Studies in Avian Biology No. 34:65–72

ESTIMATING NEST SUCCESS: A GUIDE TO THE METHODS

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Abstract. A field biologist interested in analyzing data on the nest success of birds faces a bewildering array of literature on the topic. Methods proposed to treat these data range from the simple and easily calculated, to the complex and computationally challenging. Many methods have received little use, so it is difficult to assess how well they perform in the real world. The apparent estimator, the fraction of nests found that ultimately succeed, is seldom applicable. The Mayfield estimator, despite its extremely restrictive assumption that the daily survival rate is the same for all nests and all days, has fared surprisingly well in many applications. A few methods are too demanding to warrant routine use; for example, they might require daily visits to nests, which are rarely practical and may markedly influence the outcome of a nesting attempt. Many methods require that the age of each nest be known; other methods need this information only if age-related variation in daily survival rate is a concern, or is marked enough to require age-specific estimates to generate a satisfactory overall estimate. The use of survival-time methods is questionable because of their limited ability to handle left truncation and interval censoring.

Key Words: guide, Mayfield, nest success, recommendations, survival.

ESTIMANDO ÉXITO DE NIDO: UNA GUÍA PARA LOS MÉTODOS

Resumen. Un biólogo de campo interesado en el análisis de datos de éxito de nido enfrenta un desconcertante acomodo en la literatura respecto a este tema. Métodos han sido propuestos para tratar estos datos, los quales van desde lo simple y fácilmente calculado, hasta lo complejo y retador en términos computacionales. Muchos métodos han sido poco utilizados, por lo que es difícil valorar qué tan bien funcionan en el mundo real. El estimador aparente y la fracción de nidos encontrados que finalmente tuvo éxito es raramente aplicada. El estimador Mayfield, a pesar de su supuesto extremadamente restrictivo de que la tasa diaria de sobrevivencia es la misma para todos los nidos y todos los días, ha resultado sorpresivamente buena en muchas aplicaciones. Pocos métodos son lo suficientemente demandantes como para autorizar su uso rutinario; por ejemplo, quizás requieran visitas diarias a los nidos, lo cual es raramente práctico y quizás influyan de manera muy marcada los resultados del intento de anidación. Muchos métodos requieren que la edad de cada nido sea conocida; otros métodos requieren esta información solo si la variación relacionada con la edad en la tasa de sobrevivencia diaria es una preocupación, o es suficientemente marcada para requerir estimaciones específicas de edad para generar estimaciones totales satisfactorias. La utilización de métodos de sobrevivencia de tiempo es cuestionable debido a su limitada habilidad para manejar el redondeo de izquierda y examinadores de intervalo.

It is widely recognized that nest success is a major factor in the dynamics of bird populations and one that contributes substantially to the viability of those populations. Although other aspects of the life cycle (e.g., adult survival, propensity to nest and renest, clutch size, and survival of young birds) certainly influence population size, most of them pale in comparison to the effect of nest success (Johnson et al. 1992, Hoekman et al. 2002). Furthermore, in many situations nest success is more amenable to management than many of the other components and is more readily measured than most other critical components of population dynamics.

As a partial testament to the value of information on nest success, the literature on the topic of estimating nest success of birds is large and still growing. By my count, 44 articles have been published on this topic, all in the past half-century. Perhaps surprisingly, the rate of publication has been increasing, especially in the past few years (Fig. 1). This trend suggests that issues related to the topic are not settled, and that certain questions remain unresolved. To a field biologist seeking to analyze data on nest success, the volume of literature can be perplexing—what method should be used? Until about 1960, the decision was easy, as was the analysis. If you found and monitored, say, 50 nests, and 30 of them produced young, you estimated nest success as 60%.

Eventually, some problems associated with this simple method (which came to be known as the apparent estimator) were revealed, and most knowledgeable investigators adopted the method proposed by Mayfield (1961), which required keeping track of how many days each nest was under observation. By summing those values across all nests and dividing into the

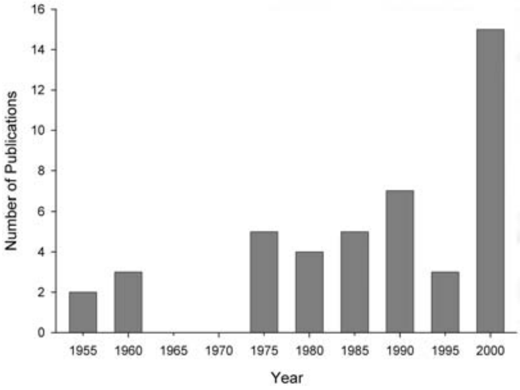

FIGURE 1. Number of methodological papers on estimating nest success published, by 5-yr period.

