An Evaluation of an Avian Diversity Model

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AN EVALUATION OF AN AVIAN DIVERSITY MODEL

By

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Abstract: Diversity exists at all temporal and spatial scales but has been studied largely at the community level because of the limited availability of regional or nation-wide data. In the U.S. both the Breeding Bird Survey (BBS) and the Breeding Bird Census (BBC) provide large-scale observations of avian populations over periods of decades and offer a potential source of information. A large-scale model of avian diversity based on the BBS has been developed by O’Connor et. al. (1996). The BBC serves as a source for independently obtained species richness estimates used to evaluate the ability of the model to generate corresponding predictions. Overall, the species richness estimates obtained from the BBC data were consistently less than the model predictions. Differences between the BBC and BBS sampling methods offer an explanation for this bias. The BBC data set suffered many limitations; however, when species richness estimates were obtained from sites representative of the surrounding habitat, the model offered the strongest correlation.

Introduction

Diversity issues in ecology are often discussed in terms of species richness for a specific local community, but there is a need to examine diversity at larger scales (Samson and Knopf 1982, Ricklefs 1987, Hunter 1987, Ricklefs and Schluter 1993). Some patterns of species distribution become obvious only at a regional or continental scale. Underlying regional characteristics can affect local community structure (Ricklefs 1987). Large-scale patterns of
species richness have been explored for vertebrates and plants in relation to energetic factors (Maurer and Brown 1988, Currie 1991, Brown 1995) and for birds in relation to environmental correlates (O'Connor et. al. 1996). Examining diversity at this large scale requires a broad base of consistently collected and widely geographically distributed data. The need for sources of data that meet these criteria has long been recognized (Sanderson et. al. 1979, Hirsch et. al. 1979, Flather and Hoekstra 1989, Gall and Christian 1984).

The Breeding Bird Census (BBC) and the Breeding Bird Survey (BBS) are examples of existing nation-wide sources of avian population data. The BBS employs the point count technique to sample avian populations on approximately 2000 routes each year. BBS routes tend to be relatively inefficient at detecting all species present on a route (Citation), but because of the convenience of the BBS methodology, the survey routes tend to be revisited consistently from year to year. This allows repeated opportunities to observe additional species.

The BBS data set is therefore quite inclusive over both time and space, and was intended for use with large-scale analysis (Robbins et. al. 1986). The BBS has been shown to be useful in conjunction with habitat data (Weber and Theberge 1977) and vegetation data (Flather et. al. 1992). Avian distributions are also associated with environmental factors such as minimum January temperatures, mean annual precipitation, and elevation (Root 1988). The BBS data were well suited to the construction of a large-scale model of avian diversity in the U.S. related to environmental factors by O'Connor et. al. (1996).

Evaluation of the O'Connor et. al. (1996) model is important because of its potential to be a reliable indicator of avian species diversity. Such a large-scale model of species richness could be valuable in revealing continental patterns in the distribution of species or giving insight into reasons for these distributions. A national model of avian species richness may, for
example, prove useful in answering questions about the decline of songbird communities or the
effect of human development on diversity. For this model to be useful, it is first necessary to
determine whether the predictions it produces are consistent with data other than the BBS routes
it was created from.

The Breeding Bird Census (BBC) data, although not nearly as extensive as the BBS data
set, reaches across the United States and is an independent source against which the predictions
of this model can be tested. To estimate avian population levels, the BBC employs a technique
(Van Velzen 1972, Hall 1964, Pough 1947) that is essentially spot-mapping (Engstrom and
James 1984, Robbins 1970, Franzeb 1977). This method is more time consuming and labor
intensive than the point count method and only approximately 100 sites are censused annually.
The BBC is consequently more limited in sample size than the BBS. However, this method is
more thorough in detecting all species present and was anticipated to provide reliable species
richness estimates across the United States. It is therefore used here in an attempt to validate the
usefulness of the O'Connor et. al. (1996) avian diversity model.

