EXTENDING METHODS FOR MODELING HETEROGENEITY IN NEST-SURVIVAL DATA USING GENERALIZED MIXED MODELS

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Abstract. Strong interest in nest success has led to advancement in the analysis of nest-survival data. New approaches allow researchers greater flexibility in modeling nest-survival data and provide methods for relaxing assumptions and accounting for potentially important sources of variation. The most flexible method uses linear-logistic models with a random-effects framework to both incorporate potential covariate effects and model remaining heterogeneity. With the goal of increasing the use of more flexible methods, we provide additional detail regarding linear-logistic mixed models and their implementation. We use an example dataset to (1) demonstrate data preparation for analysis in PROC NLMIXED of SAS, (2) describe the use of code for evaluating competing models, (3) illustrate implementation of models with and without random effects and that evaluate potential effects of observer visits to nests, and (4) present methods of obtaining estimates of nest-survival rate for various covariate conditions of interest. We also conduct Monte Carlo simulations to evaluate the performance of linear-logistic mixed models of nest-survival data. We present the results of evaluation for one scenario and show that the estimation procedure as implemented in PROC NLMIXED is effective and that simulation can be used to gain insights into the advantages and disadvantages of various study designs. We encourage the development of further advancements that will allow greater flexibility in modeling.

Key Words: generalized mixed model, nest survival, population dynamics, random-effects statistics.

AMPLIACIÓN DE MÉTODOS PARA MODELAR LA HETEROGENEIDAD DE DATOS DE SOBREVIVENCIA DE NIDO UTILIZANDO MODELOS GENERALIZADOS MEZCLADOS

Resumen. El fuerte interés respecto a al éxito de nido, ha llevado al avance del análisis de datos de sobrevivencia de nido. Nuevos enfoques permiten a los investigadores tener mayor flexibilidad en el modelaje de datos de sobrevivencia de nido, y proveer métodos para suavizar las suposiciones y el conteo de fuentes potenciales importantes de variación. El método más flexible utiliza modelos lineares logísticos con un marco de efectos al azar, tanto para incorporar efectos covariantes potenciales, como para modelar la heterogeneidad restante. Con el objeto de incrementar la utilización de métodos más flexibles, proporcionamos detalle adicional respecto a modelos lineares logísticos mezclados y su implementación. Utilizamos un ejemplo de conjunto de datos para (1) demostrar la preparación de datos para el análisis en PROC NLMIXED de SAS, (2) describir la utilización del código para evaluar modelos competentes, (3) ilustrar la implementación de modelos con o sin efectos al azar y que evalúan potenciales efectos de visitas observadas a nidos, y (4) presentar métodos de estimaciones obtenidos de tasas de sobrevivencia de nido para varias condiciones covariantes de interés. También condujimos simulaciones Monte Carlo para evaluar el desempeño de modelos lineares logísticos mezclados de datos de sobrevivencia de nido. Presentamos los resultados de la evaluación para un escenario y mostramos que el procedimiento de estimación como el implementado en PROC NLMIXED es efectivo, y que la simulación puede ser utilizada para aumentar la penetración en las ventajas y desventajas de varios diseños de estudios. Promovemos el desarrollo de futuros adelantos que permitan mayor flexibilidad en el modelaje.

Methods for estimating nest survival rate have received considerable attention (Mayfield 1961, Johnson 1979, Bart and Robson 1982, Natarajan and McCulloch 1999, Farnsworth et al. 2000, Dinsmore et al. 2002). Williams et al. (2002) provide a useful review of historical development, available approaches, and estimation programs. Information regarding how daily survival rates and overall nest success are calculated is provided by Dinsmore et al. (2002).

The Mayfield (1961) method, either in its original form or as expanded by Johnson (1979) and Bart and Robson (1982), requires the assumption of a constant daily survival rate for all nests in a sample over the time period being considered. However, heterogeneity in daily survival rates among members of the study population can cause estimates of nest success and, in some cases, daily survival rate to be biased (Farnsworth et al. 2000, Rotella et al. 2000).

To allow greater flexibility in modeling nest-survival data in the presence of heterogeneity, numerous publications have presented methods for relaxing assumptions and account for potentially important sources of variation

(Dinsmore et al. 2002, Rotella et al. 2004, Stanley 2004a). Most troubling has been the assumption of the absence of overdispersion. Overdispersion occurs when the variance of the response variable exceeds the nominal variance. Overdispersion can be caused by lack of independence among animals and heterogeneity in the probabilities beyond that specified by the model. Overdispersion in count-based models can have profound inferential consequences. If not adjusted for, overdispersed count data will lead to inter-related problems: (1) model-selection procedures selecting over-parameterized models, (2) hypothesis tests that are too liberal, and (3) parameter confidence intervals that are too short (Lebreton et al. 1992, Fitzmaurice 1997, Ennis 1998). Lebreton et al. (1992) introduced a quasi-likelihood-based adjustment of a generalized variance-inflation factor. This adjustment influences both model identification and parameter confidence intervals but not parameter estimates (Lebreton et al. 1992).

Quasi-likelihood is not the only device for coping with overdispersion. An alternative approach is to model explicitly the random effects generating the overdispersion (Hinde and Demetrio 1998, Lee and Nelder 2000). The most flexible methods explicitly for nest-survival analysis were linear-logistic models that use covariate-based fixed effects and random effects to incorporate overdispersion (Natarajan and McCulloch 1999). Their approach can also incorporate nest-encounter probabilities (Pollock and Cornelius 1988, Bromaghin and McDonald 1993a, McPherson et al. 2003).

