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Scott W. Manley
Mississippi State University

Jeffrey M. Lee
Mississippi State University

R. Shane Fuller
Mississippi State University

John P. Carroll
University of Georgia

Leonard A. Brennan
Tall Timbers Research Station

COMPARISON OF TWO METHODS FOR QUANTIFYING NORTHERN BOBWHITE HABITAT USE

Scott W. Manley[1]
Mississippi State University, Department of Wildlife and Fisheries, Box 9690, Mississippi State, MS 39762

Jeffrey M. Lee[2]
Mississippi State University, Department of Wildlife and Fisheries, Box 9690, Mississippi State, MS 39762

R. Shane Fuller[3]
Mississippi State University, Department of Wildlife and Fisheries, Box 9690, Mississippi State, MS 39762

John P. Carroll
University of Georgia, Daniel B. Warnell School of Forest Resources, Athens, GA 30602

Leonard A. Brennan
Tall Timbers Research Station, 13093 Henry Beadel Drive, Tallahassee, FL 32312-0918

ABSTRACT

Habitat use is an important ecological parameter that is used to make informed decisions about quail management and research. Statistical methods for quantifying habitat use are numerous, but few objective criteria are available to support the selection of a particular analytical approach. Therefore, we compared breeding season habitat use by radio-marked northern bobwhites (*Colinus virginianus*) at 2 study sites in Mississippi with 2 widely used statistical methods; Chi-square goodness-of-fit test with Bonferroni confidence intervals, and compositional analysis. These statistical methods produced similar results for both study areas; however, more detailed habitat use information was provided by compositional analysis when performed using the customary hierarchical approach. Therefore, for analysis of radio-marked quail, we recommend this method due to its effective hierarchical approach, improved statistical validity, and ability to incorporate other population parameters (e.g., survival) into statistical models of habitat use by northern bobwhites.

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INTRODUCTION

Habitat use and selection are fundamental concepts in the study of vertebrate ecology and management. Following definitions from Hilden (1965) and others (Johnson 1980, Hutto 1985, Block and Brennan 1994), habitat use is simply an association of an animal with a particular habitat (i.e., collection of physical and biological features supporting life requisites). Habitat selection, however, implies a behavioral process whereby an animal chooses among alternative habitats. The result of most analyses of habitat selection is typically some level of use where one habitat is occupied disproportionate to its availability. Habitat selection can occur at a variety of different spatial and temporal scales (e.g., geographical or within an animal's home range, seasonal). In theory, animals select habitats that optimize their survival and fitness.

Habitat use and selection are important population parameters used as a basis to make informed decisions about northern bobwhite management. Bobwhites most likely select habitats at various spatial and temporal scales; a reflection of specific habitat needs for survival and reproduction. Success of management actions to increase food, cover, and other important resources which affect survival and reproduction can be evaluated with analyses of habitat use.

Following Stoddard's (1931) landmark life history study, perhaps the greatest technological advancement in the study of bobwhite habitat use and selection was development of miniaturized radio transmitters. Although not without liabilities (see Samuel and Fuller [1994] for review), use of radio transmitters to mark individual bobwhites has provided new insight on movements, habitat use, behavior, survival, and breeding biology.

Methods to analyze habitat use data based on ra-

[1] Present address: Ducks Unlimited, Inc. 4511 East 43rd Street, North Little Rock, AR 72117.
[2] Present address: Dahomie National Wildlife Refuge, U.S. Fish & Wildlife Service, % Mississippi Wetlands Management District, P.O. Box 1070, 16736 Highway 8 West, Grenada, MS 38902.
[3] Present address: St. Joe Land and Timber Company, Route 1, Box 60, Lamont, FL 32366.

dio-marked animals, and test for selection, are numerous (see Alldredge and Ratti [1986, 1992] for review). All methods have limitations and advantages. One analytical method proposed by Neu et al. (1974) uses Chi-square goodness-of-fit procedures to test whether observations of habitat use follow the expected pattern of occurrence based on availability. If the Chi-square test detects a significant difference in use versus availability, a Bonferroni *z*-statistic (Miller 1981) is used to determine which habitat types are used more or less frequently than expected. This method is widely applied when use and availability were estimated at the population level and individual animals could not be uniquely marked as to generate individual case histories. As a result, the method must assume equal availability and selection among all individuals. With respect to radio telemetry data, this method forgoes the detailed information derived from individually marked animals and the more complete data structure that is provided. Nonetheless, the Neu et al. (1974) method is widely used for telemetry data (e.g., Killbride et al. 1992, Whiting and Sloan 1993, Dixon et al. 1996), is based on straightforward and easily applied calculations, and is thought to produce satisfactory results when the pooled number of marked individuals and radio locations per individual are sufficiently large (Alldredge and Ratti 1986).

