A UNIFIED APPROACH TO ANALYZING NEST SUCCESS

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Abstract.—Logistic regression has become increasingly popular for modeling nest success in terms of nest-specific explanatory variables. However, logistic regression models for nest fate are inappropriate when applied to data from nests found at various ages, for the same reason that the apparent estimator of nest success is biased (i.e. older clutches are more likely to be successful than younger clutches). A generalized linear model is presented and illustrated that gives ornithologists access to a flexible, suitable alternative to logistic regression that is appropriate when exposure periods vary, as they usually do. Unlike the Mayfield method (1961, 1975) and the logistic regression method of Aebischer (1999), the logistic-exposure model requires no assumptions about when nest losses occur. Nest survival models involving continuous and categorical explanatory variables, multiway classifications, and time-specific (e.g. nest age) and random effects are easily implemented with the logistic-exposure model. Application of the model to a sample of Yellow-breasted Chat (*Icteria virens*) nests shows that logistic-exposure estimates for individual levels of categorical explanatory variables agree closely with estimates obtained with Johnson's (1979) constant-survival estimator. Use of the logistic-exposure method to model time-specific effects of nest age and date on survival of Blue-winged Teal (*Anas discors*) and Mallard (*A. platyrhynchos*) nests gives results comparable to those reported by Klett and Johnson (1982). However, the logistic-exposure approach is less subjective and much easier to implement than Klett and Johnson's method. In addition, logistic-exposure survival rate estimates are constrained to the (0,1) interval, whereas Klett and Johnson estimates are not. When applied to a sample of Mountain Plover (*Charadrius montanus*) nests, the logistic-exposure method gives results either identical to, or similar to, those obtained with the nest survival model in program MARK (White and Burnham 1999). I illustrate how the combination of generalized linear models and information-theoretic techniques for model selection, along with commonly available statistical software, provides ornithologists with a powerful, easily used approach to analyzing nest success. *Received 23 April 2003, accepted 14 January 2004.*

Resumen.—La regresión logística se ha hecho cada vez más popular para modelar el éxito de nidificación en términos de variables explicativas específicas para los nidos. Sin embargo, los modelos de regresión logística para el éxito de los nidos son inapropiados cuando se aplican a datos de nidos de diferentes edades, por la misma razón que el estimador aparente del éxito de nidificación está sesgado (i.e. nidadas más viejas son probablemente más exitosas que nidadas más jóvenes). Aquí se presenta e ilustra un modelo lineal generalizado que les brinda a los ornitólogos una alternativa flexible y adecuada a la regresión logística que es apropiada cuando los períodos de exposición varían, como sucede a menudo. A diferencia del método de Mayfield (1961, 1975) y del modelo de regresión logística de Aebischer (1999), el modelo logístico de exposición no requiere suponer cuándo ocurre la pérdida de los nidos. Los modelos de supervivencia de los nidos que incluyen variables explicativas continuas y categóricas, clasificaciones de múltiples vías y efectos temporales específicos (e.g. edad del nido) y aleatorios, son implementados fácilmente con el modelo logístico de exposición. La aplicación del modelo a una muestra de nidos de *Icteria virens* mostró que las estimaciones de los niveles individuales de variables categóricas explicativas coinciden en gran medida con las obtenidas con el estimador de supervivencia constante de Johnson (1979). El uso del método logístico de exposición para modelar los efectos temporales específicos de la edad y fecha del nido en relación con la supervivencia de nidos de *Anas discors* y *A. platyrhynchos* brinda resultados comparables con aquellos suministrados por Klett y Johnson (1982). Sin embargo, el enfoque del modelo logístico de exposición es menos subjetivo y mucho más fácil de implementar que el método de Klett y Johnson. Además, las estimaciones de la tasa de supervivencia del método logístico de exposición están restringidas al intervalo (0,1), mientras que las estimaciones de Klett y Johnson no lo están. Cuando el método logístico de exposición

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es aplicado a una muestra de nidos de *Charadrius montanus*, los resultados son idénticos o simi-
lares a los obtenidos con el modelo de supervivencia de nidos del programa MARK (White y
Burnham 1999). Aquí muestro cómo la combinación de modelos lineales generalizados y técnicas
de información teóricas de selección de modelos, junto con paquetes estadísticos comúnmente
disponibles, les brindan a los ornitólogos un enfoque poderoso y fácil de usar para analizar el
éxito de nidificación.

Determining the influence of various factors on natality and mortality is crucial to understanding the dynamics of an animal population. Nest success is an important component of natality for many species of birds. Methods for estimating nest success have received considerable attention in the ornithological and biometrics literature (e.g. Mayfield 1961, Johnson 1979, Klett and Johnson 1982, Bromaghin and McDonald 1993, Aebischer 1999, Rotella et al. 2000, Stanley 2000, Dinsmore et al. 2002). In a typical nesting study, investigators periodically search for nests, discover them at various stages of development (ages), and revisit them one or more times to monitor status until nests either succeed (i.e. eggs hatch or nestlings fledge) or fail. Thus, time from discovery to expected date of termination (hatch or fledge) varies among clutches. Because presence of an adult is often used as a primary cue for locating nests, clutches that survive for only a short time are easily missed by investigators and tend to be underrepresented in samples. Mayfield (1961, 1975) observed that older clutches, because they are closer to hatching (or fledging), are more likely to be successful than younger ones and that the apparent estimator of nest success (proportion of observed clutches that are successful) overestimates actual nest success. He proposed an *ad hoc* estimator based on calculating a daily survival rate, assumed constant from day to day and nest to nest, and raising it to a power equal to the number of days from initiation to a successful outcome. To calculate daily survival rate, one first computes daily mortality rate by dividing number of nest failures by total exposure days for all nests under observation during the period of interest. Because clutches typically are not monitored daily, the date of failure, and hence the period of exposure, for failed nests is unknown and must be assumed. Mayfield assumed that failure would occur midway between visits. Whereas Mayfield based his midpoint assumption on studies of passerine species in which intervals between visits to nests were short, Miller and Johnson

(1978) recommended that unsuccessful waterfowl nests be credited with surviving only 40% of the interval between visits (the "40-percent Mayfield estimator") to account for longer visitation intervals typical of waterfowl studies.

Johnson (1979) provided the mathematical framework for Mayfield's method and developed a large-sample variance estimator. Johnson (1979) and Bart and Robson (1982) developed a maximum-likelihood estimator that does not require knowledge of the date of nest loss (the "Johnson estimator"). Comparing Mayfield's estimator, the 40-percent Mayfield estimator, and the Johnson estimator on several data sets, Johnson (1979) observed that Mayfield's method and the more computationally intensive Johnson estimator gave similar results, especially when visitation intervals were short. The 40-percent Mayfield estimator performed slightly better than the original Mayfield method when applied to data sets with longer intervals between visits. Johnson concluded that Mayfield's method, perhaps with an adjustment in exposure for infrequently visited nests, is adequate when data are limited but recommended the Johnson estimator for comprehensive analyses of large data sets. Although Mayfield's concern over bias in the apparent estimator was slow to gain recognition, his method or suitable modification is now widely used.

