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PROPORTIONAL USE OF SUBSTRATES BY FORAGING BIRDS: MODEL CONSIDERATIONS ON FIRST SIGHTINGS AND SUBSEQUENT OBSERVATIONS

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Abstract. This study presents a mathematical approach to comparing results from initial observations of foraging birds to sequential observations of repeated foraging maneuvers by the same individuals. We consider the case in which the objective is to compare the proportions of use of each of several substrates by a single species. Results suggest that only initial observations should be used, and that subsequent observations do not carry information about the question of proportional use. Generalizations are given for a wide class of probability distributions and also to the problem of comparing proportional use by two bird species.

Key Words: Birds; foraging behavior; initial observations; sequential observations; mathematical models; substrate comparisons.

Avian ecologists use two basic approaches when collecting data on foraging behavior. In the first, the observer records only one event from each bird observed. In the second, the observer records each event in a sequence of events by each bird for as long as it can be observed. Modifications of the second approach have included time-based and location-based constraints on data collection, as well as various criteria for truncating sequences (see Hejl et al., this volume, for examples). Although sequential observations of this sort generate longer sample sizes than if only one event were recorded, the samples are flawed for certain kinds of analyses by a lack of independence. Studies about behavioral transitions of foraging birds must, of course, record sequential events. However, when using foraging observations to characterize the proportional use of different substrates, sites, maneuvers, or other categorical measures, observations should be independent or some adjustment should be made for dependency among observations.

Application of a chi-square goodness-of-fit test to test the null hypothesis of equal proportions among substrates used by birds, for example, assumes independent events, which is a problem when using sequential observations. One way to use sequential observations and to be reasonably assured of independence among units is to treat all foraging attacks of a single bird as a unit, as done by Airola and Barrett (1985). (Note, however, that different record lengths among individual birds may create problems of unequal weighing.) Another approach is to use Markov chain analyses or bootstrapping to assess the effects of dependency among observations on results (e.g., Hejl et al., this volume; Raphael, this volume). Tests of independence can be applied to sequential data but should consider the advice about power given by Swihart and Slade (1986).

Studies that assume independence among sequential observations when data are analyzed also assume that each event in a sequence adds to our knowledge of proportional use of categorical measures. Our primary objective here is to test that assumption mathematically. We describe possible mathematical models, giving specific assumptions, resulting probability distributions, and some of the parameters of those distributions. We further describe likelihood-ratio tests of the hypothesis of equal proportions. Although we use the substrate at which a bird is observed directing an apparent foraging attack as the measure for consideration, results would be the same for whatever categorical measure we might have selected.

MODELS AND ASSUMPTIONS

Let there be k substrates in all. Assume that birds are detected singly and forage from one of the substrates, with the detections following a Poisson process. The number of birds to be observed is not fixed in advance and this is a case of Poisson sampling (Fienberg 1980:15). The intensity of the process (the mean of the Poisson) will be denoted as λ_i in the ith substrate. If the means for all substrates are equal, the proportions are equal. The λ_i values may depend on a variety of factors, including: (1) the quantity of the resources available, (2) the nutritional and energetic values of the different resources, (3) the weather conditions, (4) the apparent safety from predators, and (5) the effects of interference from other individuals of the same or different species.

Once a bird has selected a substrate and made a foraging strike, it is counted for that substrate. The total number of birds for the whole sampling period will be denoted by X_i for the ith substrate. The random variables $X_1, X_2, \ldots, X_k$ are assumed to be independent, making their sum,

TABLE 1. FIELD COUNTS OF INITIAL OBSERVATIONS (X), SUBSEQUENT OBSERVATIONS (Y), AND TOTAL OBSERVATIONS (T) OF BUSHTITS

Substrate	Period 1			Period 2		
	X	Y	T	X	Y	T
1	11	4	15	10	6	16
2	42	15	57	40	39	79
3	8	1	9	31	24	55
4	38	24	62	35	17	52
5	7	11	18	3	0	3
6	5	0	5	10	20	30

TABLE 2. SOME MOMENTS OF THE RANDOM VARIABLES—FIRST SIGHTINGS, SUBSEQUENT OBSERVATIONS, AND TOTAL, PER SUBSTRATE (SUBSCRIPT SUPPRESSED)

Moment	X	Y (conditional)	Y (unconditional)	T
Mean	λ	$x\mu$	$\lambda\mu$	$\lambda(1 + \mu)$
Variance	λ	$x\mu$	$\lambda\mu(1 + \mu)$	$\lambda(1 + 3\mu + \mu^2)$
Correlation $(X, Y) = \mu/[\mu(1 + \mu)]^{0.5}$				