number of losses recorded, one could estimate a daily mortality rate for the sample of nests. Subtracting that result from one gave a daily survival rate (DSR), which could then be projected to the entire lifetime of a nest to estimate nest success. The Mayfield estimator is a somewhat more complicated procedure but one with much less bias than the apparent estimator; it has received a great deal of use by biologists, especially after standard errors for the estimator were developed (Johnson 1979).

Not content with the Mayfield method, investigators continued to develop new techniques for analyzing nest success information, especially to account for age-related variation in DSR. Few of these other methods received much use by practicing biologists, however. Then in the past few years, several papers were published that offered greater flexibility in the analysis of nesting data (reviewed by Johnson, *chapter 1, this volume*). The new methods were based on more sophisticated statistical models and required more computational abilities, leaving biologists to wonder if the new methods are worth the greater time and effort and, if so, which of them should be used.

The major objective of this paper is to offer guidance to biologists on how to select a method to analyze nesting data. First, I describe the major assumptions and requirements of the various methods and note their advantages and disadvantages. From that information, I develop guidelines for choosing a method, based on the objectives of the nesting study, features that characterize the study, and properties of the resulting data.

A generalized description of nesting studies is as follows. (see Klett et al. [1986] and Manolis et al. [2000] for more details on waterfowl and passerine studies, respectively). An investigator searches for the nests of birds, finding them by any of a variety of methods. Typically, nests are not discovered at their initiation, but are found only after they have progressed for some time. In some studies, nests that fail before nest searching begins, or are initiated but fail between nest visits, can be found, but in most studies such nests are hard to detect. Nests that failed early and thus are not included in the sample represent an example of left truncation, in the terminology of survival analysis (Heisey et al., *this volume*).

For virtually all methods (except life-table methods), nests must be monitored subsequent to their detection. Nests may be checked daily, but visits to nests usually are less frequent, partly because of logistic constraints and partly to reduce the effect of visitation on the fate of the nest (Götmark 1992). If nests are not visited daily, and a nest fails between two visits, the exact date of loss usually is uncertain. Analytic methods vary in how they treat such interval-censored data; the visitation frequency needed for a method varies from none to daily. Sometimes nests are not followed until termination—they may not have been relocated, or field work might have ended. Such nests are right-censored, in that the ending date is not known. Note that this definition of right-censoring differs from the usual definition in survival analysis; in that context, a nest that succeeds would be considered right-censored because its failure had not occurred when monitoring ceased.

Nesting studies differ in their objectives. Many studies seek only an estimate of the overall nest success rate. Others may focus on how DSRs vary by age of the nest. Some studies may address the influence on nest survival of other variables, such as date within the nesting season, habitat type, distance from various features, etc. Such covariates may be either group-specific (e.g., applying to all nests within a certain habitat type) or nest-specific (having individual values for each nest). Others may be time-specific (e.g., age of nest or date within season). Analytic methods differ in their abilities to accommodate these various objectives.

Some of the methods assume no variation in the DSR, by age, date, or nest. Others can accommodate various types of heterogeneity in DSR. By stratification, any method can accommodate variation among groups of nests, such as those in one type of habitat versus those in another type. Such stratification requires large sample sizes, however, so that nest success within each group can be estimated with adequate precision. The type of variation most commonly incorporated is that associated with the age of a nest. Certain methods, especially the more recently developed ones, allow a wider variety of influences on DSR, including age-specific, date-specific, and nest-specific covariates. In some situations it may be necessary to account for the effects of explanatory variables such as nest age to estimate nest success accurately (Grant et al. 2005).

Another consideration is the computational ease with which estimates of nest success can be calculated. Some estimators can be computed easily by hand. Others require only some fairly basic data processing. Some estimators demand knowledge of sophisticated software. Yet others need custom-designed programs that may not be generally available or well supported.

