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Spatial and predictive foraging models for gray bats in northwest Georgia and a comparison of two acoustical bat survey techniques

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**SPATIAL AND PREDICTIVE FORAGING MODELS FOR GRAY BATS IN
NORTHWEST GEORGIA AND A COMPARISON OF
TWO ACOUSTICAL BAT SURVEY TECHNIQUES**

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ABSTRACT

Spatial and Predictive Foraging Models for Gray Bats in Northwest Georgia and a
Comparison of Two Acoustical Bat Survey Techniques

Joshua B. Johnson

The federally endangered gray bat (*Myotis grisescens*) is an obligate, year-round, cave-dwelling species. Efforts to protect caves occupied by gray bats have proved beneficial to recovery. Specific gray bat foraging area characteristics also are critical to gray bat population recovery and maintenance. In summer 2000 and 2001, I determined gray bat presence/absence with Anabat II acoustic bat detectors in potential foraging areas near 2 bachelor colonies in northwest Georgia. In 2000, I systematically sampled 213 locations near water sources over an 8.3×9.4 km sampling grid that was established over a 5,100 km^2 study area. Each sampling point was monitored for 20 minutes. A predictive landscape-level model was developed in a Geographic Information Systems (GIS). In summer 2001, to further refine gray bat spatial activity patterns on a macro-habitat level, I sampled 114 locations that were predicted on a landscape level as gray bat foraging areas based on data from 2000.

In 2000, 6,314 echolocation call sequences were collected using Anabat6 software and analyzed using Analook software. I identified 237 gray bat calls at 34 locations. Gray bats were detected 1.6 km to 28.0 km straight-line distance and 66 km riparian corridor distance from the 2 bachelor colony roost caves. Spatial data suggested the presence of 2 additional gray bat colonies and that gray bats foraged along major riparian corridors nearest to their roost sites. A GIS model incorporating the 2 known roost caves and the 2 predicted roost caves contained the largest waterway near each roost cave and its tributaries up to a minimum third-order stream. The GIS model contained 79% of locations where gray bats were detected and included 14% (1,235 km) of streams and rivers in northwest Georgia. Gray bats were detected in low valleys more often than ridge tops and mountains. Gray bats were detected at lotic water sources in greater proportion than lentic water sources.

In 2001, I developed a macro-habitat foraging model based on 5,124 echolocation call sequences collected at 114 locations within gray bat foraging areas delineated by the GIS model. I collected 620 gray bat calls at 87 locations. Gray bats were detected more often in larger, downstream portions of foraging areas than narrow, cluttered, upstream portions.

The use of ultrasonic detectors to survey bat species presence is common. Echolocation call quality differs between call sequences recorded directly to a laptop computer and sequences recorded to tape, but few studies have quantified the magnitude of difference and its potential effect on bat survey results. In 2000, I sampled 213 locations in northwest Georgia passively with an Anabat II bat detector (Titley Electronics, Ballina, Australia) linked to a tape recorder and actively with an Anabat II detector linked to a laptop computer (hereafter referred to as tape recorder and laptop, respectively). On average, the laptop recorded >2× as many species/site as the tape recorder. Moreover, I detected 3 bat species with the laptop system that I did not detect with the tape recorder. The laptop system detected all species detected by the tape recorder. I was able to identify to species 53.2% of recorded calls on the laptop in contrast to only 28.0% of

tape-recorder calls. My results suggest that actively monitoring with an Anabat detector linked directly to a laptop computer records more bat call sequences and produces higher quality call recordings, resulting in a more complete bat community survey than passively monitoring with an Anabat detector linked to a tape recorder.

ACKNOWLEDGMENTS

TABLE OF CONTENTS

LIST OF TABLES

List of Tables (continued)

LIST OF FIGURES

INTRODUCTION, RESEARCH JUSTIFICATION, AND OBJECTIVES

Gray bats (*Myotis grisescens*) are a year-round, cave-dwelling species with a range restricted to the karst areas of the southeastern United States. Approximately 95% of the gray bat population hibernates in only 9 caves (Tuttle 1979). Human disturbance of hibernacula and maternity caves caused major population declines in the 1960s and 1970s (Tuttle 1979). Gray bat population declines also were attributed to pesticides that reduced gray bat food resources and poisoned gray bats through bioaccumulation (Tuttle 1979). Gray bats were federally listed as endangered in 1976 (*Federal Register*, 28 April, 1976) and a recovery plan was completed in 1982 (Brady et al. 1982). Gates and fences were erected to protect high-priority caves that contained large numbers of hibernating gray bats or maternity colonies from human disturbance. Gray bat populations have shown signs of recovery through cave protection efforts. For example, in Arkansas, 2 gray bat colonies increased from <100 individuals before protection, to >10,000 individuals after protection (Harvey 1994). Although protecting gray bat roosts is imperative to their survival, conservation of specific foraging areas also may be critical to individual gray bat colonies and further species recovery.

Gray bats primarily forage over open waterways such as rivers and reservoirs (LaVal et al. 1977, Best and Hudson 1996, Menzel et al. 2000b) that are within 4 km of their caves (Tuttle 1976). It has been suggested that forest cover near roost caves and foraging areas is important to gray bats because it protects gray bats from predation and protects water quality (Tuttle 1979). Physical characteristics of the water source where gray bats forage and its surrounding vegetation may affect species composition and abundances of aquatic macroinvertebrates, which develop into an important gray bat food source (Brady et al. 1982). No previous studies in the

species range have quantitatively analyzed specific habitat characteristics within foraging areas that may be important to gray bats.

Past efforts to use radio-telemetry to determine gray bat foraging areas have met with varying degrees of success (Rueter et al. 1992, Best and Hudson 1996, Menzel et al. 2000b). Flight speeds of gray bats have been estimated as high as 39 km/hour (LaVal et al. 1977), making contact with radio-transmittered gray bats difficult. Gray bats emit a unique echolocation call that allows them to be distinguished from other Myotids via ultrasonic detection equipment (Henry et al. 1992, Menzel et al. 2000b). Acoustic detection also is useful in determining spatial activity patterns of bats (Grindal 1995, Hayes and Adam 1996, Krusic et al. 1996). However, many acoustic sampling techniques exist and each has advantages and limitations that should be considered before selecting equipment and sampling protocols (Parsons et al. 2000, Fenton et al. 2001). As of summer 2000, 2 caves in northwest Georgia were known to contain gray bats during summer months (April-September). The caves are occupied by small colonies (<10,000 individuals) of male gray bats (Martin and Sneed 1990, Buhlmann 1996). Although the caves are protected through limited access, the foraging areas of these colonies are uncertain and require further investigation. Determining the spatial extent and important characteristics of the foraging areas would be an important first step in the delineation and protection of specific foraging areas. Changes in landuse near foraging areas may occur in the future due to suburban sprawl associated with the nearby metropolitan areas of Atlanta, Georgia and Chattanooga, Tennessee. Adverse effects on the gray bat foraging areas, such as pollution or sedimentation, would negatively affect gray bat populations in northwest Georgia.

