

FURTHER COMPARISON OF SOME STATISTICAL TECHNIQUES FOR ANALYSIS OF RESOURCE SELECTION

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Abstract: Many biologists and statisticians still have questions about analysis of resource selection data. Consequently, we compared 4 statistical methods for analysis of habitat selection by considering hypotheses, assumptions, and methods of calculation. We used detailed calculations on gray partridge (*Perdix perdix*) habitat-use data to note factors that may cause the methods to give disparate results. The factors we identified were the emphasis or relative weight placed on within- versus between-animal observations, independence and variability assumptions, and the relationship between the statistical hypothesis and the biological hypothesis. These factors serve as criteria for choosing a method of statistical analysis for data on resource selection.

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This paper considers questions raised by an earlier paper (Allredge and Ratti 1986), which compared 4 statistical methods for analysis of resource selection. The exceptional number of reprint requests for that paper indicated great interest in this topic. Subsequent discussions with wildlife biologists and statisticians disclosed that many questions and some confusion remained about analysis of resource selection data. This paper presents further comparisons of the hypotheses, assumptions, and methods of calculation inherent in the Neu et al. (1974) method, the Johnson (1980) test, the Friedman (Friedman 1937, Iman and Davenport 1980) test, and the Quade (1979) test.

Results of >50,000 computer simulations of field data indicated no clear choice of method that was best in all cases (Allredge and Ratti 1986). The conflicting results obtained for different numbers of habitats were due primarily to the values chosen for simulated percent selected and percent availability, and the simulation method. The simulations illustrated the advantage of increasing the number of animals observed, the number of observations per animal, and limiting the number of habitat types; but even these intuitively obvious results were somewhat obscured because of differences in simulated values as the number of habitats changed.

A clearer choice among the statistical techniques emerges when we examine the methods of calculation for each procedure. The way data are treated determines the hypotheses being tested and which method would be best for a particular data set.

The methods discussed here are a small subset

of those useful for exploring resource selection. Other methods for analysis of habitat use have been reported by Kincaid and Bryant (1983), Suring and Vohs (1979), and Talent et al. (1982). The Johnson (1980) and Neu (1974) methods are commonly reported in the literature. The Friedman (1937) test is a well-known and often used nonparametric method. The Quade (1979) test is a modification of the Friedman test which allows assigning greater weight to observations from some animals. All 4 methods consider analysis of data where resources are considered as categorical rather than continuous variables. All methods compare habitat use to corresponding habitat availability. We impose the conditions that availability is measured without error to be able to compare the Neu method, which requires this assumption, with the other methods, even though they do not require this restriction. The impact of this restriction is discussed by Thomas and Taylor (1990). We assume that the sample of observations on individual animals and the sample of animals represent the population of interest. For statistical inferences about a population to be strictly valid, all samples must be random. It is doubtful that random sampling can be achieved in practice in most studies with radio-tagged individuals. However, we must strive to conduct studies that do not violate basic assumptions. When such a study is not possible, results must be interpreted with caution, and the assumption violations should be reported.

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COMPARISON OF METHODS

The analysis described by Neu et al. (1974) (Neu method) compares the observed occurrence to the expected occurrence for each habitat category. The hypothesis tested is that each habitat category is used in exact proportion to its occurrence within the study area. The alternative hypothesis is that at least 1 habitat is used disproportionately to its availability. The data that are analyzed consist of counts or number of observations in each habitat category. Thus, 20 observations on 1 animal in a habitat are treated the same as 1 observation on 20 different animals in the same habitat (i.e., the Neu method weights each observation equally). A critical assumption is that all observations are independent. From a practical viewpoint, observations on the same animal, even when separated in time, violate this assumption. Intuitively, this lack of independence is predictable because if an animal is observed in a habitat at 1 time, the probability of observing that animal in the same habitat at some future time is increased. Observations on different animals will not be independent if the animals tend to aggregate or avoid other individuals.