Explicitly modeling fixed and random effects in a generalized mixed model is an attractive way of addressing overdispersion. First, because the random effects are estimated jointly with the fixed effects, there will be a reduction in bias of the estimated fixed effects. As with normal mixed models, this effect is generally small (Cox 1983, McCullagh and Nelder 1989), but on occasion, as with normal mixed models, more substantial differences can occur. Secondly, comparisons of models incorporating random effects in a variety of ways yield greater biological insight into the genesis of the overdispersion than does the calculation of a single overarching variance-inflation factor. Such insight may lead to the inclusion of further covariates in the fixed effects that reduce the overdispersion. Williams et al. (2002:349) concluded that the approach is a reasonable and natural way to view nest survival, but also noted that, at present, the complexity of the computations may limit the ability of many biologists to apply this approach. To date, this impairment appears real, because we are unaware of any published study that has implemented the full approach.

Despite the computational complexities of mixed models, several benefits can be gained from using mixed models when they are appropriate. In some situations, the precision of estimates will be increased. Incorporation of random effects can allow one to make broader inferences. For example, if a random effect of study site is present and mixed models are used, inferences can be made about the actual population of study sites from which samples were drawn. In contrast, if fixed-effects-only models were used and each study site were treated as a fixed effect, then inferences would be limited to only those specific sites used in the study. Finally, information about random effects can motivate thinking about the process underlying the structure of the data and missing covariates that could be measured in the future to explain the random effects.

Mixed models are appropriate if levels of some covariates represent all possible levels, or at least the levels for which inferences are desired (these are fixed factors), whereas for others covariates, the levels observed are only a random sample of a larger set of potential levels of interest (these are random factors; Breslow and Clayton 1993, Littell et al. 1996, Pinheiro and Bates 2000). Examples of covariates that might be treated as random effects are study site or individual. This is true because it will often be the case that the particular experimental units such as the sites or individuals studied are selected at random from the population of sites or individuals, which are of interest. Pinheiro and Bates (2000: 8) stated that they are random effects because they represent a deviation from an overall mean. Thus, the effect of choosing a particular site, year, or individual may be a shift in the expected response value for observations made on that experimental unit relative to those made on other experimental units experiencing the same levels for the fixed effects. In other words, multiple observations made on the same site, year, or individual may be correlated, and if so, this should be accounted for in the analysis.

In a broad discussion of data analysis, Littell et al. (1996) stated they believe that valid statistical analysis of most data sets requires mixed-model methodology. Given the potential utility of such an approach, our objective here is to provide further details of the method beyond those presented previously (Rotella et al. 2004, Shaffer 2004a, Stephens et al. 2005). Although some material presented here has

been presented previously (Rotella et al. 2004), we repeat it here to provide a more coherent treatment of the subject. We also provide additional information of how to implement the technique by analyzing an example dataset. In so doing, we review the programming statements written that can be used with SAS (SAS Institute 2004) for conducting necessary computations for a suite of candidate models, and consider a variety of important aspects of interpreting the output from generalized mixed models of daily survival rates. Sturdivant et al. (*this volume*) developed a goodness-of-fit test for the nest-survival model reviewed here, and they illustrate its implementation with the same example dataset used here and in Rotella et al. (2004). We conclude by presenting alternative analysis approaches that could be used and by pointing out the need for future improvements.

A GENERALIZED LINEAR-MIXED-MODELS APPROACH FOR NEST SURVIVAL

The nest-survival model employed by Stephens et al. (2005) generalizes the model described by Bart and Robson (1982). The model employs a generalized linear-models approach (McCullagh and Nelder 1989) based on a binomial likelihood, where daily survival rates are modeled as a function of nest-, group-, and/or time-specific covariates. Daily survival rates can then be estimated from the resulting model and multiplied together, as appropriate, to estimate nest success.

To illustrate the model likelihood, let S_i (daily survival rate) denote the probability that a nest survives from day i to day $i + 1$. Consider a nest that was found on day k was active when revisited on day l, and was last checked on day m ($k < l < m$). Because the nest is known to have survived the first interval, its contribution to the likelihood for that interval is $S_k S_{k+1} \dots S_{l-1}$. During the second interval, the nest either survives with probability $S_l S_{l+1} \dots S_{m-1}$ or fails with probability $(1 - S_l S_{l+1} \dots S_{m-1})$. The likelihood is thus proportional to the product of probabilities of observed events for all nests in the sample (Dinsmore et al. 2002).

A link function is used to characterize the relationship between daily survival rate and the covariates of interest. A variety of link functions can be used (White and Burnham 1999, Williams et al. 2002). Here, focus will be on use of the logit link (and the logistic inverse link) as it is the natural link for the binomial distribution (McCullagh and Nelder 1989). The logit link is frequently used in mark-resighting modeling, provides a flexible form, and bounds estimates of survival in the (0, 1) interval.

Stephens et al. (2005) used the logit link in their work, and Lebreton et al. (1992) presented methods for estimating confidence intervals and back-transforming to model parameters and estimates of their variances and covariances when the logit link is used.

