22 days, using the RANBIN function in SAS (SAS 1990). This function generated random variates (0 or 1 for success or failure) from a binomial distribution with a mean that we specified. In one scenario, we set the mean daily mortality rate (DMR) at 0.04 for each of the 22 days to simulate a constant DMR (constant DMR scenario). In another scenario,

we set the mean daily mortality rate to 0.04 for the first 16 days and 0.10 for days 17 to 22, allowing evaluation of Mayfield approaches when daily mortality was not constant (nonconstant DMR scenario). Constant DMR is a key assumption of the Mayfield estimator, and it is well known that violations of the assumption will produce biased estimates (Klett and Johnson 1982). We wished to examine whether this source of bias, particularly resulting from a change in DMR during the potential fledging interval, could be minimized by any of the approaches to Mayfield estimation in Table 2.

The model allowed identification of exact failure day. Nests were "checked" every four days for the first 16 days. Because the length of the nesting cycle varies in nature, we selected potential fledging dates between days 18 and 22 using a discrete random uniform function. A nest was considered fledged (successful) if it did not fail before or on the randomly selected fledging date. If a nest survived beyond day 16, it was "checked" again on day 20, and if it survived beyond day 20 it was checked again on day 22. These visit intervals were used to calculate exposure based on different exposure-period termination methods. To simulate different levels of fate uncertainty, the RANBIN function was used to generate an uncertainty variable for each nest that survived to the potential fledging interval (1 for uncertain fate, 0 for certain fate). Because we knew the actual outcomes of simulated nests, we could compare known survival rates with estimates calculated under different levels and approaches to fate uncertainty.

We simulated effects of six levels of nest-fate uncertainty (0, 10, 20, 30, 40, and 100% of nests that reach the potential fledging interval) on Mayfield estimates that were calculated using the approaches described in Table 2. In the Mayfield formula, we raised the daily survival rate to the power of 20 days. For each alternative method (using uncertain nest fates and different exposure-termination methods), we calculated the mean Mayfield estimate over 1,000 runs (100 nests each) and calculated the mean difference from the known survival rate. Each set of 100 nests had a different known survival rate, because daily survival probabilities were drawn from a binomial distribution, rather than set exactly. Over 100 sets of 1,000 runs (100 nests each), the mean survival rate was $0.442 \pm$ SD of 0.001 for the constant daily mortality scenario and 0.345 ± 0.001 for the nonconstant daily mortality scenario. For each alternative approach to Mayfield estimation, the mean difference from the known survival rate, over 1,000 runs, was a measure of bias. Over 100 sets of 1,000 runs, the bias estimates varied by ±0.002 (SD = 0.001).

To compare methods and evaluate how well they handle uncertain nest fates, we calculated a bias index (Table 3) as the mean of the absolute values of the values in a particular row, across levels of nest-fate uncertainty. We used the absolute value because

the direction of bias can be positive or negative depending on the level of fate uncertainty. Thus, the bias index is an average measure of the magnitude of bias but does not indicate direction. Direction of bias can be assessed by examining individual values for each level of fate uncertainty. We varied two additional model variables to see if they affected the bias estimates. We ran the simulations with higher (0.08) and lower (0.02) daily mortality rates and ran the simulations with a narrower potential fledging interval (between days 19 and 21, instead of days 17 and 22).

In addition to simulations, we evaluated real data from nests found in north-central Minnesota in 1992 and 1994. We restricted our analyses to Least Flycatcher and Ovenbird nests and believe the contrasting nesting behaviors and associated monitoring and observation problems for these two species represent the range of problems encountered in many studies of nesting success. Ovenbirds nest on the ground and have a very short nestling period (8 to 10 days), making it difficult to check nests frequently enough to unambiguously determine nest fate. Least Flycatchers have a longer nestling period (12 to 16 days), but nests in our study area occur up to 20 m high in trees. With high nests, it can be difficult to determine nest activity, nest stage, transition dates between nesting stages, and age of the young.