Virtually all the methods treat the survival process as discrete. That is, the process being modeled is whether a nest survives or not during a discrete time period, usually a day. In actuality, survival of nests is a continuous process, because deaths can occur at any time during a 24-hr period (Heisey et al., *this volume*). The discrete model is appropriate, however, for the observations resulting from the survival process, because nests are generally not under continuous observation. In most nesting studies, nests are checked daily or usually less frequently, so a finer resolution than a day is not feasible. And nests generally are checked at approximately the same time each day, consistent with the 24-hr period of a discrete model.

I am not considering the assumptions that are required for all the methods, such as the nests being a random or representative sample from the population to which inferences are to be drawn (but see Shaffer and Thompson [*this volume*] for use of model-based rather than design-based estimators to overcome non-representative samples); or that fates of nests are independent of one another (unless random effects are included); or that ages, if needed, are assigned correctly; or that fates are accurately determined; or that survival from day to day is conditionally independent (that is, DSRs can be multiplied). All methods assume that the monitoring process does not affect the fate of the nest, although several investigators (Bart and Robson 1982, Nichols et al. 1984, Sedinger 1990, Rotella et al. 2000) have addressed estimation or adjustment for the effects of observers on nest fate.

Table 1 briefly describes how various methods of estimating nest success accommodate particular features of the data. Included are the objectives of the study, whether or not a method satisfactorily deals with the exclusion of nests that were destroyed before they could be discovered, and the ability of a method to handle nests for which the age is unknown. Certain methods require that the age of the nest at discovery be known; others need that information only if age-specific analysis is desired. Many methods can use age to estimate the date of hatching, if nests are not visited daily. Although techniques for estimating the age of a nest sometimes can be employed, accurate aging often is a problem, especially for nests that ultimately fail and cannot be aged by counting backward from the date of hatching or fledging. Also Table 1 indicates whether or not the method accommodates right censoring—e.g., if it uses data from nests that could not be relocated or were still active after the study terminated, interval censoring—in which losses occur on an unknown day between visits to a nest, the types of heterogeneity in DSR that a method is designed to accommodate, and the relative effort needed in the field to provide data necessary for analysis with the method. In many cases this feature is closely tied to the ability of a method to handle uncertain failure dates and thereby the need for daily checks on nests.

In Table 2, I present the computational ease for the same methods, which indicates whether commonly available and easy-to-use software is available to apply the method. Results presented in Tables 1 and 2 lead to the guidelines offered in Table 3. There a researcher can respond to a few questions about the study and resulting data, and narrow down the choice of most appropriate methods. The questions involve the objectives of the study, the visitation schedule, whether or not the age of a nest when found is known, and whether or not failed nests are as detectable as active nests.

For example, if interest lies in the effect of some group covariate, say habitat type, then the choice narrows to methods 1–3, 5–7, 12, 13, and 18–22. If nests can be revisited only periodically and not on a rigid schedule, method 13 is eliminated from consideration. If nests cannot be aged accurately, we eliminate methods 7, 18, 19, and probably 20. Method 1 will not work if destroyed nests are less likely to be detected than active ones. That reduces the possibilities to methods 2, 3, 5, 6, 12, 21, and 22. Methods 2, 3, 5, and 6 require the estimation of DSR for each group (and hence large sample sizes) and subsequent comparisons. Methods 12, 21, and 22 can incorporate the group effect directly in the analysis. Method 12 relies on a midpoint approximation when nests are not visited daily.

CONCLUSIONS

The 23 methods of estimating nest success, outlined in Tables 1 and 2, offer a bewildering choice to a biologist posing a rather simple but important question—what is the success rate of a group of nests? Only a few of the methods

Table 1. This table summarizes the methods of estimating nest success, the objectives each method addresses, whether or not various features of nesting data are accommodated, and the degree of field effort required to obtain data appropriate for the method. ID is an identification number; method is either a name commonly associated with the method or an original reference to the method; objectives addressed is whether the method can address the effect of various covariates on survival. Accommodates indicates whether the method satisfactorily deals with: left truncation—the exclusion of nests that were destroyed before they could be discovered; unknown age, nests for which the age is unknown; uncertain fate, right censoring; uncertain failure date, interval censoring; and variation in DSR—the types of heterogeneity in DSR that the method is designed to accommodate. Field effort required describes the relative effort needed in the field to provide data necessary for analysis with the method.

