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Douglas H. Johnson

Northern Prairie Wildlife Research Center

Terry L. Shaffer

Northern Prairie Wildlife Research Center

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ESTIMATING NEST SUCCESS: WHEN MAYFIELD WINS

DOUGLAS H. JOHNSON AND TERRY L. SHAFFER

*U.S. Fish and Wildlife Service, Northern Prairie Wildlife Research Center,
Jamestown, North Dakota 58402 USA*

ABSTRACT.—The Apparent estimator of nest success may be severely biased because unsuccessful nests are less likely to be found than are successful nests. The Mayfield estimator is a preferred alternative. The situation is somewhat different for nests in colonies or on islands because of greater visibility of nests, higher synchrony of nesting, and often higher hatch rates than dispersed mainland nests. Also, destruction is more likely to occur catastrophically, which violates an assumption of the Mayfield method that the mortality rate is constant. By simulation we investigated the performance of the Apparent and Mayfield estimators under a variety of circumstances.

We found that when mortality rate was constant, the Mayfield estimator generally performed well regardless of whether or not nesting was synchronous or whether mortality was high or low. The Apparent estimator required more searches and higher detectability of nests. When mortality was mostly catastrophic, the Mayfield method performed poorly. The Apparent method was better, but high levels of detectability were needed for accurate estimates. We reached similar conclusions for attempts to estimate the number of nests initiated. *Received 31 July 1989, accepted 5 January 1990.*

ORNITHOLOGISTS have come to realize that the traditional estimate of nest success (the fraction of observed nests that are successful) may be severely biased. This unwelcome result exists because unsuccessful nests may be active only briefly and are less likely to be observed than are successful nests, which persist for the entire laying and incubation period. Although Snow (1955), Hammond and Forward (1956), and others alluded to the bias, it was not formally dealt with until Mayfield (1961, 1975) proposed a solution. Johnson (1979) provided the statistical underpinnings of the method, which is similar to estimating an exponential survival function with censoring (e.g. Gross and Clark 1975).

Problems that require a Mayfield treatment are somewhat different for nests on islands or in nesting colonies for four reasons, some of which Ely and Raveling (1984) identified. First, nest success is often much higher on islands than on mainlands. This reduces the bias of the Apparent hatch rate, and minimizes the need for the Mayfield method. Second, nesting on islands or in colonies is often fairly synchronous, which facilitates nest finding in early stages, before many of them are destroyed. Third, mortality of clutches in island or colonial nests is more often catastrophic than in mainland or isolated nests. The Mayfield method assumes that a constant mortality rate applies. Fourth, the small size of the nesting area, and

high density and high visibility of nests, often permit many destroyed clutches to be found, which reduces the bias in the Apparent hatch rate. Additionally, nests destroyed before discovery are not used in the Mayfield calculation. In island or colonial situations these may be numerous, and biologists are tempted to include them to enhance sample sizes.

METHODS

We devised a simulation model of a population of nests, to which we applied simulated nest-searching patterns. Although the method is general, we specified parameters such as clutch size and incubation period. For simulation, we chose values appropriate to the Mallard (*Anas platyrhynchos*). The model was written in SAS for personal computers (SAS Institute Inc. 1988), as were programs for analyzing results.

We simulated nest populations with different levels of nesting synchrony, constancy of mortality rate (steady mortality rate vs. catastrophic mortality), and survival rate of clutches. Simulated searches were made with different frequency and various levels of detectability of clutches (in laying, incubation, hatched, and destroyed categories).

All simulated nests were initiated between 16 April and 16 June. To obtain two levels of nesting synchrony, we used as initiation dates random variates drawn from a beta distribution with parameters $\alpha = 10$ and $\beta = 20$ for the more synchronized population, and parameters $\alpha = 1.25$ and $\beta = 2.5$ for the population with low synchrony (Fig. 1).