RESULTS AND DISCUSSION

The Exclusion method resulted in the highest levels of negative bias of all methods (Table 3). With high levels of fate uncertainty, the bias was severe for both constant and nonconstant DMR scenarios. For the nonconstant DMR scenario, the extent of bias was under-represented in the simulations, because two sources of bias canceled each other out. Excluding nests with uncertain fate resulted in negative bias, and the higher mortality rate during the potential fledging interval resulted in positive bias. The bias found in the Exclusion method with the nonconstant DMR scenario would be more pronounced if DMR was lower during the potential fledging interval than during the earlier part of the nesting cycle. The extent of fate uncertainty is rarely documented in the literature, and it can vary across studies depending on frequency of nest visits, height of nests, and criteria used to determine fate.

We measured extent of fate uncertainty in our Minnesota data based on criteria in Table 1. Fates for nests that met the criteria were considered known, and fates that did not meet any of the criteria were considered uncertain. Fates

TABLE 3. Mean difference from known nesting-success rate for approaches to Mayfield estimation in Table 1, based on 1,000 simulation runs of 100 nests each. Values not in parentheses based on constant daily mortality rate = 0.04; values in parentheses based on daily mortality rate = 0.04 for days 1 to 16 and 0.10 for days 17 to 22.

Sub-group	Percent of nest fates uncertain[a]						Bias index[b]
	0	10	20	30	40	100	
Exclusion							
A	−0.016	−0.039	−0.065	−0.094	−0.127	—	0.068
	(+0.017)	(−0.001)	(−0.022)	(−0.046)	(−0.070)		(0.031)
B	−0.006	−0.028	−0.055	−0.084	−0.118	—	0.058
	(+0.027)	(+0.008)	(−0.013)	(−0.038)	(−0.062)		(0.030)
Early termination							
A	−0.007	−0.006	−0.005	−0.007	−0.007	−0.008	0.006
	(+0.091)	(+0.089)	(+0.091)	(+0.091)	(+0.091)	(+0.090)	(0.091)
C[c]	+0.071	+0.070	+0.070	+0.072	+0.071	+0.071	0.071
	(+0.169)	(+0.168)	(+0.169)	(+0.168)	(+0.167)	(+0.168)	(0.168)
C[d]	−0.006	−0.006	−0.007	−0.005	−0.007	−0.006	0.006
	(−0.006)	(−0.006)	(−0.008)	(−0.007)	(−0.005)	(−0.006)	(0.006)
Last active							
A	−0.037	−0.032	−0.027	−0.022	−0.017	+0.014	0.025
	(+0.001)	(+0.010)	(+0.019)	(+0.030)	(+0.040)	(+0.106)	(0.034)
B	−0.016	−0.013	−0.010	−0.008	−0.005	+0.014	0.011
	(+0.017)	(+0.025)	(+0.033)	(+0.041)	(+0.050)	(+0.106)	(0.045)
C	−0.006	0.000	+0.004	+0 .009	+0.014	+0.044	0.013
	(+0.027)	(+0.036)	(+0.045)	(+0.056)	(+0.067)	(+0.132)	(0.061)
Midpoint							
A	−0.017	−0.011	−0.005	0.000	+0.005	+0.038	0.013
	(+0.018)	(+0.027)	(+0.038)	(+0.049)	(+0.061)	(+0.132)	(0.054)
B	−0.006	0.000	+0.005	+0.011	+0.015	+0.048	0.014
	(+0.027)	(+0. 037)	(+0.047)	(+0.059)	(+0.070)	(+0.141)	(0.064)
Decision rule							
A[e]	—	−0.013	−0.012	−0.008	−0.005	+0.010	0.009
B[f]	—	−0.030	−0.044	−0.058	−0.072	−0.142	0.069
Last active							
B[g]	—	−0.010	−0.005	+0.001	−0.005	—	0.005
B[h]	—	−0.016	−0.016	−0.015	−0.015	—[i]	0.016

[a] Proportion of nests that survive to the potential fledging interval (near expected fledging date) that are set to have uncertain fates in simulations. Nests that failed before the potential fledging interval in simulations had known fates.

