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ESTIMATING NEST SUCCESS: THE MAYFIELD METHOD AND AN ALTERNATIVE

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ABSTRACT.—Mayfield's method for calculating the success of a group of nests is examined in detail. The standard error of his estimator is developed. Mayfield's assumption that destroyed nests are at risk until the midpoint of the interval between visits leads to bias if nests are visited infrequently. A remedy is suggested, the Mayfield-40% method. I also present a competing model, which recognizes that the actual destruction date of a failed nest is unknown. Estimated daily mortality rates and standard errors are developed under this model. A comparison of the original Mayfield method, the Mayfield-40% method, and the new method, which incorporates an unknown date of destruction, shows that the original or modified Mayfield method performs nearly as well as the more appropriate method and requires far easier calculations. A technique for statistically comparing daily mortality rates is offered; the one proposed by Dow (1978) is claimed to be misleading. Finally, I give a method for detecting heterogeneity among nests and an improved estimator, if it is found. *Received 5 March 1979, accepted 28 July 1979.*

THE well-being of an avian population lies in the delicate balance between natality and mortality. Biologists attempt to infer the status of a species by estimating rates of births and deaths and, through their comparison, determining if the former are sufficient to offset the latter. For most populations of wild birds, none of the crucial characteristics of population dynamics is easy to measure. One component of natality that seems easy to gauge is the percentage of nests that hatch, which is often used as an indirect measure of reproduction. Mayfield (1961) has demonstrated, however, serious error in the ordinary method of determining this rate: dividing the number of nests under observation into the number of those that ultimately hatch.

To overcome the difficulties he recognized, Mayfield (1961, 1975) developed an alternative method for calculating hatch rate. In it he accounts for the fact that normally not all nests are under observation from the day of initiation but are discovered at various stages of development. Nests found in a late stage are more likely to hatch than those found in an early one, because they have already survived part of the requisite time. Combining all nests, regardless of stage of development, and calculating an apparent hatch rate will result in a severely biased estimator.

Mayfield's method places all nests on a comparable basis by using only information from the period during which a nest was under observation. The length of that period he termed the *exposure,* although *risk* may be a more appropriate term. Thus, a nest that was found on 10 May and was still active on 18 May had survived 8 days of exposure. Had it been destroyed by 18 May, Mayfield would credit the nest with 4 days of exposure, under the assumption that it was at risk for half the period.

From a group of nests, Mayfield calculates the total exposure in nest-days. This number is divided into the number of nests that were destroyed while under observation. The resultant value, expressed as losses per nest-day, is the estimated *daily mortality rate* of nests. For example, in Mayfield's (1961: 258) analysis of Kirtland's Warbler (*Dendroica kirtlandii*), 154 nests seen during incubation represented a total exposure of 882.5 nest-days. (Mayfield's data have been reanalyzed here; some results differ slightly from his original presentation.) Thirty-five nests were lost (destroyed or deserted), yielding a daily mortality rate of $35/882.5 = 0.04$ losses per nest-day.

To determine the probability that a nest survives the entire period of incubation, one must know the length of that period; for the Kirtland's Warbler it is 14 days. The probability of survival for one day is 0.96 ($=1 - 0.04$), so the probability of surviving throughout the 14-day incubation period is 0.96 times itself 14 times, or $0.96^{14} = 0.56$.

Although the Mayfield method is a major advance in treating nesting data, it has been criticized (Green 1977) because of its assumption that the population is homogeneous, i.e. all nests are subject to the same rate of mortality. In addition, Mayfield provided neither variance estimates for his mortality rate nor tests of the underlying assumptions.

The present paper is intended to augment Mayfield (1961 and 1975). In it I derive his estimator, which he developed heuristically, in a more formal context. A standard error for his estimator can be calculated from this derivation. The implications of Mayfield's assumption that nests are at risk until midway between visits are considered in detail. I also propose a more realistic model, which does not require the midpoint assumption. Estimators of the daily mortality rate and its standard error are obtained under this model and compared to those of Mayfield. Finally, I discuss the importance of variation in daily mortality rates, from both identifiable and nonidentifiable causes. Methods of detecting such variability and treating it, if it exists, are presented.