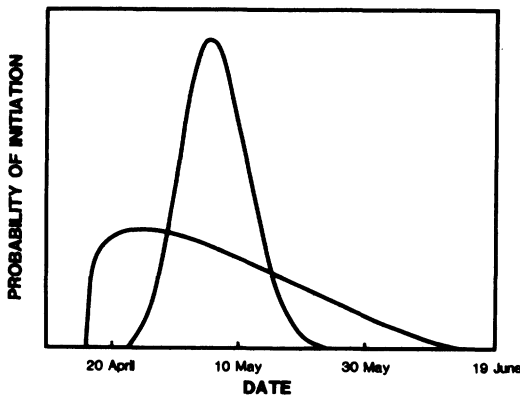


Fig. 1. The two nest-initiation curves used in the simulations.

We simulated the two extremes of mortality constancy either by a constant daily mortality rate throughout the nesting period or by catastrophic mortality on one day during the season, with low background mortality at other times. In the latter case, simulated catastrophes occurred on one of five different dates during the nesting season, approximately 5 days apart for highly synchronous nesting and 10 days apart for less synchronous nesting.

High and low hatch rates were used for both the constant mortality and the catastrophic mortality scenarios. Under constant mortality, we used daily survival rates of 0.99 and 0.95. The former results in a hatch rate ca. 0.703 for a 35-day period (9 days for laying an average-sized clutch and 26 days for incubation). The hatch rate under lower survival is ca. 0.166. For catastrophic mortality, we modeled the destruction of $1 - S_1$ of the nests active on the day of catastrophe and $1 - S_2$ of the nests on each of the other days. We found values of S_1 and S_2 by trial and error, so that hatch rates for the season were approximately 0.70 under high survival and 0.17 under low survival (Table 1).

We simulated four search patterns. One pattern comprised four searches (on 2 May, 16 May, 30 May, and 13 June). The second included three searches (on 9 May, 23 May, and 6 June). Patterns involving three or four searches were simulated only for nesting populations with low synchrony. The pattern with two searches involved the dates 16 May and 6 June. A one-search effort included a single search on 22 May.

Two extremes of nest detectability were postulated, based on personal experiences and discussions with biologists who had searched for nests in a variety of circumstances. Nests of low detectability had separate probabilities of detection for each nest stage. For nests in the laying stage, during which the female is present for longer and longer times as egg-laying progresses, the probability increases linearly from 0.16 for a one-egg nest to 0.80 for a nest with eight or

TABLE 1. Daily survival rates on days of catastrophe (S_1) and on other days (S_2) used to obtain desired hatch rates for various combinations of nesting synchrony and dates of catastrophe.

Date of catastrophe	Low mortality		High mortality	
	S_1	S_2	S_1	S_2
Low synchrony				
1 May	0.40	0.997	0.0	0.965
11 May	0.65	0.997	0.0	0.975
20 May	0.75	0.997	0.05	0.990
31 May	0.70	0.997	0.0	0.985
10 June	0.50	0.997	0.0	0.970
High synchrony				
1 May	0.0	0.994	0.0	0.955
6 May	0.50	0.997	0.0	0.965
11 May	0.70	0.997	0.05	0.990
16 May	0.75	0.997	0.25	0.990
20 May	0.75	0.997	0.20	0.990

more eggs. The probability of finding a nest during incubation is 0.80. Chances of finding terminated nests are 0.05 if the clutch hatched, and 0.10 if it was destroyed. These values are generally applicable to hidden nests for which the presence of an adult is often used to discover the nest (typical of most passerines and many other species). In the case of high nest detectability, the probability of finding a nest is 0.60 for nests with one egg, 0.75 for those with two eggs, and 0.90 for those with three or more eggs or in incubation. These rates held regardless of whether the nest was active or had been destroyed. Nests from which eggs had hatched were found with probability of 0.90. These rates may be applicable to small islands or colonial-nesting situations, where most nests are likely to be found on a single search.

Between these two extremes of nest detectability, we considered three intermediate situations. For any given nest status, let P_0 represent the probability of finding such a nest under the low detectability schedule, and let P_1 represent the probability of finding such a nest under the high detectability schedule. Define θ as an index of detectability, and P_θ as the probability of finding a nest of the given status under detectability index θ :

$$P_\theta = (1 - \theta)P_0 + \theta P_1.$$

We considered values $\theta = 0, 0.25, 0.50, 0.75, \text{ and } 1.00$.