[b] Index is the mean of the absolute values of the values in a particular row. This indicates how robust a particular method is across levels of nest-fate uncertainty.

[c] Survival estimate calculated as p^k, where k = 16 days. The early termination method terminates exposure at day 16, before the potential fledging interval begins. Bias estimate is the mean difference from the known survival rate that incorporates nest failures up to day 22.

[d] Survival estimate calculated as p^k, where k = 16 days. The early termination method terminates exposure at day 16, before the potential fledging interval begins. Bias estimate is the mean difference from the known survival rate for the period up to 16 days (failures after day 16 are not included).

[e] 50% of uncertain nests that in fact failed are considered successful.

[f] 50% of uncertain nests that in fact fledged are considred failed.

[g] Uncertainty probability 2× higher for failed vs. successful nests.

[h] Uncertainty probability 2× higher for successful vs. failed nests.

[i] If there are 0 or 100% uncertain nest fates, probability of uncertainty cannot vary among successful and failed nests.

were uncertain for 40% of the Ovenbird nests (51 of 127) and 30% of the Least Flycatcher nests (43 of 144). Excluding nests with uncertain fate resulted in severe downward bias. For Ovenbirds, the Exclusion-A method resulted in an estimate 31% lower than the estimate that included nests with uncertain fates (from 0.48 to 0.33; χ^2 = 3.63, P = 0.057). For Least Flycatchers, the Exclusion-A method resulted in a Mayfield estimate 24% lower than when these nests were included (from 0.46 to 0.35; χ^2 = 3.32, P = 0.057). Clearly, the Exclusion method should not be used, especially when the level of fate uncertainty is high.

The Early Termination-A method resulted in the lowest bias overall for the constant DMR scenario (index value = 0.006), but it resulted in substantial bias in the nonconstant DMR scenario (0.091). This bias resulted because DMR increased after the early termination date in the simulations, but failures and exposure days beyond the early termination date were not included in Mayfield calculations. Little is known about survival during the last several days of the nestling period, but F. R. Thompson (pers. comm.) observed high mortality during this period using video cameras. To the extent possible, the method of choice should be robust to such an increase in DMR. One approach (Early Termination-C; Table 3) avoids the bias associated with an increase in DMR during the potential fledging interval by estimating a different quantity for survival, p^k, where p is daily survival and k is the length of the nesting cycle up to the early termination point (16 days in our simulations; J. Nichols pers. comm.). Recall that the other methods estimate S as p^j, where j is the average length of the nesting cycle for the species in question (20 days in our simulations). We simulated Early Termination-C (Table 3). Because it estimated survival for the 16-day period rather than the 20-day period, the method resulted in a substantial upward bias from the true survival rate for both constant and nonconstant DMR scenarios (Table 3). However, because Early Termination-C actually estimated survival for the 16-day period rather than for the full nesting cycle, the estimate should also be compared with the known survival rate for the 16-day period to generate a bias estimate. Here, the bias is minimal for both constant and nonconstant DMR scenarios. This method is inappropriate if one desires an accurate estimate of nesting success as traditionally defined, but it may be appropriate if the full nesting-cycle length survival rate is not the quantity of interest (e.g. if one only wishes to compare nesting success across treatments; see below).

We did not simulate Early Termination-B (maximum-likelihood approach), but we believe the results would be similar to those of Early Termination-A or C because this method, as described by the individual who used it, also terminated exposure before the potential fledging interval began. As with Early Termination-A and C, results should vary depending on

which quantity is estimated (survival up to the early termination point, or for the full nesting-cycle length).