A frequent goal of nesting studies is to understand how nest success varies in response to changes in one or more explanatory variables. Mayfield's method can be used to address that objective, if the assumption of constant daily survival can be met and if samples of nests are adequate to estimate a daily survival rate for each combination of levels of the explanatory variables. The latter is a serious problem with continuous explanatory variables. For example, a study looking at the effect of distance from a nest to the nearest habitat edge may result in a sample of hundreds of nests, each having a different value for the explanatory variable, distance to edge. In situations like that, logistic

regression (Hosmer and Lemeshow 1989), which models probability of success as a function of the explanatory variables, has become increasingly popular (e.g. Hanski et al. 1996, Maxson and Riggs 1996, Burhans and Thompson 1999, Willson and Gende 2000, Zanette and Jenkins 2000, Davidson and Knight 2001).

Several variants of logistic regression have been used. In one variant, each nesting attempt is treated as a Bernoulli trial, and nest fate (success or failure) is related to the various explanatory variables without regard to the length of time the nest was under observation (e.g. Frederick and Collopy 1989, Maxson and Riggs 1996, Willson and Gende 2000). That approach is analogous to using the apparent estimator of nest success and suffers from the same bias noted by Mayfield and others.

In a second variant, differences in exposure period are accounted for by including the number of exposure days for each nest (e.g. Pasitschniak-Arts et al. 1998) or each nest-check interval (e.g. Garrettson and Rohwer 2001) as an explanatory variable in the logistic regression. That approach is incorrect, because the effect of exposure period is not additive on the logistic scale, yet the analysis treats it as such.

Aebischer (1999) proposed a logistic regression approach that considers each nest-day as a Bernoulli trial. The unit of analysis is the nest, the response variable is number of days of successful observation at the nest, and number of Bernoulli trials is equal to number of nest-days. By definition, number of days of successful observation is either equal to (for successful nests) or one less than (for unsuccessful nests) the number of nest-days. Aebischer's method works well when nests are visited daily (and, therefore, number of nest-days is known exactly) but is problematic when visits are not daily and nest-days must be estimated. To illustrate the problem, consider a nest that is found on 1 May and revisited on 4 May. For the clutch to survive the interval, it must survive three nest-days (i.e. 1 May, 2 May, and 3 May). Thus, a successful clutch is credited with three days of successful observation during three nest-days. If the clutch does not survive the interval, a reasonable assumption might be that it survived day 1 (1 May) but did not survive day 2 (2 May), giving rise to one day of successful observation in two nest-days. That assumption is akin to Mayfield's midpoint assumption. Now consider

a clutch found on 1 May and revisited on 5 May. If that clutch survives the interval, clearly the number of days of successful observation and the number of nest-days is four. But if the clutch fails, do we assume that it fails on day 2 (2 May) or day 3 (3 May)? Johnson (1979) used probability theory to show that the clutch would be expected to fail between day 2 and day 3. Thus, consistent application of either of the proposed failure dates (2 May or 3 May) would lead to a bias, the direction of which would be positive in one case and negative in the other. The problem of unknown failure date is exacerbated as intervals become longer and Mayfield's midpoint assumption becomes more tenuous. Mayfield (1975) and Miller and Johnson (1978) were able to effectively deal with that issue by allowing for fractional nest-days and by pooling nest-days across relatively large samples of nests. In a logistic-regression context, however, nest-days must take on integer values. Moreover, pooling across nests, which would tend to reduce the bias, does not occur, because individual nests are sample units.

The nest survival model available in program MARK (White and Burnham 1999) allows daily nest survival to be rigorously modeled as a function of nest-, group-, and time-specific explanatory variables (Dinsmore et al. 2002). The model allows visitation intervals to vary and requires no assumptions about when nest losses occur. Program MARK uses encounter histories of individual nests and likelihood-based procedures to estimate regression coefficients for explanatory variables included in the model. Values for time-specific explanatory variables, such as age, date, and precipitation, are allowed to vary daily. For ornithologists willing to learn program MARK, its nest survival model provides a highly flexible and powerful alternative to traditional constant-survival methods.

In addition to estimating daily survival rates and relating them to continuous or categorical explanatory variables, interest often lies in comparing daily survival rates among groups of nests. Johnson (1979) provided a large-sample t-test for comparing daily survival rates between two categories of nests, and Johnson (1990) extended the method to more than two categories. Sauer and Williams (1989) provided a chi-square test statistic that can be used to test for homogeneity among several survival rates and investigator-defined hypotheses. Aebischer (1999) used

generalized linear models and likelihood-ratio theory to develop hypothesis-testing procedures for complex Mayfield models for nests that were visited daily or for which date of failure could otherwise be determined.

Biologists are realizing that model selection and parameter estimation should be emphasized over hypothesis testing to advance our understanding of many ecological problems (Cherry 1998, Johnson 1999, Anderson et al. 2000). The information-theoretic approach (Burnham and Anderson 2002) offers an alternative paradigm for model selection and inference that is less subjective than statistical hypothesis testing.

Here, I offer a straightforward alternative to logistic regression, based on a generalized linear model that allows for varying visitation intervals. The method is easily implemented with readily available statistical software and requires no assumptions about when nest losses occur. I demonstrate the method by applying it to previously published data sets and illustrate how it can be used to model the effects of various biological and nonbiological factors on daily nest survival. I compare parameter estimates obtained from this method with estimates generated by the nest survival model in program MARK, and discuss similarities and differences in the two approaches. The examples I give illustrate how the combination of generalized linear models and information-theoretic methods for model selection (along with commonly available statistical software) provides ornithologists with a powerful and unified, yet easily implemented, approach to analyzing nest success data.

Methods

An Alternative to Logistic Regression

An alternative to logistic regression is based on a special class of statistical models known as generalized linear models (Nelder and Wedderburn 1972), which consist of three components: a random component identifying the probability distribution of the response, which must be a member of the exponential family; a systematic component that is a linear predictor function of explanatory variables; and a link function relating the linear predictor to the expected value of the random component. A link function must be monotonic and differentiable with respect to the unknown parameter or parameters. The logistic regression model is a generalized linear model with a binomial response distribution, a systematic component based on the logistic function (Hosmer and Lemeshow 1989), and the logit link function ($\log_e[p/(1 - p)]$, where p is the probability of a success).

Consider a single nest from a random sample of nests from some hypothetical population. Let t be the length of an observation interval (in days) for that nest. The probability that the clutch survives the interval is $\theta = s^t$, where s is a daily survival rate that depends on the value of some explanatory variable x. The random component of our generalized linear model is the binomial distribution with probability of success equal to θ.

The daily survival rate is modeled in terms of x through the choice of an appropriate predictor function, which in our case should yield values between zero and one. As is done in logistic regression, we use the S-shaped logistic function.

$$s(x) = \frac{e^{\beta_0 + \beta_1 x}}{1 + e^{\beta_0 + \beta_1 x}} \qquad (1)$$

The systematic component of our generalized linear model is then $[s(x)]^t$.
Next, we consider the function

$$g(\theta) = \log_e\left(\frac{\theta^{\frac{1}{t}}}{1 - \theta^{\frac{1}{t}}}\right) \qquad (2)$$

The above function is monotonic and differentiable with respect to θ, and it can be shown that $g(\theta) = \beta_0 + \beta_1 x$, which satisfies the criteria for a link function in a generalized linear model. Those three components—the binomial response distribution, the predictor function given in Expression 1, and the link function given in Expression 2—completely specify our generalized linear model. (hereafter "the logistic-exposure model") is similar to the logistic regression model but differs in the form of the link function. The logistic-exposure link function contains an exponent ($1/t$) in the numerator and denominator that is not present in the logistic-regression link function. The exponent is necessary to account for the fact that probability of surviving an interval depends on interval length.