The Neu method is easy to use since the calculations are a straightforward application of the Chi-square goodness-of-fit test. The observed counts in each habitat type are compared to the counts expected if each habitat type is used in proportion to its availability. When a significant difference in use versus availability is detected by the test, a Bonferroni Z-statistic (Miller 1981:219) is used to determine the habitat types used more or less frequently than expected. The Bonferroni statistic is based on a normal approximation confidence interval for a variable that follows a binomial distribution. The level of significance is altered to reflect the number of confidence intervals constructed (i.e., habitat types). The results indicate whether each habitat is used significantly more or less than expected. The ease of calculation and interpretation, as well as the fact that identification of individual animals is not necessary, makes this method a popular choice for analysis of resource selection.

Johnson (1980) (Johnson method) compares ranks of habitat use with ranks of habitat avail-

ability for each animal. Using ranks causes little loss of information in general, and methods based on ranks are preferred when use and availability data are poorly estimated. Also, the availability of many habitats (or food items) may be questionable. Johnson's method is relatively insensitive to decisions made about the availability of such resources to the animal. The data consist of some measure of use and some measure of availability of each habitat for each animal. The data for each animal are converted to ranks. We chose to assign the most used (or available) habitat a rank of 1 and the least used (or available) a rank of k , where k is the number of habitats. The hypothesis tested is that the rank ordering of habitat use is the same as the rank ordering of habitat availability when averaged over all animals. Note that the use and availability proportions could be different across the habitats while still having the same rank ordering. For example, if the use percent equals 5, 10, 35, 50, and the availability percent equals 15, 20, 25, 40, then use and availability have the same rank ordering even though the use in each habitat does not equal the corresponding availability.

The observations on each animal are compiled and used to determine a vector of ranks for that animal. Each animal is considered 1 observational unit so all animals have equal importance in the analysis, but individual observations on different animals receive unequal weights (i.e., if 1 animal is observed 100 times and another is observed 20 times, they are given equal importance in this method).

The Johnson method does not require that observations on an animal be independent of other observations on that same animal. However, we must assume that the observations on 1 animal do not influence results from other animals. Therefore, animals that exhibit attraction or avoidance behavior could violate this assumption. Johnson's method assumes the number of animals observed is large enough so that the average of differences in ranks across all animals has a multivariate normal distribution. In any given application, it is not obvious whether these assumptions would be satisfied. In studies consisting of only a few animals, the distributional assumptions are especially likely to be compromised. These assumptions can be eliminated by using permutation procedures on this test statistic (Mielke and Iyer 1982, Mielke 1986).

The Johnson method is best suited to computer analysis. A FORTRAN program (Johnson

1980) and a micro-computer program are now available (D. H. Johnson, North Prairie Res. Cent., pers. commun.). The test consists of ranking the selection array and availability array for each animal, then computing the difference in these vectors of ranks. The vectors of differences in the ranks for the animals are then used to test the hypothesis that a multivariate normal vector of means is equal to a vector of zeroes by using a Hotelling T^2 statistic (Morrison 1976: 128). The Johnson method is an application of a multivariate paired t -test where the variables are habitat types. If a significant test statistic is obtained, Johnson suggests using the Waller-Duncan multiple comparison procedure (Waller and Duncan 1969) to determine differentially selected habitats. This procedure performed well in comparative studies (Carmer and Swanson 1973). This application of a multiple comparison method is analogous to comparing treatment levels for factors in a repeated-measures experiment (Morrison 1976:147-159). The Johnson method results in an ordering of the habitats that supports relative statements about selection of 1 habitat compared to others. A problem occurs when differences between usage and availability ranks have the same value for habitats with differing relative selection. For example, suppose usage and availability percentages are 5, 15, 40, 40; and 45, 15, 20, 20, respectively (Allredge and Ratti 1986, Table 3). The ranks for usage and availability are 1, 2, 3.5, 3.5; and 4, 1, 2.5, 2.5, respectively. Differences in ranks are -3, 1, 1, 1 for the 4 habitats. This seems to indicate that the relative selection for the last 3 habitats is equal. However, habitat 2 is used in the same proportion as availability, while use of habitats 3 and 4 is twice the availability. This brief example shows why the percentage of multiple comparison Type II errors is so large for Johnson's method under some conditions (Allredge and Ratti 1986).