The Last Active-B method had the second-lowest bias index for the constant DMR scenario (0.011) and the lowest bias index for the nonconstant DMR scenario (0.045). The index for the nonconstant DMR scenario dropped to 0.033 if the 100% nest-fate uncertainty level was not included in the index calculation (100% nest-fate uncertainty is highly unlikely). Last Active-A, which was the most commonly used method in this group (19% of all respondents), produced the highest bias index within the group for the constant DMR scenario (0.025) and a similar value for the nonconstant scenario (0.034). Last Active-C performed reasonably well but not as well as Last Active-B. The Midpoint method (subgroups A and B) also performed reasonably well, but again, not as well as Last Active-B.

For the Decision Rule method, we simulated the effect of 50% fate misclassification using a decision rule. The accuracy of such rules is unknown (and difficult to test), so the possibility of inaccurate results must be considered. The bias index was small in the scenario where 50% of the uncertain nests that failed were considered successful by the rule (0.009). However, the bias index was substantial (0.069) for the opposite scenario, where 50% of the uncertain nests that actually fledged young were considered to have failed. This potential bias suggests that the Decision Rule method is not appropriate for Mayfield estimation. Regardless of the true accuracy of decision rules, final nest fates do not need to be known for Mayfield estimation, so attempting to determine fate with such rules is unnecessary.

The Last Active-B method appears to handle high levels of nest-fate uncertainty and nonconstant daily mortality well. However, one must consider potential bias that may arise if the probability of fate uncertainty is different for nests that are successful versus nests that fail. For Last Active-B, we modeled scenarios where the probability of uncertainty was twice as high for failed versus successful and successful versus failed nests (last two rows in Table 3). This differential in uncertainty probability had relatively little effect on the overall performance of the method because uncertainty occurred only in the last observation interval. Errors dur-

ing this last interval have little influence be-
cause interval status and correct number of ex-
posure days are known for previous intervals,
and previous intervals comprise the majority of
exposure days. We conclude that bias of this
type, if present, will be inconsequential and
that the Last Active-B method is still a reason-
able approach. We also tested whether higher
(0.08) or lower (0.02) daily mortality rates than
those we used in the main simulations and a
narrower potential fledging interval (3 vs. 5
days) would change the bias estimates. Bias es-
timates were consistent with those produced in
the main simulations.

The Last Active-B method appears to be the
most suitable for general use because it per-
forms well in both constant and nonconstant
DMR scenarios. This was surprising because
only 9% of survey respondents used the meth-
od. In our simulations, Early Termination-A
produced better results than Last Active-B
when daily mortality was constant. Thus, Early
Termination-A may be more appropriate for
cases or species where constant daily mortality
has been well documented. However, there are
several disadvantages to Early Termination-A
(which also would apply for Early Termination-
B and C). First, it is often difficult to predict a
fledging date accurately. For example, for many
nests a hatching or initiation (1st egg) day can-
not be determined; hence, it is impossible to de-
termine when the potential fledging interval
begins (to be certain that the early termination
date occurs before this interval). Furthermore,
because it can be difficult for visits to occur ex-
actly at the early termination date, we do not
recommend the method for general use.

Reporting nesting-success estimates.—In our
examination of these issues, we found incon-
sistent reporting of Mayfield estimates and as-
sociated variance estimates in the literature.
Quite often, Mayfield estimates were the only
values reported. Other information necessary
to interpret and compare nesting-success esti-
mates are (1) a variance estimate, (2) the length
of the period over which daily survival rates
are projected to derive period survival rates,
and (3) which periods were used (egg laying,
incubation, brood rearing, or some combina-
tion) to calculate the estimate. Of 13 recent ar-
ticles on nesting success (appearing in *Auk,
Condor, Wilson Bulletin, Journal of Field Ornithol-
ogy,* or *Journal of Wildlife Management* from 1987

to 1996), 7 did not report variance estimates, 6
did not report a period length used for projec-
tion of daily survival rates, and 3 did not report
which periods were used for calculating May-
field estimates. Variance estimates are needed
to make statistical comparisons, and the other
factors can influence the Mayfield estimate.
More consistent reporting of this information is
necessary for valid comparisons among stud-
ies.

