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METHODS OF ESTIMATING NEST SUCCESS: AN HISTORICAL TOUR

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Abstract. The number of methodological papers on estimating nest success is large and growing, reflecting the importance of this topic in avian ecology. Harold Mayfield proposed the most widely used method nearly a half-century ago. Subsequent work has largely expanded on his early method and allowed ornithologists to address new questions about nest survival, such as how survival rate varies with age of nest and in response to various covariates. The plethora of literature on the topic can be both daunting and confusing. Here I present a historical account of the literature. A companion paper in this volume offers some guidelines for selecting a method to estimate nest success.

Key Words: history, Mayfield estimator, nest success, survival.

MÉTODOS PARA LA ESTIMACIÓN DE ÉXITO DE NIDO: UN RECORRIDO HISTÓRICO

Resumen. La cantidad de artículos metodológicos en la estimación de éxito de nido es muy grande y está creciendo, y refleja la importancia de este tema en la ecología de aves. Harold Mayfield propuso hace cerca de medio siglo el método mayormente utilizado. Subsecuentemente se ha expandido ampliamente su trabajo partiendo de su método, permitiendo así a los ornitólogos encausar nuevas preguntas respecto a la sobrevivencia de nido, tales como la forma en la qual la tasa de sobrevivencia varía con la edad del nido y en respuesta a varias covariantes. El exceso de literatura en el tema puede ser tanto desalentador como confuso. Aquí presento un recuento histórico de la literatura. Algún otro artículo en este volumen ofrece las pautas para seleccionar un modelo para estimar el éxito de nido.

Ornithologists have long been fascinated by the nests of birds. To avoid predation, many species of birds are very secretive about their nesting habits; thus locating nests may become a real challenge. Curiosity about the outcome often drives the biologist to check back later to see if the nests had been successful in allowing the clutches to hatch and young birds to fledge. If enough nests are found, one can calculate the percentage of nests that were successful. Such nest-success rates are very convenient metrics of reproductive success and have been used to compare species, study areas, habitat types, management practices, and the like. Certainly, nest-success rates are incomplete measures of reproduction since they do not account for birds that never initiated nests, birds that renested after either losing a clutch or fledging a brood, and the survival of eggs and young. Nonetheless, nest success is a valuable index to reproductive success and for most populations is a critical component of reproductive success (Johnson et al. 1992, Hoekman et al. 2002). For these reasons it is important that measures of nest success be accurate.

In this chapter, I review the history of methods developed to estimate nest success. The number of these methods is surprisingly large, reflecting both the interest in and importance of the topic, as well as a lack of awareness of what others had done previously. Some wheels have been invented repeatedly. Being a historical perspective, this account will be largely chronological. I do not review methodological papers that discuss how to find nests (Klett et al. 1986, Martin and Geupel 1993, Winter et al. 2003) nor how to treat nesting data (Klett et al. 1986, Manolis et al. 2000, Stanley 2004b), although these topics clearly are important in their own right. This historical overview is complementary to Johnson (*chapter 6, this volume*), which provides some guidelines for selecting a method to use.

THE HISTORY

The measure mentioned above, the ratio of successful nests to total nests in a sample, has come to be known as the apparent estimator of nest success, and has a history that spans decades, if not centuries. It is straightforward and easy to calculate. That it can be biased, often severely, was not widely recognized in the scientific literature until 1960. Harold F. Mayfield, an amateur ornithologist (see sidebar), was compiling a large amount of information on the breeding biology of the Kirtland's Warbler (*Dendroica kirtlandii*) for a major treatise on the species (Mayfield 1960). In that book he pointed out the bias in the apparent estimator and proposed what became known as the Mayfield estimator as a remedy. Recognizing the general need for such a treatment of nesting data, Mayfield (1961) focused specifically on the methodology.

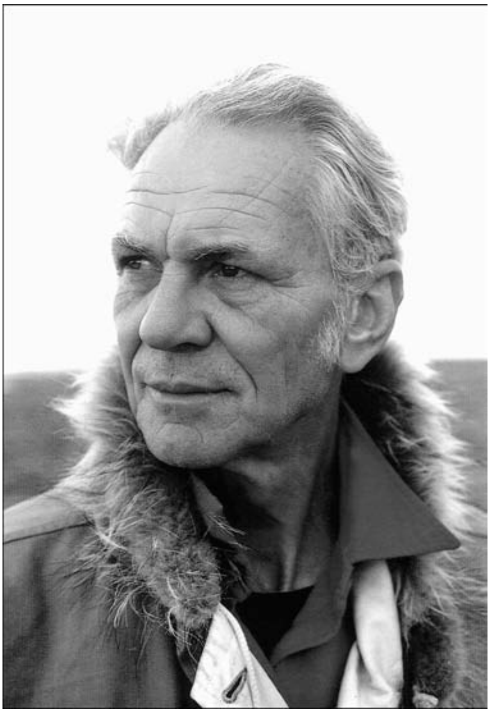

FIGURE 1. Harold F. Mayfield in 1984.

Harold F. Mayfield (Fig. 1) is perhaps best known among ornithologists as the developer of a method for estimating nest success, a method that now bears his name. Mayfield's seminal 1961 paper on the topic is the most-frequently cited ever to appear in the *Wilson Bulletin*. His ornithological credentials, however, are much greater than that single, albeit highly valuable, contribution to our science. His monograph on the Kirtland's Warbler won the Brewster Award, the top scientific honor granted by the American Ornithologists' Union. He has often trekked to the Arctic; one product of those trips was a monograph on the life history of the Red Phalarope (*Phalaropus fulicaria*). These represent just two of his approximately 300 published papers in ornithology.

Mayfield also has the distinction of being the only individual to have served as president of all three major North American scientific ornithological societies: the American Ornithologists' Union, Cooper Ornithological Society, and Wilson Ornithological Society. Among his other honors are the Arthur A. Allen award from the Cornell Laboratory of Ornithology, the Ridgway award from the American Birding Association, and the first-ever Lifetime Achievement award from the Toledo Naturalists' Association.

