

## SHORT COMMUNICATIONS

### Testing for Individual Variation in Breeding Success

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I measured the breeding success of Northern Fulmars (*Fulmarus glacialis*) in 6 consecutive years at a colony on the Semidi Islands, western Gulf of Alaska (56°N, 156°W). I tabulated the frequency distribution of the number of years successful for a sample of 244 nest sites at which breeding occurred in all 6 yr. A consistently higher probability of success occurred in some sites than in others (Fig. 1a). The same over-representation of extreme values was present in a subsample of 137 sites in which one or both members of the pair was individually known from plumage differences and no changes of identity were detected between years (Fig. 1b). More pairs were consistently successful, or consistently unsuccessful, than expected on the null hypothesis that all pairs had the same probability of breeding success in a given year.

Fulmars establish permanent nest sites to which they return annually with a high degree of fidelity. Adult mortality in the population averaged 3% per year, and nonbreeding ensued for one or more years at half of the nest sites at which a mortality occurred (Hatch 1987). Changes of mate or nest site not associated with mortality occurred at a combined rate of less than 1% per year. Thus, differences among pairs in their ability to raise young and differences among nest sites in likelihood of success were, to a large extent, confounded. There was evidence that individual variation in breeding competence was the major contributing factor (Hatch 1985), but whatever the source of variation in success, the problem of computing statistical significance is the same.

There are two ways one might calculate the expected frequency distribution in an analysis of the type presented in Fig. 1. In each of  $i$  years there is a probability of success,  $p_i$ , which is the number of successful pairs in year  $i$  divided by  $n_i$ , the total number of pairs in year  $i$ . The probability of failure in year  $i$  is denoted  $q_i$ , which is equal to  $1 - p_i$ . The weighted average success over all samples could be taken as the estimated mean probability of success  $\bar{p}$  (= total successes/total nests;  $\bar{q} = 1 - \bar{p}$ ).

For a sample of pairs observed in 3 yr, let  $P(0)$  be the probability that a pair will have 0 successes in those 3 yr,  $P(1)$  the probability of 1 success and 2 failures, and so on. The model of weighted averages just described allows probabilities to be calculated

using the binomial expansion and the estimates of  $p$  and  $q$  as follows:

$$P(0) = C(3,3) \cdot \bar{q}^3$$

$$P(1) = C(3,2) \cdot \bar{p}^1 \cdot \bar{q}^2$$

$$P(2) = C(3,1) \cdot \bar{p}^2 \cdot \bar{q}^1$$

$$P(3) = C(3,0) \cdot \bar{p}^3.$$

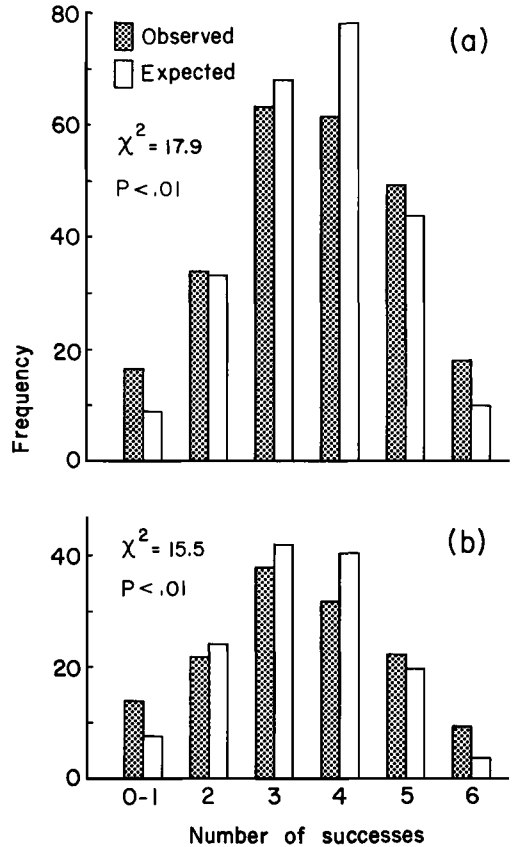


Fig. 1. Observed and expected frequencies of the number of successful breeding attempts by fulmar pairs in 6 yr. Separate analyses for (a) 244 nest sites at which the only criterion for inclusion was an unbroken record of breeding attempts in 6 yr and (b) 137 sites in which one or both birds were individually known. Sites with 0 or 1 success were pooled to avoid small expected frequencies.