The Friedman (1937) test (Friedman method) is an analysis of variance based on ranks for a randomized complete block design. Allredge and Ratti (1986) applied the test procedure to the difference between percent used and percent available for each habitat by each animal. The Friedman method is computed by ranking the differences in use and availability for each animal. The vector of ranks for an animal is a "block" of observations; habitats represent "treatments." The Friedman method combines data on individual observations of an animal to

compute use percentages. The array of differences between use and availability percentages for each animal is the input to the test procedure. Each animal is given the same weight or importance. We must assume that locations of 1 study animal are not influenced by locations of other study animals (i.e., habitat use among animals is independent). If a significant test statistic is obtained, we choose to use Fisher's least significant difference (LSD) procedure based on the difference between selection and availability. Conclusions can be reached about the relative selection of each habitat as in Johnson's method. In contrast to Johnson's method, which is based on differences in ranks, the Friedman method is based on ranks of difference in use and availability.

The hypothesis tested by the Friedman method is that ranks of the differences in use and availability are the same for all habitats (i.e., the null hypothesis is that each rank ordering of habitats for each animal is equally likely [Conover 1980]). This is very important, because if there is variation in the difference between use and availability among habitats, not all rank ordering will be equally likely. For example, assume that the average use percentages for 4 habitats are 5, 15, 35, 45, and availability percentages are also 5, 15, 35, 45. Also assume $\pm 5\%$ variation for use of the last habitat and $\pm 5\%$ variation for the other 3 habitats. Because of larger variability, the difference in use and availability for the last habitat is more likely to be the largest or the smallest difference and, thus, is more likely to be ranked first or last. Therefore, even with equal use and availability (average), not all rank orderings of the difference are equally likely. In an application with a finite number of animals, the null hypothesis more likely will be rejected.

The Quade (1979) method (Quade method), as described by Conover (1980), is a specific example of a weighted-ranking test statistic for comparing 2 or more treatments. The assumptions and form of the data are the same as for Friedman's method. Allredge and Ratti (1986) used an LSD-type multiple comparison to determine which habitats differ significantly in terms of use versus availability. The difference between Friedman's and Quade's methods is in weighting the blocks or animals. Friedman's method assigns equal weight to all animals, whereas Quade's method assigns more weight to those animals with greater observed vari-

Table 1. Habitat use by individual radio-marked gray partridge and proportion of area of 5 habitat types, South Dakota, summer, 1979 (Smith et al. 1982).

| Bird no. | No. of telemetry locations | | | | | Total |
|------------------------|----------------------------|---------|-------------|-------|-------|-------|
| | Row crop | Pasture | Small grain | Hay | Idle | |
| 1 | 8 | 20 | 0 | 0 | 2 | 30 |
| 2 | 21 | 0 | 25 | 0 | 1 | 47 |
| 3 | 11 | 0 | 17 | 0 | 2 | 30 |
| 4 | 0 | 0 | 4 | 0 | 2 | 6 |
| 5 | 0 | 9 | 20 | 0 | 0 | 29 |
| 6 | 0 | 2 | 22 | 0 | 0 | 24 |
| 7 | 7 | 0 | 0 | 6 | 1 | 14 |
| 8 | 26 | 8 | 10 | 2 | 0 | 46 |
| 9 | 0 | 0 | 21 | 4 | 3 | 28 |
| 10 | 1 | 0 | 44 | 0 | 5 | 50 |
| Total | 74 | 39 | 163 | 12 | 16 | 304 |
| Percent area available | 0.417 | 0.135 | 0.282 | 0.102 | 0.063 | |

ability of difference between percent use and percent availability among habitats, as indicated by the sample range. It is assumed that all animals have equal underlying variability, so that those with greater observed variability are providing a stronger indication for selection of habitat. Thus, data showing a greater disparity between percent use and percent availability are assumed to better reflect the choice of habitats. If the data for animals that show greater observed variability actually do indicate greater underlying variability for the animal, the Quade method will not perform well (Quade 1979).