More recently, compositional analysis has been recommended over other methods for assessing habitat selection (Aebischer et al. 1993a, 1993b). Designed for animal-specific paired vectors of use and availability, this method employs multivariate analysis of variance (MANOVA) procedures to first test for a departure from random habitat use. Assuming significant nonrandom use, comparisons of pair-wise differences between matching log-ratios of use and availability produces habitat ranks from most to least used. Compositional analysis is effectively designed to analyze resource selection at multiple spatial levels (i.e., study area versus home range and home range versus individual radio locations), treats the individual animal as the experimental unit, and circumvents statistical assumptions such as equal availability and selection among pooled individuals. Conversely, compositional analysis requires relatively complex calculations, and use of a Geographical Information System to manipulate and produce multilevel-proportion data for marked individuals. Aebisher et al. (1993a) specifically advocates use of compositional analyses for radio-marked individuals as this method more appropriately addresses the following areas of concern: (1) sampling level, (2) data pooling across individuals, (3) non-independence of habitat proportions, (4) differential habitat use by groups (i.e., sex, age class) of animals, and (5) definition of habitat availability.

Since the Chi-square and compositional analysis methods are two of the most widely used techniques for assessing habitat use by bobwhites, our objectives are to compare and contrast the following: (1) results from two different study areas, (2) logistical, statistical, and biological concerns that may affect results, and (3) inferential merits leading to the ensuing habitat management recommendations. Our goal was to provide a qualitative comparison of these two analytical methods for quantifying habitat use of bobwhites. This information will aid researchers and managers in interpretation of past studies and the design of future ones.

METHODS

Study Areas

Our habitat use study was conducted at 2 different sites where bobwhite management had recently been initiated. Copiah County Wildlife Management Area (CCWMA) spans 2900 hectares and is located within the Lower Thin Loess physiographic region of south Mississippi (see Pettry [1977] for description of soil resource areas). The area is dominated by old-field successional pine (*Pinus* spp.) that are 40–70+ years in age, with hardwood drains, and approximately 200 hectares of fields used for hay production prior to 1988. In 1992, disking and burning were employed to promote more suitable bobwhite habitat throughout the area. The second study site, Trim Cane Wildlife Demonstration Area (TCWDA), is located within an alluvial floodplain between the Interior Flatwoods and Blackland Prairie physiographic regions in northeast Mississippi. This 320 hectare study site is composed of old-field and wooded-hedgerow habitats and is surrounded by row-crop agriculture and pasture land. Last farmed in 1986, succession has led to a plant community dominated by broomsedge (*Andropogon* spp.) along with several pioneer tree species (e.g., groundsel tree [*Baccharis* sp.], and ash [*Fraxinus* spp.]). Beginning in 1991, disking and burning were employed on the area which floods regularly during winter and spring. For a more detailed description of study areas see Lee (1994) and Manley (1994).

Data Collection

Bobwhites were captured in collapsible funnel traps at each study area during February–March 1993 and affixed with a 7 g necklace-type transmitter. Bobwhites were located daily throughout the ensuing breeding season (15 April–1 September) via triangulation, radio receivers, directional antennae, and permanent telemetry stations. Triangulation error was assessed by calculating mean distance between point estimates and known locations of test transmitters distributed among all habitat types (White and Garrot 1990:80–90). Geographic Information Systems [PC ARC/INFO (ESRI 1989)] were used to process all telemetry data [TELEBASE (Wynn 1989)], home range data [HOMERANGE (Ackerman et al. 1990)], and study area data required to compare our 2 types of habitat use analyses.

Data Analyses

Addressing each study area separately, we first compared use of habitat types to availability using Chi-square goodness-of-fit tests and Bonferroni simul-

Table 1. Habitat use by northern bobwhites (n = 16), as estimated by Chi-square goodness-of-fit test followed by Bonferroni confidence intervals (Neu et al. 1974), on Copiah County Wildlife Management Area, Copiah County, Mississippi, 15 April–1 September, 1993.