Methods

BBC Methods

The BBC is a national effort that began in 1914. Today, it is organized by the Cornell
Laboratory of Ornithology. It employs the spot-mapping technique to estimate avian population
levels (Engstrom and James 1984, Robbins 1970, Franzeb 1977). The goals of the spot-mapping
technique are to record the presence and abundance of species in an individual plot and to define
their territories. The BBC protocol suggests that the plot being censused should be at least 15
acres (with a recommended size of at least 20 acres) and should be located within a
homogeneous habitat type (Hall, 1964). In 1989, actual plot sizes ranged from 9.8 acres to 162.3 acres, with a mean of 38.4 acres. The BBC technique requires a predetermined route established within the plot. An observer travels along this route and maps the locations of all singing males and breeding pairs present. Repeated visits result in multiple locations of males and pairs, which then translate into the number of territories and the number of breeding pairs located on the plot that year. The BBC methodology recommends a minimum of 8 visits to a plot during each year’s census (Hall 1964). In 1989, observers spent 3 to 199 total hours of observation on each site, with a mean of 27.7 hours.

BBS Methods

The BBS is another national avian population effort. The U.S. Fish and Wildlife Service and the Canadian Wildlife Service share joint administration. The BBS uses the point-count method to gather information on bird species presence and abundance. An observer stands at the location and records all birds seen or heard. A point count plot is circular, with a radius that varies with the observer’s ability, weather conditions and vegetation type. A BBS route is 25 miles (39.4 km) long and consists of 3-minute roadside point counts conducted at 0.5 mile (0.8 km) intervals. The 50 point count stops on a BBS route take 4-5 hours to complete.

The Model of Avian Species Diversity

Using the classification and regression tree (CART) technique (O’Connor et. al. (1996) created a model of avian species richness in the continental United States from BBS data. Because the number and type of species found on a BBS route differs from year to year, BBS data from 1981 to 1990 were combined to obtain the cumulative number of species during
the ten year period for each route. Only routes with greater than 7 years of data were used in constructing the model, because species tallies over 7, 8, 9 or 10 years could reliably be adjusted to a 10 year total. Species totals largely leveled off after 10 years (O'Connor et. al. 1996).

Each BBS route for which sufficient data were available was linked with a hexagonal unit in a spatial analysis grid (White et. al. 1992). Each hexagon was approximately 640km$^2$, with the centers approximately 27km apart. The continental United States is covered by about 12,500 hexagons. The values for various environmental characteristics (rainfall, temperature, etc.) were determined for each of these hexagons with data obtained from the Historical Climate Network Database. Each hexagon was also linked with one of 160 land classes (Loveland et. al. 1991, O’Connor 1996) obtained by from Advanced Very High Resolution Radiometer (AVHRR) data compiled by the National Oceanic Atmospheric Administration (NOAA). AVHRR data were available at 1km$^2$ resolution and each hexagon is 640km$^2$. This allowed the percentage of each land class present and landscape pattern metrics to be calculated for each hexagon.

CART analysis was used to analyze the hexagons for which bird data were available. Bird species richness was considered the dependent variable and climate and land class data were designated independent variables. As the model was developed, groups of hexagons for which BBS data were available were divided with respect to species richness into increasingly more homogeneous groups based on environmental factors such as rainfall or temperature, land use or cover type, and geographical location. In principle, it is possible for these divisions to continue until there is only one hexagon (or multiple hexagons with identical bird species richness values) in each category. This perfect fit model is not very useful for extrapolating to hexagons without bird species data because it is too specific to the areas sampled.

The challenge in creating a CART model is to determine how many divisions result in the
most accurate overall model. Cross-validation analysis was used to prune back a fully extended regression tree to a reduced number of categories that produced an optimum fit (Breiman 1986). The environmental conditions and land classes defining each of these final categories were known for the entire continental United States and therefore could be extrapolated across the continent to yield corresponding avian species richness predictions. The 1996 publication of this model consisted of only 13 generalized land classes. Subsequently it was revised to include all of the 160 AVHHR land classes. The revised version of the model evaluated here contained 33 prediction groups encompassing the continental U.S.