Within Georgia, the gray bat is little studied (Martin and Sneed 1990, Buhlmann 1996, Menzel et al. 2000b). Small streams in proximity to roost caves may be important foraging areas

2

for gray bats in Georgia because large reservoirs and rivers are >11 km from the 2 known roost caves. Because of the limited knowledge of spatial activity patterns and foraging habitat characteristics of gray bats in northwest Georgia, my objectives included:

1) determine the spatial activity patterns of gray bats in northwest Georgia with acoustic monitoring and GIS models;

2) develop a predictive foraging habitat model based on macro- and micro-habitat characteristics; and

3) quantify the differences in echolocation data, for bat species composition and activity levels, obtained by different acoustic monitoring techniques.

CHAPTER 1 — SPATIAL AND PREDICTIVE FORAGING MODELS FOR GRAY BATS IN NORTHWEST GEORGIA

INTRODUCTION

The gray bat (*Myotis grisescens*) was federally listed in 1976 (*Federal Register*, April 28, 1976) because of drastic population declines in the 1960s and 1970s. In 1982, a recovery plan was completed that detailed the reasons for population declines and needed recovery actions (Brady et al. 1982). These declines primarily were attributed to human disturbance of hibernating gray bat colonies (Tuttle 1979). Gray bat arousal in winter causes the depletion of vital fat reserves. Because of specific thermal requirements, the majority (95%) of gray bats hibernated in only 9 suitable caves in the southeastern United States in the 1960s and 1970s, making the species highly vulnerable to human disturbance (Tuttle 1979). Pesticides also caused declines in gray bat populations through harmful bioaccumulation (Clark et al. 1983, Clark et al. 1988, Clawson 1991) and reduction of arthropod food resources (Tuttle 1979). Destruction of forested waterways, the primary foraging areas of gray bats, also was believed to have a negative effect on populations. Forests adjacent to foraging areas provide protection for gray bats against predation by screech owls (*Otus asio*) and other predators (Brady et al. 1982) as well as maintaining water quality and reducing stream sedimentation (Young and Giese 1990).

Efforts to conserve and recover gray bat populations focused on protection of large maternity colonies and hibernacula as outlined in the recovery plan. Gates and fences were placed in or near cave entrances to prevent human disturbance of colonies. Marked gray bat population increases were observed in protected caves (Harvey 1994). The gray bat recovery plan also recommended that actions should be carried out to prevent adverse modification to water quality and forest cover in gray bat foraging areas and travel corridors (Brady et al. 1982).

4

The gray bat recovery plan recommended that foraging areas and travel corridors should be identified and protected for gray bat colonies (Brady et al. 1982). Despite this, few studies of gray bats have focused on foraging habitat requirements. Although gray bats are known to primarily forage over waterways such as streams, rivers, and lakes (Tuttle 1976, LaVal et al. 1977, Best and Hudson 1996, Menzel et al. 2000b), specific macro-habitat characteristics of waterways and surrounding lands important to gray bats are uncertain. Tuttle (1979) suggested that retaining forested buffers around roost caves and forested riparian corridors along gray bat foraging routes would be beneficial. Moreover, bat activity levels in forested riparian areas are higher than in non-forested riparian areas, especially in regard to most Myotids (Hayes and Adam 1996). Gray bats in Missouri foraged over waterways adjacent to forested areas more often than waterways adjacent to pastures (LaVal et al. 1977). Although in Georgia, Menzel et al. (2000b) detected gray bats primarily in riparian areas; gray bats also were detected over adjacent fields.

Physical characteristics of water sources and surrounding vegetation influence aquatic macroinvertebrate species compositions, abundances, and emergence patterns, which can affect gray bat foraging patterns. Headwater streams have reduced autotrophic inputs because of increased canopy cover and therefore rely on terrestrial inputs, whereas medium-sized streams rely on inputs from transported material from headwaters and algal and rooted vascular plant production (Vannote et al. 1980). Along this river continuum, different niches are occupied by different macroinvertebrates. Other physical characteristics of the water source, such as siltation, can negatively affect aquatic macroinvertebrate populations that can develop into gray bat food sources (Tebo 1955, Rosenberg and Weins 1978, Angradi 1999, Kaller et al. In press).

Gray bat foraging behavior also is influenced by stream size and proximity of roost caves to streams or other foraging areas. In Missouri and Alabama, gray bats used larger, downstream portions of streams and rivers more frequently than narrower, upstream portions (LaVal et al. 1977, Best and Hudson 1996). In summer, gray bats day-roost in caves that are usually located within 4 km of a major river or reservoir in Alabama, Florida, Tennessee, and Virginia (Tuttle 1976). However, on the Meramec River in Missouri, gray bats routinely traveled 30-70 km from caves when foraging (LaVal et al. 1977).

Limited quantitative data exists on the foraging patterns of gray bats in northwest Georgia. In Walker and Chattooga Counties, 2 known bachelor colonies exist, one at Frick's Cave and one at Lowery's Cave. Both of these caves are located >11 km from major waterways. Gray bats in northwest Georgia may need to travel farther to forage in larger waterways than other gray bat populations in the Southeast. Or conversely, small streams in proximity to these roost caves may be important foraging areas and travel corridors for gray bats. Although these caves are protected through limited access, the spatial extent of the colonies' foraging areas is uncertain. Preliminary radio-telemetry data suggested that gray bats from Frick's Cave used West Chickamauga Creek and its tributaries when foraging (Menzel et al. 2000b). Light-tagged gray bats from Lowery's Cave were observed flying over the Oostanaula River (Johnson et al. unpublished data). Determining the spatial extent and important characteristics of gray bat foraging areas is a crucial first step in the delineation and protection of critical habitat. The ability to predict gray bat spatial activity patterns on a landscape-scale with Geographic Information Systems (GIS) would be an efficient method of delineating critical habitat.

Consequently, the objectives of my study were to: 1) use acoustic monitoring to determine the spatial activity patterns of gray bats in northwest Georgia; and 2) develop

predictive landscape-level and macro-habitat level models of gray bat foraging patterns in northwest Georgia.