Habitat	Number of locations	Proportion: Expected use	Proportion: Actual use	Bonferroni[a] confidence interval	Result
Upland pine woods	607	0.504	0.735	0.692–0.778	Preferred
Hardwoods and drains	2	0.060	0.002	0.000–0.006	Avoided
Mixed pines and hardwoods	102	0.328	0.124	0.092–0.156	Avoided
Clearcut hardwoods	13	0.015	0.016	0.004–0.128	Proportional
Old fields and pastures	102	0.090	0.124	0.092–0.156	Preferred

[a] Confidence interval at $P < 0.05$.

taneous confidence intervals (Neu et al. 1974). Telemetry locations were pooled across animals; we assumed that habitat availability was the same for all individuals. The null hypothesis was: Use of habitat types was proportional to study area availability. Following rejection of this hypothesis, confidence intervals were used to determine which habitat types were used more or less frequently than expected.

Secondly, we considered habitat use by employing the multi-step process of compositional analysis (Aebischer et al. 1993a, 1993b, Carroll et al. 1995). We compared proportions of each habitat in the study area with proportions found in each 95% convex polygon home range (Mohr 1947). We then compared proportions of habitats in each home range with proportion of radio locations for each bird. Using MANOVA procedures (SYSTAT 1992), we tested the null hypothesis: Use of habitat types follows an expected random distribution. Following rejection of this null hypothesis, we used paired t-tests to compare relative use of each habitat with all others individually, and then ranked habitats according to relative use. Because of potential nonnormality of these data, we used randomization (Edgington 1980) to construct expected distributions for comparison of observed values. In order to account for missing values we calculated Wilk's lambda values using each habitat as the denominator (Aebischer et al. 1993a). We then calculated a weighted average of the Wilk's lambda values based on the number of missing values in each of the habitats used as the denominator.

RESULTS

Copiah County Wildlife Management Area

Between 15 April and 1 September 1993, 823 radio locations were obtained from 16 bobwhites. Mean number of locations per individual was 51 (range 25–75). Average distance between triangulated estimates and known points of test transmitters was 23.6 meters. Following Neu et al. (1974), habitat use was disproportionate to availability (χ^2 = 1478, df = 4, $P <$ 0.001), with upland pine and field habitats being preferred, mixed pine-hardwoods and hardwood drains avoided, and clear-cut habitats used in proportion to availability (Table 1).

Following compositional analysis, proportions of habitats within each home range were different from proportions within the study area (Λ = 0.067, $P <$ 0.001). Analysis of individual habitats demonstrated habitat use trends identical to those of the previous goodness-of-fit tests (Table 2). However, proportions of habitat composed from individual radio locations were not different from habitats within home ranges (Λ = 0.590, P = 0.563). In fact, there were so many missing values in habitat availability at the home range level, we were required to drop the hardwood-drain category to complete the analysis.

Trim Cane Wildlife Demonstration Area

During the 1993 breeding season, 2117 radio locations were obtained from 32 bobwhites. Mean num-

Table 2. Matrix of differences in log-ratios of habitat use by northern bobwhites (n = 16), produced by compositional analysis (Aebischer et al. 1993), comparing study area versus home range proportions, Copiah County Wildlife Management Area, Copiah County, Mississippi, 15 April–1 September, 1993.

Habitat	Upland pine[a] woods		Hardwoods and drains		Mixed pines and hardwoods		Clearcut hardwoods		Old fields and pastures	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Upland pine woods			−5.834	0.586*	−2.996	0.837*	−4.228	0.515*	−0.268	0.182
Hardwoods and drains	+5.834	0.586*			+2.838	0.905*	+1.606	0.840	+5.566	0.654*
Mixed pines and hardwoods	+2.996	0.837*	−2.838	0.905*			−1.232	0.836	+2.728	0.856*
Clearcut hardwoods	+4.228	0.515*	−1.606	0.840	+1.232	0.836			+3.960	0.440*
Old fields and pastures	+0.268	0.182	−5.566	0.654*	−2.728	0.856*	−3.960	0.440*		
Rank[b]	4		0		2		1		3	

[a] A positive value of log-ratio differences indicates that the column habitat was used more often than row habitat. A negative value indicates the opposite. An asterisk (*) means the difference is significant at $P \leq 0.05$.

[b] Ranks were determined by comparing relative use of each habitat to all other habitats. Largest rank indicates most used habitat(s), and smallest rank indicates the least used habitat.

Table 3. Habitat use by northern bobwhites (n = 31), as estimated by Chi-square goodness-of-fit test followed by Bonferroni confidence intervals (Neu et al. 1974), on Trim Cane Wildlife Demonstration Area, Oktibbeha County, Mississippi, 15 April–1 September, 1993.