			Accommodates					
ID[a]	Method	Objectives addressed	Left truncation	Unknown age	Uncertain fate	Uncertain failure date	Variation in DSR	Field effort required
1	Apparent	Nest success; group effects	No[b]	Yes	No	Yes	All[c]	Very easy
2	Mayfield (1961, 1975)	Nest success; group effects	Yes	Yes	Yes	Yes (but by assumption only)[d, e]	By group[f]	Easy
3	Johnson (1979)	Nest success; group effects	Yes	Yes	Yes	Yes	By group	Easy
4	Intercept (Johnson 1979)	Nest success	Yes	No	Yes	Yes	Heterogeneity; also age-related	Easy
5	Hensler and Nichols (1981)	Nest success; group effects	Yes	Yes	Yes	No[d]	By group	Easy
6	Bart and Robson (1982)	Nest success; group effects	Yes	Yes	Yes	Yes	By group	Easy
7	Product (Klett and Johnson 1982)	Nest success; age or group effects	Yes	No	Yes	Yes	Age, date, or any identifiable characteristic	Easy
8	Life table (Goc 1986)	Nest success; age effects	Yes	No	Yes	Yes	Age	Very easy; no checks needed
9	Pollock and Cornelius (1988)	Nest success; age effects	Yes	No	No	No	Age group	Easy
10	Bromaghin and McDonald (1993a, b)	Nest success	Yes	Yes	No	Yes	No assumptions made	Visits to nests regularly spaced
11	Heisey and Nordheim (1995)	Nest success; age effects	Yes	Yes	Yes	Yes	Age	Easy
12	Aebischer (1999)	Nest success; effects of covariates	Yes	Yes	Yes	Yes (but by assumption only)[d]	Age, date, or any identifiable characteristic	Easy
13	Natarajan and McCulloch (1999)	Nest success; heterogeneity; effects of covariates	Basic model assumes nests are found at initiation; generalization seems to assume no losses before discovery	Yes	No	Not an issue since nests need to be visited daily	Heterogeneity (nest-specific DSR); any identifiable variable, including nest- and time-specific ones	Assumes nests are visited daily or that detectability is constant

TABLE 1. CONTINUED.

			Accommodates					
ID[a]	Method	Objectives addressed	Left truncation	Unknown age	Uncertain fate	Uncertain failure date	Variation in DSR	Field effort required
14	Stanley (2000)	Nest success; age effects	Yes	No	Yes	Yes	Stage	Visits frequent enough to not miss any stage
15	Stanley (2004a)	Nest success; age effects	Yes	Yes	Yes	Yes	Stage	Visits frequent enough to not miss any stage
16	He et al. (2001)	Nest success; age effects	Yes	Yes	No	No	Age	Daily visits to nests
17	He (2003)	Nest success; age effects	Yes	Yes	No	Yes	Age	Frequent visits to nests
18	Survival time, (Aldridge and Brigham 2001, Nur et al. 2004)	Nest success; effects of covariates	No[g]	No	Yes	No[d]	Any identifiable variable, including nest- and time-specific ones	Frequent visits to nests
19	Manly and Schmutz (2001)	Nest success; age or group effects	Yes	No	Yes	Yes	Age (or date)	Easy
20	Dinsmore et al. (2002)	Nest success; effects of covariates	Yes	No[h]	Yes	Yes	Any identifiable variable, including nest- and time-specific ones	Easy
21	Stephens (2003)	Nest success; effects of covariates	Yes	Yes	Yes	Yes	Any identifiable variable, including nest- and time-specific ones	Easy
22	Shaffer (2004)	Nest success; effects of covariates	Yes	Yes	Yes	Yes	Any identifiable variable, including nest- and time-specific ones	Easy
23	McPherson et al. (2003)	Nest success; age effects	Yes; assumes some nests are found at Day 1	No	Yes	No	Age	Daily visits to nests

[a] Identification number.
[b] Unless successful and failed nests are equally likely to be found.
[c] Variation in DSR is accommodated implicitly but not specifically identified.
[d] Robust with respect to uncertainty in failure dates, as long as intervals between searches are short.
[e] Miller and Johnson (1978) modified the method for longer intervals between searches.
[f] Robust to variation among groups if variation in DSR is modest.
[g] See Heisey et al. (*this volume*).
[h] Method seems not to require known age but program MARK does.

TABLE 2. METHODS OF ESTIMATING NEST SUCCESS, THE EASE WITH WHICH ESTIMATES CAN BE COMPUTED, AND ANY OTHER DISTINGUISHING FEATURES.