Assumptions underlying the logistic-exposure model are that all nests survive or fail independently of one another and that daily survival probabilities are homogeneous among nest-days having the same values of explanatory variables. The first of those is standard for Mayfield-like estimators. The second assumption is much less restrictive than that which is necessary for Mayfield's method, namely that daily survival rates must be homogeneous within and among nests.

In terms of analysis, the parameters of interest are

Table 1. Comparison of several estimates of depredation rate of Yellow-breasted Chat nests (Burhans and Thompson 1999), including observed depredation rate (Apparent), Johnson's (1979) estimator, logistic regression of observed nest depredations assuming no interaction between parasitism status and patch size, logistic-exposure model assuming no interaction, and logistic-exposure model allowing for interaction.

Parasitized	Patch size	n	Estimated nest depredation rate (%)				
			Apparent	Johnson	Logistic regression	Logistic-exposure	
						No interaction	Interaction
Yes	Large	10	70	68	72	73	68
	Small	3	100	99	93	97	99
No	Large	13	31	47	29	39	47
	Small	20	65	71	66	73	71

the regression coefficients (β_k) that describe the effects of the explanatory variable(s) on daily survival rate. After the regression coefficients have been estimated, daily survival rate estimates for various values of the explanatory variable(s) can be computed from Expression (1). Estimates of the regression coefficients are obtained by the method of maximum likelihood, just as in logistic regression. Although the likelihood function must be maximized numerically and there are no explicit formulas for the regression coefficients, estimates and their standard errors are easily obtained with commonly available statistical software (e.g. S, SAS).

To illustrate the method, I consider data on depredation rates of 46 Yellow-breasted Chat (*Icteria virens*) nests (Burhans and Thompson 1999). The authors used logistic regression on nest fates to evaluate effects of nest parasitism (parasitized vs. not parasitized) and average patch size (small vs. large). Because both explanatory variables are categorical and take on only two values, we can estimate depredation rates for each category using standard estimators and compare them with estimates obtained with logistic regression on nest fates, and with estimates obtained with the logistic-exposure method. Somewhat surprisingly, apparent rates and those obtained with the Johnson estimator are similar for parasitized nests (Table 1), assuming 22 days from nest initiation to fledging (Thompson and Nolan 1973). However, apparent rates, because of the bias noted by Mayfield, are considerably lower than Johnson estimates for nests that were not parasitized. As expected, estimates from logistic regression on nest fates are similar to apparent rates, especially for nests that were not parasitized.

I used PROC GENMOD (SAS Institute 1997; Appendix 1) to fit a logistic-exposure model to the Yellow-breasted Chat data. Estimated nest depredation rates were generally greater than both the apparent rates and estimates derived from logistic regression on nest fates (Table 1). Logistic-exposure estimates from the model without an interaction between parasitism status and patch size were somewhat similar to Johnson estimates, and logistic-exposure estimates from the model that included an interaction term were identical to Johnson estimates.

The logistic-exposure model, like logistic regression, also can be used with continuous explanatory variables. As an example, consider the 1976 sample of Blue-winged Teal (*Anas discors*) nests from Klett and Johnson (1982; Table 2). The sample of nests is from a 37-km stretch of right-of-way along Interstate 94 in Stutsman and Kidder counties, North Dakota. Investigators recorded the perpendicular distance from each nest to the road surface. Mayfield nest success for 220 nests (sample size differs slightly from Klett and Johnson) was 28.6%, but hatch rates appeared to be greater for nests closer to the road (Table 2). I used PROC GENMOD to fit a logistic-exposure model of daily survival rate involving a linear term for distance to the road (ROAD). Coefficients for the constant term and ROAD were 3.6665 (SE = 0.1985) and –0.0161 (SE = 0.0080), respectively. Substituting those values into Expression 1 and evaluating the function over the range of observed values for ROAD gives a logistic-exposure model in which estimates of daily mortality rate (1 – daily survival rate) are close to Mayfield estimates for nests closer to the road ($\leq$25.3 m), but larger than the Mayfield estimate for nests farthest from the road (>25.3 m; Fig. 1). Under the linear logistic-exposure model, the odds ratio (Hosmer and Lemeshow 1989) for an increase of 10 m from the road is $e^{10(-0.0161)}$ = 0.85 (95% confidence interval = [0.72, 1.00]); that is, for every 10-m increase in distance to the road, the daily survival rate decreased by a factor of 0.85.

Table 2. Mayfield nest success rate of Blue-winged Teal in relation to distance from an interstate highway in North Dakota, 1976 (Klett and Johnson 1982).

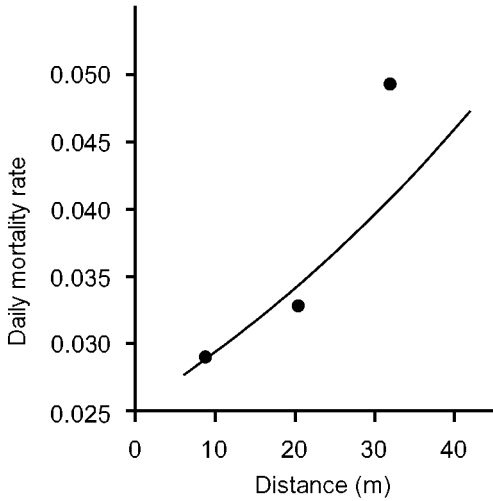| | Distance to highway (m) | | |
	0–12.8	12.9–25.3	25.4–49.7
Number of nests	74	73	73
Exposure days	1,278	1,204	977
Daily mortality rate	0.030	0.032	0.049
Mayfield success (%)	35.8	32.6	18.0

Fɪɢ. 1. Daily mortality rate of Blue-winged Teal nests in relation to distance from an interstate highway in North Dakota, 1976 (Klett and Johnson 1982). Filled circles denote daily mortality rates (Mayfield 1961) for nests grouped into three categories on the basis of distance to highway edge. Distance categories are 0–12.8 m (n = 74; median = 8.8), 12.9–25.3 m (n = 73; median = 20.4), and 25.4–49.7 m (n = 73; median = 31.9). The solid line denotes fitted values from a logistic-exposure model involving a linear term for distance to the highway edge.

Rᴇsᴜʟᴛs

Aɢᴇ- ᴀɴᴅ Dᴀᴛᴇ-ʀᴇʟᴀᴛᴇᴅ Vᴀʀɪᴀʙɪʟɪᴛʏ ɪɴ Sᴜʀᴠɪᴠᴀʟ Rᴀᴛᴇs

Here, I consider examples involving categorical and time-specific, continuous explanatory variables, and use Akaike's Information Criterion (AIC; Burnham and Anderson 2002) to rank candidate models. I re-analyze four data sets previously examined by Klett and Johnson (1982) for variation in daily survival rates related to nest age and date. The data sets are of Mallard (*A. platyrhynchos*) and Blue-winged Teal nests found along Interstate 94 right-of-way in 1976 and 1977. Basic information on each data set is given in table 1 of Klett and Johnson (1982), with the exception of the previously noted discrepancy in sample size in the 1976 Blue-winged Teal data set.

Klett and Johnson (1982) used probability theory to partition nest losses and exposure days into 5-day age classes (AGE) and 10-day calendar periods (DATE), and calculated daily mortality rates for each combination of AGE and DATE. They then used analysis of variance methods to fit various models involving linear and quadratic effects of AGE (*A* and *AA*), linear and quadratic effects of DATE (*D* and *DD*), and interaction between AGE and DATE (*AD*). They also considered joint linear models in AGE (*A1 + A2*), which intersect at the 11–15 day AGE category. Mean-square error and significance levels of each effect were used to compare models.