Species Richness Values from BBC Data

The complete BBC data sets for the years 1989 and 1990 have been published in the *Journal of Field Ornithology* as supplements (respectively Engstrom 1990, Marshall 1991). A summarized version for each year’s data appeared in *American Birds* (Van Velzen 1990, Anonymous 1991). I obtained the complete data set in electronic form via Patuxent Wildlife Research Center’s web page (http://www.im.nbs.gov/birds/bbc.html) using file transfer protocol. The BBC information was contained in 5 data files. A unique 5-digit record number identified each plot each year. The first 2 digits of this number represented the year the plot was sampled. The remaining three digits were unique for each site, but were not consistent for the same sites in different years.

The record number for each plot references all information in these files. All information existed only as the observer reported it; some categories were more consistently reported than others. The first data file (bbc1.dat) contained location information for each plot. This included latitude, longitude, year of census, country, state/province, publication information, and a
descriptive habitat name. The descriptive habitat name for each plot was similar to, but not always the same as, the published names. The second data file (bbc2.dat) contained the nearest city or town, county, USGS map quadrangle, minimum and maximum plot elevations, plot size in hectares, and the year the plot was first sampled. The third data file (bbc3.dat) included a local reference name for the plot, compiler's name, presence of other participants, and remarks. The fourth file (bbc4.dat) contained total hours spent censusing, total number of species, total number of territories, major habitat type, and detailed vegetation and water body information. The fifth data file (bbc5.dat) contained the names of species found in each plot and the number of territorial males of each species. All data files, except bbc5.dat, were converted to Excel spreadsheet format in their entirety for ease in manipulation. The bbc5.dat file contained individual species densities for many years and only the data for 1989 and 1990 were converted to the spreadsheet format.

Of the 96 sites sampled in 1989 and the 98 sampled in 1990, 67 plots were censused in both years. Because the record number for each plot varied from year to year, consecutively censused plots were determined by comparing the latitude, longitude, city, county, and descriptive habitat name between both years. One of these 67 plots was located in Canada and was disregarded because it would not contribute to the evaluation of the O'Connor et al. (1996) model of U.S. avian species diversity.

The greater the sampling effort for a site, the more accurate the species estimate is likely to be. O'Connor et al. (1996) used this principle in obtaining species richness values of BBS routes from adjusted cumulative richness totals from 7 to 10 years of data. BBC data is more limited, so paired sites were used to estimate the number of species actually present on a site in conjunction with the program SPECRICH2 (Hines et al. 1997). SPECRICH2 estimates species
richness from presence-absence data using a variation of the familiar capture-recapture modeling approach (Otis et. al. 1978, Pollock et. al. 1990, Nichols 1992, Lebreton 1992). The presence of a species in a survey or census represents the initial capture while presence of the same species in each subsequent survey or census represents a recapture.

Adaptations of capture-recapture models have been used to estimate species richness from BBS data (Boulinier et. al. 1998). Here, SPECRICH2 was used to estimate the number of species present at each of the 66 BBC sites with two sampling occasions. With two censuses of each site, some species were found during one census and not the other, while other species were found during both sampling occasions. The program requires the total number species observed on each sampling site/occasion, the number of species observed for only one site/occasion, and the number of species observed for both sites/occasions. SPECRICH2 then reports an estimate of the total number of species on the site and its standard error.

Statistics

Once these estimates were obtained, GIS specialist John Bartlett used the program ARC Info to match them to the hexagon of the model in which they were located. The BBC locations were identified geographically by latitude and longitude from the BBC data files, while the model was created using a Lambert equal area projection. The latitude and longitude coordinates therefore had to be projected onto the Lambert projection in order to match each location with the appropriate hexagon. When the latitude and longitudinal coordinates are converted into hexagonal locations on this type of projection, there is an increasing amount of distortion as the distance from the center of the projection increases. The center of the projection used in the model was the center of the continental United States. This increases the likelihood that a BBC
plot in coastal California, for example, could be converted to a hexagon neighboring its true location. The location of the town nearest to the BBC plot and the county the plot was located had a known hexagon location. To correct for the possibility of the BBC plot being located in the incorrect hexagon, the town and county hexagon identification numbers were compared to the BBC plot hexagon identification numbers. Where these numbers apparently differed due to the distortion of the projection, the hexagon ID of the correct town and county replaced the original value. Finally, the species richness estimate for each BBC plot was matched to the appropriate model prediction for the hexagon where the plot was located (Table 1).