What may be most surprising is that Mayfield is not a professional ornithologist; he is an amateur in the true sense of the word, someone who does something out of love, not for compensation. His paying profession was in personnel management. He is accomplished in that field, too, having published more than 100 papers in its journals. Mayfield in fact traces the roots of the Mayfield method to his background in industry, where safety was measured in terms of incidents per worker-day exposure.

When I most recently visited Harold and his wife Virginia in 1995, at their home in Toledo, he was still intellectually active at age 85. To illustrate, he had come up with a new hypothesis to explain the migration path of Kirtland's Warblers.

More personally, Harold Mayfield has been a gracious supporter of my own work on the topic of estimating nest success. When I developed the maximum likelihood estimator that allowed for an uncertain termination date (Johnson 1979), I thought it would be useful to compare estimates from that method with estimates Mayfield had obtained with his method. When I wrote to state an interest in obtaining the data he used, he generously provided his original data on Kirtland's Warblers. Further, he continued to write to me, encouraging me, and expressing his satisfaction that someone was taking a more rigorous look at the topic. His enthusiastic support continued to his death in 2006.

In hindsight, but hindsight only, his method was simple and the need for it obvious. A nest that is found, say, 1 d prior to hatching has a high probability of success, because it has to survive only one more day. Conversely, a nest found early in its lifetime has to survive many more days to succeed, and its chances of success are lower. So the fates of a sample of nests found at different ages are not likely to represent the likelihood of a nest surviving from initiation until hatching. The problem, in statistical jargon, is one of length-biased sampling. That is, the chance that a unit (nest, in this case) is included in a sample depends upon the length of time it survives. One way to overcome this bias is to use in the analysis only nests found at the onset, but in most studies this restriction would result in the omission of many nests. Mayfield (1960, 1961) suggested that the time that a nest is under observation be considered; he termed this period the exposure. He further suggested the nest-day as the unit of exposure. Then, the number of nest failures observed divided by the exposure provides an estimate of the daily mortality rate, which when subtracted from one yields a daily survival rate (DSR). To project DSR to the length of time necessary for a nest to succeed yields an estimate of nest success. When nests fail between visits, Mayfield assumed the failure occurred midway between visits and assigned the exposure as half the length of that interval. He acknowledged his assumption of constant DSR throughout the period. Also key is the assumption that DSR does not vary among nests.

It can be noted (Gross and Clark 1975) that Mayfield's estimator is the maximum likelihood estimator of the daily survival rate under the geometric model, the discrete analog of the exponential model, both of which assume a constant hazard rate.

Other investigators too had noted the bias in the apparent estimator. For example, Snow (1955) observed that nests nest found at an advanced stage of the nesting cycle will bias the percentage in favor of success if included in the analyses. He alluded to a rather laborious mathematical procedure to compensate for the bias and indicated an intention to deal fully with the mathematical procedure in a forthcoming paper (Snow 1955). In a 1996 letter to me (D. W. Snow, pers. comm.), he indicated that the paper never was published.

Coulson (1956) also recognized the bias and suggested a remedy. He reasoned that, on average, a failed nest would be under observation for only half the period necessary to succeed, so the chance of finding a failed nest would be only half the chance of finding a successful one. Thus, the actual number of failed nests would be twice the number observed. So, whereas the apparent estimator of nest success is 1 – failed/(failed + hatched), Coulson generated an estimate of 1 – (2 × failed)/(2 × failed + hatched). This ad hoc procedure seemed to receive little use (but note Peakall 1960) and did not closely approximate Mayfield's estimator of nest success rate in some example data sets (D. H. Johnson, unpubl. data).

Hammond and Forward (1956) also recognized a problem with the apparent estimator—neglecting to consider the length of time nests are under observation as compared with the total period they are exposed to predation would lead to a recorded success higher than that actually occurring (Hammond and Forward 1956). Note that they used the term exposed, much as Mayfield did. Hammond and Forward (1956), in fact, developed a Mayfield-like estimator of nest-survival rate, and scaled it to a mortality rate per week. In their data set, they noted (Hammond and Forward 1956) for 2,543 nest-days observation of group (1), the predation rate was 10.8% destroyed per week as compared with 6.7% for 728 nest-days observation of group (2) nests. They also projected the rate to the term of nesting. It is interesting that the Hammond-Forward method was used little if at all, despite being essentially the same as the Mayfield method and published 4 yr earlier than Mayfield's article. Possibly if Hammond and Forward (1952) had presented a paper focused directly on the methodology, as did Mayfield, we might today be referring to the Hammond-Forward estimator, rather than the Mayfield estimator.

Peakall (1960) identified two problems associated with the apparent estimator. First, it does not account for failed nests that were not found; this is the same length-biased sampling concern noted above. He recommended Coulson's (1956) adjustment as a solution to this problem. Second, he indicated that it is easier to determine the fate of nests that fail than those that succeed, because successful nests last longer and the observer may not be persistent enough to learn their fate. Peakall (1960) proposed a new method, which is akin to the Kaplan-Meier method (Kaplan and Meier 1958). It can use only nests found at onset, however. For the example he cited, the apparent estimate was 52.6% and his estimate was 44.6%. It should be noted that if only nests found at initiation are used, then the apparent estimator itself is unbiased.

Gilmer et al. (1974) and Trent and Rongstad (1974) each used Mayfield-like estimators, although without citing Mayfield, in applications to telemetry studies. Gilmer et al. (1974) defined a daily predation rate as the number of predator kills per duck tracking day. They projected the DSR (1 minus the daily predation rate) to a 120-d breeding season. Trent and Rongstad (1974) also presented confidence limits for the survival-rate estimate, based on treating days as independent binomial variates, and approximating the binomial distribution with a Poisson distribution. Trent and Rongstad (1974) identified the key assumptions: (1) each animal day was an independent trial, and (2) survival was constant over time (and, unstated among animals). They similarly projected DSR, and its confidence limits, to a 61-d period.

