

SUGGESTIONS FOR CALCULATING NEST SUCCESS

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Reports of nesting success that do not take into account the time span of observation for each nest usually understate losses, and sometimes the error can be very large. More than a decade ago I pointed out this problem and proposed a way of dealing with it (Mayfield 1960:192-204; 1961). Since that time many field students have used the method, and it has proved especially helpful in combining fragments of data from many sources, as in the North American Nest-record Program at Cornell University. However, not every published report shows awareness of the problem, and letters of inquiry have shown that some people are deterred from dealing with it because of difficulty with details. Therefore, I offer these further suggestions to simplify the procedure as much as possible.

THE PROBLEM

All nests are not found at the very start. Indeed, most nests of small open-nesting birds are not found until incubation is well under way or until the young have hatched. The observed success in such a sample will be greater than the true nesting success of the species.

The shorter the time span of observations, the less the observed losses; that is, nest mortality—loss by destruction or desertion—is a function of time. Since nearly all field studies contain a mixture of nests found early and late, as customarily reported they show nesting success higher than reality; but the amount of error is indeterminable because the time each nest entered the sample is not reported. For precise analysis of mortality and survival, it is not enough merely to count nests, eggs, and young. The elapsed time of the observations must also be considered.

To illustrate the main difficulty, suppose you found a series of nests when incubation was far advanced. Hatching success would be nearly 100%; and in nests containing large young when found, fledging success would be nearly 100%. Yet you would hesitate to present these figures because it is plain that not enough time elapsed for many accidents to befall. In this extreme case the pitfall is obvious, but in a mixed bag of data, this kind of error may slip through unnoticed.

What you are trying to determine is the nesting success of a population. Ideally you would like to find all the nests started by the birds in that population, watch all these nests from their beginnings, and observe everything that happened up to the fledging of young. Usually this is impossible and you have to settle for a good deal less, namely, a sample that is anything but

neat and complete. Some nests in the population are not found at all, some are not under observation for their full duration—found early, found late, or not followed to a conclusion.

What do you do with these incomplete records, which often comprise the larger part of the data? Customarily, some aspects of the problem are ignored. Nests found late are lumped with nests found early and considered alike. The result is to understate mortality and overstate success, as mentioned earlier.

Not everyone dodges the issue. In his study of the Yellowhammer (*Emberiza citrinella*), Peakall (1960) used only the subsample of nests observed from the very start. But this course brings 3 objections: First, very few field studies contain enough nests found before incubation began; second, the nests disqualified contain valuable information that should be used if possible; and third, the subsample of nests found earliest may not be typical. Perhaps they were easier to find because of their locations or because the vegetation concealing them was not yet far advanced.

In some elusive species the eggs and young may be found almost at random times throughout the duration of the nesting cycle. If so, the average period of observation is about half the duration of the nesting cycle, and the observed losses are about half the true losses. Coulson (1956) recognized this fact in his study of the Meadow Pipit (*Anthus pratensis*) and corrected the observed figures by doubling the known losses.

Up to this point I have discussed nests not observed from the start, but what of nests not followed to a conclusion? At one extreme there is the case of an ornithologist whose field records each year did not begin until he arrived at his summer cottage after the close of the school term, and at the other extreme are the members of expeditions and the vacationers who are obliged to leave a region while some nests are still active. Samples containing the work of many years are likely to contain records of both kinds.

Customarily, I suspect, nests with outcomes unknown are excluded from samples used in calculating success. Yet, this too is regrettable, because it tends to exaggerate losses. That is, a nest lost early becomes a part of the record, whereas a nest that persists is thrown out.

Finally, the sorriest data are those on nests whose beginnings are shrouded in doubt and whose outcomes are also unknown. These are certain to be discarded in calculations of success. The effect on the sample is uncertain, but any loss of data is regrettable and any discards may introduce bias.

No field student is happy to see a simple concept like nesting success made to appear complicated. Yet everyone who has undertaken a nesting study knows that his own data embody not only hard facts but also elements of judgment that might have been handled differently by another worker. None

of this difficulty is apparent in published tables of figures, which convey an air of indisputable finality.

A review of nest success in altricial birds by Nice (1957) is widely quoted. Yet Woolfenden and Rohwer (1969) examined about half the 35 summarized studies of open-nesting birds included; in not one did the original author tell how he dealt with these difficulties. Ricklefs (1969) offered a sophisticated analysis of mortality in small altricial birds but threw up his hands at trying to disentangle these tissues in published studies, and treated all nests as if "found before the initiation of laying."

