such a downward movement during mid-day by much of the avian community in a tropical dry forest of Peru, and attributed these to high temperatures and/or insect movement. If Brown Jays are not responding to heat or insect movement, their downward shift in height may be a result of a movement to a preferred foraging zone after initial canopy rallying.

We wish to thank E. Shanley and P. Cantle for field assistance. K. A. Arnold, N. Silvy, S. Beasom, and W. A. Brown read earlier drafts of the manuscript.—MICHAEL L. MORRISON AND R. DOUGLAS SLACK, *Dept. of Wildlife and Fisheries Sciences, Texas A&M Univ., College Station, 77843.* *Accepted 16 Aug. 1976.*

Do more birds produce fewer young? A comment on Mayfield's measure of nest success.—Fretwell (Populations in a Seasonal Environment, Princeton Univ. Press, Princeton, NJ, 1972) has considered the effect of nest density on nesting success of Field Sparrows (*Spizella pusilla*). He used the method of Mayfield (Wilson Bull. 73:255–261, 1961) to calculate a daily mortality rate and from this the overall nest survival rate. Fretwell concluded that the nesting success rate decreases as density increases. A closer look at the data, pictured in Fretwell's Figure 44, suggests that not only does the survival rate decrease with increasing density but, in fact, the decrease in survival rate is actually so great that at higher densities the larger total number of breeding adults would produce a lower total number of young than would a smaller number of less crowded adults. The data given are not sufficient to draw this conclusion explicitly and Fretwell does not do so, but it is implicit in his schematic Figure 45 which shows overall nest survival decreasing very rapidly as nest density increases.

It is theoretically possible that more birds might produce fewer young but this seems sufficiently improbable to require an examination of the method used to estimate nesting success. Examination shows that Mayfield's method of estimating nesting success may be biased if not all nests have the same chance of success. This bias will be negligible for low or moderate nest mortality but for high nest mortality it may substantially exaggerate nest mortality.

Mayfield's measure of nesting success was designed to eliminate the bias in earlier methods of estimating nesting success. In using Mayfield's method, first a daily nest mortality rate, p, is estimated by dividing the number of nest failures by the number of nest-days at risk. Then the overall survival rate is calculated to be $(1 - p)^n$, where n is the nest lifetime. Mayfield's method assumes that the risk is the same for all nests and for all days. If, in fact, different nests have different probabilities of surviving then Mayfield's method will produce a biased estimate of the nesting success rate. In general, the estimated success rate will tend to be less than the actual success rate if the nests differ.

There is some evidence that nests may actually differ in survival probability. Nice (Trans. Linn. Soc. N. Y. 4:1–247, 1937) in her work on Song Sparrows (*Melospiza melodia*) observed that well-concealed nests are less likely to be destroyed than badly-concealed nests. Baptista (Auk 89:879–882, 1972) conjectured that the parasitism of White-crowned Sparrows (*Zonotrichia leucophrys*) by Brown-headed Cowbirds (*Molothrus ater*) that he observed in San Francisco may have been due to the suboptimum habitat which didn't offer the White-crowns adequate cover. Krebs (Ecology 52:2–22, 1971) observed that Great Tits (*Parus major*) nesting in hedgerows had less success than birds nesting in woodlands.

The bias in Mayfield's procedure when nests have different survival probabilities may be illustrated in a simple example. Assume that a nesting population consists of birds of

TABLE 1

THE EFFECTS OF BIAS IN MAYFIELD'S MEASURE OF NEST SUCCESS IF NESTING SUCCESS RATES ARE VERY DIFFERENT

Proportion of "young" α	Number of "young" N_y	Number of "adults" N_a	Success Rate per nest		Total number of Successful Nests	
			True S_1	Apparent S_2	True	Apparent
.000	0	100	.668	.668	66.8	66.8
.500	100	100	.340	.282	67.9	56.5
.667	200	100	.230	.162	69.1	48.5
.750	300	100	.176	.109	70.2	43.6
.800	400	100	.143	.082	71.4	40.8

2 types. Let proportion α of the nests be of one type, say of young birds nesting for the first time, which produce nests all of which have the same daily risk p_y. Let the remaining proportion $1-\alpha$ of the nests be of another type, say of experienced adults, which produce nests all of which have the same daily risk p_a. Then the actual nesting success rate will be $\alpha(1-p_y)^n + (1-\alpha)(1-p_a)^n$.