THE MAYFIELD MODEL

Let s be the (constant) daily survival rate of a population of nests, and $m = 1 - s$ the daily mortality rate. Suppose a nest is found, then visited t days later. The probability that it survived that interval is s^t. The probability that it survived, say, k days and was then destroyed is $s^k (1 - s)$. Throughout this paper I treat survival times as discrete, in integral numbers of days.

For intervals between visits of one day ($t = 1$), a nest is destroyed, with probability $1 - s$, or survives, with probability s. For intervals greater than one day, we assume that a destroyed nest was at risk for half the interval, i.e. it survived half way minus one day of the interval, and was then destroyed. The probability of this event is $s^{\frac{1}{2}t-1} (1 - s)$. A nest survives the interval with probability s^t.

Assume a sample of nests is found at various ages. The number of nests found that were due to hatch t days later, or were visited t days later, is denoted n_t. Of these, h_t hatched or remained viable, and f_t failed by the subsequent visit. If we assume that all failures occurred on the midday of the interval, we get a likelihood function that is the product of the probabilites of all events, *viz.*

$$\binom{n_1}{h_1} s^{h_1}(1 - s)^{f_1} \prod \binom{n_t}{h_t} (s^t)^{h_t} [(s^{\frac{1}{2}t-1})(1 - s)]^{f_t},$$

where the product extends over all interval lengths $t > 1$. The value of s that maximizes this quantity is the maximum likelihood estimator, which enjoys many desirable statistical properties (e.g. Kendall and Stuart 1967). It is usually easier to work with the logarithm of this quantity, known as the log likelihood function. Both quantities are maximized by the same value of s.

The log likelihood function is then

$$L = \text{constant} + h_1 \log s + f_1 \log(1 - s) + \sum_t \{th_t \log s + f_t[(\tfrac{1}{2}t - 1)\log s + \log(1 - s)]\}.$$

The summation includes terms $t > 1$. This function can be conveniently maximized by differentiating it and equating the result to zero. After some algebra, the solution for s, or equivalently m, is found to be

$$\hat{m} = 1 - \hat{s} = \frac{f_1 + \sum f_t}{h_1 + \sum th_t + f_1 + \tfrac{1}{2} \sum tf_t}.$$

This value is the most likely value of m given the model and the data that were observed. The numerator is the total number of nest failures. The denominator is the total exposure of hatched nests, plus the exposure of nests destroyed between visits one day apart plus one-half the maximum exposure of nests destroyed during longer intervals. This quantity is seen to be Mayfield's estimator.

Because it is now obtained as a maximum likelihood estimator, rather than heuristically, we can calculate its large sample variance as

$$\left\{-E\left[\frac{\partial^2 L}{\partial s^2}\right]\right\}^{-1}$$

(Kendall and Stuart 1967). We first take the second derivative of the log likelihood function with respect to s. This is

$$-\frac{\{h_1 + \sum th_t + \tfrac{1}{2} \sum tf_t - \sum f_t\}}{s^2} - \frac{\{f_1 + \sum f_t\}}{(1 - s)^2}.$$

The true value of s is unknown, so we replace it by its estimator $\hat{s}$. The above quantity then becomes

$$\frac{-(\text{exposure})^3}{(\text{exposure} - \text{losses}) \times \text{losses}},$$

where exposure $= h_1 + \sum th_t + f_1 + \tfrac{1}{2} \sum tf_t$ and losses $= f_1 + \sum f_t$. We can then calculate the above quantity, change its sign, and invert it to obtain a large-sample estimator of the variance of Mayfield's estimator. Its standard error is the square root of the variance.

Returning to the Kirtland's Warbler data as an example, we have losses $= 35$, exposure $= 882.5$, $\hat{s} = 0.9603$, so the variance of $\hat{s}$ is estimated by the inverse of

$$\frac{(882.5)^3}{(882.5 - 35) \times 35} = 23{,}170.55,$$

yielding standard error $= \text{SE}(\hat{s}) = 0.00657$. Approximate 95% confidence limits for s can be calculated as the estimated value ± 2 standard errors, or $\hat{s} - 2\,\text{SE}$ to $\hat{s} + 2\,\text{SE}$. In the present example, these limits become $0.9603 - 2(0.00657)$ to $0.9603 + 2 \cdot (0.00657)$ and equal 0.9472 to 0.9734.