I treated each visitation interval for a nest as an observation and computed the average age (in days) and average date (Julian) during each interval. For example, a 6-day-old nest found on day 140 and revisited on day 147 was assigned an age of 9 days and a date of 143. I used PROC GENMOD to fit logistic-exposure models that included the same terms considered by Klett and Johnson (1982). In addition, I considered a constant-survival logistic-exposure model (*CONSTANT*) in which time of loss is unknown. I used a second-order variant of AIC (AIC$_c$; Burnham and Anderson 2002) to rank candidate models from most to least supported. I used the number of observation intervals as the sample size (n) when computing AIC$_c$. Values of ΔAIC$_c$, the difference in AIC$_c$ between the model in question and the one with lowest AIC$_c$, were computed for each model. Small values of ΔAIC$_c$ indicate models that have substantial support that should be considered when making inferences (Burnham and Anderson 2002). I also computed the Akaike weight (w_i; Burnham and Anderson 2002) that can be considered as the weight of evidence supporting model *i*.

For the 1976 Blue-winged Teal data set, no single model stands out as clearly best (Table 3). The model involving a linear effect of age has the lowest AIC$_c$ and largest w_i, followed closely by the *CONSTANT* model. Either model has more support than the *A + D* model, which is Klett and Johnson's (1982) best-fitting model. For Mallards in 1976, the *A1 + A2* model has the most support and is also Klett and Johnson's (1982) best-fitting model. For Blue-winged Teal in 1977, the *A1 + A2* model stands out as clearly best and is consistent with findings of Klett and Johnson (1982). A linear effect of age is the best-fitting model for Mallards in 1977, whereas Klett and Johnson (1982) selected the *A1 + A2* model. Inspection of the plot of raw daily mortality rates (*m*) versus nest age reveals why the *A1 + A2* model was Klett and Johnson's (1982) best-fitting model (Fig. 2). The

Table 3. Effects of nest age and date on daily mortality rates of Mallard and Blue-winged Teal nests along an interstate highway in North Dakota, 1976–1977 (Klett and Johnson 1982). Scaled values of Akaike's Information Criterion (ΔAIC_c) and Akaike weights (w_i) are presented for nine logistic-exposure models. CONSTANT is a constant-survival model; A and D represent linear effects of age and date; AA and DD represent quadratic effects; AD represents the interaction; and A1 and A2 represent linear effects of age for <13 and ≥13 days.

| | 1976 | | | | 1977 | | | |
| | Blue-winged Teal | | Mallard | | Blue-winged Teal | | Mallard | |
Model	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i
$S_{CONSTANT}$	0.22	0.18	0.42	0.22	7.39	0.01	8.98	<0.01
S_A	0.00	0.21 [b]	2.16	0.09	2.77	0.10	0.00	0.31 [b]
S_{A+AA}	1.96	0.08	1.57	0.12	2.18	0.14	1.80	0.13
S_{A1+A2}	1.17	0.11	0.00	0.27 [a,b]	0.00	0.41 [a,b]	1.43	0.15 [a]
S_{A+D}	0.65	0.15 [a]	3.60	0.04	4.47	0.04	1.26	0.17
S_{A+D+AD}	1.62	0.09	5.64	0.02	5.75	0.02	2.84	0.08
S_{A+AA+D}	2.62	0.06	2.92	0.06	3.84	0.06	3.15	0.06
$S_{A1+A2+D}$	1.83	0.08	1.15	0.15	1.52	0.19	2.86	0.07
$S_{A+AA+D+DD}$	3.36	0.04	4.87	0.02	5.58	0.03	5.20	0.02

[a] Klett and Johnson's (1982) best-fitting models.
[b] Best-fitting logistic-exposure models on the basis of AIC_c.

logistic-exposure model, although linear in the logistic scale, implies a curvilinear relationship between m and age that closely matches the raw data, and, therefore, Klett and Johnson's (1982) A1 + A2 model. That illustrates an important
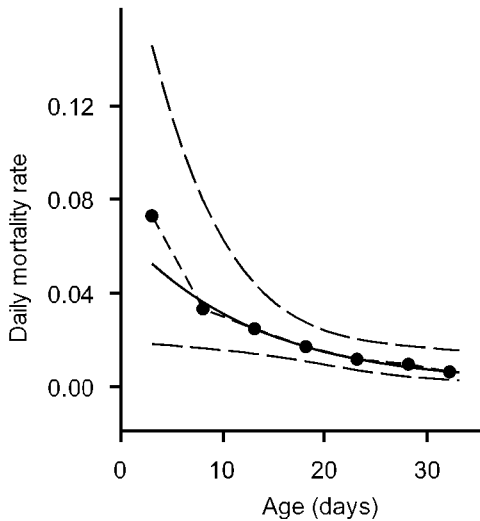

Fig. 2. Daily mortality rate of Mallard nests along an interstate highway in North Dakota in 1977, in relation to number of days since initiation. Filled circles and short-dashed line denote observed mortality rates from figure 1 of Klett and Johnson (1982). The solid line is the logistic-exposure model involving a linear effect of age. Long-dashed lines represent 90% confidence limits for the logistic-exposure age model.

advantage of the linear logistic-exposure model, namely, that it has one fewer parameter than Klett and Johnson's (1982) A1 + A2 model and is, therefore, more parsimonious.

As an alternative to analyzing the four data sets separately, the logistic-exposure method can be used to analyze them comprehensively, allowing for effects of species (S) and year (Y). To illustrate, I used AIC_c to evaluate 24 candidate models, including the CONSTANT model; models involving various combinations of Y, S, A, D, and AD; and models involving combinations of Y, S, A1, A2, and D. Before proceeding with the analysis, it is advisable to examine the adequacy of the global model (candidate model with the most parameters) for goodness-of-fit (Anderson and Burnham 2002). Failure of the global model to adequately portray variation in the data would indicate either a structural problem with the model (e.g. omission of an important explanatory variable), or perhaps an invalid assumption (e.g. assuming that survival rates are homogeneous when they are not). Hosmer and Lemeshow (1989) proposed a test based on grouping the values of estimated probabilities into deciles and calculating a Pearson chi-square statistic ($\hat{C}$) from the 2 × 10 table of observed and expected outcomes. In the present example, $\hat{C}$ = 4.07 for the model involving Y, S, A, D, and AD, which, when compared to a chi-square distribution with df = 8, gives P = 0.85. Thus, the global model fits the data well.

Of the 24 candidate models, the two most supported models had ΔAIC_c values <1 and Akaike weights >0.2 (Table 4). Both models involved effects for species, year, and either linear or joint-linear effects of age. Year was obviously an important effect, occurring in all models with Akaike weights >0.001. Age effects, whether linear or joint-linear, were also important, occurring in all models with Akaike weights >0.01. Burnham and Anderson (2002) advocate taking a weighted average of parameter estimates across all models, using the w_i as weights, and computing variance estimates that reflect both uncertainty in parameter estimates from a given model and uncertainty in selecting that model. Model averaging supported the above findings and indicated that date effects, including the age × date interaction, were negligible (Table 5), which suggests that estimated hatch rates for each species–year combination could be calculated as the product of age-specific daily survival rates (Johnson 1979). That method resulted in estimated Mallard hatch rates equal to 0.19 and 0.53, compared with Klett and Johnson's (1982) estimates of 0.17 and 0.43 for 1976 and 1977, respectively. Blue-winged Teal hatch rates were 0.26 and 0.59 in 1976 and 1977, respectively, compared with Klett and Johnson's (1982) 0.30 and 0.51.