For the constant mortality situations, four different types of nesting populations were thus generated, with all combinations of low and high synchrony, and high and low survival. For the catastrophic situations, four types of nesting populations were generated for each of five dates of catastrophe. We replicated each of the 24 resulting combinations five times, with different sequences of random numbers. This process resulted in 120 populations of nests. To each,

TABLE 2. Conditions under which Mayfield and Apparent estimators of nest success are accurate (root mean squared error ≤ 0.05), according to timing of mortality, synchrony of nesting, and mortality rate. Number of searches is k , and index of detectability is θ .

Timing of mortality	Nesting synchrony	Mortality rate	Acceptable conditions			
			Mayfield		Apparent	
			k	θ	k	θ
Constant	low	low	1	≥ 0.75	1	≥ 0.75
			2-4	all	2	≥ 0.50
					3-4	≥ 0.25
Constant	low	high	1-2	≥ 0.50	1-2	≥ 0.50
			3-4	all	3-4	≥ 0.25
Constant	high	low	1-2	all	1	≥ 0.75
					2	≥ 0.50
Constant	high	high	1-2	all	1-2	≥ 0.50
			Catastrophic	low	low	none
2	≥ 0.50					
3-4	≥ 0.25					
Catastrophic	low	high	none	1	≥ 0.50	
					2-4	≥ 0.25
Catastrophic	high	low	none	1	1.00	
					2	≥ 0.50
Catastrophic	high	high	none	1	≥ 0.75	
					2	≥ 0.50

we applied the specified search options: one to four searches made with detectability indices $\theta = 0, 0.25, 0.50, 0.75$, and 1.00 . Each simulated population contained 150 nests. We assumed that nests would not be checked between searches.

The Apparent hatch rate was calculated simply as the fraction of the found nests that hatched, either before or after discovery. We calculated the Mayfield (1961) estimator according to common practice for waterfowl. The 40% method (Johnson 1979) was used if searches were more than 14 days apart, otherwise half the interval between visits was taken for exposure if a nest had been destroyed during an interval.

To estimate the number of nests initiated in the area, we used the number of nests found for the Apparent method. For the Mayfield method we divided the number of found nests that were successful by the Mayfield estimate of nest success. The rationale for that procedure (Miller and Johnson 1978) is as follows. The number of successful nests is the total number of nests initiated times the hatch rate. Thus, the total number of nests initiated can be estimated by the number that are successful divided by the estimated hatch rate.

We evaluated both the Apparent and Mayfield estimators on the basis of how close each was to the actual hatch rate, which we knew for our simulated populations. We did similarly for the number of nests initiated. The criterion of closeness was the root mean squared error (RMSE). To obtain this value, we squared the difference between the estimate and the true value, averaged these over the replications (5 for con-

stant mortality; 25 for catastrophic, including the five dates of catastrophe), then took the square root of the resulting value. Root mean squared error conveniently incorporates both the bias of an estimator and its sampling variability: $RMSE = (\text{bias})^2 + \text{variance}$. For hatch rate, we defined as acceptable those conditions resulting in $RMSE \leq 0.05$. For number of nests initiated, the criterion was $RMSE \leq 15$.

RESULTS

Estimates of hatch rates.—When mortality occurred with constant probability throughout the nesting season, the Mayfield estimator was accurate for a wide range of number of searches and detectability of nests (Table 2). With low nesting synchrony and only one or two searches, however, fairly high detectability ($\theta \geq 0.75$ for low mortality, $\theta \geq 0.50$ for high mortality) was required to obtain accurate Mayfield estimates. The Apparent estimator generally was accurate only for high detectability ($\theta \geq 0.75$). With low nesting synchrony and three or four searches, accurate estimates resulted with modest detectability ($\theta \geq 0.25$).

When mortality was mostly catastrophic, the Mayfield method did not perform satisfactorily (Table 2). The Apparent method usually offered accurate estimates as long as two or more searches were made and detectability was fairly

TABLE 3. Conditions under which Mayfield and Apparent estimators of number of nests are accurate (root mean squared error ≤ 15), according to timing of mortality, synchrony of nesting, and mortality rate. Number of searches is k , and index of detectability is θ .