It is true that nests of some species are more likely to be found during the building stage than during incubation, and some field workers—notably, the oologists—are particularly adept at finding nests before the eggs are laid, but these circumstances are not universal. My own experience in the field and consultations with others about their data lead me to suspect that raw data on species with hard-to-find nests commonly reveal a mortality only a little more than half the true mortality. This problem needs to be dealt with in one way or another.

In this whole discussion I emphasize small open-nesting birds, because the problem of finding nests early is much more acute in such species than in those nesting in boxes or other predetermined sites.

A SOLUTION

There is a straightforward way of dealing with these problems that makes use of nearly every bit of data collected. In principle it treats nests in terms of mortality and survival over observed periods of time. Survival is the converse of mortality. For mathematical elegance, we deal with both as probabilities.

Nest success may be viewed in 5 stages: (1) survival during the building of the nest; (2) survival during the egg-laying period; (3) survival during incubation; (4) hatching of eggs, which is assumed to take place at a point in time when the first young bird breaks free of the shell; (5) survival of young to fledging. Here I will focus attention on the last 3 stages.

The number of observed losses will depend on the number of nests in the sample and the amount of time each nest is under observation—that is, the exposure. A convenient unit for measuring exposure is the nest-day (one nest for one day). For example, 2 nests both under observation for periods spanning 6 days represent an observed exposure of 12 nest-days; this is equivalent to 3 nests observed for 4 days or one nest for 12 days. The time span is the crucial factor even though the nest was not actually visited on all the days in it. By dividing the total number of losses by the total number of nest-days, you get the mortality and survival rates (probability) for any period.

For the greatest precision by this method, if your sample were large enough, you might calculate a separate survival rate for each day of each stage, and compute the probability of survival for n days by the product $P_1 P_2 P_3 \dots P_n$, where P_1 is the probability of survival on day 1, P_2 is the probability of survival on day 2, and P_n is the probability of survival on day n . However, very few studies will have samples of sufficient size to yield a reliable separate rate for each day. So, if losses do not bunch up early or late in any stage, the practical course is to calculate an average mortality and survival rate across each stage of the nest. Since the conditions at the nest are usually different for each stage, we would expect to find, for example, a survival rate during incubation different from the survival rate during the nestling stage.

Here is an example. In my study of the Kirtland's Warbler (*Dendroica kirtlandii*) (Mayfield 1960:193), 35 nests were lost during 878 nest-days of incubation, and the mortality was therefore $35/878 = .040$ per nest-day. If so, the survival rate was $1 - .040 = .960$ per nest-day. Now we can use what we have learned from the entire sample to predict the probability of success for a nest through the full 14 days of incubation. Since the probability of successive events is the product of their probabilities, the probability a nest will survive 14 days is .960 multiplied by itself 14 times, or $.960^{14} = .56$.

In raising decimals to high powers, it is best to use as many decimal points as practical at each step, because repeated rounding off of decimals will cause errors to pyramid.

In calculating nest success—defined as the survival of any contents of the nest—you ignore partial losses through the failure of some but not all eggs to survive and hatch, and proceed immediately to the nestling period, which you handle in the same way. For example, in the Kirtland's Warbler (Mayfield 1960:198) in 735 nest-days with young in the nest, 22 nests were lost. So the mortality rate was $22/735 = .030$ per nest-day, and the probability of survival was $1 - .030 = .970$ per nest-day. Hence, with a nestling period of 9 days, the probability of survival of a nest with young was $.970^9 = .76$.

Combining these probabilities, we have the probability of survival of a nest from the start of incubation to the fledging of young, $.56 \times .76 = .43$. Note that nest success is usually somewhat larger than egg success, because some eggs do not hatch and some eggs and young are lost from nests whose contents otherwise remain intact.

A separate calculation gives the hatching rate—the probability that eggs present at hatching time actually produce living young. Divide the number of young by the number of eggs present just before hatching. In Kirtland's Warblers (Mayfield 1960:197) this probability was .73; that is, 27% of the eggs present at hatching time did not hatch.

If there are no significant losses of eggs or young without the loss of entire nests, the 3 probabilities calculated in the previous paragraphs may be combined to arrive at the probability an egg present at the start of incubation will produce a fledgling. We multiply the probability an egg will survive the incubation period, by the probability an egg will hatch, by the probability a young bird will survive the nestling period; thus, $.56 \times .73 \times .76 = .31$.