With the logit link, daily survival rate of a nest on day i is modeled as:

$$\frac{\exp(\beta_0 + \sum_j \beta_j x_{ji})}{1 + \exp(\beta_0 + \sum_j \beta_j x_{ji})}$$

where the x_{ji} ($j = 1, 2, \dots, J$) are values for J covariates on day i and the are coefficients to be estimated from the data. Logit transformation of the above expression yields

$$\beta_0 + \sum_j \beta_j x_{ji}.$$

Thus, the relationship between the logit of S_i, i.e., $\ln(S_i/(1 - S_i))$, and the covariates is linear, whereas the relationship between S_i and the covariates is logistic or S-shaped. Once the are estimated, an estimate of the parameter(s) of interest (S_i) is generated by solving the regression equation and then back transforming the answer. Note that the above formulation allows daily survival rates to vary among groups of nests based on group-specific covariates, among individual nests based on nest-specific covariates, and among days based on time-specific covariates.

The parameters β_j of competing models are estimated iteratively by the method of maximum likelihood using computer code designed for generalized linear models. Accordingly, a variety of likelihood-based methods are available for evaluating competing models. Likelihood ratio tests can be used to formally test hypotheses about whether specific covariates are associated with variation in nest survival (but see Anderson and Burnham 2002). If a set of candidate models is used, then information-theoretic measures such as Akaike's information criterion (AIC) and AIC_c can be used to select which model or models to use for inference (Burnham and Anderson 2002). Model-selection inference will be most robust if the model set is selected a priori, but nevertheless, useful inferences of a weaker epistemic standing can still be made with a post hoc model set (Taper and Lele 2004).

Assumptions of the daily nest-survival model described here are: (1) homogeneity of daily survival rates as modeled (e.g., if the model contains nest age and no other covariates, then all nests of a given age are assumed to have the same daily survival rate), (2) nest fates are correctly determined on each visit after the first one, (3) nest discovery and subsequent

nest checks do not influence survival (although see below for methods of modeling the effects of nest visits and relaxing this assumption), (4) nest fates are independent or sources of dependency are appropriately modeled, (5) all visits to nests are recorded, (6) the age of nests can be determined correctly so that the day of hatching, or fledging can be determined correctly, and (7) nest checks are conducted independently of nest fate. If data are available for more than one interval length, an extension of the model presented by Rotella et al. (2000) can be used to evaluate and possibly relax assumption three. Assumption one, by virtue of the fact that daily survival rates can be modeled as a function of group-, nest-, and time-specific covariates, is far less restrictive than is necessary for Mayfield's (1961) method. If nest age is to be considered in models of daily survival rate, then it is also assumed that the age of nests can be determined correctly when first found (Dinsmore et al. 2002). Although it is analytically possible to estimate age-specific daily survival rates for nests of all ages, logistical constraints may prevent this. If nests are rarely found early in the laying stage, then estimates may be lacking or very imprecise for this period. If visits to nests containing older nestlings commonly cause nestlings to leave their nest prior to the expected fledging age, then it may not be possible to estimate daily survival rates for nests beyond some threshold age. The method requires no assumptions about when nest losses occur during the interval between two nest visits.

DATA INPUT FORMAT

Each row of data input typically contains information for one observation interval for an individual nest as this allows a complete record of all nest observations and nest visits to be entered. An observation interval is the length of time (t; an integer, typically measured in days) between any two successive nest visits. Note that for a given nest, different observation intervals do not need to be of the same length. The minimum data that must be provided are the length of the interval (t) and the nest's fate for the interval (Ifate; 1 = successful, 0 = unsuccessful). In addition, individual and group- and time-specific covariates can be included. For example, the date (StartDate) and age of the nest (StartAge) at the start of the interval might be recorded. If each interval starts with an observer visit to the nest, and all visits involve similar activities by observers, then information about observer visits is not needed even if one is interested in estimating observer effects on daily survival rate (see below). However, if all

intervals do not start with a nest visit such as when telemetry is used to remotely check nest status for many intervals, or, if activities during visits differ among occasions, then it may be useful to provide information about the nature of visits with a covariate (see below). Other individual covariates such as habitat measures associated with the nest site could be included. Covariates associated with a group of nests (group covariates) such as weather or year could also be included.

To illustrate the data format, we utilize an example dataset for Mallard (*Anas platyrhynchos*) nests that were monitored during 2000 in the Coteau region of North Dakota as part of a larger study (Stephens et al. 2005). The example dataset contains nest-, group- and time- specific covariates and contains information from 1,585 observation intervals for 565 nests monitored on 18 sites during a 90-d nesting season. Interval lengths ranged from 1–18 d and were most commonly 4, 5, or 6 d (frequencies of observations for interval lengths of 1, 2, 3, 4, 5, 6, 7, 8, 10, 11, 12, and 18 d were 50, 27, 150, 475, 542, 245, 63, 21, 4, 6, 1, and 1, respectively). Here, the following subset of the covariates measured by Stephens et al. (2005) was considered for each observation interval: (1) nest age at the start of the interval (Age, 1–35 d), (2) day of the nesting season at the start of the interval (Date, 1–90), (3) vegetative visual obstruction at the nest site (Robel et al. 1970), (4) the proportion of the study site (10.4 km^2) containing the nest that was in grassland cover (PpnGr), (5–7) the habitat type in which the nest was located (three dummy variables were used to distinguish among native grassland (NatGr), planted nesting cover (PlCov), wetland vegetation (Wetl), and roadside right-of-way (Road), (8) study site (Site), and (9) nest-visitation status on each day of the interval (Ob, a dummy variable coded as 1 on the day a nest was visited and 0 otherwise). Nest-visitation status did not appear in the original input file as this variable was created with programming statements during the analysis (see below).