Timing of mortality	Nesting synchrony	Mortality rate	Acceptable conditions			
			Mayfield		Apparent	
			k	θ	k	θ
Constant	low	low	2	≥ 0.75	2	≥ 0.75
			3-4	all	3	≥ 0.50
Constant	low	high	4	≥ 0.75	4	≥ 0.25
					2	1.00
					3	≥ 0.75
Constant	high	low	1	1.00	1	1.00
			2	all	2	≥ 0.50
Constant	high	high	none		2	≥ 0.75
					3	≥ 0.50
Catastrophic	low	low	none		2	≥ 0.75
					3	≥ 0.50
					4	≥ 0.25
Catastrophic	low	high	none		2	1.00
					3	≥ 0.75
					4	≥ 0.50
Catastrophic	high	low	none		2	≥ 0.75
					2	≥ 0.75
Catastrophic	high	high	none		2	≥ 0.75

high ($\theta \geq 0.50$ usually). With a single search, very high levels of detectability (typically $\theta \geq 0.75$) were required for accurate estimates.

Estimates of number of nests initiated.—If mortality occurred at a steady but low rate, the Mayfield estimate of number of nests was accurate with three or more searches of a less synchronized population and two or more searches of a more synchronized population (Table 3). For similar situations, the Apparent estimator of number of nests required higher detectability to yield an accurate value. For populations with constant but high mortality, accurate Mayfield estimates of number of nests resulted only with four searches and high detectability ($\theta \geq 0.75$). Under the same conditions, the Apparent estimate was accurate in some cases where the Mayfield was not.

If mortality was catastrophic, the Mayfield estimate of nest number never was accurate. Apparent numbers for catastrophic situations were close whenever two or more searches were made and detectability was high.

Detectability.—The quantity θ that we use as an index to detectability admittedly is not an intuitive measure. To lend it some solidity, we calculated the percentage of simulated nests that were found, in relation to θ , for both high and low synchrony and for various numbers of

searches (Table 4). The range in percent of nests found indicates the variability over high and low survival rates, and constant and catastrophic mortality. It is obvious that, even with what we term low detectability, the percentage of all nests found can be high.

Although this information cannot be used to tell an investigator which value of θ is applicable to a study, it can provide some measure of confidence in the study design. For example, suppose a study involves two searches of a high-

TABLE 4. Range in percentage of nests found in simulated searches of nest populations, according to nesting synchrony and number of searches, for all combinations of high and low mortality rates and constant and catastrophic mortality.

No. of searches	Detectability (θ)				
	0	0.25	0.50	0.75	1.00
High synchrony					
1	25-68	38-71	55-76	71-83	85-91
2	32-84	55-90	75-93	90-97	96-99
Low synchrony					
1	14-61	25-65	45-70	59-73	73-80
2	32-83	54-86	74-90	87-93	92-97
3	51-89	71-92	85-94	92-97	95-98
4	56-90	77-95	89-97	94-99	98-99

ly synchronized nesting population. To use the Apparent rate of nest success, an observer should insure that $\theta \geq 0.50$ to be assured of reasonable accuracy (Table 2). Then, according to Table 4, 75–93% of all nests initiated should be found. The comfort with which the investigator can make this assumption, or—better yet—verify it, determines the comfort with which the estimates of nest success can be embraced. Nests must be detectable, and current nests must be distinguished from old nests, and actual nests from dummy nests. These distinctions are made more difficult if nests have been destroyed or if nests are not found until after they have been terminated.

DISCUSSION

The appropriate method.—The optimal method depends on which set of circumstances prevails in the nesting population. We considered five attributes: synchrony of nesting, steady vs. catastrophic mortality, survival rate, number of searches, and detectability. The survival rate of clutches is unknown, and is in fact the object of most nesting studies. Nonetheless, previous experience in the study area and knowledge of nesting studies conducted in similar situations may give the investigator some idea of the expected hatch rate. The number of searches is under the control of the investigator. Synchrony of nesting usually can be anticipated by familiarity with the species under study and the site latitude.

Determining whether mortality of clutches is catastrophic or occurs at a relatively constant rate is less clear-cut. There may be evidence of catastrophe after the fact. For example, a severe weather phenomenon that destroyed many nests might be recorded; or repeated searching might indicate high survival of clutches until one search shows destruction of most clutches. Designing a nesting study to accommodate catastrophic mortality requires the anticipation of the event, which is highly problematic. Only a familiarity with the area and the nesting population can give the investigator some idea of the likelihood of such events.