STUDY AREA

I conducted my study in the Cumberland Plateau and Ridge and Valley physiographic provinces in northwest Georgia (Catoosa, Chattooga, Dade, Floyd, Gordon, Murray, Walker, and Whitfield Counties). Chattanooga, Tennessee is approximately 30 km north of Frick's Cave and Atlanta, Georgia is approximately 100 km southeast of Lowery's Cave. This area is characterized by long, linear ridges and plateaus with sharp escarpments rising 300-400 m above valley floors. River valleys are wide and flat in the Ridge and Valley province to the east, with water courses forming deeply cut, narrow gorges to the northwest on the Cumberland Plateau province. Approximately 8,820 km of streams and rivers run through the study area. Oak (*Quercus* spp.) -pine (*Pinus* spp.) forests predominate in uplands. Riparian areas include communities with sweetgum (*Liquidambar styraciflua*), sycamore (*Platanus occidentalis*), yellow-poplar (*Liriodendron tulipifera*) or shrub wetlands where buttonbush (*Cephalanthus occidentalis*) and black willow (*Salix nigra*) occur. Much of the valley area in the Ridge and Valley has been cleared for pasture and row crops. Limestone geology occurs throughout the area and is unique among Georgia's physiographic provinces for its abundance of caves (Wharton 1978). Eight species of bats are confirmed in the area, including: gray bat, small-footed myotis (*Myotis leibii*), little brown bat (*M. lucifugus*), northern long-eared myotis (*M. septentrionalis*), Indiana myotis (*M. sodalis*), silver-haired bat (*Lasionycteris noctivagans*), eastern red bat (*Lasiurus borealis*) and eastern pipistrelle (*Pipistrellus subflavus*). Additionally, Rafinesque's big-eared bat (*Corynorhinus rafinesquii*), big brown bat (*Eptesicus fuscus*), hoary

bat (*L. cinereus*), and evening bat (*Nycticeius humeralis*) also may occur in the area (Menzel et al. 2000a), but have not been confirmed.

METHODS

Acoustical Monitoring

To investigate spatial activity patterns of gray bats on a landscape level and on a macro-habitat level in summer 2000 (June-August), I sampled 213 sites near water sources by actively monitoring and recording bat activity with an Anabat II (Titley Electronics, Australia) bat detector linked to a laptop computer (Fig. 1-1). An 8.3 × 9.4 km sampling grid was established over a 5,100 km^2 study area in the northwestern corner of Georgia (Fig. 1-1). Each grid crossing ($n = 69$) was sampled by locating 3-4 water sources within 4 km of each grid intersection on a topographic map (Fig. 1-2). Water sources included ponds, lakes, streams, and rivers. The Anabat II bat detector was held approximately 1 m above the ground and was slowly swept back and forth to scan for activity over the water. When activity was detected, the detector was oriented to capture as much of the bat call sequence as possible. I monitored bat activity at each site ($n = 213$) for 20 minutes between 2115 and 0200 hours (3-10 sites per night). Sampling was not conducted during periods of high wind or rain.

Calls sequences were recorded to a Compaq Presario 1200 computer (Compaq Computer Corporation, Houston, Texas, USA) via an Anabat V Zero-Crossing Analysis Interface Module (ZCAIM) and Anabat 6.2d software (Corben 1999). Calls were analyzed with Analook 4.7j software (Corben 1999). I used qualitative and quantitative methods to identify calls. I identified all calls to reduce variation in identification accuracy (O'Farrell et al. 1999) and only identified call sequences containing ≥3 pulses. I examined calls using Analook software with filter parameters similar to those described by Britzke and Murray (2000). Filters were necessary to

preserve the diagnostic portion of the echolocations calls, while screening out the unnecessary portions that would interfere with quantitative techniques used for identification, particularly the slope of Myotid calls. I qualitatively identified calls of non-Myotids by comparing structures and frequencies of unknown calls to known calls of hand-released bats marked with chemiluminescent tags (Fenton and Bell 1981). The library of known calls was comprised of calls from bats across the southeastern United States (Menzel et al. In press). I quantitatively identified Myotids based on frequency and slope characteristics of calls (O'Farrell 1999, Britzke and Murray 2000).

Habitat Sampling

I measured 23 habitat variables at each sampling location that would likely influence gray bat presence either directly or indirectly. Certain water and vegetation variables could influence macroinvertebrate species compositions, abundances, and emergence patterns, therefore influencing gray bat presence. Other potential variables (e.g. water chemistry) were not measured because of time constraints and/or lack of appropriate equipment. The 23 variables that were measured were defined as follows:

1) Shrub (shrub; Table A-1) was an estimate of the amount of clutter (e.g. vegetation, tree limbs) over the water sources that could potentially impede the flight of bats. I separated the stream at each location into 20 1-m segments; 10 upstream and 10 downstream from the sampling location. Each segment was tallied if there was clutter within the segment and <3 m of the water's surface, therefore giving a total value of 0-20. On ponds and lakes a value of 0 was automatically given unless there was clutter that would warrant a tally;

2) Percent canopy cover (%canopy) over each sampling location was estimated at 5 points (5-m spacing); 1 at the sampling location, 2 upstream and 2 downstream from the sampling location. At each point, the percent canopy cover was estimated as 0, 25, 50, 75, or 100%. The values for the 5 points were then averaged for each sampling location;

3) Number of snags (>4 m height and >10 cm DBH; snags) within 50 m of each sampling location was counted. Trees with cavities and/or dead limbs were counted;

4) Number of trees (>4 m height and >10 cm DBH) within 50 m of each sampling location with exfoliating bark (exfobark), such as shagbark hickory (*Carya ovata*), was counted. It was possible to also count a tree in this category as a snag;

5) Clarity of the water (clarity) at each sampling location was classified as clear, semi-turbid, or turbid. I defined turbid water as having obvious suspended sediment that made viewing the substrate at depths greater than 15 cm impossible. Semi-turbid water made viewing the substrate possible only to a depth of 30 cm. Clear water made viewing substrate possible at depths >30 cm;

6-7) The width (m) of the forest immediately adjacent to the water source on each bank at each sampling location (sside1 and sside2) was measured with a laser range finder from the water's edge to the nearest opening (e.g. field, road) perpendicular to the shoreline;

8) The temperature (°C) of the water (wtemp) at each sampling location was determined with an aquarium thermometer;

9) The height (m) of the forest (forestht) adjacent to the water source at each sampling location was determined using a laser range finder to measure the distance to the forest. A clinometer was then used to measure the angle to the top of the canopy. The distance and

angle metrics were then entered into the trigonometric formula for measuring tangents to obtain the height;