Uncertain nest fates in causal analysis.—Al-
though nests with uncertain fate can be readily
used in Mayfield estimation, they can be prob-
lematic for other analyses conducted in nesting
studies. It is important to clarify different anal-
ysis goals, because uncertain fates can have dif-
ferent effects depending on the type of analy-
sis. Most of our discussion has focused on nest-
ing-success estimation, where it is important to
obtain an accurate and precise estimate of nest-
ing success. Accurate estimates of nesting suc-
cess are needed if they are used in demograph-
ic models or compared among species. How-
ever, in many analyses, the objective is not to
estimate nesting success, but to examine factors
that affect nesting success (causal analysis).
Here, accuracy of nesting-success estimates
may not be critical as long as any biases are
consistent across treatments or factors thought
to affect nesting success. Causal analyses can
be broken down into several categories: simple
comparisons, explanatory models, and predic-
tive models. Mayfield estimates often are used
for estimating nesting success and for simple
comparisons. For example, Donovan et al.
(1995) used Mayfield estimates as inputs for
source-sink models (where accuracy is critical)
and also compared Mayfield estimates among
levels of habitat fragmentation to investigate
whether fragmentation affected nesting suc-
cess. Robinson et al. (1995) developed explan-
atory linear regression models using percent
forest cover as a predictor and daily mortality
rate as an outcome variable. In both of these ex-
amples, uncertain nest fates should not be a
problem, because the Mayfield estimator or
daily mortality rates are the values compared
or evaluated in regression models. However,
these approaches have a major drawback in
that data from individual nests must be col-
lapsed into rates for groups or treatments. With
such collapsing, it can be difficult (in some cas-
es impossible) to evaluate the effects of multi-

ple variables, and sample sizes are much reduced.

Because of this limitation, many recent papers use techniques that treat every nest as a unit of analysis in explanatory or predictive models. For example, Li and Martin (1991) used discriminant function analysis to compare successful and failed nests to identify habitat variables associated with successful reproduction. Similarly, Hanski et al. (1996) used logistic regression (with nest fate as the outcome variable) to identify factors associated with nest survival. These approaches are limited when uncertain fates are present, because nests with uncertain fate must be excluded from analysis. This reduces statistical power, and results can be biased if excluded nests have higher or lower mortality rates than included nests. Finally, when nest fate is a required variable, investigators may be tempted to classify fate when information is ambiguous and insufficient to make such a decision.

Some investigators use decision rules to classify ambiguous or uncertain nest fates. For example, Mayfield (1960:190) used a simple rule to classify nest fate for Kirtland's Warblers when he lacked empirical fate cues. He considered nests to be successful if nestlings reached seven days of age, when the average fledging age was nine days. He assumed that seven-day-old chicks could survive outside the nest. Another rule, used by the BBIRD program (Martin et al. 1997), reads "In the absence of other cues, we assume chicks fledged successfully if the median date between the last nest check during which the nest was active and the final nest check when the nest was empty was within two days of predicted fledging date." These rules can be difficult to apply because chick age often is unknown, or fledging dates are difficult to predict accurately. Manolis (1996) formalized and evaluated modifications of these rules. He suggested that if structured properly and if used consistently among researchers, such rules could reduce subjectivity involved in fate classification. However, the decision rules he suggested are limited in that they cannot classify the fates of all nests, many of which will remain uncertain. In addition, the accuracy of these decision rules is unknown and difficult to evaluate.

For evaluating effects of explanatory variables on nest survival, an approach that does not require knowledge of final nest fate is Cox regression (also known as proportional hazards regression; Cox 1972). Used frequently in medical studies, this approach models the effects of predictor variables on survival times. Times for individual subjects are measured from the start of the study (or from entry time into the study) until an event of interest occurs (e.g. death). In many cases, subjects will leave the study before it ends or will remain living at the end of the study. In survival analyses, such observations are said to be "censored," and Cox regression is designed to incorporate them. Nests with uncertain fate are simply censored in Cox regression (analogous to a patient withdrawing from a study), in basically the same way that nests with uncertain fates are included in Mayfield estimation.