ΣX_i, a Poisson variate with parameter $\Sigma \lambda_i$ (Hogg and Craig 1978:131). After the initial foraging strike, the bird may make additional strikes on the same substrate (perhaps interspersed with other activities) or leave the area. (Other possibilities exist: [1] The bird may disappear from view but still be on the same substrate, and then reappear to be counted again. The frequency of such events cannot be known and is ignored here. [2] The bird may exhibit a transition to a different substrate. We do not address such events here, as transition to a new substrate by the same bird cannot be treated as the beginning of an independent sequence of observations.) Additional strikes by the bird on the substrate are assumed to follow another Poisson process, with intensity μ_i in the ith substrate. Counts of the number of subsequent strikes by different birds are assumed to be independent, thus their sum is Poisson, this one denoted by Y_i in the ith substrate. (Note that we do not adopt a notation for the number of strikes made by a single bird, only for the total made by all birds on that substrate.) The sum that yields Y_i has x_i terms, once $X_i = x_i$ is observed, hence the Y_i rate is $x_i\mu_i$. Thus the Y mean depends on the number of individual birds seen, as does Y itself. To summarize, Y is a Poisson random variable with parameter $x\mu$ conditional on the number of birds seen.

A logical trap exists at this point. The X data and their associated parameters are of primary interest for comparing proportional use of substrates. The Y data (number of subsequent foraging attacks) might be expected to carry additional information about the X parameters, because the Y's depend directly on the X's. Some observers may combine the two counts, letting $X_i + Y_i = T_i$ denote the total in the ith substrate. This is not implausible, because T_i is the total number of foraging strikes seen. On the other hand, T is a total with mixed units, individual birds and foraging strikes, which helps focus attention on the issue addressed in this study.

Additional random variables exist in this setting. The unconditional distribution of Y_i, obtained by averaging over all possible values of X_i, is that of a Neyman Type A random variable and T is known as a Thomas variable. These are two of the well-known "contagious" distributions used for modeling clumped or clustered data (references in Johnson and Kotz 1969:213–215, 236–237; Pielou 1977:118–123).

Foraging data collected by these methods on Bushtits (*Psaltriparus minimus*) (Table 1) can be used to clarify the notation. For example, consider Substrate 5, Period 1. Before observations began, we expected to obtain values for three random variables, X_5, Y_5, and T_5. The observed counts were $x_5 = 7$ birds sighted, $y_5 = 11$ additional strikes made by those 7 birds, and $t_5 = 18$ total foraging strikes seen. The latter number, by itself, conceals important details about the distribution of observations. They might have resulted from single observations of 18 different birds, from 18 observations of a single bird, or from some intermediate combination. Also, 7 is an observed value of a Poisson variable with parameter λ_5 and, conditional on $x_5 = 7$, 11 is an observation on a Poisson variable with parameter $7\mu_5$.

The theoretical or expected performance of these random variables may be summarized by their means, variances, correlations, or other moments. These may be found in Johnson and Kotz (1969:209, 218); some are shown in Table 2. Two columns are needed for Y, as it may be treated conditionally or unconditionally. Note the equality of the mean and variance for X and Y (conditional) but not for Y (unconditional) or for T. The λ factor in some of the Y moments suggests that the subsequent observations can be used in a chi-square test of equal proportions across substrates. The absence of the λ factor in the correlation suggests that the correlative information available does not refer to the λ's.

HYPOTHESES AND TESTS

Two main possibilities are considered in this section. A test may be based on X, Y, or T, or on some combination of these variables. These are addressed as univariate tests or bivariate tests, respectively. In the following paragraphs, log refers to natural logarithm; alternative hypotheses are logical alternatives of the null hypothesis, and approximate chi-square test statistics are denoted by χ^2.

UNIVARIATE TESTS

The null hypothesis is that the rates are equal, $\lambda_1 = \lambda_2 = \ldots = \lambda_k$. Once the total of the X_i is known, the set of substrate counts is a multinomial random variable, with proportion $\lambda_i/\Sigma\,\lambda_j$ for the ith substrate (Johnson and Kotz 1969: 93). Thus a chi-square test of equal proportions or a G-test (e.g., see Sokal and Rohlf 1981:705–708) may be used, provided expected counts are not too small. For the first sighting data from Period 1, $\chi^2 = 76.40$, with 5 degrees of freedom ($P < 0.001$). This test should not be run on the Y (or T) data alone, because both Y and T depend on two parameters per substrate, and we cannot estimate two parameters from a single observation. Formally, this is a problem of identifiability (Ferguson 1967:144). Intuitively, a decision based on the T data, for example, cannot be attributed to differential values of the λ's or differential values of the μ's. While univariate tests must be restricted to the X data, it seems possible that in a bivariate test the Y data can be used to supplement the information from the X's.