The BBC plots were then sorted by general habitat type to see if their correlation with the model predictions differed with habitat type. The habitat types used were deciduous forest, coniferous forest, mixed forest, open (non-forested) land, and wetlands (Table 2). Each BBC site was assigned to one of these categories according to the descriptive habitat name associated with the site. If this name did not clearly classify the site, the presence, absence, and primary composition of canopy species were used to assign a type. Because these habitat types that are assigned to the BBC plots are much more generalized than the 160 AVHHR categories, I will use the term “habitat type” to refer to the five generalized types used here and “land class” or “land classification” to refer to the AVHHR categories.

A Kruskal-Wallis test was performed to compare between BBC species richness estimates for the five generalized habitat types. Because deciduous and open sites were the most numerous of the five habitat types, correlation coefficients were calculated comparing deciduous and open habitat BBC estimates with the corresponding model predictions. A BBC plot may be representative of the surrounding habitat or it might be a small patch inconsistent with the surrounding area. Because patch size has a substantial effect on the species richness of the plot (Yahner 1995, Harris 1984, Galli et al. 1976, Lynch and Whigham 1984, Diamond 1975), additional correlations were performed for
both deciduous and open habitat types. A correlation coefficient was calculated only for species richness estimates of BBC sites that occurred in hexagons where the primary land cover class constituted >50% of the area of the hexagon and corresponded to the BBC plot habitat type. For example, only deciduous BBC plots that occurred in hexagons with >50% of the area in a single deciduous land class (or in a habitat matrix that included deciduous land cover) were correlated with the model predictions. The purpose of this second comparison was to determine if a better correlation existed when the habitat type of the BBC plot was consistent with the surrounding landscape. Further analysis of the deciduous habitat type was performed using Scedecor and Cochran’s (1967) z-transformation process to determine the respective effects of the group of plots located in hexagons with a dominant deciduous land class and the group of plots located in other hexagons.

Results

The species estimates obtained from the BBC data were consistently less than corresponding predictions of the CART model. SPECRICH2 yielded species richness estimates for the BBC plots ranging from 6 to 71, while the avian diversity model yielded species richness prediction values for each of the corresponding hexagons ranging from 44.9 to 99.0 (Table 1). The BBC species richness estimates exhibited a negative bias as indicated by their location below the 1:1 line in Figure 2.

Due to the limited and clustered nature of the BBC data, an overall evaluation of the model was not appropriate. Only 19 of the 33 predictive regions identified by the CART model were represented in the BBC data (Fig. 1). This uneven distribution of sample points is further illustrated by the location of multiple BBC plots within a single hexagon, with the 66 BBC plots corresponding to only 43 hexagons.

However, the available BBC data was sufficient for a more limited evaluation within
specific habitat types. The non-parametric Kruskal-Wallis test was used to compare the species richness values between habitat types because visual inspection of the data (Fig. 2) indicated a non-normal distribution of BBC estimates. This test returned a significant statistic of 30.843 (P < 0.000). This indicates that species richness varies with habitat type and analysis to determine if any significant correlation exists within individual types is justified.

Analysis within habitat type was performed for the open (unforested) and deciduous habitat types. These habitat types were chosen to be tested for two reasons. First, they were the two most frequently occurring types, each accounting for roughly a third of the 66 BBC plots sampled (Table 2). Second, there was a large amount of geographic and vegetative variability within the smaller habitat types. For example, the coniferous sites varied from a New York Christmas tree farm to a Ponderosa pine stand in Colorado.

The 18 open BBC sites were first tested to determine the correlation between the species richness estimates and the corresponding diversity model predictions (r = 0.103). Next, the relationship of only those estimates with predictions embedded in hexagons with a dominant (>50%) open land class was tested (r = -0.016, n = 12). Neither correlation exhibited significance, however the open habitat sites did demonstrate the geographic and vegetative variability observed in the less frequent types.