Variables required for using nesting-success data that contain variable entry times (nests found at different times) in Cox models are (1) a censor variable (e.g. 0 for successful or uncertain, 1 for failure), (2) the estimated age in days when the nest was found (time from when the first egg was laid), and (3) the estimated age in days when the nest failed (for uncensored observations) or was last observed (for censored observations). Data collected for Mayfield estimation can be converted to this format. Cox regression models can evaluate the contribution of any combination of categorical and continuous predictor variables to nest survival.

A basic assumption of Cox regression is proportionality of hazard functions. This means that hazard functions for individuals in a study should be proportional, or parallel to each other, although the hazard functions can take any shape. For example, for a group of nests, the hazard function could be low during the egg-laying period, higher but flat during the incubation period, and rise steadily during the nesting stage. This differs markedly from the Mayfield estimator, which assumes a constant hazard rate. If hazard functions are found to be nonproportional, adjustments can often be made in Cox models so that they remain valid. These adjustments are made through introduction of time-dependent covariates or through stratification (Allison 1997). Another important assumption of Cox regression is that random censoring should be noninformative. Random censoring is the type of censoring that is beyond the researcher's control. For example, a

patient withdraws from a study, or a nest fate is uncertain during the potential fledging interval, for reasons described earlier. Censoring is informative if the probability of failure after censoring at time C_i is higher or lower than for individuals that survive to but are not censored at time C_i (Allison 1997). For example, for all nests that survive to day 18, the probability of failure after day 18 should not be different for nests that become uncertain on day 18 versus those whose outcome is known after day 18. Informative censoring may occur if fate evidence generally is more clear for either failures or successes. However, because the censoring times (C_r) for these randomly censored observations are so close to those for nests that actually fledge or for failure times that occur after C_r, the effect of such informative censoring should be slight. The slight level of bias produced when we simulated informative censoring in the Mayfield estimator (last two rows in Table 3) supports this conclusion.

Cox regression has not been used frequently in avian nesting studies, but it has several advantages in addition to its ability to incorporate censored observations. In many cases, survival time may be a more appropriate dependent variable than nest fate. Analyses that use nest fate as the dependent variable (i.e. logistic regression) ignore the length of time nests are observed. Nests observed for short periods receive the same weight as those observed for long periods, but nests observed briefly should receive less weight because they give less information about the contribution of covariates to survival. Cox regression uses observation length (exposure period) for each nest in a manner similar to the Mayfield estimator and weights observation lengths appropriately. In addition, survival functions and confidence limits are readily derived. Survival estimates derived from proportional hazards regression do not assume constant mortality, a major limitation of the Mayfield estimator (Klett and Johnson 1982, Johnson and Shaffer 1990).

When using proportional hazards regression, consistent criteria (such as those in Table 1) should be used to judge evidence for nest failure, but if it is not clear that a nest failed, the observation should be censored. We recommend terminating survival times in the same manner as for Mayfield estimation (Last Active-B; Table 2). Numerous statistical programs offer Cox regression, and the ones that offer "late entry" or truncated observations (such as SAS, S-PLUS, STATA, EGRET) are most appropriate for analyzing nesting-success data. Nesting studies usually involve truncated observations because nests are found at different stages of the nesting cycle. Allison (1997) is a suitable text on Cox regression and survival analysis in general.

SUMMARY AND RECOMMENDATIONS

As more studies of avian nesting success are undertaken, especially of species that exhibit short incubation and nestling periods, it is important that data collection and analyses are standardized to allow spatial and temporal comparisons. Investigators generally have not acknowledged that inconsistencies in data collection and analyses exist, particularly those related to uncertain nest fates and exposure-period termination methods used for Mayfield estimation. The effects of these inconsistencies can be significant. We recommend the following:

1. Nests with uncertain fate should not be excluded from Mayfield estimates of nesting success or a downward bias will result.