BIVARIATE TESTS

We now consider hypotheses based on the joint distribution of X and Y. This discussion is based on the likelihood ratio (e.g., see Morrison 1976: 17–22), a test principle that leads to G-tests or other approximate chi-square tests. The likelihood function is essentially the product of the density function of the random variable, the product extending over the sample. After the data are obtained, the likelihood function depends only on the parameters. Parameters are estimated to maximize this function twice, once under the constraints of the null hypothesis, H, and then with no constraints. If the ratio of the maximum of the likelihood function constrained by H to the unconstrained maximum is denoted by L, then $-2 \log L$ is an approximate chi-square variate.

Consider the composite hypothesis that the substrates are equally used while the within-substrate foraging rates are unconstrained.

$$H_{01}\colon \lambda_1 = \lambda_2 = \ldots = \lambda_k; \quad \mu_1, \mu_2, \ldots, \mu_k \text{ are unspecified.}$$

For this hypothesis

$$\chi^2 = 2\left(\sum x_i \log x_i - \sum x_i \log \bar{x}\right).$$

Note the absence of y's in this expression. The test based on the joint distribution of the X's and Y's uses only the data on the X's. It is the same test found using the distribution of the X's only. (It is not exactly the same as the chi-square test usually applied; it is more similar to the G-test; see Kendall and Stuart 1967:421.)

Consider next a hypothesis that does constrain the μ's:

$$H_{02}\colon \lambda_1 = \lambda_2 = \ldots = \lambda_k, \text{ and } \mu_1 = \mu_2 = \ldots = \mu_k.$$

The approximate chi-square for testing this hypothesis is

$$\chi^2 = 2\left(\sum x_i \log x_i - \sum x_i \log \bar{x}\right) + 2\left[\sum y_i \log(y_i/x_i) - \sum y_i \log\left(\sum y_i / \sum x_i\right)\right].$$

The first line of this expression is the χ^2 of the previous hypothesis, so

$$\chi^2(H_{02}) = \chi^2(H_{01}) + \text{other terms.}$$

The "other terms" in this expression can be shown to be those obtained to test

$$H_{03}\colon \mu_1 = \mu_2 = \ldots = \mu_k,$$

with no constraints on the λ's. Evidently the X's carry information about the Y's, but not conversely. This is consistent with the observation made about the correlation.

We consider only one further hypothesis; this time the two parameter sets are related proportionately.

$$H_{04}\colon \lambda_1 = \lambda_2 = \ldots = \lambda_k; \quad \mu_i = c_i\lambda_i,\ c_i \text{ unspecified}, \quad i = 1, 2, \ldots, k.$$

It can be shown that the approximate chi-square statistic is now exactly that for H_{01}. The likelihood ratio essentially ignores the subsequent observations.

OTHER RESULTS

We have generalized the problem in several ways, but do not include the details here. We have proven that the overall results hold when comparing the substrate distribution for two species and also for comparing two sampling periods. We have also extended the results by replacing the Poisson distribution of X by any single parameter-discrete random variable and Y by any discrete variable whose parameter depends on the observed value of X. The test statistics are different, but conclusions remain unchanged.

QUALITATIVE ASSESSMENT OF ASSUMPTIONS

POISSON ASSUMPTIONS

Consider first the Poisson assumptions. From the previous paragraph, it is clear that the results are virtually independent of these assumptions. Almost any pair of discrete random variables will lead to the same conclusions.

INDEPENDENCE ASSUMPTIONS

These are critical, and probably least amenable to verification. The first is the requirement that observations be of birds foraging singly. Our modeling did not address the problem of species that forage in flocks, although results may still apply if observation is limited to a lead bird. Independence between substrates is easier to accept, because data from additional substrates must come from sightings of different individual birds. Finally, we assumed that birds within a substrate act independently. This may require that we have only one bird in sight at a time.

THE CASE WHEN X IS UNKNOWN

We may wish to assume that X is unknown (per substrate), or that we are unsure of how many distinct birds have contributed to our counts. Then we treat Y in its unconditional distribution and Y must be taken to carry all information about both the numbers of birds and extent of their foraging. In the k substrate problem, we have $2k$ parameters, but only k data values. Additional data must be obtained to carry out any useful test on the substrate proportions. Additional data can perhaps be collected by another observer in a different area, or by means of shorter, repeated, observation periods.