RESULTS

Example Calculations

Data from 10 radio-marked gray partridge (Smith et al. 1982) are used to demonstrate calculations. However, we do not recommend using all of these methods for any given set. The data are from only 1 time period (Table 1) in a study conducted over 6 time periods.

Neu Method.—There were 304 radio-telemetry observations of gray partridge. The expected number of observations in the 5 habitats under the null hypothesis of no habitat selection are: row crop = 126.768, pasture = 41.040, small grain = 85.728, hay = 31.008, idle = 19.152, where $126.768 = 304 \times 0.417$ (Table 1). The Chi-square goodness-of-fit calculations are:

$$\begin{aligned} \chi^2 &= [74 - 126.768]^2 / 126.768 \\ &+ [(39 - 41.040)^2 / 41.040] \\ &+ \dots + [(16 - 19.152)^2 / 19.152] \\ &= 103.74 \end{aligned}$$

Comparing this computed Chi-square value to a tabled Chi-square with 4 degrees of freedom indicates that the null hypothesis should be rejected ($P < 0.001$). The Bonferroni Z-statistic approach may be used by the general formula:

$$p \pm Z_{1-\alpha/2k} \sqrt{p(1-p)/n}$$

where p is proportion of use in a habitat, n is the total number of observations, and k is the number of habitats. The analysis for the row crop, for example, is computed as follows for $\alpha = 0.05$: $p = 74/304 = 0.243$; lower confidence limit =

$$0.243 - (2.58)\sqrt{(0.243)(1-0.243)/304}$$

$$= 0.243 - 0.064 = 0.179; \text{ upper confidence limit} \\ = 0.243 + (2.58)\sqrt{(0.243)(1-0.243)/304}$$

$= 0.243 + 0.064 = 0.307$. The proportion of the area in row crop habitat is 0.417, which is not contained in the confidence interval. The conclusion resulting from the Neu method of analysis is that the row crop was used less than expected. Similar confidence intervals may be constructed for other habitat types.

Johnson.—Recall that for the Johnson method, the ranks of habitat use and habitat availability for each animal must be determined (Table 2). For this example, it is assumed that availability is the same for all animals, although the assumption is not necessary for use of this method. The difference between rank of habitat use for an animal and the rank of availability is computed (i.e., the proportion of an area in this example). These differences are shown in

Table 2. Rank of habitat use (difference between use and availability ranks) by individual radio-marked gray partridge in 5 habitat types, South Dakota, summer, 1979 (Smith et al. 1982).

| Bird no. | Row crop | Pasture | Small grain | Hay | Idle |
|----------|-----------|------------|-------------|------------|----------|
| 1 | 2 (1.0) | 1 (-2.0) | 4.5 (2.5) | 4.5 (0.5) | 3 (-2.0) |
| 2 | 2 (1.0) | 4.5 (1.5) | 1 (-1.0) | 4.5 (0.5) | 3 (-2.0) |
| 3 | 2 (1.0) | 4.5 (1.5) | 1 (-1.0) | 4.5 (0.5) | 3 (-2.0) |
| 4 | 4 (3.0) | 4 (1.0) | 1 (-1.0) | 4 (0.0) | 2 (-3.0) |
| 5 | 4 (3.0) | 2 (-1.0) | 1 (-1.0) | 4 (0.0) | 4 (-1.0) |
| 6 | 4 (3.0) | 2 (-1.0) | 1 (-1.0) | 4 (0.0) | 4 (-1.0) |
| 7 | 1 (0.0) | 4.5 (1.5) | 4.5 (2.5) | 2 (-2.0) | 3 (-2.0) |
| 8 | 1 (0.0) | 3 (0.0) | 2 (0.0) | 4 (0.0) | 5 (0.0) |
| 9 | 4.5 (3.5) | 4.5 (1.5) | 1 (-1.0) | 2 (-2.0) | 3 (-2.0) |
| 10 | 3 (2.0) | 4.5 (1.5) | 1 (-1.0) | 4.5 (0.5) | 2 (-3.0) |
| Rank* | 1 | 3 | 2 | 4 | 5 |