Data were originally recorded in interval-specific form, and thus, each row of data contained information for one observation interval for an individual nest (Table 1). All analyses that appear below were conducted on this dataset and input format. However, it is possible to do a great deal of modeling with a reduced version of the dataset. If the possible observer effects on daily survival rates are not of interest, and, if nest age and date are the only nest-specific time-varying covariates to be considered, then the interval-specific data can be collapsed with no loss of information.

TABLE 1. INPUT FORMAT FOR INTERVAL-SPECIFIC NEST-SURVIVAL DATA.[a]

ID	Species	Site	Hab	Int	t	IFate	SDate	Sage	Robel	PpnGr
1	MALL	14	PlCov	1	5	1	1	1	4.50	0.96
1	MALL	14	PlCov	2	5	1	6	6	4.50	0.96
1	MALL	14	PlCov	3	4	1	11	11	4.50	0.96
1	MALL	14	PlCov	4	6	1	15	15	4.50	0.96
1	MALL	14	PlCov	5	5	1	21	21	4.50	0.96
1	MALL	14	PlCov	6	5	1	26	26	4.50	0.96
1	MALL	14	PlCov	7	4	1	31	31	4.50	0.96
2	MALL	14	PlCov	1	5	1	1	3	0.88	0.96
2	MALL	14	PlCov	2	5	1	6	8	0.88	0.96
2	MALL	14	PlCov	3	4	1	11	13	0.88	0.96
2	MALL	14	PlCov	4	6	0	15	17	0.88	0.96
2,206	MALL	16	Road	1	4	1	73	13	6.00	0.80
2,206	MALL	16	Road	2	5	1	77	17	6.00	0.80
2,206	MALL	16	Road	3	4	1	82	22	6.00	0.80
2,206	MALL	16	Road	4	3	1	86	26	6.00	0.80

[a] (ID—nest number, Species—species code, Site—study site, Hab—habitat code, Int—observation interval, t—interval length (d), Ifate—nest fate for the interval, SDate—date at the start of the interval, SAge—nest age at the start of the interval, Robel—vegetative visual obstruction at nest site, and PpnGr—proportion of grassland cover on the 10.4-km^2 study site.

The critical information to retain for each nest consists of (1) the age of the nest when it was found, (2) the day the nest was found, (3) the last day the nest was checked alive, (4) the last day the nest was checked, and (5) the fate of the nest (successful or unsuccessful) on the last visit. For successful nests, the dates in items (3) and (4) above will be equal, and the entire set of re-visit intervals can be collapsed into one interval (one row of data with Ifate = 1). For unsuccessful nests, the dates in items (3) and (4) above will be different, and data may need to be presented as one or two rows of data depending on the timing of nest failure. For nests that fail by the end of the first re-visit interval, the relevant data are contained in a single row of data (with Ifate = 0). For nests that fail after the end of the first re-visit interval, two rows of data are required: one row of data will consist of a successful interval (Ifate = 1) starting on the day the nest was found (item 2 above) and ending on the last day the nest was checked alive (item 3 above); a second interval (with Ifate = 0) will start on the last day the nest was checked alive (item 3 above) and end on the last day the nest was checked (item 4 above). Analysis of data in this reduced format will not be considered further here but can be accomplished with the methods described below. It is worth noting that data in this reduced format do prevent the evaluation of possible visit effects on nest fate.

GENERALIZED MIXED MODELS IN PROC NLMIXED

Because interval lengths typically are >1 d, it is necessary to use programming statements from within NLMIXED to iteratively do the logit survival value for each of the days in an interval (see below). Through programming statements, covariates such as date and age that vary across an interval in a predictable fashion can be included in each day of an interval.

Consider a model that includes (1) a covariate x_1 that does not vary by time, (2) nest age, and (3) date. This method models a nest's fate for a given interval as:

$$Ifate_i = \prod_{k=0}^{t-1} \left(\frac{\exp(\beta_0 + \beta_1 x_{1i} + \beta_2(StartAge_i + k) + \beta_2(StartDate_i + k)}{1 + \exp(\beta_0 + \beta_1 x_{1i} + \beta_2(StartAge_i + k) + \beta_2(StartDate_i + k)} \right).$$

Applying this model to a 2-d observation interval that started on the 20th day of the nesting season for a nest that was 15-d old at the start of the interval and whose value for covariate x_1 was 10 would yield:

$$\left(\frac{\exp(\beta_0 + \beta_1 10 + \beta_2 15 + \beta_2 20)}{1 + \exp(\beta_0 + \beta_1 10 + \beta_2 15 + \beta_2 20)} \right)$$

$$\left(\frac{\exp(\beta_0 + \beta_1 10 + \beta_2 16 + \beta_2 21)}{1 + \exp(\beta_0 + \beta_1 10 + \beta_2 16 + \beta_2 21)} \right)$$

Because the method allows covariates to be specified differently on different days within an interval, observer effects on nest survival can be modeled in a straightforward manner. Specifically, an index variable (visit) is created with programming statements such that it takes on a value of one for the first day of an interval (day the nest was visited) and zero otherwise. This variable can then be used to evaluate

whether variation in daily survival rates was associated with observer visits. If additional covariates contain information on the nature of a nest visit, these covariates can be allowed to interact with the visit variable to test for their potential influence on survival rate. To illustrate, consider a 2-d interval and a model that includes the effect of an observer visit and a single covariate (x_1) on daily survival rate.

$$Ifate_i = \left(\frac{\exp(\beta_0 + \beta'_0 \, visit + \beta_1 x_{1i})}{1 + \exp(\beta_0 + \beta'_0 \, visit + \beta_1 x_{1i})} \right)$$

$$\left(\frac{\exp(\beta_0 + \beta_1 x_{1i})}{1 + \exp(\beta_0 + \beta_1 x_{1i})} \right)$$

Thus, procedures in SAS allow for examination of a rich collection of models for nest-survival data.