Mayfield (1975) revisited the issue, because many studies were ignoring the difficulty he raised, and he often was being asked for guidance in applying his method. He noted that not every published report shows awareness of the problem and that some people have difficulty with details (Mayfield 1975). He mentioned that, no field student is happy to see a simple concept like nest success made to appear complicated (Mayfield 1975). That paper had other interesting observations. Mayfield commented on the effect of visitation on nest survival by alluding to a biological uncertainty principle whereby any nest observed is no longer in its natural state (Mayfield 1975). And, wisely, he cautioned against pooling data even if differences are not significant, a mistake many professional scientists still make.

Mayfield's method began to draw some critical attention 15 yr after first publication. Göransson and Loman (1976) tested the validity of the assumption that the hazard rate is constant with a study of simulated Ring-necked Pheasant (*Phasianus colchicus*) nests. They found that mortality was low for the first day, high for the next 3 d, then low for the rest of the period. They concluded that the Mayfield method in that situation would not be suitable for the laying period.

Green (1977) suggested that Mayfield's estimator would be biased if DSR was not constant. He argued that such heterogeneity would bias the estimator downward. Later, Johnson (1979) pointed out that Green's (1977) concern would manifest itself only if all nests were found at initiation, and that the bias would be in the opposite direction under the usual conditions that nests are found later in development.

Dow (1978) argued that Mayfield's (1975) test for comparing mortality rates between periods—based on a chi-square contingency table test between days with and without losses—is inappropriate. Dow (1978) proposed an analogous test that used nests rather than nest-days as units. Johnson (1979) pointed out that Dow's (1978) test is inappropriate in general unless the lengths of the periods are the same.

Miller and Johnson (1978) drew attention to the Mayfield method by illustrating its applicability to waterfowl nesting studies Townsend (1966) was noted as the only other waterfowl study to use Mayfield's method. They observed that the Mayfield method had not been widely adopted (Miller and Johnson 1978) and provided a detailed illustration of the bias associated with the apparent estimator and an explanation of the Mayfield method. A figure in Miller and Johnson (1978) illustrated the length-biased nature of the sampling problem. They also demonstrated the importance of the bias of the apparent estimator even for comparing treatments, with an example of Simpson's paradox (Simpson 1951).

Miller and Johnson (1978) suggested that the midpoint assumption of Mayfield was too generous in assigning exposure for the examples they considered—which were waterfowl nests typically visited at intervals of 14–21 d—and proposed that intervals with losses contribute only 40%, rather than 50%, of their length to exposure calculations. They supported this recommendation by calculating the expected exposure under a variety of scenarios. That estimator became known as the Mayfield-40% estimator.

Miller and Johnson (1978) further indicated how an improved estimate of the number of nests initiated could be made, by dividing the number of successful nests by the estimated success rate. Because the number of successful nests is the number of nests initiated times the nest-success rate, an estimator of the number of nests initiated is the number of successful nests divided by the nest-success rate. This estimator is more accurate than just the number of nests found because it is often feasible to accurately determine the total number of successful nests, since such nests persist for rather long times.

Johnson (1979) demonstrated that the Mayfield estimator is in fact a maximum likelihood estimator under a particular model, one that assumes that DSR is constant and that the loss of a nest occurs exactly midway through an interval between visits to the nest. As a maximum-likelihood estimator, it possesses certain desirable properties. Johnson (1979) developed an estimator of the standard error of Mayfield's estimator. He further explored the midpoint assumption and found that, for intervals averaging up to about 15 d and for moderate daily mortality rates, Mayfield's assumption was reasonable. For long intervals—such as were common with waterfowl studies—the midpoint assumption assigns too much exposure to destroyed nests, as Miller and Johnson (1978) had indicated.

Johnson (1979) also developed a model for which the actual time of loss was unknown and determined a maximum likelihood estimator for DSR under that less restrictive model. Iterative computation was required, which, at that time limited its applicability. Further, a comparison of the new estimator with Mayfield's and the Mayfield-40% estimators suggested that the new one most closely matched the original Mayfield values if intervals between visits were short, and was closer to the Mayfield-40% values if intervals were long. Johnson (1979) recommended routine use of the Mayfield or Mayfield-40% estimators because of their computational ease.

Johnson (1979) also considered variation, due either to identifiable or to non-identifiable causes, in the DSR. He calculated separate estimators for different stages of the nesting cycle and used t-tests to compare them statistically. He considered heterogeneity in general and suggested a graphical means for detecting it and exploiting it if it exists. This has been called the intercept estimator; it does, however, require that detectability of nests not vary with nest age.

Willis (1981) credited Snow (1955) and others with noting the bias of the apparent estimator. Mistakenly, he suggested that Mayfield's estimator would be biased because it allotted a full day of exposure to a nest destroyed during a day. Willis (1981) suggested that only a half-day be assigned in such a situation. That recommendation was later withdrawn, but only in an easily overlooked corrigendum (Anonymous 1981).

Hensler and Nichols (1981) proposed a model of nest survival based on the assumption that nests are observed each day until they succeed or fail. The maximum-likelihood estimator under that model turned out to be the same as Mayfield's. The standard error they computed was also the same as that derived by Johnson (1979) for Mayfield's model. Hensler and Nichols (1981) incorporated encounter probabilities, representing the probability that an observed nest was first found at a particular age. These turned out to be irrelevant to the estimator, although they may contain information that could be exploited. Hensler and Nichols (1981) provided some sample size values needed for specified levels of precision.