* Rank of percent of area (availability rank).

parentheses in Table 2. The average of these differences across all animals gives an indication of how much deviation there is between use and availability. If the 5 averages, 1 for each habitat type, are all close to zero, there is little evidence of habitat selection. In this example the averages of the difference in the ranks for the 5 habitat types are: row crop = 1.75, pasture = 0.45, small grain = -0.2, hay = -0.2, idle = -1.8. The calculations involve estimating the $k \times k$ variance-covariance matrix for all habitats. The covariance between habitats i and j is estimated by:

$$V_{ij} = (b-1)^{-1} \sum_{m=1}^b (t_{im} - \bar{t}_i)(t_{jm} - \bar{t}_j),$$

where b is the number of animals, t_{im} is the difference in the use and availability ranks for the m^{th} animal in the i^{th} habitat, and \bar{t}_i is the average of the difference in the ranks for the i^{th} habitat. For example, the estimated covariance for the row crop and pasture habitats is:

$$\begin{aligned} V_{12} &= (1/9)[(1.0 - 1.75)(-2.0 - 0.45) \\ &+ (1.0 - 1.75)(1.5 - 0.45) + \dots + \\ &+ (2.0 - 1.75)(1.5 - 0.45)] \\ &= -0.18. \end{aligned}$$

The variance-covariance matrix for all habitats is singular, so 1 habitat is deleted from the analysis. The same answer is obtained regardless of which component is deleted. Let U_{ij} represent the designated element of the inverse matrix of the $(k-1) \times (k-1)$ variance-covariance matrix. The F -statistic is calculated as follows:

$$\begin{aligned} F &= \frac{b(b-k+1)}{(b-1)(k-1)} \sum_{i=1}^{k-1} \sum_{j=1}^{k-1} \bar{t}_i \bar{t}_j U_{ij} \\ &= \frac{10(10-5+1)}{(10-1)(5-1)} (1.75)(1.75)(1.73) \\ &+ (1.75)(0.45)(0.95) + \dots \\ &+ (-0.2)(-0.2)(2.32) \\ &= 8.42 \end{aligned}$$

Table 3. Percent use by individual radio-marked gray partridge and proportion of area in 5 habitat types, South Dakota, summer, 1979 (Smith et al. 1982).

| Bird no. | Row crop | Pasture | Small grain | Hay | Idle | Total |
|-----------------|----------|---------|-------------|-------|-------|-------|
| 1 | 0.267 | 0.667 | 0.000 | 0.000 | 0.067 | 30 |
| 2 | 0.447 | 0.000 | 0.532 | 0.000 | 0.021 | 47 |
| 3 | 0.367 | 0.000 | 0.567 | 0.000 | 0.067 | 30 |
| 4 | 0.000 | 0.000 | 0.667 | 0.000 | 0.333 | 6 |
| 5 | 0.000 | 0.310 | 0.690 | 0.000 | 0.000 | 29 |
| 6 | 0.000 | 0.083 | 0.917 | 0.000 | 0.000 | 24 |
| 7 | 0.500 | 0.000 | 0.000 | 0.429 | 0.071 | 14 |
| 8 | 0.565 | 0.174 | 0.217 | 0.044 | 0.000 | 46 |
| 9 | 0.000 | 0.000 | 0.750 | 0.143 | 0.107 | 28 |
| 10 | 0.020 | 0.000 | 0.880 | 0.000 | 0.100 | 50 |
| Percent of area | 0.417 | 0.135 | 0.282 | 0.102 | 0.063 | |

Under the null hypothesis that all habitats are used with equal intensity, this test statistic has an F -distribution with $k - 1 = 4$ and $b - k + 1 = 6$ degrees of freedom. As reported by Allredge and Ratti (1986), there is a significant F -value ($P = 0.012$) indicating that these sample data are sufficiently different from a vector of zeroes to conclude that not all habitats are used with equal intensity. The Waller-Duncan multiple comparison procedure provides statistical evidence that the row crop is the least selected and idle is the most selected habitat.