RANDOM EFFECTS AND MIXED MODELS

Well-designed nesting studies often feature replication in space, time, or both. The aim of multisite, multiyear studies is to help ensure that results are as broadly applicable as possible by considering spatial and temporal variation in the process under study. If the study sites or study years can reasonably be assumed to represent a random sample from some larger set of sites or years, then those factors are most appropriately modeled as random effects. In contrast, variables of specific interest, such as habitat type or management treatment, are typically treated as fixed effects. Mixed models include both random and fixed effects. Generalized linear mixed models (Breslow and Clayton 1993) allow for inclusion of random effects in generalized linear models. Random effects are typically assumed to follow normal distributions with zero mean and unknown variances, termed "variance components."

I illustrate use of the logistic-exposure

TABLE 4. Model selection criteria for the six most supported logistic-exposure models of daily survival rate of Mallard and Blue-winged Teal nests found along an interstate highway in North Dakota, 1976–1977 (Klett and Johnson 1982). Twenty-four candidate models, including a constant-survival model; models involving various combinations of effects for year (Y) and species (S), linear effects of nest age (A), date (D), and their interaction (AD); and models involving combinations of Y, S, linear effects of age for nests <13 ($A1$) and ≥13 days ($A2$), and D were considered. K is the number of parameters in the model, $Log_e(L)$ is the value of the maximized log-likelihood function, AIC_c is Akaike's Information Criterion adjusted for small-sample bias, ΔAIC_c is the scaled value of AIC_c, and w_i is the Akaike weight. The remaining candidate models had $\Delta AIC_c > 3.6$ and $w_i < 0.05$.

Model	K	$Log_e(L)$	AIC_c	ΔAIC_c	w_i
$S_{Y+S+A1+A2}$	5	−669.2	1,348.5	0.0	0.29
S_{Y+S+A}	4	−670.6	1,349.1	0.7	0.21
$S_{Y+A1+A2}$	4	−671.1	1,350.3	1.8	0.12
$S_{Y+S+A1+A2+D}$	6	−669.2	1,350.5	2.0	0.11
S_{Y+A}	3	−672.4	1,350.9	2.4	0.09
$S_{Y+S+A+D}$	5	−670.5	1,351.1	2.7	0.08

TABLE 5. Model-averaged estimates of regression coefficients from logistic-exposure models relating daily survival rate of Mallard and Blue-winged Teal nests (Klett and Johnson 1982) to year, a linear effect of nest age, a linear effect of Julian date, age × date interaction, and joint-linear effects of age for nests <13 and ≥13 days old. Standard errors reflect both uncertainty in parameter estimates from a given model and uncertainty in selecting that model (Burnham and Anderson 2002).

Effect	Coefficient	Standard error
Intercept	4.055	0.476
Species		
Mallard	−0.175	0.104
Blue-winged Teal	0	0
Year		
1976	−0.966	0.153
1977	0	0
Age	0.011	0.011
Date	<0.001	0.002
Age × date	<0.001	<0.001
Age <13	−0.042	0.026
Age ≥13	0.007	0.007

method in a mixed-model setting with data from Reynolds et al. (2001). Systematic searches for duck nests were conducted in two cover types (Conservation Reserve Program [CRP] fields and planted cover on U.S. Fish and

Wildlife Service Waterfowl Production Areas [WPAs]) on a sample of 10.4-km^2 plots from the U.S. prairie pothole region. Reynolds et al. (2001) treated the plots as random effects in a randomized block design and used ANOVA to estimate the difference in daily survival rates between the two cover types. I used PROC NLMIXED (SAS Institute 1999; Appendix 2) to fit a logistic-exposure model to data for 2,698 Blue-winged Teal nests from 97 plots that were searched in 1992–1995. The model included cover type as a fixed effect and plot as a random effect. The estimated difference in the logit scale between CRP and WPA cover types was 0.0097, with a standard error of 0.0577. An approximate 95% confidence interval for the logit difference is 0.0097 ± 2 × 0.0577, which includes zero and supports the conclusion of Reynolds et al. (2001) that nests in CRP cover and nests in WPA cover survived at about the same rate. The logistic-exposure approach has at least two advantages over Reynolds et al.'s approach: (1) estimated survival rates are constrained to the (0,1) interval with the logistic-exposure approach; and (2) the logistic-exposure model can be used with group-, nest-, and time-specific explanatory variables, whereas Reynolds et al.'s approach can be used only with group-specific explanatory variables.

Logistic-Exposure Compared with Program MARK

Dinsmore et al. (2002) used the nest survival model in program MARK to model the daily survival of Mountain Plover (*Charadrius montanus*) nests as a function of the sex of the incubating adult, year, linear, and quadratic terms for time (T and TT), and linear terms for nest age (AGE), maximum daily temperature (TEMP), and daily precipitation (PRECIP). Twelve candidate models were ranked on the basis of AIC$_c$ values. I used PROC GENMOD to apply the logistic-exposure method to each of the 12 candidate models and computed AIC$_c$ for each model. I averaged daily values of AGE, T, TEMP, and PRECIP within each observation interval ($\overline{x}$ = 4.3 days, n = 1,336) and used the averages as explanatory variables in logistic-exposure models.

Three of the 12 candidate models ($S_{CONSTANT}$, S_{SEX}, and S_{YEAR}) did not involve time-specific effects. Deviance values from those three models were identical for the logistic-exposure and program MARK methods (Table 6). Deviance is a measure of discrepancy between observed and fitted values and is defined as –2× the difference of the log likelihood of the

Table 6. Model selection results of analyzing daily survival rates of Mountain Plover nests (Dinsmore et al. 2002) with the logistic-exposure (L-E) method, compared with results of using the nest survival model of program MARK. Explanatory variables are sex, year, nest age (AGE), precipitation (PRECIP), maximum temperature (TEMP), and linear (T) and quadratic (TT) effects of time. Program MARK used daily values for AGE, PRECIP, TEMP, T, and TT; whereas logistic-exposure results are based on average values for each observation interval. K is the number of parameters, and w_i is the Akaike weight. Deviance is a measure of discrepancy between observed and fitted values and is defined as –2× the difference of the log likelihood of the model of interest and the saturated model for the data. Program MARK results are from Dinsmore et al. (2002).