Klett and Johnson (1982) explored the key assumption of the Mayfield estimator, that daily survival is constant with respect to age and to date. They examined the variation in daily mortality rate, using waterfowl nests in their examples. Klett and Johnson (1982) found that the daily mortality rate tended to decline with the age of nest. Seasonal variation also was evident. They developed a product estimator that accounted for such variation by taking the product of individual age-dependent survival probabilities. The stratification necessary for the product estimator required detailed allocation of losses and exposure days to categories of age and date. In their example, the product estimator, based on age-specific survival rates, did not differ appreciably from the ordinary Mayfield estimator. Klett and Johnson (1982) also computed intercept estimators (Johnson 1979) for their data. They found that the Mayfield estimator was robust with respect to mild variation in DSR. They further doubted that pure heterogeneity existed in their data sets; the intercept estimators were not useful. Klett and Johnson (1982) also provided some sample-size recommendations.

Bart and Robson (1982) also developed maximum-likelihood estimators, giving guidance for iteratively solving them. They also used power analysis to generate some sample-size requirements.

Johnson and Klett (1985) clearly demonstrated the bias of the apparent estimator, being greater when the survival rate is low to medium or when nests are found at older ages. They proposed a shortcut estimator of nest success, which uses the apparent rate and the average age of nests when found. The approximation is made by assuming that all nests were found on that average day. Several examples indicated that the shortcut estimator was closer to Mayfield values and Johnson (1979) maximum likelihood values than was the apparent estimator.

Hensler (1985) developed estimators for the variance of functions of Mayfield's DSR, such as the survival rate for an interval that spans multiple days.

Goc (1986) proposed estimating nest success by constructing a life table from the ages of nests found. He indicated that the frequency of clutches recorded in consecutive age groups would correspond to the survival of clutches to the respective ages (Goc 1986). Stated requirements for the method were: (1) large sample sizes (300–500 nest checks), (2) sampling to occur throughout the season, and (3) detectability of nests being equal for nests of all ages. Goc (1986) did not address the need for independence of nest checks, which would seem necessary and which would make the data requirements very demanding. Further, in most situations the detectability of nests varies rather dramatically by age of the nest. The influence of such variation on survival estimates based on this method bears scrutiny.

A nice mathematical property of the constant-hazard (exponential) model is its lack of memory. This lack-of-memory property means that no additional information is gained by knowing the nest's age, which is extremely appealing because many nests are difficult to age. But constant-hazard models are often unrealistic, and all other models require some consideration of age, usually in the form of age-specific discovery probabilities. Age-specific discovery probabilities were introduced but turned out to be irrelevant in the Hensler and Nichols (1981) model, a consequence of the very special lack-of-memory property of their model. Pollock and Cornelius (1988) apparently were the first to address the issue of estimating age-dependent nest survival in the situation where nest ages are not known exactly but for which bounds were known. Their estimator allowed the survival rate to vary among stages (age groups). In addition to survival parameters, their model requires the estimation of discovery parameters. Because their estimator basically treated all nests in a stage as if they were found at the beginning of the stage, it has the same problem, but at a smaller scale, as the apparent estimator; it was shown to be biased high by Heisey and Nordheim (1990).

Green (1989) suggested a transformation of the apparent estimator to reduce its bias. The fundamental idea is that the numbers of nests found at a particular age should be proportional to the numbers surviving to that age. Its validity depends on the detectability of nests being constant over age of the nests, which is unlikely in most situations (Johnson and Shaffer 1990). It also requires that the observed nests be but a small fraction of the nests available for detection or that nest searches are infrequent relative to the lifetime of successful nests.

Johnson (1991) revisited Green's (1989) procedure and noted that it involved a mixture of a discrete-time model and a continuous-time model of the survival process. By example, Johnson (1991) clarified the distinction between the two modeling approaches. This has been a source of confusion in some published papers (Willis 1981). Johnson (1991) proposed a new formulation that was consistent in its reliance on the discrete-time approach. It turned out to be slightly more complicated than Green's (1989) original method in that it required separate specification of the daily survival rate and the length of the interval a clutch must survive in order to hatch. Johnson's (1991) modification always produces slightly higher estimates of nest success than the original Green (1989) version. A comparison of several estimators with both actual and simulated data sets indicated the Johnson (1979) or Mayfield method to be preferred, but if exposure information is not available, the Johnson-Klett (1985), Green (1989), or Johnson-Green (Johnson 1991) estimators performed similarly.

Johnson (1991) also indicated that the assumptions of Green's (1989) estimator could be checked by plotting the log of the number of nests found at each age against age. Based on this relationship, one could estimate the DSR solely from the age distribution of nests when found (cf. Goc 1986).

Johnson and Shaffer (1990) considered situations in which the daily mortality rate is likely to be severely non-constant, specifically when destruction of nests occurs catastrophically. The Mayfield estimator, with its assumption of constant DSR, was shown to be inaccurate in such situations. Apparent estimates were satisfactory when searches for nests were frequent and detectability of nests was high. Johnson and Shaffer (1990) specifically considered island nesting situations, which often differ from those on mainland due to: (1) generally high survival of nests, and therefore lower bias of the apparent estimator, (2) greater synchrony of nesting, which facilitates finding nests early and thereby reduces the bias of the apparent estimator, (3) catastrophic mortality being more likely on islands, due to extreme weather events or the sudden appearance of a predator, therefore violating the key assumption of the Mayfield estimator, and (4) destroyed nests being more likely to be found, again reducing the bias of the apparent estimator.

Johnson and Shaffer (1990) also described conditions under which apparent and Mayfield estimates of nest success led to reasonable estimates of the number of nests initiated. Mayfield estimates were better in situations with constant and low mortality rates. When mortality was high and constant, or catastrophic, the apparent estimator led to acceptable estimates of number of nests initiated only when many searches were made and detectability of nests was high.