ID	Method	Computational ease[a]	Other
1	Apparent	Hand	Failed and active nests must be equally detectable.
2	Mayfield (1961, 1975)	Hand	Assumes DSR is the same for all nests and nest-days in group (method is robust to modest variation); assumes losses between visits occurred at midpoint of interval.
3	Johnson (1979)	STATware	Same as Mayfield except midpoint assumption not needed.
4	Intercept (Johnson 1979)	STATware	Need to know age of nest when found; detectability must be the same for all ages and all nests; large sample required.
5	Hensler and Nichols (1981)	Hand	Same as Mayfield; also, strictly, requires exact failure date; in practice usually works with mid-point assumption when nest visits are not daily.
6	Bart and Robson (1982)	AUTHORware	Same as Mayfield except midpoint assumption not needed.
7	Product (Klett and Johnson 1982)	AUTHORware	Need to know age of nest when found.
8	Life table (e.g., Goc 1986)	STATware	Need to know age of nest when found; detectability must be the same for all ages and all nests; large sample required; must sample throughout season.
9	Pollock and Cornelius (1988)	AUTHORware	Generally produces biased estimators (Heisey and Nordheim 1990).
10	Bromaghin and McDonald (1993a, b)	AUTHORware	Detectability must be the same for all ages and all nests; rigid sampling design required.
11	Heisey and Nordheim (1995)	AUTHORware	
12	Aebischer (1999)	STATware	Strictly, requires exact failure date; in practice usually robust under mid-point assumption when nest visits are not daily.
13	Natarajan and McCulloch (1999)	AUTHORware	Random effects modeling; assumptions and properties not clear.
14	Stanley (2000)	AUTHORware	Need to know age of nest when found.
15	Stanley (2004a)	AUTHORware	No longer need to know age of nest when found.
16	He et al. (2001)	AUTHORware	Bayesian.
17	He (2003)	AUTHORware	Bayesian.
18	Survival time (Aldridge and Brigham 2001, Nur et al. 2004)	STATware	Need to know fairly precisely age when found and when lost. Care required to ensure that left truncation is properly handled by the software, and some nests need to be discovered at initiation (Heisey et al., *this volume*).
19	Manly and Schmutz (2001)	AUTHORware	An extension of Klett-Johnson (1982); need to know age of nest when found.
20	Dinsmore et al. (2002)	MARKware	
21	Stephens (2003)	STATware	Developed SAS code to perform method of Dinsmore et al. (2002); also allowed single random effect.
22	Shaffer (2004)	STATware	
23	McPherson et al. (2003)	AUTHORware	Requires daily checks of nests; some nests must be monitored from initiation.

[a] Hand—calculations can be done on a hand calculator or with simple spreadsheet, STATware—computations can be performed with general purpose statistical software such as SAS, MARKware—method requires special-purpose software that is readily available and well supported, AUTHORware—method uses specially written software available from the author and with limited support.

TABLE 3. A GUIDE TO SUITABLE METHODS OF ESTIMATING NEST SUCCESS AND EFFECTS OF ASSOCIATED VARIABLES, BASED ON THE OBJECTIVES OF THE STUDY, THE VISITATION SCHEDULE INVOLVED, WHETHER THE AGE OF A NEST AT DISCOVERY CAN BE DETERMINED, AND WHETHER OR NOT DESTROYED NESTS ARE AS READILY DISCOVERED AS NESTS THAT ARE ACTIVE.

Objective, if your objective involves:	Then consider methods:
Nest success only	Any
Age effects	7–9, 11–23
Group covariates	1, 2, 3, 5, 6, 7, 12, 13, 18–22
Individual covariates	12, 13, 18, 20–22
Visitation schedule:	
No revisit	8
Revisited after anticipated termination date	1, 8
Check only periodically	1–9, 11, 12, 18–22
Fairly rigid schedule	1–12, 14, 15, 17–22
Check daily	Any
Age of nest at discovery:	
Known	Any
Unknown	1, 2, 3, 5, 6, 10–13, 15–17, 21, 22
Detectability of failed nests:	
Same as successful	Any
Lower than successful	2–23

have received much use, beyond an example application in the paper that introduced the method. These little-used methods have not faced testing in the real world.

I think that the requirements of certain methods are too demanding to warrant frequent use. For example, methods 13, 16, and 23 require that nests be visited daily to meet their assumptions. Such a rigid schedule is hardly ever practical in field studies, and the effect on the fate of such intensive monitoring may be severe (Götmark 1992).