10) The substrate of each water source (substrate) was qualitatively classified as clay/mud, sand, gravel, cobble, or bedrock;

11) The surface of the water (actflo) was qualitatively classified as pool, run, riffle, or rapid;

12) The current speed of the water source (sspeed) at each sampling location was qualitatively assessed as still, slow, or fast;

13) I noted if the sampling location was within 50 m of a bridge, and if so, whether the bridge was unimproved, gravel, single-lane paved, double-lane paved, or expressway (bridge);

14) The water source at each sampling location was qualitatively assigned to alluvial bottom, narrow bottom, terraced bottom, or incised stream (immland);

15) The land surrounding each sampling location as was qualitatively assigned as flat peneplain, rolling hills, knobs, linear ridges, or mountains (surrland);

16) The width (m) of each water source (actwid) was measured with a laser range finder or tape measure;

17) The channel width (m) of the stream (bankfull) was measured with a laser range finder or tape measure;

18-19) The depth of each water source at the bank (dbank) and at the center (dcent) was classified as 0-15 cm, 16-90 cm, or >90 cm;

20) I noted if the sampling location was located within 50 m of a waterfall/discernable plunge pool system or not (wfall);

21) I noted if none, one, or both streambanks were undercut from erosion by the water (undercut);

22) I noted if none, one, or both streambanks were vegetated (veg); and

23) I noted if none, one, or both streambanks were forested (forest).

GIS Analysis

I used ArcView 3.2 (ESRI 1999a) and Spatial Analyst 2.0 (ESRI 1999b) to acquire and analyze landscape-level data. County-wide digital elevation models (DEM; 30-m resolution) were obtained from Georgia Spatial Data Infrastructure (GSDI 2000) and were assembled using the Mosaic function in Map Calculator. Digital line graphics (DLG) of all streams and rivers (scale 1:24,000) and polygons of ponds and lakes (scale 1:12,000) also were obtained from GSDI (2000). I used a landuse/landcover theme (30-m resolution) from the United States Geological Survey Gap Analysis Program (USGS GAP 2000) that contained 16 landuse/landcover types (Table A-2).

I measured 17 habitat variables with GIS, defined as follows:

1-13) The percent of each landuse/landcover type (e.g. %11, Table A-2) in a 1-ha area surrounding each sampling location was determined by creating a 56.4 m buffer around the center of each sampling location and using the Tabulate Areas function in the Analysis menu of ArcView;

14) Stream order (sorder) was determined for each stream segment in the DLG by using the Strahler method (Strahler 1964);

15) The distance (m) from each sampling location to each cave (distnear) was calculated by using UTM coordinates of the caves and sampling locations entered into the Pythagorean Theorum;

16) The elevation (m; elev) of each sampling location was obtained by using the Summarize Zones function in the Analysis menu of ArcView; and

17) A model within a GIS was developed to predict gray bat spatial activity patterns over the study area. Preliminary radio-telemetry data collected by Menzel et al. (2000b) indicated that bats from Frick's Cave primarily foraged over West Chickamauga Creek. Light-tagged gray bats traveling from Lowery's Cave were observed from bridges on the Oostanaula River (Johnson et al. unpublished data). Acoustic data collected in summer 2000 suggested the presence of 2 additional gray bat colonies; one near the town of Ringgold in Catooosa County and one in Dade County (possibly in Sitton's Cave that was historically a gray bat cave).

To determine if there was a spatial pattern to sampling locations that produced gray bats, I hypothesized that gray bats use the nearest and largest stream to their cave and the tributaries of that stream to some threshold width. I divided the study area into 4 areas, one for each gray bat colony (Fig. 1-3), based on the likelihood that a maximum of 4 gray bat colonies (one near Ringgold, Frick's Cave, Lowery's Cave, and Sitton's Cave) existed in northwest Georgia. Separation among colonies was based on likely topographic barriers such as Lookout Mountain, drainage basin delineations, and halfway distances between caves. I determined the riparian corridor distance from the nearest point of the main foraging stream to the cave, to the farthest sampling location that produced a gray bat that likely came from that cave. I used this greatest distance for any cave and applied it to all caves. Gray bats from any cave could travel as great a distance, upstream or downstream from the point on the main foraging stream closest to the cave, as any gray bat from any other cave. I limited the distance a gray bat could fly upstream on a tributary from the main foraging stream (if not first limited by stream width) to the distance from the intersection of the tributary and the main foraging stream to the greatest likely

13

distance traveled on the main foraging stream from that intersection. The sum of the distance traveled upstream on the tributary and the distance traveled on the main foraging stream from the point closest to the cave would equal the greatest distance traveled on the main foraging stream.

Additionally, I hypothesized that gray bats would use any size stream within a certain distance of their cave for purposes of traveling to the main foraging stream. A buffer around each cave was created that included the maximum proportion of sample locations producing gray bats with the least amount of area included. In ArcView3.2, I selected all segments of the main foraging stream for each cave, both upstream and downstream from the point closest to the cave, within the aforementioned greatest distance. I selected all tributaries to each main foraging stream based on criteria described above. All streams within a 3.5-km buffer of each cave were selected with the Select by Theme function in the Theme menu. A new theme was created in ArcView comprised of the selected stream segments. I used the Create Buffers function in the Theme menu to create a 150-m buffer around the stream segments in the new theme. All sampling points within the buffer were selected using the Select by Theme function to create a binary variable (i.e. within buffer and without buffer) for each sampling location (GIS model). A 150-m buffer was an arbitrary value used to include sampling locations that may have differed from their true geographic position due to GPS variation or locations that had GPS data collected a negligible distance from the correct sampling location. The threshold minimum stream order was determined by excluding all first-order streams from the GIS model and determining the proportion of locations producing gray bats within the GIS model. Iteratively, I excluded all second-order streams, all third-order

streams, and so on, until the maximum proportion of locations producing gray bats was retained with the largest, minimum stream order included. I then determined if actual stream width was significantly correlated with stream order (ProcCorr; SAS Institute Inc. 1990); if stream orders were significantly different based on their corresponding widths, which stream orders corresponded to the mean and range of stream widths was determined by a Kruskal-Wallis test and Duncan's New Multiple Range Test (Proc Npar1way; SAS Institute Inc. 1990). The proportion of streams in the study area included in the GIS model was determined by converting the DLG stream theme and the GIS model theme into a 10 × 10 m grid theme and then dividing the number of cells in the GIS model by the number of cells in the DLG stream theme.