The survival rate for a period of length t days is calculated as $\hat{s}^t$. Lower and upper confidence limits for this parameter can be gotten by raising the corresponding confidence limits for the daily survival rate to the power t. For the Kirtland's Warbler data, $\hat{s} = 0.9603$, and $t = 14$ days, so $\hat{s}^t = (0.9603)^{14} = 0.5671$. Confidence limits for this are $(0.9472)^{14}$ and $(0.9734)^{14}$, or 0.4679 and 0.6856.

MAYFIELD'S MIDPOINT ASSUMPTION

Mayfield calculated the exposure of a nest destroyed between visits several days apart as one-half the length of the interval. In actuality, the expected days at risk could be greater than or less than that value, depending on the daily survival rate and the interval length. In this section I present a formula for the expected days at risk of a destroyed nest.

Suppose the daily survival rate of a nest is s, and sometime during a t-day interval a nest is destroyed. What is the expected number of days at risk (exposure), given that it did not survive the full t days? A straightforward argument using conditional probabilities yields the following result:

$$\text{expected days at risk} = \frac{1 - s^t(t + 1 - st)}{(1 - s)(1 - s^t)}$$

The following table displays some differences between this expected risk and the midpoint as used by Mayfield, for selected values of t and s:

	$t = 4$	$t = 15$	$t = 34$
$s = 0.95$	2.44	7.05	12.80
$s = 0.98$	2.47	7.62	15.57
Midpoint	2.00	7.50	17.00

For intervals between visits averaging up to about 15 days, and for moderate values of s, Mayfield's midpoint assumption is reasonable. For very long intervals, such as are often obtained in studies of waterfowl nesting, the midpoint assumption gives too much exposure to destroyed nests. For this reason and because the expected exposure is difficult to calculate, Miller and Johnson (1978) recommended that destroyed nests be assigned exposure of 40% of the interval between visits. Their modification will be referred to as the Mayfield-40% method and in a subsequent section compared with the original Mayfield estimator and a new estimator.

MODEL IN WHICH TIME OF LOSS IS UNKNOWN

The Mayfield model involves the assumption that the date of destruction is known. In actuality, we ordinarily know only that the nest was destroyed sometime between two visits. In this section I develop a more realistic model, which accommodates an unknown date of destruction, and provide the appropriate maximum likelihood estimator.

In our earlier notation, and for an interval between visits of t days, the probability that the nest survives that period is s^t. The probability that it is destroyed by the next visit is simply $1 - s^t$. The likelihood of the observed sample described earlier (h_t out of n_t surviving intervals of length t days) is

$$\prod_t \binom{n_t}{h_t} (s^t)^{h_t} (1 - s^t)^{f_t}.$$

Taking logarithms yields

$$\text{constant} + \sum_t th_t \log s + \sum_t f_t \log(1 - s^t),\tag{1}$$

where the constant term does not involve s and the summation is over all $t \geq 1$. If we differentiate (1) and set the resulting expression to zero, we obtain the following equation for the maximum likelihood estimator:

$$\frac{1}{s} \sum_t th_t = \sum_t \frac{tf_t s^{t-1}}{1 - s^t}.$$

Unlike the Mayfield model, there is no closed expression for the solution $\hat{s}$; that is, we cannot get s on the left-hand side of the equation and an expression independent of s on the right-hand side. The equation must be solved by using one or another of the numerous computer routines for numerical maximization that are available.

The large-sample variance of $\hat{s}$ can be estimated by the inverse of

$$\frac{\sum th_t}{s^2} + \sum tf_t \left[\frac{(t - 1)s^{t-2} + s^{2t-2}}{(1 - s^t)^2} \right],\tag{2}$$

in which s is replaced by its estimate $\hat{s}$.

As an example, consider the sample of 1,900 nests of Blue-winged Teal (*Anas discors*) reported by Miller and Johnson (1978). The estimated daily survival rate for these nests is 0.9564, which was obtained by using the Nelder-Mead method (O'Neill 1971) to maximize numerically the log likelihood function (Equation 1). The standard error of the daily survival rate, from Equation 2, is 0.00137.

In the next section I compare this estimator to the original Mayfield and the Mayfield-40% estimators.

COMPARISON OF ESTIMATORS

The various estimators described earlier will be applied to four sets of data. One is a set of Mallard (*Anas platyrhynchos*) data reported by Cowardin and Johnson (1979). The second consists of Blue-winged Teal data cited by Miller and Johnson (1978). The third is the subset of the second involving only those nests found with one egg. The fourth is of Kirtland's Warbler nests observed during incubation (Mayfield 1961).