Another method for handling this case would be to simply record all foraging strikes, making no attempt to separate sightings from subsequent observations. These data, from Thomas distributions, again depend on two parameters, and some device must be employed to replicate the sampling.

ILLUSTRATIONS WITH FIELD DATA

The following analysis is based on data in Hejl et al. (this volume), recorded at the San Joaquin Experimental Range, in Madera County, California, during March through May 1980. Field observations were made on a 19.8 ha (300 × 660 m) plot, gridded into quadrats 30 m on each side. To gather foraging information, observers walked back and forth along alternate gridded lines on the study area. The lines walked and the direction of travel were selected to ensure even coverage of all segments of the grid during daylight hours. When a bird was detected, one that had not obviously been disturbed, it was selected for observation. To reduce dependence of the data between individual birds, information was recorded only for the first bird detected in a flock or pair of birds and only if that bird species had not been seen in the last 30 m or for the last 10 min. The activity of the bird was noted at the count of "5". If it was foraging, then sequential observations were recorded for each apparently successful foraging strike that was noted up to 11 observations. Counts were made for several categorical variables including foraging substrate. Foraging substrate as used in Table 1 included plant species, the ground, and the air. In the modeling discussion, "substrate" could represent either foraging substrate or any other categorical variable.

An inconsistency between our assumptions and the study as done was the fact that sequences were truncated at 11 observations, but no adjustment was made for this. Truncation was rarely needed, however, because birds could seldom be followed for that many consecutive foraging strikes.

The data on foraging Bushtits (Table 1) can be used to test the Poisson assumptions for X_i and Y_i, provided we assume that the means did not change between periods. Poisson variables have a variance-to-mean ratio of 1.0. The average variance-to-mean ratio for X between periods across substrates was 3.40, but dropped to 1.36 on deletion of Substrate 3. Using the results of Ratcliffe (1964), these gave (approximate) chi-square values of 20.38 and 6.82, with 6 and 5 degrees of freedom, respectively. The apparent shift in mean for Substrate 3 caused the large value; the remaining data did not contradict the Poisson assumption. For Y the mean ratio was 10.73, with a chi-square of 64.42, far too large to confirm Poisson variation with constant means.

The field objective of substrate comparisons should be addressed by only the data on first sightings. The chi-square values were 76.40 and 56.81 for the separate periods, indicating that some substrates were used more frequently than others. When the same computations were done on total foraging strikes, the values were 114.01 and 100.33, biased upwards in this case by likely differences in the Y rates. By studying the conditional distributions of the subsequent observations, one could test the equality of the within-substrate foraging rates, but this lies outside the scope of this paper. Finally, consider the T data again. Substrate 2, across periods, furnished a good example of the risks inherent in this problem. Virtually the same numbers of birds gave quite different values of t.

CONCLUSIONS

The objective at the outset was to consider the information furnished about one process by data from another. The data on the discovery process seemed straightforward, but the status of the data on subsequent observations was less clear. The two extremes of data analysis are to use only numbers of distinct birds or to use counts of all observed foraging acts. A reasonable compromise was to model the two main aspects of the problem as related processes.

Of the many possible ways to model the joint distribution of initial detections and subsequent events, we have dealt with only one. We focused on the ultimate totals of birds and subsequent events per substrate, since that seemed the natural way to summarize the data. As a result, our modeling of the actions of a single bird may seem artificial; the reproductive property of Poisson variables (totals of Poissons are Poissons) had some influence on our choice of model since it makes the mathematics tractable. However, reproductivity is not really necessary. The total of subsequent strikes need not follow the same distributional form as the variables in the sum.

We have also limited the scope of this discussion by insisting that the question is to discover what subsequent observations tell about proportional use of substrates. The broader question of what can be done with those observations has not been addressed; questions that are within-substrate in content seem more approachable by these data. Hejl et al. (this volume) apply and discuss some methods appropriate for analysis of the subsequent observations.

The use of subsequent observations in the present problem is clearly a case of pseudoreplication (Hurlbert 1984). It is similar to the use of multiple readings per experimental unit in a treatment design. One can know more about the experimental unit by subsampling, but gains no degrees of freedom to compare the treatments. In the same way, subsequent observations tell more about the individual birds that forage on a substrate, but give no advice about the comparison of proportions.

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