In some species a considerable number of eggs or young may vanish from nests that are not lost totally. If so, the probability of these events must be superimposed on the previous calculations. The principle is the same, but now it is necessary to introduce a smaller unit of exposure, the egg-day or the nestling-day. That is, a nest with 5 eggs observed for one day has an exposure of 5 egg-days. Similarly, nestling-days measure the exposure of young in the nest. Note that when more than one egg or nestling is in the nest, the exposure in egg-days or nestling-days is much larger than when measured in nest-days, and for nests not suffering internal variations, it is a multiple of the number of nest-days.

The total number of individual eggs lost without the loss of all eggs in the clutch divided by the total number of egg-days gives the mortality per egg-day. For example, in the Kirtland's Warbler I noted 6 eggs lost individually during incubation where the exposure was 3181 egg-days. (This number was small because most eggs removed by cowbirds vanished before incubation began.) The mortality was .002 and the survival was .998 per egg-day, and the probability of an egg surviving the incubation period in a persisting nest was $.998^{14} = .97$. A similar calculation may be made for nestlings surviving in persisting nests.

Often, as in my example, these categories of loss are very small, or, conversely, the probability of survival of eggs and young in continuing nests is very high. If so, it is doubtful if this refinement is justified by the limited accuracy of the basic data. However, to pursue the example given, if the only adjustment to be made is for eggs lost individually, we multiply this last probability by the previously calculated probability of survival of nests from the start of incubation to fledging (which ignored losses of individual eggs and nestlings) and get a slightly reduced probability of success; $.97 \times .31 = .30$. If there is also a significant loss of individual nestlings, this will call for a further adjustment downward of the ultimate probability of success from the start of incubation to fledging.

ARE MORTALITY RATES OF SEPARATE STAGES REALLY DIFFERENT?

In the foregoing example I have treated the incubation period separately from the nestling period (ignoring nest-building and egg-laying stages). This step may not always be necessary. In precocial birds the nestling period

TABLE I
COMPARISON OF MORTALITY IN INCUBATION AND NESTLING PERIODS OF KIRTLAND'S
WARBLER*

	Nest-days with losses	Nest-days without losses	Total nest-days
Incubation period	35	843	878
Nestling period	22	713	735
Totals	57	1556	1613

$\chi^2 = 1.16, P > .25$

* This contingency table, constructed to appraise by the chi-square test if there is a real difference in mortality between the incubation period and the nestling period, shows that the observed difference might have been expected by chance in about a quarter of samples of this size; i.e., a significant difference is not proven, although a larger sample might show a real difference to exist.

shrinks toward the vanishing point, and in some altricial birds the mortality in the two periods may not be significantly different.

To appraise the difference, we construct a 2×2 contingency table, as shown in Table I, and apply the chi-square test. The test reveals the observed difference is not statistically significant for the entire population at a high level of probability. This is plausible because the variants (losses) are relatively small numbers, and chance effects could have a major influence on the differences. Therefore, on the basis of this sample, the observed difference cannot be taken as virtually certain; that is, the difference does not meet the 1% or 5% test of significance commonly used by statisticians to be assured the difference could be explained on the basis of chance alone in less than 1 or 5 times out of 100. However, the difference may still be real. A larger sample might increase the confidence level.

Changing to a smaller unit—say, nest-hours—might seem to hold out promise of a different result, since it multiplies the sample size without enlarging the losses; but in this instance it still yields a chi-square and probability of the same order, and therefore does not alter the general conclusion.

In these circumstances, what are the alternatives? By lumping the 2 stages, you enlarge the sample and increase the confidence in the single mortality rate across both. Sometimes this is the wise course. Yet, to do so, may mask real differences that ought to be recognized for some purposes. It would be astonishing to find survival rates identical in the 2 stages, since desertion is usually more prevalent during incubation and predation is usually more likely when activity at the nest increases after the hatching of young. The observer should state reasons for whatever course taken.

In this example, lumping the stages to get a single rate brings little change

in the final results. The survival rate per day for the entire 23 days of incubation and young is .96466 (instead of .96 and .97 for the respective stages). Using this rate for both, we find the probability of survival for the incubation period is .60 (instead of .56); for the nestling period is .76 (the same as before); for the product of the two is .46 (instead of .43); and for the entire 23 days of both stages considered as a unit is .44. At no point do the 2 methods give survival probabilities differing by more than .04.