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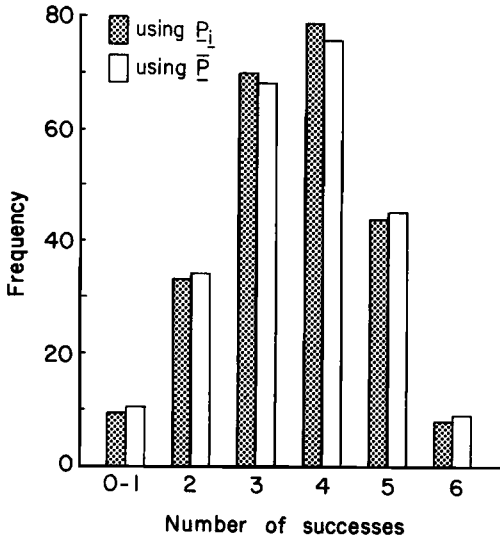


Fig. 2. Comparison of expected frequency distributions (number of successful breeding attempts in 6 yr) calculated by two methods.

$C(k,r)$  is combinatorial notation for the number of ways a pair could have  $r$  successes in  $k$  years. It is evaluated as  $r!/[k!(r-k)!]$ . These coefficients can also be obtained directly from Pascal's triangle (Sokal and Rohlf 1981).

The above formulation is based on the generally unrealistic assumption of no variation among years in the probability of nest success. An alternative, less restrictive model uses the individual  $p_i$  and  $q_i$  from each year in the appropriate combinations, as follows:

$$P(0) = (q_1 \cdot q_2 \cdot q_3)$$

$$P(1) = (p_1 \cdot q_2 \cdot q_3) + (q_1 \cdot p_2 \cdot q_3) + (q_1 \cdot q_2 \cdot p_3)$$

$$P(2) = (p_1 \cdot p_2 \cdot q_3) + (p_1 \cdot q_2 \cdot p_3) + (q_1 \cdot p_2 \cdot p_3)$$

$$P(3) = (p_1 \cdot p_2 \cdot p_3).$$

The two methods yield different expected frequencies. Specifically, Method 1 places more of the distribution in the extreme values and reduces the expected frequencies near the mean (Fig. 2). A more intuitive statement of the same principle is that annual variation in success ( $p_i$ ) tends to push the expected distribution toward the center as the component of variation among pairs becomes relatively smaller. A consequence of using Method 1, therefore, is that the test for individual variation in success is less likely to detect such variation when it exists (greater probability of a Type II error).

In my study of fulmars, the proportion of nests successful differed significantly among years ( $\chi^2 = 58.5$ ,  $P < 0.001$ ,  $df = 5$ ), and the appropriate model therefore allows  $p_i$  to vary. In Fig. 1 I used expected values generated by Method 2, although in this instance the observed and expected frequencies differed significantly by either method. I used 4 df for the Chi-square tests, which is the number of cells in the analysis (6) minus 1 df for the fixed sum (244 or 137) and 1 df for the fitted parameters  $\bar{p}$  or  $p_i$ . Observed and expected frequencies of 0 and 1 success were combined to avoid expected frequencies less than 5 (Sokal and Rohlf 1981).

A complete array of years and nest sites (no missing values) is needed to generate expected frequencies by either method. The resulting tests are conservative, however, because pairs that failed to lay in one or more years, and perhaps also the least desirable sites, are excluded. The likelihood of detecting among-pair variation is also constrained by the mean value of  $p$ : the closer  $\bar{p}$  is to 0.5, the smaller the variance of the binomial expansion and, therefore, the greater the potential for significant variation among pairs. In this respect fulmars were almost ideally suited for detecting individual variation in success ( $\bar{p} = 0.520$ ).

The potential for reaching different conclusions using Method 1 or Method 2 underscores the importance of choosing an appropriate model for annual variation when testing for individual variation. Readers also may wish to consider the use of a randomization test (Bradley 1968, Sokal and Rohlf 1981) as a computationally involved but potentially powerful alternative to either of the tests for individual variation described here.

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