Model	K	Deviance		AIC$_c$		ΔAIC$_c$		w_i	
		MARK	L-E	MARK	L-E	MARK	L-E	MARK	L-E
$S_{SEX+AGE+T+TT+PRECIP}$	6	858.29	855.57	870.39	867.64	0.00	0.00	0.56	0.83
$S_{SEX+AGE+T+TT}$	5	862.09	862.03	872.15	872.07	1.76	4.44	0.23	0.09
$S_{SEX+AGE}$	3	868.12	868.11	874.14	874.12	3.75	6.49	0.09	0.03
$S_{SEX+AGE+T+TT+TEMP}$	6	862.06	862.01	874.16	874.07	3.76	6.43	0.09	0.03
$S_{SEX+AGE+T}$	4	868.05	868.04	876.10	876.07	5.71	8.44	0.03	0.01
$S_{SEX+T+TT}$	4	888.92	889.02	896.97	897.05	26.58	29.41	0.00	0.00
$S_{YEAR+T+TT}$	8	885.07	885.14	901.25	901.25	30.85	33.62	0.00	0.00
S_{SEX+T}	3	895.61	895.61	901.64	901.63	31.25	33.99	0.00	0.00
S_{SEX}	2	897.76	897.76	901.77	901.76	31.38	34.13	0.00	0.00
$S_{CONSTANT}$	1	902.29	902.29	904.29	904.29	33.90	36.65	0.00	0.00
S_{YEAR}	6	893.30	893.30	905.40	905.36	35.01	37.72	0.00	0.00
S_{YEAR+T}	7	891.54	891.54	905.68	905.62	35.29	37.99	0.00	0.00

model of interest and the saturated model for the data (McCullagh and Nelder 1989). The saturated model contains a parameter for each data point, thus providing a perfect fit to the data, and the maximum possible log likelihood. Logistic-exposure and program MARK results for all models involving time-specific effects were nearly identical, except for the model involving PRECIP. Both methods identified that model as the most supported on the basis of AIC_c (Table 6). The best-fitting logistic-exposure model (standard errors are shown below in parentheses) was

$\log_e (s/[1-s]) =$

$\quad 3.71 + 0.38 \times SEX + 0.06 \times AGE -$
$\quad (0.43) \quad (0.17) \qquad (0.01)$

$\quad 0.06 \times T + 0.001 \times TT - 2.09 \times PRECIP$
$\quad (0.03) \qquad (0.0004) \qquad (0.79)$

Dinsmore et al.'s (2002) best-fitting model was

$\log_e (s/[1-s]) =$

$\quad 3.23 + 0.37 \times SEX + 0.06 \times AGE -$
$\quad (0.61) \quad (0.17) \qquad (0.01)$

$\quad 0.06 \times T + 0.001 \times TT - 1.08 \times PRECIP$
$\quad (0.04) \qquad (0.0007) \qquad (0.48)$

The logistic-exposure method estimated a stronger negative effect of precipitation than program MARK. In addition, the logistic-exposure model resulted in a smaller deviance value, which suggests that it fit the data better than the program MARK model.

Discussion

More than 40 years have passed since Mayfield (1961) drew attention to the bias in the apparent estimator of nest success. In that time, numerous papers have been published that emphasized or illustrated Mayfield's point, offered solutions to the problem, evaluated or compared alternative estimators, and assessed the influence of various violations in assumptions. The bias in the apparent estimator of nest success is now widely recognized, and Mayfield's method or some suitable alternative has become the norm for estimating nest success.

Despite all the attention the problem has received, numerous papers have appeared recently that present results of logistic regression analyses on nest fate (e.g. Hanski et al. 1996, Burhans and Thompson 1999, Willson and Gende 2000). In many papers, the authors employed Mayfield's method (or some alternative [e.g. Bart and Robson 1982]) for estimating nest success, indicating that they were aware of the bias in apparent nest success, yet they conducted logistic regression analyses on what is essentially apparent nest success (e.g. Frederick and Collopy 1989, Maxson and Riggs 1996, Zanette and Jenkins 2000). I suspect that authors recognized the bias associated with logistic regression on nest fate, but were unsure how to deal with it. For example, Burhans et al. (2002) acknowledged that their logistic models did not account for the effect of exposure period. They attempted to minimize the effect by locating nests early in incubation, so that exposure would not vary greatly among nests. Pasitschniak-Arts et al. (1998) and Garrettson and Rohwer (2001) also recognized the problem and tried to deal with it by including number of exposure days as an explanatory variable in their logistic regression models. Willson and Gende (2000) were obviously aware of the problem and justified their use of logistic regression by noting that apparent and Mayfield nest success rates were "closely correlated."

Whatever the reason for its misuse, logistic regression (in which the unit of analysis is the nest and nest fate is the response) is inappropriate when applied to a sample of nests found at various ages, unless inactive nests can be found with the same probability as active ones. Those are exactly the same conditions under which the apparent estimator of nest success is unbiased, and those conditions rarely occur in real-world nesting studies.

Fortunately for ornithologists, the logistic-exposure model provides access to all the advantages of logistic regression, while accounting for the bias noted by Mayfield (1961, 1975) and others. The difference between logistic regression and the logistic-exposure model is in the link function. The link function for the logistic-exposure model contains a "nuisance" variable, reflecting the fact that nests vary in their exposure time. This link function will always yield an estimate of the daily survival rate between 0 and 1. Because it is a generalized linear model, the logistic-exposure model can be implemented using any generalized linear-models software

that accepts user-defined link functions. Analysts who are familiar with logistic regression techniques should have little difficulty implementing the logistic-exposure method.

The primary strength of logistic regression lies in dealing with explanatory variables that are measured on a continuous scale. The logistic-exposure model makes this type of analysis possible with nest success data, as illustrated by the example relating daily survival of Blue-winged Teal nests to distance to a highway. Standard summary statistics for presenting logistic regression results, such as odds ratios, are equally applicable to logistic-exposure models.

One alternative to the logistic-exposure approach involves collapsing continuous explanatory variables into two or more categories and comparing daily survival rates among them (e.g. Winter et al. 2000). That procedure has several drawbacks. First, the choice of categories, including how many and how broad, is arbitrary and is often dictated by sample-size considerations rather than by other, possibly more relevant, criteria. Second, loss of information occurs, particularly when sample sizes are small, leading either to imprecise daily survival-rate estimates for categories with limited sample sizes or to unsatisfactorily broad categories.

Another alternative to the logistic-exposure model is the logistic regression approach of Aebischer (1999), which can be considered a special case of the logistic-exposure model in which visits to nests occur daily. For most studies of nesting birds, especially when the period under study is more than a few days, daily visits are either logistically infeasible or ill-advised because of the potential effects of increased disturbance on nest survival. The logistic-exposure model requires only that the length of the interval and fate of the clutch during the interval be known. Aebischer's (1999) method can be used when visitation intervals are longer than one day, but it requires that failure dates for unsuccessful nests be assumed (Table 7). Although the midpoint assumption, which can lead to partial exposure days, may be acceptable with Mayfield's estimator, it is problematic with Aebischer's (1999) method, for which observation days must be integers. Johnson (1979) recommended the unknown-date-of-loss Johnson estimator over Mayfield's method for comprehensive analyses of large data sets. By way of analogy, the unknown-date-of-loss logistic-exposure model would be expected to perform better than Aebischer's (1999) method.

Time-specific effects.—The logistic-exposure approach can be used to model effects of time-specific variables (Table 7). Logistic-exposure analyses of four Mallard and Blue-winged Teal data sets for time-specific effects of nest age and date gave results similar to those reported by Klett and Johnson (1982), who used a cumbersome analytic method. Because the logistic-exposure model is based on the S-shaped logistic function, estimates of daily survival rate are constrained between 0 and 1, which is not the case for Klett and Johnson's (1982) method. In addition, nonlinear effects can sometimes be modeled using fewer parameters with the logistic-exposure model than with Klett and Johnson's (1982) method.

Length of visitation intervals is a consideration when designing nesting studies in the presence of possible time-specific effects. More-frequent visits mean shorter intervals and more precise information on time-specific effects.

Table 7. Key differences and similarities among five methods for analyzing nest success. Assumptions common to all methods (e.g. that clutches survive or fail independently of one another) are not listed.