The estimators of daily survival rate are based on: (1) the original Mayfield method, (2) the Mayfield method with exposure of destroyed nests set equal to 40% of maximum (Miller and Johnson 1978), and (3) the maximum likelihood method derived from the new model. I compare both the estimated daily survival rates (Table 1) and the estimated standard errors of those rates (Table 2).

The data from ducks differ from those of the Kirtland's Warbler with respect to the average length of interval between visits. To minimize interference with nesting hens, waterfowl researchers ordinarily do not revisit a nest after discovery until its calculated hatch date is past. Thus, the interval between visits may average 20 days or more. In contrast, most Kirtland's Warbler nests were checked within 1–6 days, which resulted in shorter intervals. The assumptions of the original Mayfield method would appear to be more justified for the warbler data, and those of the Mayfield-40% method for the duck data.

The maximum likelihood (ML) estimator under the new model is an efficient estimator based on a model that is more appropriate than Mayfield's, although small

TABLE 1. Comparison of estimated daily survival rates obtained from the original Mayfield method, the Mayfield-40% method, and the new maximum likelihood method, as applied to four sets of data.

| Data set | Mayfield | | Maximum likelihood |
	Original	40%	
Mallard	0.9509	0.9437	0.9430
Blue-winged Teal	0.9593	0.9551	0.9564
Blue-winged Teal (1-egg only)	0.9637	0.9586	0.9585
Kirtland's Warbler	0.9603	0.9601	0.9605

samples can result in biased estimators. The last column in each of Table 1 and Table 2 thus serves as a standard to use in evaluating the original Mayfield method and the Mayfield-40% method.

It is clear that in all four examples, Mayfield's original method and the Mayfield-40% method yielded estimators very close to the maximum likelihood (Table 1). Moreover, for the three sets of duck data, the Mayfield-40% method was extremely close to the ML; the differences between estimates of daily survival rates were 0.0007, −0.0013, and 0.0001. The original Mayfield method, as conjectured, yielded better results for the oft-visited Kirtland's Warbler nests. The estimated daily survival rate differed from the ML estimate by only −0.0002.

Estimated standard errors gave analogous results (Table 2). Differences between Mayfield-40% and ML standard errors for the three duck data sets were −0.00119, −0.00002, and −0.00068. The differences between the original Mayfield and ML standard error for the Kirtland's Warbler data was only 0.00002.

It is reassuring, and perhaps a bit surprising, that the Mayfield method performs as well as it does. Adopting the assumption that we know the exact date of destruction of an unsuccessful nest does not seem to affect the inferences drawn from the analysis.

The apparent conclusion is that the Mayfield method, perhaps with an adjustment if intervals between visits are long, performs nearly as well as the maximum likelihood estimator of the more strictly appropriate model. In addition, it is much easier to calculate, and estimated standard errors are now available.

VARIABILITY IN DAILY MORTALITY RATES—IDENTIFIABLE CAUSES

An assumption common to the Mayfield method and the other method developed here is that daily mortality rates of nests remain constant, throughout the lifetime of the nest, throughout the nesting season, among nests, etc. In this section I examine this assumption, suggest methods for detecting variability from known or suspected causes, and present a technique for treating data that are subject to such variability.

TABLE 2. Comparison of standard errors of estimated daily survival rates obtained from the original Mayfield method, the Mayfield-40% method, and the new maximum likelihood method, as applied to four sets of data.

| Data set | Mayfield | | Maximum likelihood |
	Original	40%	
Mallard	0.00889	0.01015	0.01134
Blue-winged Teal	0.00122	0.00135	0.00137
Blue-winged Teal (1-egg only)	0.00662	0.00753	0.00821
Kirtland's Warbler	0.00657	0.00660	0.00655

TABLE 3. Example of comparison of mortality during incubation and nestling periods of Kirtland's Warbler, following Dow (1978).

	Daily mortality rate	Average mortality rate for period	Calculated number of nests lost	Calculated number of nests succeeded	Total nests found
Incubation period	0.035	0.39	60.1	93.9	154
Nestling period	0.035	0.27	38.9	105.1	144
Totals			99.0	199.0	298

$\chi^2 = 4.84$; df = 1; $P < 0.05$

Variability can arise from any of a number of identifiable causes, e.g. age of nest—rates may differ between laying and incubating periods; date within season—nests may be more vulnerable early in the season than later; or habitat—nests in one habitat may be safer than those in another. If daily mortality rates are suspected to vary among categories, the following test can be employed.