In summer 2001, I sampled 114 locations that were predicted on a landscape level as gray bat foraging areas based on data from 2000 to further refine gray bat spatial activity patterns on a macro-habitat level (Fig. 1-4). Active acoustic monitoring to a laptop computer was primarily conducted from a boat to access points not accessible by foot, boat ramps, or bridges. All sampling protocols established in summer 2000 were used except for the sampling grid. None of the locations sampled in 2000 were re-sampled in 2001.

Statistical Analysis

I used a chi-square test (Proc Freq; SAS Institute Inc. 1990) to determine if the number of sampling locations producing gray bats and the number of sampling locations not producing gray bats were proportional to the number of sampling locations at lentic (ponds and lakes) water sources and the number of sampling locations at lotic (streams and rivers) water sources. If there was disproportionate use of lentic and lotic water sources, I focused the logistic analyses on the water source type that gray bats used greater than expected.

I examined independent variables in each analysis for collinearity (Proc Corr; SAS Institute Inc. 1990) before logistic analyses were executed. Collinearity in the datasets did not require remedial action. To determine if gray bat presence could be predicted on a landscape level (i.e. study area), I conducted a logistic analysis on the landscape-level variables (distnear, elev, GISmodel, immland, surrland) measured in 2000. To determine if gray bat presence could be predicted on a macro-habitat level, I conducted a logistic analysis, on data from locations sampled in 2000 that were predicted to produce gray bats by the landscape-level model and data from all locations sampled in 2001. All variables were tested that were not used in the landscape-level analysis for the entire study area ($n = 35$). Stepwise variable selection was used in logistic analyses. Jackknife (Ctable option; Proc Logistic; SAS Institute Inc. 1990) and bootstrap procedures (SAS Institute Inc. 1995) were used to determine the classification accuracy of each model. Hosmer and Lemeshow goodness-of-fit tests, generalized coefficients of determination, and adjusted generalized coefficients of determination were computed for each model (Lackfit and Rsq options; Proc Logistic; SAS Institute Inc. 1990). Brier scores were used to compare predictive abilities of models (Brier 1950).

RESULTS

Acoustical Monitoring

I collected a total of 6,314 echolocation calls at 213 sampling locations in summer 2000. I identified calls of big brown bats ($n = 50$) at 32 locations, eastern red bats ($n = 307$) at 34 locations, hoary bats ($n = 5$) at 5 locations, gray bats ($n = 237$) at 34 locations, little brown bats ($n = 56$) at 28 locations, northern long-eared bats ($n = 23$) at 13 locations, Indiana bats ($n = 2$) at 2 locations, unidentified species of Myotids ($n = 157$) at 66 locations, and eastern pipistrelles

(n = 2,626) at 156 locations. A total of 2,851 (45%) echolocation calls were unidentifiable at 192 locations. Only 16 (7.5%) sampling locations produced no bat activity.

Spatial Patterns

Sampling locations (n = 213) ranged from 1.2 km to 46.3 km straight-line distance from the nearest gray bat cave. Gray bat presence (n = 34) was recorded from 1.6 km to 28.0 km straight-line distance from the nearest gray bat cave. The maximum riparian corridor distance from a gray bat cave to a sampling location that produced gray bats was 66.0 km from Lowery's Cave to a sampling location on the Oostanaula River. Therefore, it was assumed that any gray bat in northwest Georgia could fly up to 66.0 km riparian corridor distance from its cave while foraging.

Gray bats used lotic water types in greater proportion to lentic water types (χ^2 = 4.15; P = 0.040). Therefore, all sampling locations at lentic water types were deleted from subsequent analyses, which excluded 30 sampling locations and approximately 22% of water surface area in northwest Georgia.

I detected gray bats at 2130 hours at one sampling location on South Chickamauga Creek near Ringgold. Assuming that gray bats exited caves at approximately 2100 hours, it was unlikely that they could travel from the nearest known gray bat roost cave (Frick's) to the sampling location (34.2 km) in 30 minutes. I observed gray bats exiting Lowery's Cave at 2100 hours, 1 week after the aforementioned location was sampled. On the basis of these findings, I speculated that a previously unknown gray bat colony existed near Ringgold, possibly Chickamauga Cave. Spatial data also suggested the presence of a fourth gray bat colony in Dade County, possibly Sitton's Cave, which was historically occupied by gray bats. Therefore, I considered all 4 caves when constructing the spatial foraging model.

Lookout Creek was the nearest and largest stream to Sitton's Cave (approximately 4 km); West Chickamauga Creek was the nearest and largest stream to Frick's Cave (approximately 4 km); South Chickamauga Creek was the nearest and largest stream to Chickamauga Cave (0 km); and the Oostanaula River was the nearest and largest stream to Lowery's Cave (approximately 12 km). When all streams within 66 km riparian corridor distance of the nearest point on the main foraging stream to the cave were included in the GIS model, 87 of 213 sampling locations were within 150 m of the streams in the model. Gray bats were detected at 28 of 87 (32.2%) sampling locations. However, approximately 48% (4,234 km) of all streams and rivers in northwest Georgia were included in the model (Fig. 1-5, Table 1-1). When only second-order and larger streams were included in the GIS model, 84 of 213 (39.4%) sampling locations were within 150 m of the streams in the model. Gray bats were detected at 28 of 84 (33.3%) sampling locations. Approximately 23% of all streams and rivers in northwest Georgia were included in the GIS model. When third-order and larger streams were included in the GIS model, 76 sampling locations were within 150 m of streams in the model. Gray bats were detected at 27 of 76 (35.5%) sampling locations. Approximately 14% (1,235 km) of all streams and rivers in northwest Georgia were included in the model. When fourth-order and larger streams were included in the GIS model, 53 sampling locations were within 150 m of streams in the model. Gray bats were detected at 20 of 53 (37.7%) sampling locations. Approximately 7% of streams and rivers in northwest Georgia were included in the model. The GIS model that included only third-order and larger streams retained 79.4% of sampling locations producing gray bats and included 14.4% of streams and rivers in northwest Georgia (Fig. 1-6). This model was used in further analyses because it contained a relatively high proportion of sample points that produced gray bats and a relatively low proportion of all streams and rivers in northwest Georgia.

Stream order was significantly correlated with the actual width of streams and rivers across the landscape (2000 and 2001 data combined; $r^2 = 0.776$; $P < 0.001$). Some stream orders were significantly different based on their corresponding actual widths (Table 1-2; $P < 0.001$).