	Mayfield (1961, 1975)	Johnson (1979)	Aeibischer (1999)	Dinsmore et al. (2002)	Logistic-exposure (this article)
Explanatory variables					
Group-specific (categorical)	Yes	Yes	Yes	Yes	Yes
Nest-specific (continuous)	No	No	Yes	Yes	Yes
Time-specific (e.g. age)	No	No	No	Yes	Yes
Complex models possible	No	No	Yes	Yes	Yes
Mixed models possible	No	No	No	No	Yes
Hand-calculations possible	Yes	No	No	No	No
Assumptions					
Survival is constant day-to-day	Yes	Yes	Yes	No	No
Failure dates are known	Yes	No	Yes	No	No

However, increasing visitation frequency can increase disturbance to the nest and elevate concerns over potential observer effects (Götmark 1992). That important issue must be considered regardless of the method of analysis that is used. Klett and Johnson (1982) recommended that, when the objective is to estimate the hatch rate of duck nests with minimum bias, nest searches should be made approximately weekly throughout the nesting season during the hours when most laying occurs. If time-specific effects are likely, I would add that duck nests also should be rechecked at approximate one-week intervals to facilitate estimation of time-specific effects. More-frequent visits are necessary for passerines and other species with nesting periods considerably shorter than those of ducks.

Random effects and mixed models.—With data from Reynolds et al. (2001), I illustrated how the logistic-exposure method can be applied in a mixed-model setting using commonly available software. The method can be used with group-, nest-, or time-specific effects (Table 7). Each random effect contributes one parameter (variance component) to the model. In contrast, each fixed effect contributes one parameter for each level of the effect. When using information criteria, such as AIC, to evaluate mixed models, analysts need to be wary of values generated by certain software packages that fail to include the variance components in the parameter count.

Model selection.—Deciding which variables to include in a model and the form in which to include them is critically important in many types of data analyses, including analyses of nest success. Information-theoretic techniques for model selection have numerous advantages over traditional methods that are based on some form of hypothesis-testing, step-wise, or best-subsets procedure (Burnham and Anderson 2002). Information-theoretic methods based on AIC are well suited for logistic-exposure modeling of nest success. Hopefully, by identifying and reporting all models that are at least somewhat supported by the data and applying model-averaging techniques, ornithologists can avoid situations in which two or more investigators studying the same question report conflicting results because of uncertainty in model selection.

Comparison with program MARK.—The nest survival model in program MARK and the logistic-exposure method gave similar results when used to model survival of Mountain Plover nests (Dinsmore et al. 2002). Deviance values were identical for models not involving time-specific effects, and only slightly different for models that included time-specific effects of nest age, time, temperature, or precipitation. Parameter estimates for the effects of nest age and time were nearly identical in the program MARK and logistic-exposure analyses, but the estimated precipitation effect was stronger (but in the same direction) in the logistic-exposure analysis. Those results can be explained by examining the assumptions that underlie each method. Consider a clutch that is found on day 1 and revisited t days later. Let θ denote the probability that the clutch survives the interval. In program MARK, θ is modeled as a product of day-specific survival rates: $\theta_{MARK} = s(x_1) s(x_2)...s(x_{t-1})$, where $s(x)$ is the logistic function given in Expression (1), and $x_1, x_2,...x_{t-1}$ are daily values of the explanatory variable x. Denote the variance among the $s(x_i)$'s as σ^2. Implicit in the logistic-exposure approach is an assumption of constant daily survival within each interval of observation: $\theta_{L-E} = [s(\overline{x})]^{t-1}$, where $\overline{x}$ is the average of the x_i's. If x is non-time-specific, then $\sigma^2 = 0$ and $\theta_{MARK} = \theta_{L-E}$, and the two methods are equivalent. If x is time-specific, then $\theta_{MARK} \neq \theta_{L-E}$ (in general), and the two approaches differ.

The magnitude of the difference $| \theta_{MARK} - \theta_{L-E} |$ will depend on the magnitude of σ^2. As σ^2 increases, we can expect $| \theta_{MARK} - \theta_{L-E} |$ to increase. Three factors contribute to the value of σ^2: (1) length of the observation interval, (2) strength of the time-specific effect (β), and (3) variance in x_i. Length of the observation interval is under the control of the investigator and can usually be kept sufficiently short (e.g. 3–5 days for passerine species and 7–10 days for waterfowl). It seems reasonable to expect that most time-specific effects will be relatively weak (i.e. small changes in x will result in small changes in $s[x]$) and will not contribute substantially to σ^2, especially when observation intervals are short. Variance in x_i is the one factor that probably has the most potential to substantially elevate the value of σ^2. Values of variables, such as nest age and time, change sequentially one day at a time; therefore, their variance should be sufficiently small not to pose a concern. In contrast, weather-related variables, such as precipitation, can experience sudden and extreme shifts in values from one

day to the next and result in dramatic fluctuations in the daily survival rate. When such an event occurs within an observation interval, the value of σ^2 may increase, causing $\mid \theta_{MARK} - \theta_{L-E} \mid$ to increase. That appears to be what happened with the Mountain Plover data. Interestingly, however, the fit of the logistic-exposure model was better than that of the program MARK model.

In addition to how time-specific effects are modeled, other differences and some similarities exist in the logistic-exposure and program MARK approaches. Neither method requires that failure dates be known (Table 7). Probably the most important difference between the two methods is in the computer software used to perform the analyses. Analysts who are familiar with program MARK should have little difficulty using the nest survival model available in that program. Analysts who have not used program MARK, but who know how to use logistic regression or generalized linear-models software, such as SAS PROC LOGISTIC (SAS Institute 1997) or the S function GLM (Hastie and Pregibon 1992), will likely find the logistic-exposure method easier to use than program MARK. One advantage of program MARK is that AIC model-selection and model-averaging capabilities are built into the software, whereas these computations entail additional programming in SAS, although macros for performing the computations are available (see Acknowledgments).

Both the logistic-exposure model and program MARK are likelihood-based methods, relying on iterative procedures to maximize the likelihood function. The logistic exposure-method, as implemented with PROC GENMOD, does not require that starting values for the parameters be specified. I did not experience any difficulties getting PROC GENMOD to converge. On the other hand, program MARK can be sensitive to the choice of starting values for the parameters, sometimes leading to convergence problems (S. J. Dinsmore pers. comm.).

Recommendations.—In typical situations where the apparent estimator of nest success is inappropriate, logistic regression on nest fate is also inappropriate. The logistic-exposure model presented here gives ornithologists access to a flexible, suitable alternative to logistic regression that is appropriate when exposure periods vary. In addition, the information-theoretic approach to model selection provides a framework that can be easily and consistently followed by ornithologists involved in analyses of nest success data. I believe that the advantages afforded by the information-theoretic approach make it a logical choice over traditional hypothesis-testing methods. Used together, the logistic-exposure model and AIC provide a unified analysis tool that has potential to markedly accelerate our understanding of factors that influence nest success.

Although I developed the logistic-exposure method to facilitate complex modeling of daily nest survival rates (i.e. models with multiple explanatory variables of different types with or without interactions), I recommend the method for simple models also. For example, because it is a unified approach, the logistic-exposure method can be used instead of the Mayfield method to estimate nest success for one or more populations of nests for which daily survival rates are assumed constant. That approach obviates the assumption that nest failure dates are known (e.g. Mayfield's midpoint assumption; Table 7). Furthermore, daily survival-rate estimates obtained with the logistic-exposure method under the assumption of constant daily survival can be directly compared with results from previous studies that reported daily survival rates, including those that used Mayfield's or Johnson's method. The major advantage of using the logistic-exposure method for simple models is that the appropriateness of those models can be judged by comparing them to more complex models via information-theoretic techniques, thereby providing objective justification (or lack thereof) for a simple model.

available macros for performing the computations, please see www.npwrc.usgs.gov/resource/tools/ nestsurv/nestsurv.htm.