As stated earlier, the NLMIXED procedure also allows models to include random effects (associated with a single factor) as well as fixed effects; hence, it allows mixed models (SAS Institute 2004). The random effects are assumed to follow normal distributions, typically with zero mean and unknown variances. In the NLMIXED procedure, all random effects must be associated with a single factor (termed the subject variable in PROC NLMIXED) for which multiple observations made at the same level of the factor may be correlated. For example, study site might be considered as a factor having random effects on nest survival because fates of nests on the same site (same factor level) might be correlated to some degree.

Multiple random effects can be modeled in PROC NLMIXED as long as they are all associated with a single factor, and we now consider some of the mixed models that may be of interest in studies of nest survival. When presenting mixed models below, we follow a common convention (Littell et al. 1996) of using Greek symbols to refer to regression coefficients that are assumed to be fixed effects and using Latin symbols to refer to those that are random. Because random effects in PROC NLMIXED are assumed to follow normal distributions, typically with zero mean and unknown variances, it is appropriate to consider them as a random sample of deviations from some population regression model (Littell et al.1996). Thus, random effects can be used to model deviations in one or more of the fixed-effect coefficients (various combinations of the intercept and slope terms) associated with different levels of the random factor being considered.

To illustrate, consider a 1-d interval and a model that includes the effect of a single covariate (x_1) on daily survival rate. A model that also includes a random effect of study site on the model's intercept term would be:

$$Ifate_{ij} = \left(\frac{\exp((\beta_0 + b_{0j}) + \beta_1 x_{1i})}{1 + \exp((\beta_0 + b_{0j}) + \beta_1 x_{1i})} \right),$$

where b_{0j} represents the random effect on the intercept term that is associated with the *j*th study site. Alternatively, a model with

$$Ifate_{ij} = \left(\frac{\exp(\beta_0 + (\beta_1 + b_{1j})x_{1i})}{1 + \exp(\beta_0 + (\beta_1 + b_{1j})x_{1i})} \right)$$

could be used to include a random effect on the model's slope term, (b_{1j}), or both types of random effects could be considered:

$$Ifate_{ij} = \left(\frac{\exp((\beta_0 + b_{0j}) + (\beta_1 + b_{1j})x_{1i})}{1 + \exp((\beta_0 + b_{0j}) + (\beta_1 + b_{1j})x_{1i})} \right).$$

PROC NLMIXED will estimate the values for each of the elements of the variance-covariance matrix of the random effects that are specified in the model. For example, if the model included both b_{0j} and b_{1j}, the variance of each random effect and the covariance between b_{0j} and b_{1j} would be estimated.

In the NLMIXED procedure, mixed models are fit by maximizing an approximation to the likelihood that is integrated over the random effects (SAS Institute 2004). Accordingly, calculations may take some time and convergence is not guaranteed. Starting values are not required for PROC NLMIXED but may be helpful, and the procedure has tools for implementing a variety of starting values. The procedure has a variety of integral approximations and alternative optimization techniques available, and these may be helpful in some cases. Finally, it may be useful to run fixed-effects models prior to mixed models to obtain reasonable starting values for the fixed-effects parameters of mixed models.

PROC NLMIXED also enables one to calculate user-specified functions of the parameters and to compute the approximate standard errors using the delta method (Seber 1982). This is useful for estimating daily survival rate and nesting success from the parameter estimates by back-transformation through the inverse or logistic link function (Lebreton et al. 1992). If the user specified function only involves parameters representing fixed effects, the calculation can be made in SAS with an ESTIMATE statement. If on the other hand, the specified function includes random effects, either alone or in combination with fixed effects, a PREDICT statement must be used (SAS Institute 2004).

EXAMPLE ANALYSIS OF NEST-SURVIVAL DATA IN PROC NLMIXED

Here, we use the example Mallard dataset and a brief model list to illustrate the implementation of the methods described here using PROC NLMIXED and simple programming statements (Rotella et al. 2006). We analyzed a set of 10 fixed-effects models and two mixed models using PROC NLMIXED, where study site was considered a random effect in the mixed models (Table 2). Models included various combinations of nest-, group-, and time-specific covariates. This list included simple models that have been commonly employed in past studies of nest survival. The simplest model was an intercept-only model that held S_i constant for all groups, nest ages, dates, and habitat conditions, and which is similar to that of Johnson (1979) and Bart and Robson (1982). A model that allowed S_i to vary among groups (nests in different habitat types in this example) was analogous to (but more efficient than) conducting a stratified analysis with methods of Johnson (1979) and Bart and Robson (1982) and testing for homogeneity among group-specific survival rates with methods of Sauer and Williams (1989). For a more thorough analysis of the full data set from which this example was extracted, see the analysis and results presented by Stephens et al. (2005).