Assume that nests are observed daily from the time the eggs are laid. Then Mayfield's method will produce an estimate of overall nesting success which will be approximately $(1-p)^n$, where

$$p = \frac{\alpha(1-q_y^n) + (1-\alpha)(1-q_a^n)}{\alpha(1-q_y^n)/p_y + (1-\alpha)(1-q_a^n)/p_a} \tag{1}$$

where $q_y = 1 - p_y$ and $q_a = 1 - p_a$. A derivation of (1) is given in Appendix 1.

A few calculations will show the effect of the bias if nesting success rates are very different. Let $n = 20$, $p_y = .2$, $p_a = .02$, let S_1 denote the true success rate and let S_2 denote the apparent success rate using p as calculated in (1). Assume that there are a fixed number of "adult" birds' nests, $N_a = 100$, and different numbers of "young" birds' nests, $N_y = 0, 100, 200, 300$, or 400. Then we can find the "true" total number of successful nests and the "apparent" number of successful nests (Table 1). Here $\alpha = N_y/(N_y + N_a)$.

These calculations show that it is possible that an increasing population of breeding birds might produce an increasing (although here only slowly increasing) number of young while the apparent number of young produced might decrease quite sharply. In the example considered here there are a fixed number of "adult" birds likely to be successful whose success rate is unaffected by density. The increase in the number of nesting birds is due solely to an increase in the number of "young" birds whose nests are subject to high risk.

The reason that Mayfield's method produces a biased estimate of nesting success if different nests have different daily mortality rates is that the nests which are at greater risk are not only more likely to be destroyed, but if they are destroyed it will tend to occur earlier than for the nests at less risk. Thus the nests with greater chance of failing will contribute less than their share to the number of nest days.

The bias in estimating nesting success due to differences in success rate from nest to nest will be negligible if the rates are not very different or if the success rates are high.

The bias will only be significant if risks are high and are quite different from nest to nest. This would be the case, however, if the effect of increasing nesting density was not to increase the risk of all nests uniformly but was rather to increase the number of nests that were at greater risk.

The question of whether nests are all at the same risk is an important one and it could be tested. If the daily risk is the same for all nests and all days then the number of days each nest is at risk will have a "censored" geometric distribution. That is, the number of days at risk will have a geometric distribution except that since a nest cannot be at risk more than the normal nest lifetime, n days, all the probability that would otherwise be assigned to values greater than n will be concentrated at n. The observed distribution of the number of days each nest is at risk may be compared with this expected distribution and a chi-squared test performed. This test is described in Appendix 2.

Appendix 1. Derivation of (1):

$$p = \frac{\alpha(1-q_y{}^n) + (1-\alpha)(1-q_a{}^n)}{\alpha(1-q_y{}^n)/p_y + (1-\alpha)(1-q_a{}^n)/p_a}.$$

The estimate p is the ratio of the number of nest failures to the number of days at risk. The numerator of (1) is the probability that a randomly chosen nest will fail since proportion α of the nests are of "young" birds and each such nest has probability $q_y{}^n$ of succeeding, where q_y is the daily survival rate. The failure rate for "young" bird nests is $(1-q_y{}^n)$ and the failure rate for "adult" bird nests is $(1-q_a{}^n)$. Proportion $1-\alpha$ of the birds are "adults."

The denominator of (1) is the expected number of days at risk for a randomly chosen nest. If X is the number of days that a "young" bird's nest is at risk then $P(X \geqslant k) = q_y{}^{k-1}$ for $k = 1, 2, \ldots, n$. To find the expected number of days at risk we find $EX = \sum_{k=1}^{n} P(X \geqslant k) = (1-q_y{}^n)/p_y$. Similarly, for "adult" birds the expected number of days at risk is $(1-q_a{}^n)/p_a$. Proportion α of the nests are of "young" birds and proportion $1-\alpha$ are of "adult" birds.

For large numbers of nests the estimated value of p will be close to that given by (1). For small numbers of nests the estimated value may be larger or smaller than that given by (1) but it will tend to be larger.

Appendix 2. Testing for homogeneity of nest mortality. If nests are observed daily from the time laying is completed the assertion that daily risk is the same for all nests and all days may be tested by finding the expected frequency of nests that survive exactly until the *kth* day (are at risk for k days): Npq^{k-1} for $k = 1, 2, \ldots, n-1$ and Nq^{n-1} for $k = n$, where N is the number of nests observed, p is the daily risk estimated by Mayfield's method and $q = 1 - p$. These expected frequencies may be compared with the observed frequencies using a chi-squared test where the number of degrees of freedom is two less than the number of categories (of numbers of days at risk) used.—RICHARD F. GREEN, *Dept. of Statistics, Univ. of California, Riverside 92521. Accepted 17 Dec. 1975.*