Comparison of estimated rates with their standard errors.—If two categories of nests are suspected to differ in daily mortality rate, the difference is measured by $\hat{m}_1 - \hat{m}_2 = \hat{s}_2 - \hat{s}_1$, where the subscript denotes the category. If the nests in the two categories are independent, the variance of this difference equals the sum of the variances of $\hat{s}_1$ and $\hat{s}_2$. (The standard error is the square root of the variance.) The ratio of the difference to its standard error, under the hypothesis that daily mortality rates do not differ between categories, will be distributed for large samples as a normal variate with zero mean and unit variance. Thus, large (positive or negative) values of the ratio will cast doubt upon the assumption of equal rates. The following example will illustrate the method.

Mayfield (1961) presented separate estimates of daily mortality rates for Kirtland's Warbler nests according to their stage, incubation versus nestling. During incubation, $\hat{m} = 0.0399$ with a variance of 0.00660^2. In the nestling period, $\hat{m} = 0.0299$ and its variance is 0.00629^2. Thus the difference between the two rates ($0.0399 - 0.0299 = 0.01$) will have a variance equal to the sum of the variances ($0.00660^2 + 0.00629^2 = 0.00912^2$). The ratio of the difference to its standard error, $0.01 \div 0.00912 = 1.096$, will be approximately normally distributed. The resulting value is not extreme enough ($P > 0.25$) to suggest that the difference is non-zero. Hence, the test does not reject the null hypothesis that daily mortality rates are the same during incubation and nestling periods.

If the rates had differed significantly, or if the investigator believed from other knowledge that they were truly different (the non-significance of the test being a result of inadequate sample size), then the rates could be combined in the following manner. The probability that a nest survives through both incubation period and nestling period is $s_I{}^I \times s_N{}^N$, where s_I is the daily survival rate during incubation, I is the length of the incubation period in days, s_N is the daily survival rate during the nestling period, and N is the length of the nestling period. In the Kirtland's Warbler example, $\hat{s}_I = 0.9601$, $I = 14$ days, $\hat{s}_N = 0.9701$ and $N = 9$ days. Thus survival throughout both periods is estimated by

$$(0.9601)^{14} \times (0.9701)^9 = 0.4303.$$

About 43% of nests beginning incubation can be expected to survive through the end of the nestling period.

An inappropriate procedure.—Dow (1978) suggested a way to compare mortality rates estimated by Mayfield's method. In his example, Dow used the estimated daily mortality rate during the incubation period (0.04) and the total number of nests found (154) to calculate the expected number of nests lost during incubation (67.8) and the expected number that succeed (86.2). The corresponding estimates derived for 144 nests observed during the nestling period with $\hat{m} = 0.03$ are 34.6 nests lost and 109.4 nests succeeding. He compared these two sets of numbers in a 2 × 2 contingency table and calculated a Chi square test statistic of 13.20. With one degree of freedom, this value is significant, which led Dow (1978: 294) to conclude that the rates differ between periods, and that "there would seem little justification for lumping the 2 stages to obtain a single rate."

Dow's method is misleading because his Chi square test statistic reflects not only differences in daily mortality rates, but also differences in length of period. A significant test can result from comparing identical mortality rates if they pertain to different periods of time. In fact, the data Dow used will yield a significant χ^2 even if daily mortality rates for the two periods are identical. Suppose, instead of $m = 0.04$ for the incubation period and $m = 0.03$ for the nestling period, that $m = 0.035$ held throughout both periods. Then, following Dow's calculations, Table 3 would result. The resulting $\chi^2 = 4.84$ is significant ($P < 0.05$). Dow would then have us conclude that mortality rates are different, even though daily mortality rates are the same, and data from the two periods should be lumped. The problem, of course, is that his test compares mortality rates *for periods,* not on a daily basis. If period lengths differ, as they usually do, the test is misleading.