Friedman and Quade.—The first step in preparing observational data for both Friedman and Quade methods is to compute the percent use for each habitat by each animal and the percent of each habitat available to each animal (Table 3). In this example we have assumed that habitat availability values are the same for all animals. Then, compute the differences between percent of habitat use and percent of availability for each animal. The final step is to rank these differences within each animal (Table 4).

The computations for Friedman's test are straightforward. Using Conover's (1980) notation we calculate:

$$A_2 = bk(k + 1)(2k + 1)/6 \\ = (10)(5)(5 + 1)(10 + 1)/6 \\ = 550$$

where b is the number of animals observed, k is the number of habitats, and 6 is a constant. We then calculate the term:

$$B_2 = \sum_{j=1}^k R_j^2 / b \\ = [(23)^2 + (27)^2 + \dots + (34)^2] / 10 \\ = 464.2$$

where R_j is the sum of the ranks for the j th habitat. The test statistic is:

$$T_2 = (b - 1)[B_2 - bk(k + 1)^2/4] / (A_2 - B_2) \\ = 1.49$$

where 4 is a constant. If T_2 exceeds the $1 - \alpha$ quantile of the F -distribution, with $k - 1 = 4$ and $(b - 1)(k - 1) = 36$ degrees of freedom, the null hypothesis is rejected. In this example we fail to reject ($P = 0.226$) the null hypothesis and conclude that there is not enough evidence to claim selection of any habitat. This conclusion is supported by examining ranks of differences

between percent habitat use and percent available (Table 4). There is little consistency among the birds in the pattern of habitat-selection values observed.

The Quade method involves making a few more calculations than Friedman's method. Ranks are assigned to the animals according to size of the sample range within observations for each animal (Table 5). Because there are no ties, we calculate the simplified version of the test statistic (Conover 1980):

$$A_1 = b(b + 1)(2b + 1)k(k + 1)(k - 1)/72 \\ = 10(10 + 1)(20 + 1)(5 + 1)(5 - 1)/72 \\ = 3,850$$

where 72 is a constant. Next, calculate the term:

$$B_1 = \sum_{j=1}^k S_j^2 / b \\ = [(-76)^2 + (-6)^2 + \dots + (30)^2] / 10 \\ = 1,126.4$$

The test statistic is:

$$T_1 = [(b - 1)B_1 / (A_1 - B_1)] \\ = [(10 - 1)1,126.4] / (3,850 - 1,126.4) \\ = 3.72$$

We reject the null hypothesis if T_1 exceeds the same critical value as was used for the Friedman test. In this example, we reject the null hypothesis ($P = 0.012$) and conclude that gray partridge do exhibit selection for some habitat types. The LSD multiple comparison procedure used by Allredge and Ratti (1986) indicated that small grain was selected relative to row crops and hay, while idle habitat was selected over row crops.

DISCUSSION

Statistical techniques for the analysis of resource selection may give conflicting results. We have identified some reasons why the 4 methods considered (Allredge and Ratti 1986) could give different results and demonstrated through calculations of data from a field study the potential magnitude of differences. The calculations in Tables 2-5 and the formulas show what statistical hypotheses are being tested by the methods.