SOME CAUTIONS

A basic underlying assumption of this method is that mortality is approximately even across each stage. That is, we judge in a particular study that nests are about as likely to fail early in incubation as late in incubation, and about as likely to fail early in the nestling period as late in the nestling period. For several species I have examined, this appears to be true, but to prove it rigorously would require a very large sample. Lacking this, we may judge the distribution of losses approximately by inspecting the total losses for each day in the nesting cycle, which may be entered at the foot of the column for each day on the worksheet suggested here. A notable concentration of losses anywhere should be apparent.

In the Mourning Dove (*Zenaida macroura*), which builds a flimsy and often exposed nest, Woolfenden and Rohwer (1969:38) found losses within the incubation period much more likely to occur near the beginning. So a flat mortality rate across the incubation period proved inappropriate for analysis of this portion of the nesting cycle.

The unit of time suggested here is one day, because nests are commonly visited on a daily schedule and recorded by days. Many observers avoid visiting a nest more often than once a day lest they interfere with its normal progress. Skutch (1966:5) expressed concern about visits even this frequent and saw here an objection to the use of this method.

Intuitively one feels some predators may follow human beings to bird nests, but it is also possible some predators may be repelled by the presence or scent of people—as fur trappers tend to believe. In any case, we are faced with a kind of biological “uncertainty principle” whereby any nest observed is no longer in its *natural* state.

Willis found a way to compare survival rates of visited and unvisited nests of Bicolored Antbirds (*Gymnopithys bicolor*) in the forest of Barro Colorado Island, Panama. Applying his test, he found “survival rates of visited and unvisited nests are very similar” (Willis 1973:264).

However, daily visits are not a cornerstone of this method. Rather, the key concept is the *time span* of observations, which may be measured even though days may be missing from the record. The emphasis here is not on the way information is gathered but on the way it is used after it is collected.

TABLE 2
SAMPLE ENTRIES IN WORKSHEET, LEFT SIDE

Nest no.	Incubation		Days before hatching															Comment			
	Egg-days	Nest-days	-17	-16	-15	-14*	-13	-12	-11	-10	-9	-8	-7	-6	-5	-4	-3		-2	-1	0**
73-1	69	14	1	2	3	4	5	5	5	5	5	5	5	5	5	5	5	5	5	4/1	1. Gap in record.
73-2	50	10						5	5	5	5	5	5	5	5	5	5	5	5	3/2	2. Start not observed.
73-3	24	5				4	5	5	5			0									3. Nest destroyed.
74-1	14	3			3	4	5	5	5												4. Nest deserted.
74-4	19	4				4	5	5	5	5											5. Human disturbance.
Totals																					
Losses by days																					
74-2	25	5					5	5	5	5	5										6. Start & outcome unknown.
74-3	0	0					5														7. One visit only.

* Incubation begins on next-to-last egg, day -14.
** Hatching begins on day zero.

TABLE 3
SAMPLE ENTRIES IN WORKSHEET, RIGHT SIDE

Nest no.	Days after hatching										Nests with young		Comment			
	0	+1	+2	+3	+4	+5	+6	+7	+8	+9	+10	+11		+12	Nest-ling-days	
73-1	4:1	5	5	5	5	5	5	5	5	5	5			10	50	8. Record complete.
73-2	3:2	5	4	3	3	3	3	3	3	3	3			10	33	9. Partial loss.
74 5					4	4	4	4	4	0				3½	14	10. Age estimated. 11. Total losses by days.

There is nothing magic about a day as a unit. Conceivably, with automatic recording of events in the nest, a half-day or an hour might suit special purposes. However, we should be wary of being lured into a fictitious appearance of precision. Any method we use will give no more than an approximation of the truth, and this method merely helps avoid certain gross errors that are common. In birds with very long nesting periods and widely spaced visits, time units larger than one day may be suitable. By using the largest practical unit, we minimize the pyramiding of small errors when raising inexact numbers to high powers.

In addition to matters treated here, there are many problems that are not circumvented by mathematics. In samples of modest size, stochastic variables may be important and seriously interfere with generalization to larger populations. Fortuitous influences may vary from year to year and place to place—predation, competition, weather, sex ratios, and so on.

WORKSHEET

You will simplify analysis if you enter all your nest data on one large worksheet. I prefer to use ruled ledger paper, splicing sheets together to any desired width and length. For hundreds of nests the sheet may be so long it must be rolled like a scroll or folded like a computer printout.