VARIABILITY IN DAILY MORTALITY RATES—NONIDENTIFIABLE CAUSES

A more subtle wrinkle in nesting data is the possibility that daily mortality rates may differ among nests, but not in relation to any variable the investigator is able, or likely, to measure. For example, suppose (as did Green 1977) that a nesting population of birds consists of two components, novice nesters and experienced nesters, whose nests are likely to differ in daily mortality rates. If nests of novices are appreciably more vulnerable to predation and desertion, then they will survive on the average a shorter time, and therefore be less likely to be found than those of the experienced nesters. The composite daily mortality rate for both novice and experienced nesters, assuming their nests cannot be differentiated in the field, will be biased low, because the high-risk nests of novices are underrepresented in the sample. [The direction of the bias is opposite that noted by Green (1977), who considered an example in which all nests were observed from the time eggs were first laid.] In this section I discuss the potential bias caused by heterogeneity among nests, and how it can be detected and treated.

First of all, it should be noted that the bias is not appreciable unless (1) the differences in daily mortality rates among groups are large, and (2) the proportion of birds with heightened vulnerability is also large. In the case of a population consisting of 1,000 "high-risk" nests ($m = 0.10$) and 1,000 "low-risk" nests ($m = 0.05$), with a period length of 10 days, the average hatch rate for the population is

$$\frac{1,000 \times (1 - 0.05)^{10} + 1,000 \times (1 - 0.10)^{10}}{2,000} = 0.4737.$$

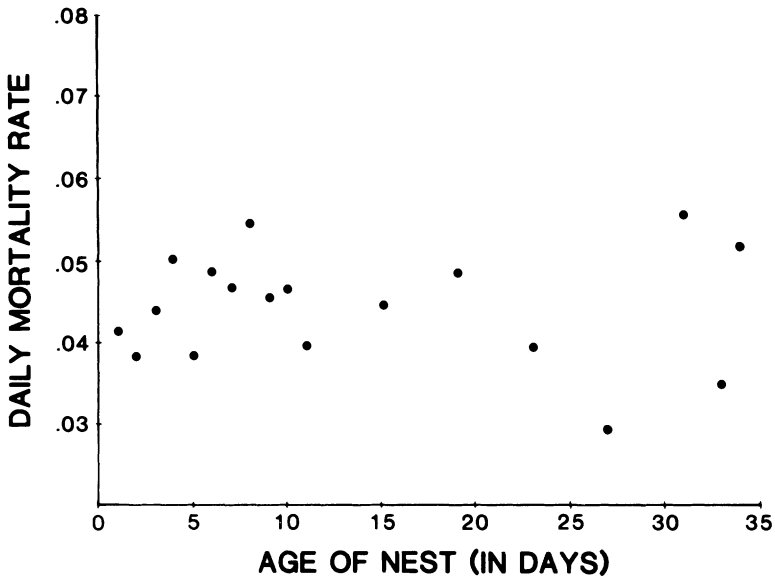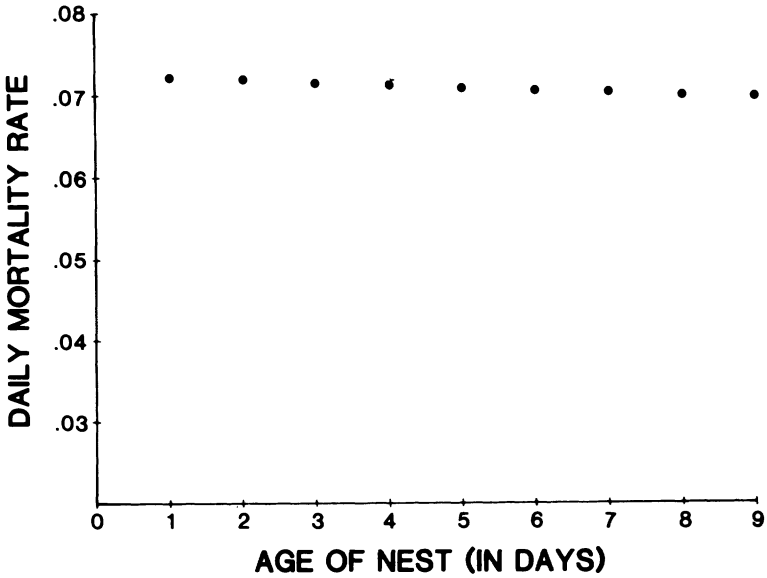If nests were found at random in proportion to the length of time they survive, the

Fig. 1.   Estimated daily mortality rates according to age of nest when found. 1A (top)—hypothetical example. 1B (bottom)—Blue-winged Teal example.

expected daily mortality rate for the sample would be 0.0713, which projects to a hatch rate of $(1 - 0.0713)^{10} = 0.4773$. The difference between this value and 0.4737 is miniscule, considering the two-fold difference in daily mortality rates between the two components of the population.