Johnson and Shaffer (1990) observed that, if detectability is independent of age of clutch, then a plot of the logarithm of the number of nests found at a particular age against age should be linear aand decreasing. In the Blue-winged Teal (*Anas discors*) example they cited (Miller and Johnson 1978), the pattern was increasing, indicating that detectability of nests in fact varied by age.

Johnson (1990) justified a procedure that he had used for some time to compare daily mortality rates for more than two groups. It extended the two-group t-test of Johnson (1979) to more than two groups by showing that multiple mortality rates could be compared by using an analysis of variance on the rates, with exposure as weights, and referring a modified test statistic to a chi-square table. The original publication contained a typographical error, which was corrected in the Internet version (Johnson 1990)

Bromaghin and McDonald (1993a, b) developed estimators of nest success based on encounter sampling, in which the probability of a nest being included in a sample depends on the length of time it survives and on the sampling plan used to search for nests. Bromaghin and McDonald (1993a) presented the framework for a general likelihood function, with component models for nest survival and nest detection. This general model uses the information about the age of a nest that is contained in the length of time a nest is observed, e.g., a successful nest is known to have survived the entire period and a nest observed for k days is known to be at least k-days old. They provided two examples based on the Mayfield model and demonstrated that the models of Hensler and Nichols (1981) and Pollock and Cornelius (1988) are special cases of their more general model. Bromaghin and McDonald (1993b) presented a second model employing systematic encounter sampling and Horvitz-Thompson (Horvitz and Thompson 1952) estimators. Unique features of this model are that no assumptions about nest survival are required and that additional parameters, such as the total number of nests initiated, the number of successful nests, and the number of young produced, can be estimated.

Bromaghin and McDonald's (1993a, b) methods are innovative but require more complex estimation procedures than many other estimators. They assume that the probability of detecting a nest is the same for all nests and for all ages, although this assumption could be generalized. As noted above, the length-biased sampling feature associated with most nesting studies leads to a severe bias of the apparent estimator. Incorporating detection probabilities into the estimation process essentially capitalizes on the problem associated with length-biased sampling. Also, Bromaghin and McDonald (1993a, b) treated the nest, rather than the nest-day, as the sampling unit. Their methods are not appropriate for casual observational studies, but rather require field methods to be carefully designed and implemented so that detection probabilities can be estimated.

Heisey and Nordheim (1995) addressed the same basic problem as Pollock and Cornelius (1988)—estimating age-dependent survival when nest ages are not known exactly. Their goal was to avoid the bias issues of Pollock and Cornelius (1988) by constructing a likelihood that more accurately represented the actual exposure times of the discovered nests. Their approach simultaneously estimated age-dependent discovery and survival parameters using almost-nonparametric, stepwise hazard models. The likelihood was relatively complicated and much of the paper focused on numerical methods for obtaining maximum likelihood estimates via the expectation-maximization (EM) algorithm (Dempster et al. 1977). The calculation by Miller and Johnson (1978) of the expected time of failure anticipated the application of EM; it is essentially an E-step. Heisey (1991) extended the method to accommodate effects of covariates (including time) on both discovery and survival rates. Because of its complexity and lack of available software, the Heisey-Nordheim method (Heisey and Nordheim 1995) has received little application by ornithologists. Using the basic likelihood structure they had proposed, however, Stanley (2000), He et al. (2001), and He (2003) later explored computationally more tractable approaches to estimation.

Aebischer (1999) clearly articulated the assumptions of the Mayfield estimator. He also developed tests to compare daily survival rates based on the deviance, in particular one comparing more than two groups (cf. Johnson 1990). Aebischer (1999) showed that Mayfield models can be fitted within the framework of generalized linear models for binomial trials. Based on this latter result, he indicated that Mayfield models can be fitted by logistic regression where the unit of analysis is the nest, the response variable is success/failure, and the number of binomial trials is the number of exposure days. The same method had been used somewhat earlier by Etheridge et al. (1997). Hazler (2004) later re-invented Aebischer's (1999) method and demonstrated in her examples its robustness to uncertainty in the date of loss, when nest visits were close together.

Although not explicitly stated, strict application of Aebischer's (1999) method requires that the date of loss is known exactly (Shaffer 2004). Nonetheless, like the original Mayfield estimator, it performs well when one assumes the date of loss to be the midpoint between the last two nest visits, especially if nest visits are fairly frequent. Aebischer (1999) did not indicate how to treat observations for which the midpoint is not an integer, as is typically required for logistic regression. Some users of the method round down and round up alternate observations. That device may induce a bias, however, if nests are not analyzed in random order, so Aebischer (pers. comm.) recommends making a random choice between rounding down and rounding up. A slightly more complicated procedure, but one that should perform better, would be to include two observations in the data set for any nest for which the midpoint assumption results in a non-integral number of days. One observation would have its exposure rounded down, the other, rounded up. Each observation would be weighted by one-half. More accurate weights (Klett and Johnson 1982) could be computed, but they likely would offer negligible improvement.

Natarajan and McCulloch (1999:553) noted that constant-survival models can seriously underestimate overall survival in the presence of heterogeneity. They described random-effects modeling approaches to analyzing nest survival data in the presence of either intangible variation (pure heterogeneity) or tangible variation (reflecting the effects of covariates) among nests. They also assumed the absence of confounding temporal factors. In the first of their two approaches, Natarajan and McCulloch (1999) allowed for pure heterogeneity among survival rates of nests. That is, each nest has its own DSR, which remains unchanged with respect to age (or any other factor). It is assumed that values of DSR follow a beta distribution with parameters α and β. Estimates of α and β, as well as of nest survival itself, can be obtained numerically. In their second approach, Natarajan and McCulloch (1999) outlined a method to incorporate heterogeneity associated with measured covariates (explanatory variables). They did this by allowing DSR values to be logistic functions of the covariates. In both of their approaches, Natarajan and McCulloch (1999) discussed situations in which all nests are found immediately after initiation. They relaxed that assumption to some degree by considering a systematic sampling scheme (Bromaghin and McDonald 1993a), in which the probability of detecting a nest is assumed to be constant across nests and ages.