2. For Mayfield estimation, Last Active-B (Table 2) appears to be the most appropriate model for general use. Here, exposure is terminated with the last observed active date for nests with uncertain fate and with the midpoint between the last observed active and the first observed inactive dates for nests of known fate.

3. When reporting Mayfield estimates, variance estimates and the period lengths used to estimate survival rates should also be reported. Periods used in the calculation (egg laying, incubation, brood rearing, or some combination) should be specified. In addition, the number of exposure days and the number of failed, successful, and uncertain nest fates should be reported.

4. Uncertain and ambiguous nest fates can be problematic for analyses that use fate as a categorical variable, and such analyses are commonly used to examine factors that affect nesting success. Cox regression does not require knowledge of nest fate and has a number of desirable features, even for cases where all nest fates are known. We recommend it for in-

vestigating factors that influence nesting success, particularly when uncertain nest fates are present.

LITERATURE CITED

ALLISON, P. D. 1997. Survival analysis using the SAS system: A practical guide. SAS Institute, Inc., Cary, North Carolina.

COX, D. R. 1972. Regression models and life tables. Journal of the Royal Statistical Society Series B 30:187–220.

DONOVAN, T. M., F. R. THOMPSON III, J. FAABORG, AND J. R. PROBST. 1995. Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology 9:1380–1395.

HANSKI, I. K., T. J. FENSKE, AND G. J. NIEMI. 1996. Lack of edge effect in nesting success of breeding birds in managed forest landscapes. Auk 113:578–585.

HENSLER, G. L., AND J. D. NICHOLS. 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.

JOHNSON, D. H., AND T. L. SHAFFER. 1990. Estimating nest success: When Mayfield wins. Auk 107:595–600.

KLETT, A. T., AND D. H. JOHNSON. 1982. Variability in nest survival rates and implications to nesting studies. Auk 99:77–87.

LI, P., AND T. E. MARTIN. 1991. Nest site selection and nesting success of cavity-nesting birds in high elevation forest drainages. Auk 108:405–418.

MANOLIS, J. C. 1996. Minimizing subjectivity in nesting success estimation: A prototype decision support system and modeling results. M.S. thesis, University of Minnesota, St. Paul.

MARTIN, T. E. 1992. Breeding productivity considerations: What are the appropriate habitat features for management? Pages 455–473 in Ecology and conservation of Neotropical migrant birds (J. M. Hagan III and D.W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.

MARTIN, T. E., AND G. R. GEUPEL. 1993. Nest-monitoring plots: Methods for locating nests and monitoring success. Journal of Field Ornithology 64:507–519.

MARTIN, T. E., C. R. PAINE, C. J. CONWAY, W. M. HOCHACHAKA, P. ALLEN, AND W. JENKINS. 1997. BBIRD field protocols. Unpublished report, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula. <http://pica.wru.umt.edu/bbird/>

MAYFIELD, H. F. 1960. The Kirtland's Warbler. Cranbrook Institute of Science, Bloomfield Hills, Michigan.

MAYFIELD, H. F. 1961. Nesting success calculated from exposure. Wilson Bulletin 73:255–261.

MAYFIELD, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

MILLER, H. W., AND D. H. JOHNSON. 1978. Interpreting the results of nesting studies. Journal of Wildlife Management 42:471–476.

RALPH, C. J., G. R. GEUPEL, P. PYLE, T. E. MARTIN, AND D. F. DESANTE. 1993. Handbook of field methods for monitoring landbirds. United States Forest Service General Technical Report PSW-GTR-144.

ROBINSON, S. K., F. R. THOMPSON III, T. E. DONOVAN, D. R. WHITEHEAD, AND J. FAABORG. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987–1990.

SAS INSTITUTE 1990. User's guide, version 6, 4th ed. SAS Institute, Inc., Cary, North Carolina.

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