Detecting heterogeneity.—If heterogeneity does exist among nests with respect to daily mortality rates, then nests found at initiation will be expected to contain nests

of the various groups in proper proportions. Samples of nests at later ages will contain disproportionately fewer nests of the more vulnerable groups. Suppose again that the population contains 1,000 nests of each of two groups, with daily mortality rates of 0.05 and 0.10. At initiation (0-day-old nests), there are 1,000 of each, so a sample would be expected to contain 50% of each. Of the first group, 950 survive to be 1-day-old nests, while only 900 of the second group do so. A sample of 1-day-old nests would then be expected to contain 51.4% of the first group. At the 9-day-old stage, 63% of the first group and 38.7% of the second group would be expected to remain, so a sample should contain about 61.9% of the first group. This example illustrates how the difference in daily mortality rate affects the composition of a sample of nests at various ages.

One obvious solution to the problem of heterogeneity is to use only nests found immediately after initiation, but in many nesting studies virtually all data would be discarded by this criterion.

A more satisfactory approach is to employ the knowledge that heterogeneity will result in an increasingly biased sample among older nests. In the example of 1,000 nests of each of two groups, the expected daily mortality rate calculated only from 0-day-old nests is 0.0724. The rate for only 1-day-old nests would be 0.0720, etc. By plotting these rates against the age of nests when found (Fig. 1A), we note that they decline nearly linearly. (Remember that these data contain no sampling variability; such precision is not to be expected in field studies.) The fact of the decline points to heterogeneity. The near-linearity of the decline suggests that the estimated intercept (0.0723) can be used as an estimate of the daily mortality rate of the entire population *accounting for the disparity between the two groups*. This value projects to a hatch rate of 0.4721, which is somewhat closer to the true population value of 0.4737 than is the value of 0.4773 obtained from a straightforward analysis by Mayfield's method.

This technique will be illustrated with data on Blue-winged Teal reported by Miller and Johnson (1978). Daily mortality rates plotted against age of nest when found (Fig. 1B) display only a slight decline with increasing age, suggesting little if any heterogeneity. The regression equation for these points yields an intercept of 0.0447, very close to the value of 0.0449 obtained by the Mayfield-40% method ignoring heterogeneity.

Other data sets may involve more heterogeneous nests than those included in this example. If the number of nests is sufficient to warrant an examination as suggested here, it should be performed.

DISCUSSION

The net result of all the mathematics presented here is, I believe, a clearer understanding of the Mayfield method. It turns out to be better than might be expected, despite concerns voiced by Green (1977) and Dow (1978). A slight modification in calculating exposure is called for when the intervals between nest visits are long, but otherwise several features of the Mayfield method recommend it.

First, the standard error of the Mayfield estimator is now available. With it, confidence limits can be constructed either for the daily mortality rate or for the mortality rate for an interval, such as the incubation period. Also, daily mortality rates can be compared one to another, e.g. incubation vs. nestling, nests in one habitat vs. those in another, nests of yearlings vs. nests of older birds.

Second, Mayfield's method yields results that are very close to the maximum likelihood estimators under the more appropriate model incorporating an unknown date of destruction. Standard errors, as well as estimates, are similar. Moreover, computation of the Mayfield estimator and its standard error is far easier than for the more appropriate model.

Third, the Mayfield method has been shown to be fairly robust with respect to heterogeneity among nests. Green (1977) suggested that there might be a problem if subpopulations of nests differ in daily mortality rate but, unless a large proportion of the nests have appreciably higher daily mortality rates than the others, the actual bias in the Mayfield estimator is slight. If heterogeneity is suspected, methods given in the present paper can be employed to check for it in large samples, and to treat it if it exists.

The model introduced here, which incorporates an unknown date of destruction, is more appropriate than Mayfield's original method. It is to be recommended if a detailed analysis involving large numbers of nests is undertaken. In more modest treatments, or if data are limited, the original Mayfield method, perhaps with an adjustment in exposure for infrequently visited nests, should serve very nicely.

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