Farnsworth et al. (2000) applied Mayfield and Kaplan-Meier methods to a data set involving Wood Thrushes (*Hylocichla mustelina*). They found essentially no difference between the methods in the estimated success rates; they also noted no variation in DSR with age and no evidence of pure heterogeneity.

Stanley (2000) developed a method to estimate nest success that allowed stage-specific variation in DSR. The underlying model was similar to that of Klett and Johnson (1982), but Stanley (2000) addressed the problem through the use of Proc NLIN in SAS, instead of the cumbersome method used by Klett and Johnson (1982). Stanley's (2000) method requires that the age of the nest be known; Stanley (2004a) relaxed that assumption. Stanley (2004a) assumed that nests found during the nestling stage would be checked on or before the date of fledging. Armstrong et al. (2002) used Stanley's (2000) method but encountered occasional convergence problems with the computer algorithm.

Manly and Schmutz (2001) developed what they termed an iterative Mayfield method, which they indicated was a simple extension of the Klett and Johnson (1982) estimator. The extension primarily involved the way that losses and exposure days are allocated to days between nest visits—Klett and Johnson (1982) assumed a constant DSR for this allocation, whereas Manly and Schmutz (iteratively) used DSRs that varied by age or date.

By assigning prior probabilities to the discovery and survival rates, He et al. (2001) and He (2003) developed a Bayesian implementation of the likelihood structure used by Heisey and Nordheim (1995). He et al. (2001) consider the special case of daily visits, while He (2003) generalized it to intermittent monitoring. He (2003) used the Bayesian equivalent of the EM algorithm for incomplete data problems, which involves the introduction of auxiliary, or latent, variables—so-called data augmentation. Both approaches, the EM algorithm and data augmentation, iteratively replace unknown exact failure times (including failure times of nests that were never discovered because they failed before discovery) by approximations; the procedure is then repeatedly refined. The advantage of a Bayesian-Markov chain Monte Carlo approach is that it allows the fitting of high-dimensional (many-parameter) models that would be intractable in a maximum likelihood context. This benefit comes at the cost of potentially introducing artificial structure via the assumed prior distributions. In examples with simulated data, the Bayesian estimator was closer to the known true daily mortality rates (and nest success rates) than was the Mayfield estimator. The method, however, often produces biased estimates for the survival rate of the youngest age class unless some nests were found at initiation and ultimately succeeded (Cao and He 2005). Cao and He (2005) suggested three ad hoc remedies that appeared to resolve the difficulty.

Williams et al. (2002) reviewed several of the approaches to modeling nest survival data including models with nest-encounter parameters and traditional survival-time methods such as Kaplan-Meier and Cox' proportional-hazards models. They also offered some guidelines for designing nesting studies.

A new era of nest survival methodology arrived with the new millennium, with three sets of investigators working more or less independently. Dinsmore et al. (2002) were the first to publish a comprehensive approach to nest survival that permitted a variety of covariates to be incorporated in the analysis. They allowed the DSR to be a function of the age of the nest, the date, or any of a variety of other factors. Survival of a nest during a day then was treated as a binomial variable that depended on those covariates. Analysis was performed using program MARK (White and Burnham 1999). Data files can become large and cumbersome, especially for long nesting seasons and numerous individual or time-dependent covariates (Rotella et al. 2004). This approach is discussed more fully in Dinsmore and Dinsmore (*this volume*).

Stephens (2003, also see Stephens et al. 2005) developed SAS software to analyze nesting data with the same model developed by Dinsmore et al. (2002). He further allowed for random effects to be included in models.

Shaffer (2004) applied logistic regression to the nest-survival problem. Others had attempted to do so before, but they had used fate of a nest as a binomial trial, either ignoring differences in exposure or incorporating exposure as an explanatory variable; neither approach is justified. Like the method of Dinsmore et al. (2002), Shaffer's (2004) logistic-exposure method is extremely powerful and accommodates a wide variety of models of daily nest survival.

The primary difference among the new methods is the use of program MARK (Dinsmore et al. 2002) versus the use of a generalized linear-model program (Shaffer 2004, Stephens et al. 2005). Another difference that may sometimes be relevant involves covariates that vary across an interval between nest checks, such as the occurrence of weather events. The effects of such covariates would be averaged over the interval in Shaffer's (2004) method but assigned to individual days in Dinsmore et al.'s (2002) method. Rotella et al. (2004) compared and contrasted the methods of Dinsmore et al. (2002), Stephens (2003), and Shaffer (2004). They also provided example code for various analyses in program MARK, SAS PROC GENMOD, and SAS PROC NLMIXED.

McPherson et al. (2003) developed estimators of nest survival and number of nests initiated based on a model involving detection probabilities and survival probabilities. The former component is comparable to the encounter probabilities of Pollock and Cornelius (1988), incorporating the daily probabilities of detection and survival. The second component, survival, is basically a Kaplan-Meier series of binomial probabilities. The McPherson et al. (2003) method assumes that nests were searched for and checked daily, which may be applicable to the telemetry study to which their method was applied but is generally unrealistic and excessively intrusive in most nesting studies. Their estimator of number of nests initiated was a modified Horvitz-Thompson estimator (Horvitz and Thompson 1952) and was a generalized form of that used by Miller and Johnson (1978). In the example given, the new estimate was virtually identical to that of Miller and Johnson (1978) but had a smaller standard error. The McPherson et al. (2003) survival model allowed for age-related, but not date-related, survival. In their example, they found very little variation due to age. McPherson et al. (2003) indicated it was essential to follow some nests from day one. They also noted that estimates of survival are expected to be robust with respect to heterogeneity in the actual survival rates (analogous to mark-recapture studies).