Evidence for the level of detectability can come from at least four sources. The first is subjective, based on the general appraisal of the habitat, the size of the nesting area, the hiding potential of the vegetative cover, the intensity of the searches, thoroughness of the investi-

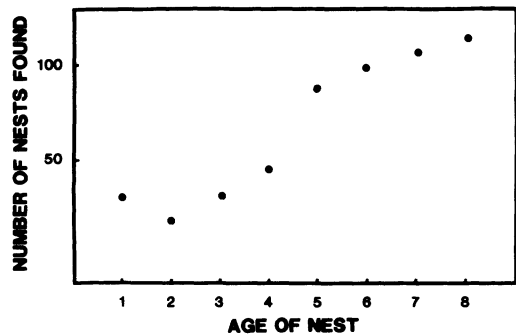


Fig. 2. Number of Blue-winged Teal nests found at specified ages.

gator, behavior of the species, etc. This is the kind of evidence usually reported. The second type is circumstantial, based on the size of the breeding population and estimates of the number of nests each pair initiates. For example, suppose a study population contains 50 breeding pairs, and with renesting each pair initiates an average of two nests. If 50 nests were found, that would indicate a value of $\theta = 0.50$, at least approximately. The third type of evidence involves the proportion of active nests found on one search but not found during a previous search. It is based on repeated searches over the site, preferably at short intervals (A. T. Klett and D. H. Johnson unpubl. data). The fourth kind of evidence is based on the distribution in the sample of the age of clutch when found. If nests are initiated during a fairly long period of time (low synchrony), several searches are made, and the sample of nests (N) is large, then the number of nests i days old (n_i) found during any search should follow a geometric distribution

$$n_i = Ns^i,$$

where s is the daily survival rate of clutches. Taking logarithms,

$$\log(n_i) = \log(N) + i \log(s),$$

so the regression of $\log(n_i)$ against i should be linear, with a negative slope equal to $\log(s)$. Departures from linearity suggest that detectability varies with age of clutch.

Consider as an example the data on Blue-winged Teal (*Anas discors*) reported by Miller and Johnson (1978: 473). Because teal generally lay 1 egg/day, the clutch size of an unincubated

nest when found represents the age of that clutch. We include nests found with 1–8 unincubated eggs. The number of nests found at a particular age increased with age (Fig. 2), rather than the converse. From this we conclude that nests in early stages of laying are less detectable than those in later stages.

General recommendations.—The following recommendations are based on this study of simulated Mallard nests as well as previous investigations (also see Klett and Johnson 1982):

1. The accuracy needed for a nesting study depends on the objectives of the study. For example, an evaluation of two alternative nesting habitats might require only fairly accurate indices of nest success in each habitat, so that the better one could be determined. A study to assess the population dynamics of a species would require greater accuracy of nest success estimates, because an error of only a few percentage points can make the difference between a population projected to be declining and one thought to be increasing.
2. The sample size of nests must be adequate for the objective. Sample sizes are often increased by pooling over species, study areas, time periods, etc. This procedure may be misleading if the data sets that are pooled actually differ.
3. A minimum of three or four searches of a population nesting asynchronously, and two of a synchronous population, is required to estimate accurately hatch rate, unless detectability of nests is high.
4. If mortality occurs at a constant rate, the Mayfield method generally gives better estimates of hatch rate than the Apparent, unless detectability is high.
5. If mortality occurs catastrophically, the Apparent estimator of hatch rate is generally better, but this estimate is accurate only if detectability is fairly high.
6. To estimate the number of nests initiated when the mortality rate is constant, the Mayfield procedure is better than the Apparent for low mortality. For high mortality situations, the Apparent estimator is accurate, but only for repeated searches and high detectability.
7. Mayfield estimates of number of nests when mortality occurs catastrophically are never very accurate. The Apparent estimator is satisfactory with repeated searches and high detectability.
8. A single method may not be optimal for all populations of nests, even within a single study. One may wish to use, for example, Apparent estimates for nests on islands and Mayfield estimates for mainland nests, and ultimately produce a combined estimate.

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