The apparent estimator (method 1) is reasonable only if destroyed nests can be detected as readily as active nests. Rarely is that condition met (Johnson and Shaffer 1990), so this estimator is seldom applicable. The apparent estimator seems largely to have fallen out of use, at least in North America, but Armstrong et al. (2002) recently indicated that it remains in common use in New Zealand.

Many methods (4, 7, 8, 9, 14, 18, 19, 23, and generally 20) require that the age of each nest be known. Other methods need this information only if age-related variation in DSR is an objective of the study, or is marked enough to require age-specific estimates to generate a satisfactory overall estimate (Grant et al. 2005). Ascertaining the age of nests accurately is fairly straightforward in some studies but nearly impossible in others.

Survival-time methods, which are widely used in many other applications, have been suggested for nest survival as well (Nur et al. 2004). Concerns about their suitability for routine use in nest-survival studies, remain, however, such as their ability to handle left truncation and interval censoring (Heisey et al., *this volume*).

The Mayfield estimator, despite its basis on what appears to be an extremely restrictive assumption (that DSR is the same for all days and all nests), has borne out rather well. In a number of comparisons with more sophisticated methods, it has proven competitive (Johnson, *chapter 1, this volume*). The Johnson (1979) variant, which obviates the need for Mayfield's midpoint assumption, likely will be useful in many situations, unless age-related variation in DSR is pronounced and sample sizes are large. Further, it can be readily calculated analogously to Shaffer's (2004) logistic-exposure method with a log link rather than a logistic link (T. L. Shaffer, pers. comm.). By doing so, biologists can compare the model with constant DSR to more complex models.

When more complex models are of interest, the choice usually is between the program MARK approach of Dinsmore et al. (2002)—or Stephens' version (2003) of that approach—and the logistic-exposure method of Shaffer (2004). The models are substantially similar, although program MARK generally requires that the ages of each nest be known. One difference arises when time-specific (or age-specific) covariates are included in the model. If visits to a nest are several days apart, the logistic-exposure method assumes the time-specific influence is the same on each day. In contrast, the program MARK approach allows the time-specific influence to vary day to day. It is unclear how frequently this difference will be appreciable. It should be noted that these approaches can be used with simple as well as complex models, and they lend themselves to addressing most common objectives. For example, if an objective is to estimate overall nest success, these methods can generate a pooled estimate that is comparable to, say, a Mayfield estimate. But, in addition, one can construct model-based estimators of nest success that can overcome biases resulting from the sample of nests being non-representative (Shaffer and Thompson, *this volume*).

Also, some methods, including those of Shaffer (2004) and Stephens (2003), readily permit random effects to be included in fitted models. Generally, the inclusion of random effects for factors such as study sites or years allows more appropriate inference to be made to the population of sites or years rather than merely to those sites and years that were sampled. The usual assumption that the mean of a random effect is zero is inappropriate for left-truncated data, however (Heisey et al., *this volume*), so the role of random effects in nest survival analysis is not yet clear.

Perhaps the greatest difference among the methods of Dinsmore et al. (2002), Stephens (2003), and Shaffer (2004) lies in the computer software requirements. To employ the first approach requires the user to be familiar with program MARK (White and Burnham 1999), a very powerful suite of software used to analyze mark-recapture data under a broad variety of models. The program and its documentation are freely available, but a substantial learning curve is involved. The latter two methods require the biologist to use generalized linear models software. Examples of such software include PROC GENMOD and PROC NLMIXED of SAS and the S function GLM. See Shaffer (2004) and Rotella et al. (2004) for further comparisons.

ACKNOWLEDGMENTS

Thanks to S. L. Jones and G. R. Geupel for organizing the symposium and inviting my participation. This report benefited from comments by S. L. Jones and T. L. Shaffer. I appreciate comments provided by authors of many methods I described, including N. J. Aebischer, J. F. Bromaghin, S. J. Dinsmore, R. E. Green, K. R. Hazler, C. Z. He, G. A. Jehle, B. F. Manly, C. E. McCulloch, R. Natarajan, N. Nur, J. J. Rotella, C. J. Schwarz, T. R. Stanley, S. E. Stephens, and especially D. M. Heisey. Each author helped me learn more about the methods they presented. C. J. Schwarz suggested the categorization of computation difficulty of the various methods.