Table 2 illustrates the left portion of such a sheet (egg-laying and incubation), and Table 3 illustrates the right portion of the same sheet. A "Comment" column is useful for noting special circumstances when entering data on the sheet, but I have used it here to identify some common problems selected for illustration. In this example I focus on the nest stages from the start of incubation to the fledging of young. Similar attention may be given to nest-building and egg-laying stages if the samples are large enough.

1. *Gap in record.* Nest 73-1 (code designates nest No. 1 of 1973) was not visited for a period of 5 days, but this did not detract from the record in any way, since no change in nest contents occurred in the interval. On handwritten worksheets it is convenient to circle all numbers representing eggs.

2. *Start not observed.* Nest 73-2 was found during incubation, and these entries were positioned on the table after the hatching day was determined.

3. *Nest destroyed.* Nest 73-3 was not visited between day -11 and day -7, when it was empty. Destruction is assumed to have occurred midway between the last two visits, namely, on day -9. If the gap in observations had been between day -11 and day -8, the midpoint would have been day $-9\frac{1}{2}$, and this would be taken into account in the nest-day and egg-day entries at left, where fractions present no difficulties. The estimated failure date is not precisely at the midpoint between the 2 observations; it is a little earlier, but not enough to make an appreciable difference for these purposes. (If the loss rate is constant, the numerical size of the losses declines steadily, and therefore the mean age of those lost in any time interval will always be less than the mean point in the interval.)

4. *Nest deserted.* Nest 74-1 was not attended by adults and the eggs were cold when it was visited on day -11. Desertion is assumed to have occurred on the day when noted since the nest was active the previous day. An extra visit or some other clue often gives the observer an inkling about the time at which the loss occurred that is better than any arbitrary rule. The observer's judgment might place this loss at day $-11\frac{1}{2}$.

5. *Human disturbance.* Nest 74-4 was subjected to experimental removal of eggs on day -9, and the nest was promptly deserted as a result. This record was admitted to the sample for 4 days of its observed period but disqualified henceforth. A portion or all of a record may be excluded for any human disturbance judged serious enough to affect the outcome, such as a gross alteration in the environment, photography, or other disruptions.

6. *Start and outcome unknown.* Because of their unknown chronology, nests 74-2 and 74-3 are segregated so they do not figure in any totals by days. Nest 74-2 was visited on 6 successive days, which constitute a time span of 5 days observation. Although this record cannot be used in analysis of events attributed to specific days, it can be used as a part of total exposure during incubation. With some species the extent of incubation may be judged by examination of the eggs, but this is not always feasible.

7. *Single visit.* Nest 74-3 was visited only once and therefore is excluded from all calculations because the period of observation does not cover a full day. Entries must show observations on 2 days, separated by at least 24 hours, to constitute a time span of a day or more. A nest visited only once may provide data for other purposes, but it is not useful for records of mortality and survival. The exposure in nest-days is zero.

The remaining examples appear on Table 3, representing the righthand side of the worksheet.

8. *Record complete.* Nest 73-1, appearing also in Table 2, remained intact until found empty on day +11. Fledging may be assumed even though the young are not seen, since young in this species sometimes leaves the nest as early as day +9. Finding all the fledglings after they have been out of the nest a few hours is very difficult in some species and unnecessary for this purpose, where attention is on survival for a stated period.

9. *Partial loss.* Nest 73-2 lost one young bird on day +2 and another on day +3, but the nest endured, and the remainder of the young fledged normally. The number of nest-days was not affected by the losses, but the number of nestling-days reflected them. Losses of individual eggs from continuing nests would be treated similarly in Table 2, the lefthand portion of the worksheet.

10. *Age estimated.* Nest 74-5 was found after hatching and destroyed before fledging, but an experienced observer can position the nest approximately in the table at his first inspection of the young.

11. *Total losses by days.* At the bottom of each column representing a day in the nesting cycle, you enter the number of nests lost that day. It helps the eye catch these losses in a large and intricate table if conspicuous red marks are made in the body of the table at points when losses are believed to have occurred. The totals for the columns show the distribution of mortality by days.

SUMMARY

In field studies of nesting birds, many nests are not found at the very beginning or are not followed to a conclusion. When nests are not under observation for their full duration, the observed loss rates are less than the actual rates of the species. The amount of error varies according to the total exposure of all nests not spanned by human observation in the sample. A way of incorporating the time span of observations is to measure the exposure in nest-days, and calculate mortality and survival rates in these units at each stage of the nesting cycle. This method allows pieces of data to be used that would be discarded in customary analyses. A suggested worksheet simplifies analysis, and illustrations answer some questions that troubled users of this method.

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