Predictive Models

Surrounding landclass ($P = 0.038$) and GIS model ($P < 0.001$) variables were significant predictors of gray bat presence on the landscape scale (Table 1-3, Table A-3). The GIS model had a max-rescaled R^2 value of 0.229. The landscape model:

Gray bat presence = – 1.7425 – 0.6074(Surrland) + 2.2793(GISmodel)

had a max-rescaled R^2 value of 0.273. There were no significant correlations ($r^2 < 0.366$) between the variables "GISmodel" and "Surrland" with any other independent variables. The jackknife procedure indicated that the landscape model correctly classified 54.1% of observations at $P = 0.05$ (Table 1-4) while the bootstrap method indicated that 83.6% of observations were correctly classified at $P = 0.05$ (Table 1-4). False positives outweighed false negatives in both classification methods. However, the bootstrap method indicated that the model classified 'no events' more consistently (96.0%) than 'events' (27.3%), while the jackknife indicated that the model classified 'events' more consistently (81.8%) than 'no events' (48%). The model produced a Brier score of 0.11 (Brier scores range from 0-1; scores approaching 0 indicate an improving model). The bootstrap method predicted gray bats at 15 locations. Only 9 of the 15 (60.0%) produced gray bats in 2000 and 14 of 15 (93.3%) fell within the GIS model. To predict gray bats on a macro-habitat scale with logistic analysis, more than 15 sampling locations were required (Neter et al. 1989).

Therefore, to develop a macro-habitat model, I collected 5,124 echolocation calls at 114 sampling locations in summer 2001. I identified calls of big brown bats ($n = 57$) at 13 locations,

eastern red bats ($n = 83$) at 28 locations, hoary bats ($n = 5$) at 1 location, gray bats ($n = 620$) at 87

locations, little brown bats ($n = 17$) at 8 locations, northern long-eared bats ($n = 18$) at 10

locations, eastern pipistrelles ($n = 1,841$) at 83 locations, and undetermined eastern red

bat/eastern pipistrelles ($n = 10$) at 6 locations. A total of 1,865 (36.4%) echolocation calls were

unidentifiable from 111 locations. All sampling locations produced bat activity in summer 2001.

A total of 129 sample points were used to execute macro-habitat logistic analysis (15

from 2000 that were predicted with the landscape model and all 2001 data). Stream order had the

highest max-rescaled R^2 value in the model (0.124), followed by clarity (0.059), shrub (0.048),

and percent pasture (0.037) (Table 1-5, Table A-4). The macro-habitat model:

Gray bat presence = 0.3743 + 0.9156(sorder) − 1.6038(clarity) + 1.7705(percent pasture)

− 0.2073(shrub)

had a max-rescaled R^2 value of 0.293. Stream order was significantly correlated with actwid

($r^2 = 0.768$; $P < 0.001$), bankfull ($r^2 = 0.759$; $P < 0.001$), clarity ($r^2 = 0.672$; $P < 0.001$), shrub

($r^2 = -0.578$; $P < 0.001$), %canopy ($r^2 = -0.529$; $P < 0.001$), dcent ($r^2 = 0.505$; $P < 0.001$), and

dbank ($r^2 = 0.502$; $P < 0.001$). Clarity was significantly correlated with actwid ($r^2 = 0.774$;

$P < 0.001$), bankfull ($r^2 = 0.767$; $P < 0.001$), shrub ($r^2 = -0.540$; $P < 0.001$), and %canopy

($r^2 = -0.529$; $P < 0.001$). Shrub was significantly correlated with bankfull ($r^2 = -0.528$;

$P < 0.001$) and actwid ($r^2 = -0.526$; $P < 0.001$). The percent of land cover in pasture/hay in the

hectare surrounding each sample point was not significantly ($P < 0.438$) correlated with any

independent variable. An analysis of the percent of land cover in a 56.4 m buffer around the GIS

model revealed that deciduous forest was the most frequent landuse (27%), followed by

pasture/hay (26%) across the study area. The jackknife procedure indicated that the macro-

habitat model classified 74.4% of observations correctly while the bootstrap procedure indicated

90.7% of observations were correctly classified (Table 1-6). The bootstrap procedure indicated that gray bat presence could be predicted more often than absence (96.9% vs. 72.7%). The jackknife procedure classified all observations as 'present' and no observations as 'absent'. The Brier score for the macro-habitat model was 0.09.

DISCUSSION

Data collected in 2000 suggested the presence of 2 additional gray bat roost caves. Gray bats were detected on the South Chickamauga Creek near Ringgold, Georgia at 2130 hours. The nearest known gray bat roost cave (Frick's) was 34.2 km away. Therefore, a gray bat exiting Frick's Cave at 2100 hours had to fly an unlikely average speed of 68.4 km/hour to reach this location. LaVal et al. (1977) and Menzel et al. (2000b) reported maximum gray bat flight speeds of 39 km/hour and 25.1 km/hour, respectively. In spring 2001, a colony of gray bats was located in Chickamauga Cave near Ringgold by the Georgia Department of Natural Resources. Approximately 5,000 gray bats use Chickamauga Cave according to population estimates using Tuttle's (1976) ceiling staining estimates. Gray bats also were detected on Lookout Creek in Dade County. Frick's Cave is the nearest known gray bat roost to Lookout Creek. However, Lookout Mountain stands between Frick's Cave and Lookout Creek and has an elevation of 700 m and rises 365 m above the valley floor. Best and Hudson (1996) observed that, in Alabama, gray bats will traverse over land between streams. However, the topography on their study site was relatively flat (<60 m difference). Lookout Mountain is plateau-like and has streams and ponds on top. Gray bats were not detected at any sampling locations on top of Lookout Mountain. Moreover, there was no direct riparian corridor from Frick's Cave to Lookout Creek, making it energetically expensive for gray bats to travel over Lookout Mountain to Lookout Creek. It is therefore likely that a gray bat roost cave exists in Dade County, possibly Sitton's

Cave, which historically contained gray bats. Sitton's Cave and other potential gray bat caves in the area should be surveyed for gray bats.