Of the 12 models considered, the two most parsimonious models both included a random effect of site (Table 2): the site-to-site process variance (Burnham et al. 1987) was estimated as 0.089 (SE = 0.052) by the better of these two models. Stephens et al. (2005) provided possible explanations for the presence of the random effect in these data, e.g., differing predator communities among sites. The second-most parsimonious model (ΔAIC_c = 0.33) provided some evidence of a negative effect of observer visits

on daily survival rate for the day of a nest visit = ($\hat{\beta}$ = -0.844, SE = 0.629). The point estimate indicates that the effect was potentially of a size that is of interest, but the lack of precision makes inference difficult. For example, on a site with 50% grassland cover, daily survival for a 15-d old nest would be predicted as 0.911 (SE = 0.033, 95% CI = 0.842–0.981) if it were visited and 0.960 (SE = 0.010, 95% CI = 0.939–0.981) otherwise, where the estimates were obtained using the ESTIMATE statement (one statement for each of the two scenarios) of PROC NLMIXED (Rotella et al. 2006). It is noteworthy that models that held daily survival rate constant or simply allowed it to vary by habitat type, which are the only model types that have been used in many recent publications on nest survival (see above), received no support when compared to the models discussed above ($\Delta AIC_c \geq 15.10$).

Once one has chosen an approximating model of daily survival rate, one is interested in using that model and its estimated parameter values to obtain estimates of survival over multiple days for various covariate conditions. For example, one might be interested in estimating the probability that a Mallard nest on a site with 85% grassland cover would survive the 35 d from nest initiation to hatching. To do so involves working with functions of random variables (the estimated coefficients of the approximating model). For a model that considers nest age and proportion grass on the site, one can calculate the probability that a nest would survival from age one through age 35 on a site with 85% grassland as follows:

$$\hat{S}_{35days} = \prod_{Age=1}^{35} \left(\frac{\exp(\hat{\beta}_0 + \hat{\beta}_1 Age + \hat{\beta}_2(0.85))}{1 + \exp(\hat{\beta}_0 + \hat{\beta}_1 Age + \hat{\beta}_2(0.85))} \right),$$

where S_{35days} is the probability of surviving 35 days. To derive an estimate of the variance of the transformation of the three estimated

TABLE 2. SUMMARY OF MODEL-SELECTION RESULTS OBTAINED IN PROC NLMIXED (SAS INSTITUTE 2004) FOR FIXED-EFFECTS AND MIXED MODELS OF DAILY SURVIVAL RATE FOR MALLARD NESTS STUDIED BY STEPHENS ET AL. (2005) IN NORTH DAKOTA.

Model	K	AIC_c	ΔAIC_c	w_i
$\beta_0 + \beta_1 \times Age + \beta_2 \times PpnGr + b_1 \times site$	4	1,554.013	0.000	0.529
$\beta_0 + \beta_1 \times Age + \beta_2 \times PpnGr + \beta_3 \times Ob + b_1 \times site$	5	1,554.340	0.327	0.449
$\beta_0 + \beta_1 \times Age + \beta_2 \times PpnGr + \beta_3 \times Ob$	4	1,562.265	8.252	0.009
$\beta_0 + \beta_1 \times Age + \beta_2 \times PpnGr$	3	1,563.010	8.996	0.006
$\beta_0 + \beta_1 \times Age$	2	1,564.066	10.053	0.003
$\beta_0 + \beta_1 \times Age + \beta_2 \times Robel$	3	1,565.906	11.892	0.001
$\beta_0 + \beta_1 \times Age + \beta_2 NatGr + \beta_3 \times CRP + \beta_4 \times Wetl$	5	1,567.344	13.330	0.001
$\beta_0 + \beta_1 \times PpnGr$	2	1,567.368	13.355	0.001
β_0	1	1,569.117	15.103	0.000
$\beta_0 + \beta_1 \times Robel$	2	1,570.775	16.762	0.000
$\beta_0 + \beta_1 \times Date$	2	1,570.826	16.813	0.000
$\beta_0 + \beta_1 \times NatGr + \beta_2 \times CRP + \beta_3 \times Wetl$	4	1,571.957	17.944	0.000

coefficients (or random variables) in the equation above random variables, one could use the delta method (Seber 1982, Williams et al. 2002) or simulation methods such as bootstrapping.

MONTE CARLO SIMULATIONS IN PROC NLMIXED

Monte Carlo Simulation (MCS) offers an empirical approach to examining a variety of characteristics of estimation results from analysis procedures (Fan et al. 2003). Distributional characteristics of estimated regression coefficients, and their associated estimates of precision, are of interest here, especially for the random effects, as these methods have not been employed for nest-survival data previously. MCS is also useful for evaluating the consequences of violating assumptions and for evaluating different potential sampling schemes that may be used in future research. Thus, we developed computer code that creates nest-survival data for multiple sites in interval-specific form according to an underlying model of interest (Rotella et al. 2006). Nests can vary from one another in terms of their characteristics, and nest-visitation intervals can vary in length among the samples. Nest fates, which can be affected by both fixed effects and a single random factor, are obtained using random sampling techniques. The data are then analyzed using models of interest, key results are stored, the process is repeated many times, and summary statistics of interest are calculated. The code can be adjusted to accommodate different scenarios.

Here we provide the results for a scenario where survival for an interval was modeled as

$$Ifate_{ij} = \prod_{k=0}^{t-1}\left(\frac{\exp((\beta_0 + b_{0j}) + \beta_1 x_{1i})}{1 + \exp((\beta_0 + b_{0j}) + \beta_1 x_{1i})} \right).$$

In the simulation, the true parameter values for the fixed effects were $\beta_0 = 2.0$ and $\beta_1 = 1.75$. The random effect of study site was normally distributed (mean = 0, variance = 0.25). The covariate x_1 was a uniformly distributed nest-specific covariate (range = 0–1.0). For each simulation, data were generated for 375 nests (25 nests per site for 15 different sites).