The deciduous habitat type was tested for correlation in the same manner as the open sites, and returned significant values. The deciduous sites were the most frequently occurring among the BBC plots sampled and were the less widespread geographically, with all but one site located in the eastern U. S. The initial analysis for all 25 deciduous BBC plots was mildly significant (r = 0.367, P = 0.05). For the 9 sites located in hexagons with a dominant deciduous land class, a stronger correlation was found (r = 0.600, P = 0.05). This indicates that the CART
model predictions have the best relationship to the BBC species richness estimates when compared to prediction units (hexagons) of a similar land class.

Visual inspection of the 9 data points for which this correlation was found showed one BBC estimate that was noticeably greater than the other 8. This point had a BBC species richness estimate of 65 compared to other deciduous estimates that ranged from 24 to 49. In order to rule out the possibility that this single point was weighting the correlation, the correlation between deciduous BBC plots within hexagons with a deciduous dominant land class was repeated without this value. The relationship actually increased slightly in significance ($r = 0.634$, $P = 0.00$), showing that this high value had not unduly influenced the results of the previous correlation.

Next, the possibility that the correlation of these 9 points ($r = 0.600$, $P = 0.05$) was driving the overall deciduous correlation ($r = 0.367$, $P = 0.05$, $n = 25$) was tested. This was a concern because the 16 BBC plots that did not occur in hexagons with a dominant deciduous land class did not give a significant, or even positive, correlation ($r = -0.031$). $Z$-transformed (Snedecor and Cochran 1967) correlation coefficients for the plots located in hexagons with a deciduous land class and those that were not were compared. A non-significant $\chi^2$ of 2.15 with one degree of freedom was obtained from the $z$-transformations and showed that the two samples could have been drawn from a common universe. These values could then be combined to give a pooled correlation of 0.196, which was markedly, although not significantly, less than the value of 0.367 obtained from the data. This suggests that some of the plots located in hexagons not dominated by a deciduous land class are influencing the overall correlation.
Discussion

The species richness estimates obtained from the 1989-1990 BBC data are consistently less than the CART model predictions and exhibit an obvious bias. The assumptions in the program SPECRICH2 were considered as a potential source of distortion when used to estimate the number of species on each plot. A comparison of the overall correlation of the adjusted and unadjusted species richness values for all sites addressed this concern. There is little difference between the two correlations and therefore no reason to believe the program developed by Hines et. al. (1997) is the source of this bias.

Alternative explanations for these disparities are three major differences between the census and survey methods: sample unit size, habitat homogeneity, and temporal sampling effort. First, a BBS route is 25 miles in length and spans a greater area than a BBC plot, which covers less than 40 acres on average. In traversing a greater area, a BBS route will typically include a greater number of species than a BBC plot. Secondly, a BBS route will also tend to include a greater number of habitat types within its greater area. A BBC plot constitutes a smaller and more homogeneous segment of the final prediction unit, the 640km² hexagon. The potentially greater variety of land classes that a BBS route includes may result in a greater variety of species sampled and ultimately predicted by the model. Finally, the higher predictions given by the model could be attributed to the greater sampling effort or time span over which the data for it was collected. The 10 years of BBS data used to create the model would almost necessarily include a greater proportion of uncommon or difficult to observe species than the two years of BBC data. This is likely to hold true despite the greater thoroughness of the census method because a rarer species may only occur in a particular area intermittently over a period of years.
Comparing only estimates classified in a single habitat type to the corresponding predictions attempts to evaluate a specific portion of the model. It also attempts to minimize one source of variability. However, no significant correlation was found when the open BBC plots and their corresponding predictions were compared. The variation within the open habitat type is a likely contributor to this lack of correlation. The habitat grouping in this case included geographically heterogeneous plots located in North Dakota, Iowa, and coastal California. The open or unforested habitat type is a subjective classification in this situation and there is no reason to expect that these wide-ranging plots should have similar avian populations or avian diversity predictions.

A better correlation is obtained from less widely distributed locations of the deciduous sites. All but one plot was located in the eastern U.S. and the overall correlation of the deciduous sites was significant ($r = 0.367$, $P = 0.05$, $n = 25$). When only those BBC plots that occur in hexagons with predominantly deciduous forest or deciduous forest matrix, such as suburban areas, are compared the correlation coefficient increases ($r = 0.600$, $P = 0.05$, $n = 9$). The model therefore bears the strongest correlation to the deciduous sites located in hexagons dominated by a deciduous land class, most likely because these sites have the least amount of geographic variability and the most comparable habitats.