In northwest Georgia, gray bat spatial foraging patterns were similar to those previously reported in other areas of the Southeast and Midwest (Tuttle 1976, LaVal et al. 1977, Best and Hudson 1996). Gray bats were detected along streams and rivers more frequently than near lakes and ponds. This was expected because gray bat roost caves were farther from major lakes and ponds and closer to streams and rivers. However, this does not mean that gray bats are not using ponds and lakes in northwest Georgia as foraging areas. It simply means that gray bats are not foraging over ponds and lakes to the extent that they are foraging over the streams and rivers. Gray bats likely foraged over the largest body of water and tributaries near their roost caves. All known and predicted gray bat roost caves in northwest Georgia, except Lowery's Cave, are <4 km of foraging areas, consistent with previous findings (Tuttle 1976, Best and Hudson 1996). Lowery's Cave is approximately 12 km from the Oostanaula River, which is the closest, major body of water. Gray bats in northwest Georgia were found to travel up to 66 km riparian corridor distance during foraging, which is not uncommon, based on previous studies that report foraging distances of >30 km (Tuttle 1976, LaVal et al 1977, Rueter et al. 1992, Best and Hudson 1996, and Menzel et al. 2000b). Straight-line distances from sampling points that produced gray bats to the cave from which they likely roosted ranged from 1.6 to 28.0 km, which is consistent with other gray bat studies (Tuttle 1976, LaVal et al. 1977). Menzel et al. (2000b) reported distances of gray bat foraging movements ranging from 8.9 to 18.2 km based on homerange estimates from Frick's Cave.

If there were no spatial patterns in foraging activities of gray bats other than their affinity for waterways, I would have expected to detect gray bats across the entire landscape (i.e., study

area), including over waterways on top of mountains (e.g. the plateau-like area of Lookout Mountain). I did not detect gray bats at any sampling points located on mountains and ridge tops. Moreover, the landscape-level logistic analysis indicated that lower elevations were more likely to contain gray bats. Surrounding landclass was a significant predictor of gray bat presence in the landscape-level model, which suggests that gray bats are more likely to forage in relatively flat topography rather than in mountainous landscapes. Menzel et al. (2000b) reported that gray bats from Frick's Cave foraged in valleys and avoided ridge tops, although sample size was limited. In British Columbia, Grindal et al. (1999) found an increase in bat activity in lower elevations compared to higher elevations. Gray bats in northwest Georgia foraged at low-elevation drainage basins that contained the largest body of water and its tributaries near their roost caves. The GIS model also predicted that gray bats forage over the largest body of water near their roost caves.

The GIS model contained 79% of sample points where gray bats were detected and included only 14% (1,235 km) of all streams within the study area. The model is strengthened by the fact that when systematically sampling across the landscape in 2000, only 16% of sampling locations produced gray bats, whereas 76% of sampling locations produced gray bats in 2001 within areas predicted by the GIS model. The GIS model contained third-order and larger streams that had a mean width of 5.75 m. In terms of actual width, third-order streams were not significantly different than second-order streams. However, if second-order streams were included in the GIS model, percent streams across the study area included in the model would increase to 23% (2,029 km), while only including an additional 3% of sampling locations producing gray bats. My GIS model should not be construed as suggesting that first and second-order streams are not important to gray bat foraging areas. I suspect that gray bats probably cannot efficiently forage in narrow, upstream portions of streams because of increased clutter

over the stream surface that masks prey echoes and decreases prey detection and increases flight difficulty (Mackey and Barclay 1989, Brigham et al. 1997). However, all streams, including first- and second-order, within 3.5 km of gray bat roost caves should be considered for conservation as they may be important travel corridors to larger streams and rivers that are primary foraging areas. Larger streams within the GIS model (i.e. gray bat foraging areas) will be affected by impacts, such as sedimentation, pollution, and deforestation, of the first- and second-order streams that flow into them. Deforestation of riparian areas in western Oregon has been associated with lower bat activity levels, particularly Myotids (Hayes and Adam 1996).

The macro-habitat model indicated that gray bats more frequently foraged over larger, downstream portions of streams and rivers than narrower, upstream portions in northwest Georgia. In both Missouri and Alabama, this aspect of gray bat behavior is similar (LaVal et al. 1977, Best and Hudson 1996). The correlations of independent variables in the macro-habitat model also support the previous research. Stream order was positively correlated with actual width, bankfull, clarity, depth at center, and depth at bank, and negatively correlated with shrub and percent canopy. Gray bat presence was negatively correlated with water clarity, indicating that gray bats were more likely to forage over more turbid waters. However, this is probably a factor of water turbidity being positively correlated with stream order. Larger streams were more turbid in northwest Georgia. The amount of shrub or obstruction over the water surface was negatively correlated with gray bat presence. However, 'shrub' was negatively correlated with stream order. Therefore, as a stream becomes larger (widens), the amount of open space over the water's surface increases, which increases the likelihood of gray bat presence. There are several reasons why gray bats are more likely to use the larger, downstream portions of waterways. One reason, which has already been discussed, is that gray bats probably cannot efficiently forage

24

within the narrow portions of streams that tend to have clutter over the surface. Secondly, gray bats in large colonies probably have to forage great distances to avoid competition with other gray bats within their colony. Gray bats have a unique foraging behavior in that they are restricted to waterways, which limits the areas in which they can forage. The third reason that gray bats use larger, downstream portion of waterways is that macroinvertebrate production is likely higher and more reliable in those areas. The production in medium-sized streams relies on upstream processing inefficiencies and autotrophy provided by algae and rooted vascular plants, whereas the shaded, upstream portions of streams rely heavily on terrestrial inputs, which may not be as reliable or abundant (Vannote et al. 1980). Therefore, gray bats may use the larger, downstream portions of waterways because the reliability of the food source. Other water characteristics, such as water chemistry, can affect macroinvertebrates, which in turn affect gray bats, were not measured but may warrant further investigation.

Gray bat foraging appears restricted to riparian areas (Tuttle 1976, LaVal et al. 1977, Menzel et al. 2000b), similar to several other Myotids such as *M. austroriparius* (Barbour and Davis 1969), *M. velifer* (Barbour and Davis 1969) and *M. yumanesis* (Barbour and Davis 1969, Brigham et al. 1992). In general, all bat activity is higher in riparian areas than upland areas (Grindal et al. 1999). Bat activity is generally lower in deforested areas of riparian corridors and higher in wooded sections (Hayes and Adam 1996). In northwest Georgia, it is likely that gray bats forage in the riparian areas predicted by the GIS model that are adjacent to pasture/hayfields. The percent of pasture/hayfields landuse as a significant predictor of gray bat presence in the macro-habitat model is consistent with the study by Menzel et al. (2000b) that reported that gray bats used fields more than intact forests, but less than riparian areas.

The robustness of the landscape and macro-habitat models should ultimately be tested by applying them to gray bat colonies whose foraging areas are uncertain. In northwest Georgia, foraging areas were not as obvious as in other parts of the gray bat's range where roost caves were located within 4 km of a major waterway, such as the Tennessee River-Guntersville Reservoir area in northern Alabama. The foraging areas of a gray bat colony that is not proximal to a major river or reservoir can be determined through the use of 3 powerful analytical tools; acoustic monitoring, GIS, and logistic regression.