Summary statistics based on 1,000 simulations provide evidence that the method produces estimates with little bias and reasonable precision (Table 3), at least for the scenario described above. Coverage for 95% confidence intervals was close to the nominal level for each of the parameters estimated. We have reached similar conclusions for a variety of scenarios where the samples of nests are balanced across sites.

The design of samples and experiments in a mixed model context is a subject in need of both further research and communication. But, based on the results of our simulation work, it seems clear that the bare-minimum data requirements of the mixed-models approach described here are as follows: data from ≥five levels of the factor being modeled as a random effect and data from ≥20 nests per level of the random factor. These are not hard and fast rules. For example, if one were to have data from only five study sites, then it would likely be best to treat site as a fixed effect as information is likely available from too few sites to allow accurate inference to the universe from which study sites might have been selected. Further, although 20 nests per site may be adequate for estimating landscape-level parameters if a substantial number of sites are surveyed, 20 nests per site will not yield an accurate estimate of the random effect at any given site. If estimating daily survival rate at the specific sites surveyed is of interest, considerably greater sample sizes will be required.

Heisey et al. (*this volume*) provide an important caveat regarding estimation in the presence of random effects. In typical studies of nest survival, data are left-truncated because some nests that fail early are not included in the sample (Heisey et al., *this volume*). Under these circumstances, it is easy to imagine scenarios for which estimates of survival will be biased high to some extent because nests in the sample overrepresent nests with higher underlying survival rates (Heisey et al., *this volume*).

TABLE 3. SUMMARY STATISTICS FOR 1,000 [a] MONTE CARLO SIMULATIONS.

| Parameter[b] | Mean estimate | Mean SE | 95% confidence interval | | Coverage |
			Lower bound	Upper bound	
β_0	2.13	0.19	1.72	2.54	0.98
β_1	1.76	0.30	1.17	2.36	0.97
σ^2_{site}	0.24	0.12	−0.02	0.50	0.97

[a] The general convergence criterion of PROC NLMIXED was satisfied for 985 of the 1,000 datasets. The 15 problematic datasets were discarded, and results presented are for the remaining 985 datasets. However, based on our experience with this procedure, convergence would likely have been achieved for many, if not all, of the remaining 15 datasets had we changed features such as the number of iterations, starting values, etc. (SAS Institute 2004).

[b] True parameter values were 2.0, 1.75, and 0.25, respectively.

To illustrate, we use an example where study site is a factor that is treated as a random effect. Under such a situation, a sample of sites having the same values for covariates treated as fixed effects will still vary in terms of their underlying survival rates: the unmeasured fixed effects responsible for the random effect will cause some of these sites to be better than others. All else being equal (nest densities, and search effort), sample sizes will be larger for those study sites that are associated with higher survival rates because nests in such settings are expected to survive longer and thus, have a greater chance of entering the sample. When the sample sizes are positively correlated with survival rates, estimates of survival will be biased high to some extent because nests in the sample over-represent nests with higher underlying survival rates (Heisey et al., *this volume*).

Given this fact, we conducted additional simulations for a modified version of the scenario described above in which the model structure and values for the fixed and random effects remained the same but the sample sizes varied among sites. Specifically, sample size per site was a function of the fixed effect and the random effect for the site, which caused a site's sample size to be positively related to a study site's survival rate (number of nests per site varied from ~10 for the poorest sites to ~25 on the best sites). We then evaluated the performance of two models: the generating model (mixed model) and a fixed-effects only model, which did not model the random effect. In accordance with statements made by Heisey et al. (*this volume*), estimates from the mixed model were biased. For the scenario investigated, the estimated parameter values were biased such that estimated survival rates were too high and the variation associated with the random effect of site was too low (true β_0 = 2.0, estimated β_0 = 2.5 [SE = 0.19]; true β_1 = 1.75, estimated β_1 = 1.3 [SE = 0.33]; true $\sigma^2_{random\ effect}$ = 0.25, estimated $\sigma^2_{random\ effect}$ = 0.14 [SE = 0.10]).

We believe that this result should not be interpreted as calling into question the use of mixed models for nest-survival data. This point is made clearer by considering the estimates that were obtained from the fixed-effects model for these simulations. Parameter estimates from a fixed-effects-only model had the same level of bias as did the estimates from the mixed model, but these estimates were more precise. Thus, if one were to avoid the use of mixed models, the bias due to analyzing left-truncated data in the presence of random effects would still persist. But, the inferences about the estimates would be falsely made more confidently, and, because the random effect would not be estimated, there

would be no opportunity to detect the presence of heterogeneity in the data above and beyond the fixed effects. The primary problem is whether random effects are in the data.

Clearly, if random effects might be present in left-truncated nest-survival data, the study design will have to be carefully considered. Simulation work completed to date indicates that balanced designs (equal numbers of nests found across levels of the covariate being treated as a random factor) effectively deals with this potential problem. Given that one will not typically know prior to data analysis whether or not random effects will exist in the data, it seems prudent to adjust search effort such that balanced samples are achieved. The issue of bias from left truncation has received little attention, and more work is needed to determine the magnitude of the problem under typical sampling scenarios.