Habitat	Number of locations	Proportion		Bonferroni[a] confidence interval	Result
		Expected use	Actual use		
Old field control	274	0.052	0.129	0.109–0.149	Preferred
Old field burn	170	0.116	0.080	0.064–0.096	Avoided
Old field disk	416	0.113	0.197	0.173–0.221	Preferred
Old field burn-disk	254	0.149	0.120	0.101–0.139	Avoided
Pasture	221	0.242	0.104	0.086–0.122	Avoided
Row crop soybeans	121	0.084	0.057	0.043–0.071	Avoided
Hedgerow woodlot	661	0.224	0.312	0.284–0.340	Preferred

[a] Confidence interval at $P \leq 0.05$.

ber of locations per individual was 69 (range 25–86). Average distance between estimated and known points of test transmitters was 62.0 meters. Following Neu et al. (1974), habitat use was disproportionate to availability ($\chi^2 = 685$, df = 6, $P < 0.001$), with hedgerows, strip-disked, and undamaged fields being preferred (Table 3). All other habitats were avoided.

Following compositional analysis, proportions of habitats within each home range were different from proportions within the study area ($\Lambda = 0.86$, $P < 0.001$). Comparisons of individual habitats showed hedgerows and disked fields with the most relative use. Pastures, unmanaged, and burned fields received intermediate use while row crops and burned-disked fields were least used (Table 4). Additionally, habitat proportions composed from individual radio locations were different from proportions within home ranges ($\Lambda = 0.197$, $P < 0.001$). At this level, order of use changed significantly with disked fields receiving the most relative use while hedgerows and pastures were used least. All other habitats received intermediate use (Table 5).

DISCUSSION

Comparisons of the 2 analytical methods demonstrated no difference in final results at CCWMA. Compositional analysis detected no difference in habitat use between bobwhite home ranges and individual radio locations (i.e., no 3rd order selection [Johnson 1980]). However, the 2 methods demonstrated contrasting results at TCWDA. Additionally, within the 2 levels of compositional analysis at TCWDA, significant differences in habitat use occurred between study area versus home range comparisons (i.e., 2nd order selection) and home range versus individual radio locations. Hedgerow-woodlot habitats were very important in determining where bobwhites located home ranges yet contained very few individual radio locations, suggesting a specific need for this habitat (e.g., escape cover, travel corridors). At TCWDA, the Chi-square tests with confidence intervals obscured the different habitat selection processes that occurred at different spatial scales.

Numerous concerns face researchers and managers who design and implement habitat use studies. With regard to the Chi-square-confidence interval method and radio-marked samples, we not only violated statistical assumptions when location data were pooled, but more importantly, we neglected potentially useful information based on variability of individual birds (see Schooley [1994] for review). Methods which do not pool data (e.g., compositional analysis) and have potential to consider individual variation along the year, sex, age, and other effects, provide more information on which to base management recommendations. Moreover, appropriate sampling units for a population are individuals within that population; radio telemetry allows us to estimate the habitat use of such individuals.

There are statistical and logistical constraints to the use of compositional analysis. It is not only desirable to have a large sample size of radio-marked individuals, but it is also essential that the following data be recorded for individual birds: (1) sufficient number of locations to identify the complete home range, (2) area and proportions of all habitats available, and (3) area and proportions of all habitats used. Secondly, larger sample sizes are needed if effects such as year, age, and sex are factored into the overall statistical model. Lastly, it is virtually impossible to collect and process multilevel habitat availability and use data without the aid and proficient use of GIS.

Perhaps the greatest benefit of compositional analysis is that it uses a multiscaled macrohabitat approach. As demonstrated in our comparison of data from TCWDA, this approach yields more information regarding habitat selection than the Chi-square-confidence interval method. Scale is very important in habitat selection, especially by birds, and must have serious consideration in design and interpretation of habitat studies (Wiens 1976, Orians and Wittenberger 1991, Danielson 1992). In fact, scale is likely an important factor at CCWMA, as microhabitat analyses of randomly-located plots versus those used by bobwhites showed significantly less tree basal area and density, and greater forb height in the used areas (Lee 1994). These microhabitat characteristics were missed by our 3rd order compositional analysis because so much of the available habitat proportions were upland pine woods (71% on average), with no differentiation be-

Table 4. Matrix of differences in log-ratios of habitat use by northern bobwhites (n = 31), produced by compositional analysis (Aebischer et al. 1993), comparing study area versus homerange proportions, Trim Cane Wildlife Demonstration Area, Oktibbeha County, Mississippi, 15 April–1 September, 1993.