Jehle et al. (2004) reviewed selected estimators of nest success, focusing on the Stanley (2000) and Dinsmore et al. (2002) estimators in comparison to the apparent and Mayfield estimators. In the several data sets on Lark Buntings (*Calamospiza melanocorys*) examined, they found results of Mayfield, Stanley, and Dinsmore methods to be very similar; the apparent estimator was much higher, as expected. The authors emphasized that nest visits were close together, however, being generally only a day or two apart near fledging.

Nur et al. (2004) showed how traditional survival-time (or lifetime or failure-time) analysis methods could be applied to nest success estimation. They included Kaplan-Meier, Cox' proportional hazards, and Weibull methods in their discussion. Critical to such methods is the need to know the age of the nest when found and age when failed.

Etterson and Bennett (2005) approached the nest-survival situation from a Markov chain perspective. By doing so, they were able to explore the effect on bias and standard errors of Mayfield estimates due to variation in discovery probabilities, uncertainties in dates of transition (e.g., hatching and fledging), monitoring schedules, and the number of nests monitored. They found that the magnitude of bias increased with the length of the monitoring interval and was smaller when the date of transition was known fairly accurately. The assumption that transition always occurs at the same age did not appear to induce any consequential bias in estimates of DSR.

CAUSE-SPECIFIC MORTALITY RATES

Some investigators have sought, not only to estimate mortality rates of nests, but to estimate rates of mortality due to different causes. In the survival literature this topic is referred to as competing risks; I will deal only briefly with it here. Heisey and Fuller (1985) indicated how Mayfield-like estimators could be adapted to estimate source-specific mortality rates when the cause of death can be determined. Their context involved radio-telemetry studies, but the method would more generally apply to nesting studies. Etterson et al. (in press) modified the Etterson and Bennett (2005) approach to incorporate multiple causes of nest failure while relaxing the assumption that failure dates are known exactly. Johnson et al. (1989)

related daily mortality rates (due to predation) on nests of ducks to indices of various predator species. They found associations that were consistent with what was known about the foraging behavior of the different predators.

LIFE-TABLE APPROACHES

Goc (1986) evidently was the first to suggest that nest success could be estimated by constructing a life table from the ages of nests found. Critical to that approach is the assumption that nests are equally detectable at all ages. Johnson (1991) noted that that assumption could be verified by plotting the log of the number of nests found at each age against age. Based on this relationship, one could estimate the DSR from the age distribution; that line should have slope equal to the logarithm of DSR. Johnson and Shaffer (1990) showed that the crucial assumption that detectability does not vary with age was not met in their example.

LIFETIME ANALYSIS

A wealth of literature on survival estimation was developed largely in the biomedical and reliability fields (see Williams et al. [2002] for a review from an animal ecology perspective). Well-known methods such as Kaplan-Meier and Cox regression have been applied only rarely to nest-survival studies, and it is reasonable to ask why. As noted above, however, the Mayfield estimator of DSR is in fact the maximum-likelihood estimator under a geometric-survival model, the discrete counterpart of exponential survival. The critical assumption of the geometric and exponential models, like Mayfield's, is that the daily mortality rate (hazard rate, in survival nomenclature) is constant. A valuable and distinctive feature of the exponential (or geometric) model is that, because DSR is independent of age, it is not necessary to know the age of the nest to estimate survival. More general models of survival, such as Kaplan-Meier, Cox' proportional hazards, and Weibull, require knowledge of the age. In nesting studies, this means it is essential to know both the age of a nest when it is found and when it failed. Knowing the age of a nest of course is useful when using any other method if interest is in age-specific survival rates. It is not necessary for most methods if one is solely concerned with estimating nest success, although estimates based on constant daily survival may be biased if that assumption is severely violated.

Several investigators, beginning with Peakall (1960), have applied Kaplan-Meier methods to nesting or similar data (Flint et al. 1995, Korschgen et al. 1996, Farnsworth et al. 2000, Aldridge and Brigham 2001). The method proposed by McPherson et al. (2003) likewise incorporated a Kaplan-Meier model for daily survival.

Nur et al. (2004) brought the survival methodology to the attention of ornithologists by applying Kaplan-Meier, Cox' proportional-hazards, and Weibull models to a data set involving Loggerhead Shrikes (*Lanius ludovicianus*). They further demonstrated how to incorporate covariates such as laying date, nest height, and year in an analysis.

OBSERVER EFFECTS

Several authors considered the effect of visitation on survival of nests. See Götmark (1992) for a review of the literature on the topic. Bart and Robson (1982) proposed a model in which the daily mortality rate for the day following a visit differed from the rate on other days. They identified a major problem that arises when checks of surviving nests are not recorded—investigators might note that a nest is still active and try to avoid disturbance. Nichols et al. (1984) found no difference in survival of Mourning Dove (*Zenaida macroura*) nests visited daily versus those visited 7 d apart. Sedinger (1990) regressed survival rate during an interval against the length of the interval, so that departures of the Y-intercept from 1 would reflect the short-term effect of a visit at the beginning of the interval. He found the method to be imprecise. Sedinger (1990) also visited nests and revisited them immediately after the pairs had returned, again to document short-term effects; he found a negligible effect. Rotella et al. (2000) explored essentially the same model proposed by Bart and Robson (1982) and noted that observer-induced differences that were difficult to detect statistically nonetheless could have major effects on estimated survival rates. More generally, Rotella et al. (2000) demonstrated how a covariate reflecting a visit to a nest could be incorporated into an analysis of DSR.

Willis (1973) knew enough about the breeding biology of the species he was studying so that he could ascertain the status of a nesting attempt without visiting the nest. He concluded that visits to nests seemed to accelerate destruction of easily discovered nests, but had little effect on the number of nests that finally succeeded.