Optimal study design will, of course, depend upon the particulars of each study such as effect sizes for factors of interest, process variation in system, and complexity of models being considered. In planning a study, if one knows that great variation is likely among levels of the random factor, obtaining data from nests over many levels of that factor will be more useful than will be obtaining large numbers of nests per level of that factor. For example, data from many sites with fewer nests/site will be better than data from few sites with many nests/site. Simulations can be used to gain insights into the advantages and disadvantages of various study designs, especially if pilot data are available to guide the simulation, for example simulation code that can be readily modified to suit the specific circumstances of different studies is available (Rotella et al. 2006).

FUTURE DIRECTIONS

The methods reviewed above provide several advances over the typical analysis methods used for most studies of nest survival. We have provided examples of some of the utility of the approach, but other innovative uses of existing methods will likely be useful. For example, survival rates of individual young within nests could be investigated with individual nest treated as a random effect and covariates such as egg (or nestling) size and age considered as fixed effects. However, improvement is possible. In some studies, it will be desirable to examine the relationship between nest survival and multiple random factors. For example, in studies that are well replicated in space and time (>10 sites replicated for >10 yr), it will be of interest to estimate the variance components

associated with the random effects of both study site and year.

Interest is growing in the consequences of individual variation in vital rates (Link et al. 2002), and results from models that incorporate heterogeneity indicate that the consequences on population dynamics can be substantial (Cam et al. 2002). Further, results show that sources of variation among individuals cannot always be sufficiently accounted for by age, year, or environmental conditions. That is, it may be necessary to allow each individual to have a unique mortality risk (Service 2000). One method of doing so is to use the methods described here to treat the individual as a random effect, but this cannot be done while also considering another random factor such as site or year. Thus, it is apparent that hierarchical models that permit multiple random factors are desirable.

Heisey et al. (*this volume*) raised an important issue regarding possible bias in estimates made from left-truncated data containing overdispersion due to random effects. We suggested above that balanced sampling designs may effectively deal with the problem. But, the issue of estimation bias from left truncation has received little attention, and more work is needed to (1) determine the magnitude of the problem under various sampling scenarios, (2) evaluate possible solutions that can be implemented during the analysis stage such as equal weighting of data from all levels of the random factor regardless of sample sizes, and (3) make recommendations regarding the appropriate interpretation of estimates from studies of nest-survival data when random effects may be present.

The methods presented here do not consider detection probability for nests with different characteristics as do some other methods (Pollock and Cornelius 1988, Bromaghin and McDonald 1993a, McPherson et al. 2003). Accordingly, these methods provide estimates that are conditional on the data set (Pollock and Cornelius 1988, Bromaghin and McDonald 1993a, McPherson et al. 2003). We note that the sample can also be non-representative of the entire population because the nature of the survey methods, birds, or both is such that nests can not be found until they are above some minimum age. For example, in some species it may be the case that nests can not be found prior to incubation because the birds spend little time on nests prior to incubation and the birds provide the cues used by researchers for finding nests. Or, for studies of species in which nest visits cause premature fledging, data may not be available for nests above some threshold age.

The methods presented here do not consider several other situations that may be encountered in nesting studies for some species. For some species, nest age will be a covariate of interest but be unknown for many nests (Stanley 2004a). Also, typical assumptions about the distributions of hatching and fledging events may be violated in some studies (Etterson and Bennett 2005). Under such circumstances, it will also be difficult to know the exact fledging date for nests and to time final nest checks such that nest fates can be unambiguously determined (Manolis et al. 2000). Given that these circumstances will occur regularly for some species of interest, it would be valuable to future studies of nest survival if methods for dealing with ambiguities in aging and determining fate (Manolis et al. 2000; Stanley 2000a, 2004; Etterson and Bennett 2005) could be incorporated into the methods presented here.

It seems clear that the analysis methods described here provide improvements but do not allow for complete evaluation of possible heterogeneity in nest-fate data. Analysis methods presented by Natarajan and McCullach (1999) provide conceptual solutions to the problem. However, exact solutions of the likelihoods presented are computationally intractable for modestly complex problems. An approach using accurate approximate solutions is essential, and extensions of work done by Lele and Taper (2002) may be useful in the future. Use of Markov Chain, Monte Carlo methods in a Bayesian approach (Link et al. 2002), may also prove useful for solving such complex problems with nest-survival data (He et al. 2001, He 2003). Bayesian alternatives to the approach described here can be implemented in readily available software packages such as program MARK (White and Burnham 1999) or WinBUGS (Lunn et al. 2000). Regardless of the approach used, we expect more complex hierarchical models to provide logical extensions to the concepts and analysis methods presented here. Of course, such analyses will require excellent data sets resulting from sound sampling designs.

The advances made by Mayfield (1961) and others (Johnson 1979, Bart and Robson 1982) are seminal and pivotal for continued improvement in the approaches that we use for analysis. Those historic approaches have some restrictive and potentially unrealistic assumptions that may cause biased estimates and misleading inferences if the investigator is not cautious about such pitfalls. Recent advancements in the analysis of nest-survival data and the availability of appropriate computer programs have raised the standards for assessing this important attribute of avian biology. Investigators that acquire nest-fate data collected from properly designed studies, which provide a representative sample

of nests, should use these analysis tools to make reliable inference about nest survival. We therefore submit that analysis of nest-survival data in the framework provided by programs such as MARK (Dinsmore et al. 2002) or SAS (Stanley 2000, 2004a; Shaffer 2004a) should be a minimum level of analysis for modern, avian studies. We hope investigators with specific interests in the effects of heterogeneity on nest-survival estimates or those with specific questions about levels of process variation in their population will consider some of the advanced methods described here and elsewhere.

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