Literature Cited

Aebischer, N. J. 1999. Multi-way comparisons and generalized linear models of nest success: Extensions of the Mayfield method. Bird Study 46:22–31.

Anderson, D. R., and K. P. Burnham. 2002. Avoiding pitfalls when using information-theoretic methods. Journal of Wildlife Management 66:912–918.

Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: Problems, prevalence, and an alternative. Journal of Wildlife Management 64:912–923.

Bart, J., and D. S. Robson. 1982. Estimating survivorship when the subjects are visited periodically. Ecology 63:1078–1090.

Breslow, N. E., and D. G. Clayton. 1993. Approximate inference in generalized linear mixed models. Journal of the American Statistical Association 88:9–25.

Bromaghin, J. F., and L. L. McDonald. 1993. Weighted nest survival models. Biometrics 49: 1164–1172.

Burhans, D. E., D. Dearborn, F. R. Thompson III, and J. Faaborg. 2002. Factors affecting predation at songbird nests in old fields. Journal of Wildlife Management 66:240–249.

Burhans, D. E., and F. R. Thompson III. 1999. Habitat patch size and nesting success of Yellow-breasted Chats. Wilson Bulletin 111: 210–215.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd ed. Springer-Verlag, New York.

Cherry, S. 1998. Statistical tests in publications of The Wildlife Society. Wildlife Society Bulletin 26:947–953.

Davidson, A. S., and R. L. Knight. 2001. Avian nest success and community composition in a western riparian forest. Journal of Wildlife Management 65:334–344.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. Ecology 83:3476–3488.

Frederick, P. C., and M. W. Collopy. 1989. Nesting success of five ciconiiform species in relation to water conditions in the Florida Everglades. Auk 106:625–634.

Garrettson, P. R., and F. C. Rohwer. 2001. Effects of mammalian predator removal on production of upland-nesting ducks in North Dakota. Journal of Wildlife Management 65:398–405.

Götmark, F. 1992. The effects of investigator disturbance on nesting birds. Current Ornithology 9: 63–104.

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.

Hastie, T. J., and D. Pregibon. 1992. Generalized linear models. Pages 195–247 in Statistical Models in S (J. M. Chambers and T. J. Hastie, Eds.). Chapman and Hall/CRC, Boca Raton, Florida.

Hosmer, D. W., Jr., and S. Lemeshow. 1989. Applied Logistic Regression. John Wiley and Sons, New York.

Johnson, D. H. 1979. Estimating nest success: The Mayfield method and an alternative. Auk 96: 651–661.

Johnson, D. H. 1990. Statistical comparison of nest success rates. Proceedings of the North Dakota Academy of Science 44:67.

Johnson, D. H. 1999. The insignificance of statistical significance testing. Journal of Wildlife Management 63:763–772.

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

Maxson, S. J., and M. R. Riggs. 1996. Habitat use and nest success of overwater nesting ducks in westcentral Minnesota. Journal of Wildlife Management 60:108–119.

Mayfield, H. 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.

McCullagh, P., and J. A. Nelder. 1989. Generalized Linear Models, 2nd ed. Chapman and Hall, London.

Miller, H. W., and D. H. Johnson. 1978. Interpreting the results of nesting studies. Journal of Wildlife Management 42:471–476.

Nelder, J. A., and R. W. M. Wedderburn. 1972. Generalized linear models. Journal of the Royal Statistical Society, Series A 135:370–384.

Pasitschniak-Arts, M., R. G. Clark, and F. Messier. 1998. Duck nesting success in a fragmented prairie landscape: Is edge effect important? Biological Conservation 85:55–62.

Reynolds, R. E., T. L. Shaffer, R. W. Renner, W. E. Newton, and B. D. J. Batt. 2001. Impact of the Conservation Reserve Program on duck recruitment in the U.S. Prairie Pothole Region. Journal of Wildlife Management 65:765–780.

Rotella, J. J., M. L. Taper, and A. J. Hansen. 2000. Correcting nesting-success estimates for observer effects: Maximum-likelihood estimates of daily survival rates with reduced bias. Auk 117:92–109.

SAS INSTITUTE. 1997. SAS/STAT Software: Changes and Enhancements Through Release 6.12. SAS Institute, Cary, North Carolina.

SAS INSTITUTE. 1999. SAS/STAT Users Guide, version 8. SAS Institute, Cary, North Carolina.

SAUER, J. R., AND B. K. WILLIAMS. 1989. Generalized procedures for testing hypotheses about survival or recovery rates. Journal of Wildlife Management 53:137–142.

STANLEY, T. R. 2000. Modeling and estimation of stage-specific daily survival probabilities of nests. Ecology 81:2048–2053.

THOMPSON, C. F., AND V. NOLAN, JR. 1973. Population biology of the Yellow-breasted Chat (*Icteria virens* L.) in southern Indiana. Ecological Monographs 43:145–171.

WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 (Supplement):120–139.

WILLSON, M. F., AND S. M. GENDE. 2000. Nesting success of forest birds in southeast Alaska and adjacent Canada. Condor 102:314–325.

WINTER, M., D. H. JOHNSON, AND J. FAABORG. 2000. Evidence for edge effects on multiple levels in tallgrass prairie. Condor 102:256–266.

ZANETTE, L., AND B. JENKINS. 2000. Nesting success and nest predators in forest fragments: A study using real and artificial nests. Auk 117: 445–454.

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APPENDIX 1. Code for estimating daily nest survival rates with the logistic-exposure model and PROC GENMOD (SAS Institute 1997). In this example, there are two explanatory variables, parasitism status (parastat) and patch size (patsize). The CLASS statement identifies the variables as categorical. Code is shown for the model without interaction.

```
/* Read in one observation for each interval of
exposure on each nest. */
data chats;
   length survive $3;
   input nest_id parastat$ patsize$ expos survive;
   trials=1;
   if survive='yes' then surv=1; else surv=0;
cards;                          /* sample data follow */
1 yes large 4 yes
1 yes large 3 no
2 no small 6 yes
2 no small 4 yes
more data
proc genmod data = chats;
   class parastat patsize;
   a = 1/expos;
   fwdlink link = log((_mean_**a)/(1-_mean_**a));
   invlink ilink = (exp(_xbeta_)/(1+exp(_xbeta_
)))**expos;
   model surv/trials = parastat patsize/ dist=binomial;
run;
```

APPENDIX 2. PROC NLMIXED (SAS Institute 1999) code for estimating daily nest survival rates with a logistic-exposure model that includes both a fixed (cover type) and random effect (study plot).

```
/* Read in one observation for each interval of
exposure on each nest. */
data bwt;
   length survive $3 cover $3;
   input nestid cover plot expos survive;
   if survive='yes' then surv=1; else surv=0;
   if cover = 'wpa' then treat=0;     /* create dummy
variable for cover type */
   if cover='crp' then treat=1;
cards;
1 wpa 101 7 yes
1 wpa 101 5 no
2 crp 101 6 yes
3 crp 101 4 yes
more data
proc sort data=bwt; by plot;
proc nlmixed data=bwt;
   parms a=3 b=0 s2u=1;
   eta = a + b*treat + u;
   expeta = exp(eta);
   s = expeta / (1 + expeta);
   p = s**expos;
   model surv ~ binomial(1,p);
   random u ~ normal(0,s2u) subject=plot;
run;
```