The significant correlation shown by an overall comparison of deciduous sites ($r = 0.367$, $P = 0.05$, $n = 25$) is noticeably larger than the value obtained if the sites not located in hexagons with a deciduous land class are assumed not to be unduly affecting the overall correlation ($r = 0.196$). This difference suggests that at least some of the 16 BBC plots located within hexagons without a dominant deciduous land class are contributing to the overall significance. A possible explanation for this contribution is that a single hexagon could potentially be comprised of
>50% of deciduous forest and still not be dominated a single deciduous land class. This is possible because many of the 160 AVHRR land classes are deciduous or have a deciduous matrix. Multiple deciduous land classes could exist within a hexagon, each covering an area of less than 50%, but totaling greater than 50%. By the classification used, such a hexagon would not have a dominant deciduous land class, but would at the same time consist of primarily deciduous vegetation. It is possible that this effect contributes to the significant value obtained when comparing over all deciduous sites, despite the lack of correlation among the hexagons without a dominant land class.

The problem of multiple BBC plots located within in a single hexagon should be recognized. In the deciduous data, nine BBC plots are recognized in the correlation between BBC plots and hexagons with a dominant land class. Only six hexagons are represented in this data set because four of the sites occur within a single hexagon. This is a potentially confounding effect, but the correlation does indicate that the model of avian diversity best reflects the species richness of small sites that are representative of the dominant land class of the model’s prediction unit, a hexagon.

**Conclusion**

BBC estimates of species richness are consistently lower than the predictions obtained from the revised version of the avian diversity model presented by O’Connor et. al. (1996). The most likely sources of bias are the differences in the amount of area sampled, the number of years on which species richness values were based, and the potential difference in habitat homogeneity.
The BBC data was insufficient to evaluate the diversity model as whole, but analysis was performed within specific habitat types. The results suggest the model’s predictions best correlate with the estimated species richness of a site when the estimates possess minimal geographic variability and the plot sampled is located within a hexagon dominated by the same habitat type.

**Acknowledgements**

I would like to thank Dr. Raymond J. O’Connor for his patience and careful criticism and John Bartlett for his freely given technical assistance. Both deserve recognition for their generously donated time and effort.
Figure 1. Revised classification and regression tree (CART) model for avian species richness across the continental United States. Numbers inside the end nodes (rectangles) are the mean number of species for each prediction zone. The splitting variables for each division are shown on the branches of the diagram. End nodes marked with an asterisk (*) represent the prediction zones for which species richness estimates were calculated from BBC data.
Fig. 2. Scatterplot of species richness estimates as a function of avian diversity model predictions for 66 BBC plots. All 66 BBC plots sampled are represented and classified into three categories: general plots (other), deciduous plots, and deciduous plots located in hexagons with a dominant (>50% in area) deciduous land class.
Table 1. For each BBC plot there is listed: a species richness prediction from the avian diversity model, a species richness estimate obtained from BBC data, a generalized habitat type, and the state where the plot is located.

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<th>ModelSpecies Prediction</th>
<th>Species Estimate</th>
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<td>24</td>
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<td>VA</td>
</tr>
</tbody>
</table>
Table 2. Sample size and mean species richness estimate obtained from BBC data. Kruskal-Wallis test result and probability for four degrees of freedom.

<table>
<thead>
<tr>
<th>Habitat Type</th>
<th>Number of Plots</th>
<th>Mean Species Richness Estimate</th>
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</thead>
<tbody>
<tr>
<td>Coniferous</td>
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<td>27.4</td>
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<tr>
<td>Deciduous</td>
<td>25</td>
<td>37.3</td>
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<tr>
<td>Mixed Forest</td>
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<tr>
<td>Open</td>
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<td>Wetland</td>
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<td>32</td>
</tr>
</tbody>
</table>

Kruskal-Wallis Test Statistic 30.843
Probability 0.000
Literature Cited