	Old field[a] control		Old field burn		Old field disk		Old field burn-disk		Pasture		Row crop soybeans		Hedgerow woodlot	
Habitat	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Old field control			−0.563	0.602	+0.217	0.428	−1.245	0.713	−0.566	0.531	−1.881	0.655*	+1.701	0.522*
Old field burn	+0.563	0.602			+0.780	0.363*	−0.682	0.603	−0.003	0.619	−1.318	0.504*	+2.263	0.323*
Old field disk	−0.217	0.428	−0.780	0.363*			−1.462	0.413*	−0.782	0.515	−2.098	0.553*	+1.484	0.286*
Old field burn-disk	+1.245	0.713	+0.682	0.603	+1.462	0.413*			+0.679	0.659	−0.636	0.762	+2.946	0.476*
Pasture	+0.566	0.531	+0.003	0.619	+0.782	0.515	−0.679	0.659			−1.315	0.588*	+2.266	0.479*
Row crop soybeans	+1.881	0.655*	+1.318	0.504*	+2.098	0.553*	+0.636	0.762	±1.315	0.588*			−3.581	0.403*
Hedgerow woodlot	−1.701	0.522*	−2.263	0.323*	−1.484	0.286*	+2.946	0.476*	−2.266	0.479*	−3.581	0.403*		
Rank[b]	4		3		5		1		2		0		6	

[a] A positive value of log-ratio differences indicates that the column habitat was used more often than row habitat. A negative value indicates the opposite. An asterisk (*) means the difference is significant at $P \leq 0.05$.

[b] Ranks were determined by comparing relative use of each habitat to all other habitats. Largest rank indicates most used habitat(s), and smallest rank indicates the least used habitat.

Table 5. Matrix of differences in log-ratios of habitat use by northern bobwhites (n = 31), produced by compositional analysis (Aebischer et al. 1993), comparing home range with individual radio-location proportions, Trim Cane Wildlife Demonstration Area, Oktibbeha County, Mississippi, 15 April–1 September, 1993.

	Old field[a] control		Old field burn		Old field disk		Old field burn-disk		Pasture		Row crop soybeans		Hedgerow woodlot	
Habitat	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Old field control			−1.205	0.469*	+0.059	0.338	−0.054	0.266	−1.516	0.463*	+0.335	0.417	−0.838	0.336*
Old field burn	+1.205	0.469*[a]			+1.407	0.458*	+0.641	0.489	−0.336	0.646	+0.726	0.512	−0.198	0.392
Old field disk	−0.059	0.338	−1.407	0.458*			−0.031	0.370	−1.824	0.508*	−0.839	0.308*	−1.187	0.297*
Old field burn-disk	+0.054	0.266	−0.641	0.489	+0.031	0.370			−1.487	0.467*	−0.331	0.767	−0.879	0.363*
Pasture	+1.516	0.463*	+0.336	0.646	+1.824	0.508*	+1.487	0.467*			+1.430	0.753	+0.672	0.443
Row crop soybeans	−0.335	0.417	−0.726	0.512	+0.839	0.308*	+0.331	0.767	−1.430	0.753			−1.139	0.265*
Hedgerow woodlot	+0.838	0.336*	+0.198	0.392	+1.187	0.297*	+0.879	0.363*	−0.672	0.443	+1.139	0.265*		
Rank[b]	4		2		6		4		0		4		1	

[a] A positive value of log-ratio differences indicates that the column habitat was used more often than row habitat. A negative value indicates the opposite. An asterisk (*) means the difference is significant at $P \leq 0.05$.

[b] Ranks were determined by comparing relative use of each habitat to all other habitats. Largest rank indicates most used habitat(s), and smallest rank indicates the least used habitat.

tween vegetation characteristics within these pine stands.

We recognize our comparison of two methods for analyzing bobwhite habitat use is qualitative and limited to only 2 data sets. Nonetheless, the Neu et al. (1974) approach (i.e., Chi-square goodness-of-fit tests with confidence intervals) provided results similar to Aebischer et al. (1993a) compositional analysis at CCWMA, yet lacked resolution at TCWDA. It is important to remember that the Chi-sqaure method was developed for use on unmarked individuals and is still very applicable for such data. Nonetheless, we recommend that compositional analysis be used for habitat use data derived from radio telemetry due to its improved statistical validity, hierarchical approach, and ability to incorporate other populations parameters (e.g., year, age, sex, survival) into statistical models.

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