Three main factors can be identified as causing disparate results when methods of analysis of resource selection data are applied. The factors are the method of weighting the observa-

Table 4. Difference (ranks) between percent habitat used by, and percent available to, individual radio-marked gray partridge in 5 habitat types, South Dakota, summer, 1979 (Smith et al. 1982).

| Bird no. | Row crop | Pasture | Small grain | Hay | Idle |
|--------------|------------|------------|-------------|------------|------------|
| 1 | -0.150 (2) | 0.532 (5) | -0.282 (1) | -0.102 (3) | 0.004 (4) |
| 2 | 0.030 (4) | -0.135 (1) | 0.250 (5) | -0.102 (2) | -0.042 (3) |
| 3 | -0.050 (3) | -0.135 (1) | 0.285 (5) | -0.102 (2) | 0.004 (4) |
| 4 | -0.417 (1) | -0.135 (2) | 0.385 (5) | -0.102 (3) | 0.270 (4) |
| 5 | -0.417 (1) | 0.175 (4) | 0.408 (5) | -0.102 (2) | -0.063 (3) |
| 6 | -0.417 (1) | -0.052 (4) | 0.635 (5) | -0.102 (2) | -0.063 (3) |
| 7 | 0.083 (4) | -0.135 (2) | -0.282 (1) | 0.327 (5) | 0.008 (3) |
| 8 | 0.148 (5) | 0.039 (4) | -0.065 (1) | -0.058 (3) | -0.063 (2) |
| 9 | -0.417 (1) | -0.135 (2) | 0.468 (5) | 0.041 (3) | 0.044 (4) |
| 10 | -0.397 (1) | -0.135 (2) | 0.598 (5) | -0.102 (3) | 0.037 (4) |
| Sum of ranks | 23 | 27 | 38 | 28 | 34 |

tions, assumptions required for valid application of the test, and the hypothesis to be tested. By examining these factors we can gain insight into which of the methods is appropriate for a given situation.

Method of Weighting

Each observation on each animal is given equal weight in the Neu method, although the number of observations for an individual may not be known for some applications of this method. Distribution of use is treated as a function of the number of observations and variation within an individual animal. In our gray partridge example, bird number 4 contributed only 6 observations to the study while bird number 10 contributed 50 observations. The question to ask is, should bird number 10 be given > 8 times as much importance in the study? We think not. We fear that such unequal weighting could amplify aberrant behavior by an individual. If insufficient observations exist to characterize behavior of some animals, we suggest analyzing the data with and without animals having limited observations. When we deleted bird 4, our conclusions changed for Johnson's and Quade's methods but not for Friedman's and Neu's methods. If sufficient observations are available for all animals, equal weighting seems appropriate.

Johnson's and Friedman's methods give equal importance to all animals regardless of how many observations there are on each. These methods place less emphasis on the number of observations and variation by an individual animal than the Neu method. Obviously, if the number of observations on each animal is nearly the same, the method of weighting is not critical. Our

application of Quade's method weights the animals unequally. The weights depend on the amount of variation in the difference between percent used and percent available. This method gives more weight to an animal showing a larger range of differences between availability and use percentages than to an animal which appears to use habitat in proportion to its availability. This unequal weighting would be appropriate if animals showing stronger preferences are to be given greater weight. For example, bird number 6 is given more weight than bird number 8, thus contributing to the conclusions that small grain habitat is selected more than row crop habitat (Table 5). In our gray partridge example, we do not believe that some birds should be given greater importance in inferring habitat selection, but prefer a method that best describes behavior by the majority of animals observed.

Assumptions

The main differences in assumptions concern independence and variability. All methods assume that observations for 1 animal are independent of observations for other animals. This assumption would be violated if animals exhibited territorial behavior for a selected habitat with limited availability, or if animals exhibited grouping behavior. For our partridge example, radio-tagged birds were considered 1 observation, regardless of the group size (covey) attended by that bird. If more than 1 radio-tagged bird was in a covey, data were recorded on only 1 randomly selected, marked bird. To assess potential impacts of territoriality on this assumption, specific data on this behavior are needed and must be assessed for each study.