ESTIMATING THE NUMBER OF NEST INITIATIONS

Just as the apparent estimator of nest success typically overestimates the actual nest success rate, the number of nests found in a study underestimates the number that were actually initiated. In most situations, short-lived nests are unlikely to be found. Evidently the first to use improved estimates of nest success to account for these undiscovered nests were Miller and Johnson (1978). They proposed simply dividing the number of successful nests—virtually all of which can be found in a careful nesting study—by the estimated nest success rate. The method could be applied to the number of nests that attain any particular age, as long as virtually all the nests that reach that age can be detected. Johnson and Shaffer (1990) considered the situation in which the Mayfield assumption of constant DSR is severely violated; in such situations the apparent number of nests initiated is better than the Miller-Johnson estimator but is accurate only with repeated searches and high detectability. Horvitz-Thompson approaches (Horvitz and Thompson 1952) to estimating the number of initiated nests have been taken by Bromaghin and McDonald (1993b), Dinsmore et al. (2002), McPherson et al. (2003), Grant et al. (2005), and, while advising caution, Grand et al. (2006).

DISCUSSION

It should be noted that the primary objective of estimating nest success has been transformed by most of the methods described into an objective of estimating DSR. Mathematically, these objectives are equivalent, as long as the time needed from initiation to success is a fixed constant. The influence of variation in transition times (egg hatching and young fledging) has received little attention (but see Etterson and Bennett 2005).

Although this has been a largely chronological accounting of published papers that addressed the topic of estimating nest success, some themes recurred; the notion of encounter probabilities arose frequently. Several of the methods incorporated these probabilities, which measure the chance that a nest will be first detected at a particular age. Hensler and Nichols (1981) used them in the development of their model. Those probabilities turned out to be unnecessary, because their new estimator was equivalent to Mayfield's original one, but others have suggested that observed encounter probabilities might contain useful information. Pollock and Cornelius (1988) used the same parameters in their derivation. Bromaghin and McDonald (1993a, b) exploited the relationship between the lifetime of a nest and the probability that the nest is detected through the use of a modified Horvitz-Thompson estimator (Horvitz and Thompson 1952). More recently, McPherson et al. (2003) employed a model of nest detection in their method to estimate nest success and number of nests initiated.

Encounter probabilities are intriguing measures. They reflect both the probability that a nest survives to a particular age—which typically is of primary interest—as well as the probability that a nest of a particular age is detected—which reflects characteristics of the nest, the birds attending it, the schedule of nest searching, and the observers' methods and skills. Some inferences about survival can be made by assuming detection probabilities are constant with respect to age, but that is a major and typically unsupported assumption (Johnson and Shaffer 1990). Intriguing as they are, encounter probabilities confound two processes, and their utility seems questionable unless some fairly stringent assumptions can be met.

Most of the nest-survival-estimation methods require more information than the apparent estimator does. At a minimum, the Mayfield estimator requires information about the length of time each nest was under observation. Many methods require knowledge of the age of a nest when it was found.

Several investigators have proposed methods to reduce the bias of the apparent estimator without nest-specific information. Coulson's (1956) procedure simply doubles the number of failed nests when computing the ratio of failed nests to failed plus successful nests. Hence, it can be calculated either from the apparent estimator and the total number of nests, or from the numbers of failed and successful nests. The shortcut estimator of Johnson and Klett (1985) also falls into this category. It uses the average age of nests when found to reduce the bias of the apparent estimator. Green's (1989) transformation is another such method; it requires no additional information beyond the apparent estimates, but relies on some questionable assumptions, such as detectability not varying with age of nest. Johnson's (1991) modification of Green's estimator behaves similarly.

Such methods for adjusting apparent estimates have potential utility for examining extant data sets, for which information needed to compute more sophisticated estimators is not available. For example, Beauchamp et al. (1996) used Green's (1989) transformation of the apparent estimator to conduct a retrospective comparison on nest success rates of waterfowl by adjusting the apparent estimates, which were all that were available from the older studies, to more closely match the Mayfield estimates that were used in more-recent investigations.

CONCLUSIONS

Any analysis should be driven by the objectives of the study. In many situations, all that is needed is a good estimate of nest success. In other cases, insight into how daily survival rate varies by age of nest is important; a large number of methods have addressed that question. Often information is sought about the influence on nest survival of various covariates. Assessment of those influences can be made with many of the methods if nests can be stratified into meaningful categories of those covariates; for example, grouping nests according to the habitat type in which they occur. If covariates are nest- or age-specific, however, the options for analysis are more limited; the recent logistic-type methods (Dinsmore et al. 2002, Shaffer 2004, Stephens et al. 2005) are well-suited to these objectives. Guidelines for selecting a method to analyze nesting data are offered in Johnson (*chapter 6, this volume*).

Despite the numerous advances in the nearly half-century since the Mayfield estimator was developed, it actually bears up rather well. Johnson (1979) wrote that the original Mayfield method, perhaps with an adjustment in exposure for infrequently visited nests, should serve very nicely in many situations. Others (Klett and Johnson 1982, Bromaghin and McDonald 1993a, Farnsworth 2000, Jehle et al. 2004) have made similar observations. Etterson and Bennett (2005) suggested that traditional Mayfield models are likely to provide adequate estimates for most applications if nests are monitored at intervals of no longer than 3 d. McPherson et al. (2003) drew a parallel to mark-recapture studies by suggesting that estimates of survival are expected to be robust with respect to heterogeneity in the actual survival rates. Johnson (pers. comm. to Mayfield) stated that the Mayfield method may be better than anyone could rightly expect.

The seemingly simple problem of estimating nest success has received much more scientific attention than one might have anticipated. Many of the recent advances were due to increased computational abilities of both computers and biologists. Can we conclude that the latest methods—which allow solid statistical inference from models that allow a wide variety of covariates—will provide the ultimate in addressing this problem? As good as the new methods are, I suspect research activity will continue on this topic and that even-better methods will be developed in the future.

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