Table 5. Weighted ranks of the difference between percent habitat used by, and percent available to, individual radio-marked gray partridge in 5 habitat types, South Dakota, summer, 1979 (Smith et al. 1982).

| Bird no. | Sample range | Rank Q_i | Row* crop | Pasture | Small grain | Hay | Idle |
|-----------------------|--------------|------------|-----------|---------|-------------|-----|------|
| 1 | 0.814 | 6 | -6 | 12 | -12 | 0 | 6 |
| 2 | 0.385 | 2 | 2 | -4 | 4 | -2 | 0 |
| 3 | 0.420 | 3 | 0 | -6 | 6 | -3 | 3 |
| 4 | 0.802 | 5 | -10 | -5 | 10 | 0 | 5 |
| 5 | 0.825 | 7 | -14 | 7 | 14 | -7 | 0 |
| 6 | 1.052 | 10 | -20 | 10 | 20 | -10 | 0 |
| 7 | 0.609 | 4 | 4 | -4 | -8 | 8 | 0 |
| 8 | 0.213 | 1 | 2 | 1 | -2 | 0 | -1 |
| 9 | 0.885 | 8 | -16 | -8 | 16 | 0 | 8 |
| 10 | 0.995 | 9 | -18 | -9 | 18 | 0 | 9 |
| Sum of weighted ranks | | | -76 | -6 | 66 | -14 | 30 |

* $S_{ij} = Q_i R(X_{ij}) - (k + 1)/2$, where $R(X_{ij})$ is the rank within bird i of the difference between habitat j use and percent available; S_{ij} is the weighted rank, Q_i is the rank of sample range, and k is the number of habitats.

The Neu method assumes that each observation is independent of every other observation. It seems likely that this assumption would be violated for all studies involving radio-tagged animals. Dependency among observations may be reduced by obtaining observations in all time periods in the daily cycle and over as long a period (i.e., days, months) as possible. In the partridge study, observation periods were systematically rotated among 4-hour diurnal time periods each day. As with most studies, the overall duration of observations on each marked bird was dictated by life of the radio or the bird. We recognize that most studies, for logistic and financial reasons, violate this assumption. This violation does not limit the value of the data, but does limit conclusions drawn from such data sets. If a study has dependent data from relatively few animals, *conclusions should be restricted to the study animals per se*, and we urge caution extrapolating to populations or species.

The Friedman and Quade methods assume that variation in the difference between use and availability should be the same for all habitats, otherwise, too many significant differences will be indicated. We are not aware of effective statistical tests of this assumption, thus, we recommend considering the nature of the data to decide if unequal variability is likely. For example, unequal variability would result from differences in ability to precisely determine use or availability for all habitats. The Johnson method will take unequal variation into account in the variance-covariance matrix used to compute the test statistic. The Neu method allows

estimation of variances for each habitat so unequal variation presents no problem.

Hypotheses

The hypotheses tested by the methods are clearly different. The Neu method tests whether the proportion used is equal to the proportion available. The Johnson method tests if the rank ordering of use and availability are the same. If the proportion used equals the proportion available for all habitats, the rank ordering of use and availability will be the same. However, the converse is not true, as noted in an earlier section. The Friedman and Quade methods test if each rank ordering of the difference in use and availability are equally likely. That is, do the animals consistently use some habitats more (or less) than the availability of that habitat. If so, that habitat will consistently be ranked high (or low) and some rank ordering of the habitats will occur more often than expected by chance. It may be argued that hypotheses for Friedman and Quade methods relate most directly to the modal concept embodied in the question, "What behavior describes most of the animals?"

Recommendation

The choice of method depends ultimately on which statistical hypothesis is most closely related to the biological question of interest, on how observations and individuals are weighted, and on which assumptions are most likely to be satisfied. For the gray partridge data presented here, we would recommend Friedman's method. This method tests a hypothesis related to the behavior of most birds, gives equal weight to

each bird, and does not require that repeated observations on the same bird be independent. The choice of analysis method is clearly not an entirely objective process, and alternate methods may be justified depending on the statistical and biological orientation of the researcher.

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