These models can be used to predict, prioritize, and delineate potential gray bat foraging areas for conservation. Determining the spatial activity patterns of gray bats in northwest Georgia and specific foraging areas requirements may ultimately lead to more knowledgeable land management decisions that will benefit gray bats in Georgia and across their entire range.

MANAGEMENT IMPLICATIONS

The ability to predict the spatial activity patterns of gray bats should allow for the conservation of important gray bat foraging areas rather than conservation of random riparian areas across the landscape or prioritizing riparian areas in a descending manner as distance increases from roost caves. Results from my study should enable land managers to focus their conservation efforts on gray bat foraging habitat. Once gray bat foraging areas are delineated, accurate population estimates of gray bats at each roost cave must be ascertained to ensure that gray bat numbers are stable or increasing. Frick's Cave is likely the most important gray bat cave in northwest Georgia because population estimates are approximately 10,000 individuals. Therefore, West Chickamauga Creek and its main tributaries are the most important gray bat foraging areas. West Chickamauga and South Chickamauga Creeks merge approximately 15 km riparian corridor distance northwest of Chickamauga Cave. Gray bats from Chickamauga Cave

may share West Chickamauga Creek as a foraging area with gray bats from Frick's Cave. More accurate population estimates are needed for the Chickamauga Cave colony. Efforts to protect this cave through gating or fencing may be necessary. Estimates of the number of gray bats in Lowery's Cave range from 4,000 to 9,000 individuals (Martin and Sneed 1990). The Oostanaula River and its tributaries are the most important foraging areas for this colony. Improvement of water quality and acquisition of riparian corridors on the Oostanaula River and its tributaries will be more difficult than for South and West Chickamauga Creeks and Lookout Creek because of the relatively large watershed involved. The cave that contains the gray bat colony in Dade County should be found as soon as possible and protected from human disturbance.

Table 1-1. Minimum stream orders, percent of all streams in study area, total lengths of rivers and streams, percent of all sampling locations that produced gray bats ($n = 213$), and percent of gray bat-producing locations ($n = 34$) retained within GIS model in northwest Georgia, 2000.

Minimum stream order in model	Streams in model	Total lengths (km) of rivers and streams in model	Locations within model that produced gray bats	Gray bat-producing locations within model
1	48	4,234	32	82
2	23	2,029	33	82
3	14	1,235	36	79
4	11	970	38	59
5	8	706	50	53
6	6	529	38	26
7	4	353	33	15

Table 1-2. Stream orders and corresponding actual widths (m) from 297 locations in northwest Georgia, 2000 and 2001.

Stream order	n	Actual width	
		Mean [a]	SE
1	6	3.75A	1.22
2	25	5.98AB	1.03
3	68	5.75AB	0.51
4	68	11.59B	0.67
5	57	18.51C	0.72
6	67	41.04D	1.70
7	6	90.37E	4.58

[a] Means with different capital letters differ as determined by
Duncan's New Multiple Range Test.

Table 1-3. Results of logistic analysis of landscape-scale variables where gray bats were present ($n = 33$) and absent ($n = 150$) in northwest Georgia, 2000.

Variable	Parameter estimate	SE	Wald χ^2	$P > \chi^2$	Odds ratio
Surrounding landclass	−0.607	0.293	4.287	0.038	0.545
GIS model	2.279	0.490	21.635	0.001	9.770

Table 1-4. Jackknife and bootstrap classification procedures from logistic analysis of landscape-level variables where gray bats were present ($n = 33$) and absent ($n = 150$) in northwest Georgia, 2000.

		Correct		Incorrect						
Procedure	Probability level	Event[a]	Non-event[b]	Event[c]	Non-event[d]	Correct[e]	Sensitivity[f]	Specificity[g]	False positives[h]	False negatives[i]
Jackknife	0.05	27	72	78	6	54.1	81.8	48.0	74.3	7.7
Bootstrap	0.05	9	144	6	24	83.6	27.3	96.0	40.0	14.3

[a] Observations correctly predicted for gray bat presence
[b] Observations correctly predicted for gray bat absence
[c] Observations incorrectly predicted for gray bat presence
[d] Observations incorrectly predicted for gray bat absence
[e] Proportion of event and non-event responses predicted correctly
[f] Proportion of event responses that were predicted to be events
[g] Proportion of non-event responses that were predicted to be non-events
[h] Proportion of predicted event responses that were observed as non-events
[i] Proportion of predicted non-event responses that were observed as events

Table 1-5. Results of logistic analysis of macro-habitat-scale variables where gray bats were present ($n = 96$) and absent ($n = 33$) in northwest Georgia, 2000 ($n = 15$) and 2001 ($n = 114$).

Variable	Parameter estimate	SE	Wald χ^2	$P > \chi^2$	Odds ratio
Clarity	−1.604	0.573	7.845	0.005	0.201
Shrub	−0.207	0.081	6.563	0.010	0.813
Percent pasture/hay	1.771	0.856	4.281	0.039	5.874
Stream order	0.916	0.293	9.787	0.002	2.498

Table 1-6. Results of jackknife and bootstrap classification procedures from logistic analysis of macro-habitat where gray bats were present ($n = 96$) and absent ($n = 33$) in northwest Georgia, 2000 ($n = 15$) and 2001 ($n = 114$).

| Procedure | Probability level | Correct | | Incorrect | | | | | | |
		Event[a]	Non-event[b]	Event[c]	Non-event[d]	Correct[e]	Sensitivity[f]	Specificity[g]	False positives[h]	False negatives[i]
Jackknife	0.05	96	0	33	0	74.4	100.0	0.0	25.6	0.0
Bootstrap	0.05	93	24	9	3	90.7	96.9	72.7	8.8	11.1

[a] Observations correctly predicted for gray bat presence
[b] Observations correctly predicted for gray bat absence
[c] Observations incorrectly predicted for gray bat presence
[d] Observations incorrectly predicted for gray bat absence
[e] Proportion of event and non-event responses predicted correctly
[f] Proportion of event responses that were predicted to be events
[g] Proportion of non-event responses that were predicted to be non-events
[h] Proportion of predicted event responses that were observed as non-events
[i] Proportion of predicted non-event responses that were observed as events

Figure 1-1. Study area with 213 sampling locations on an 8.3 × 9.4 km grid in northwest Georgia, 2000.

Figure 1-2. Sampling locations at water sources within a 4-km radius of a sampling grid crossing in northwest Georgia, 2000.
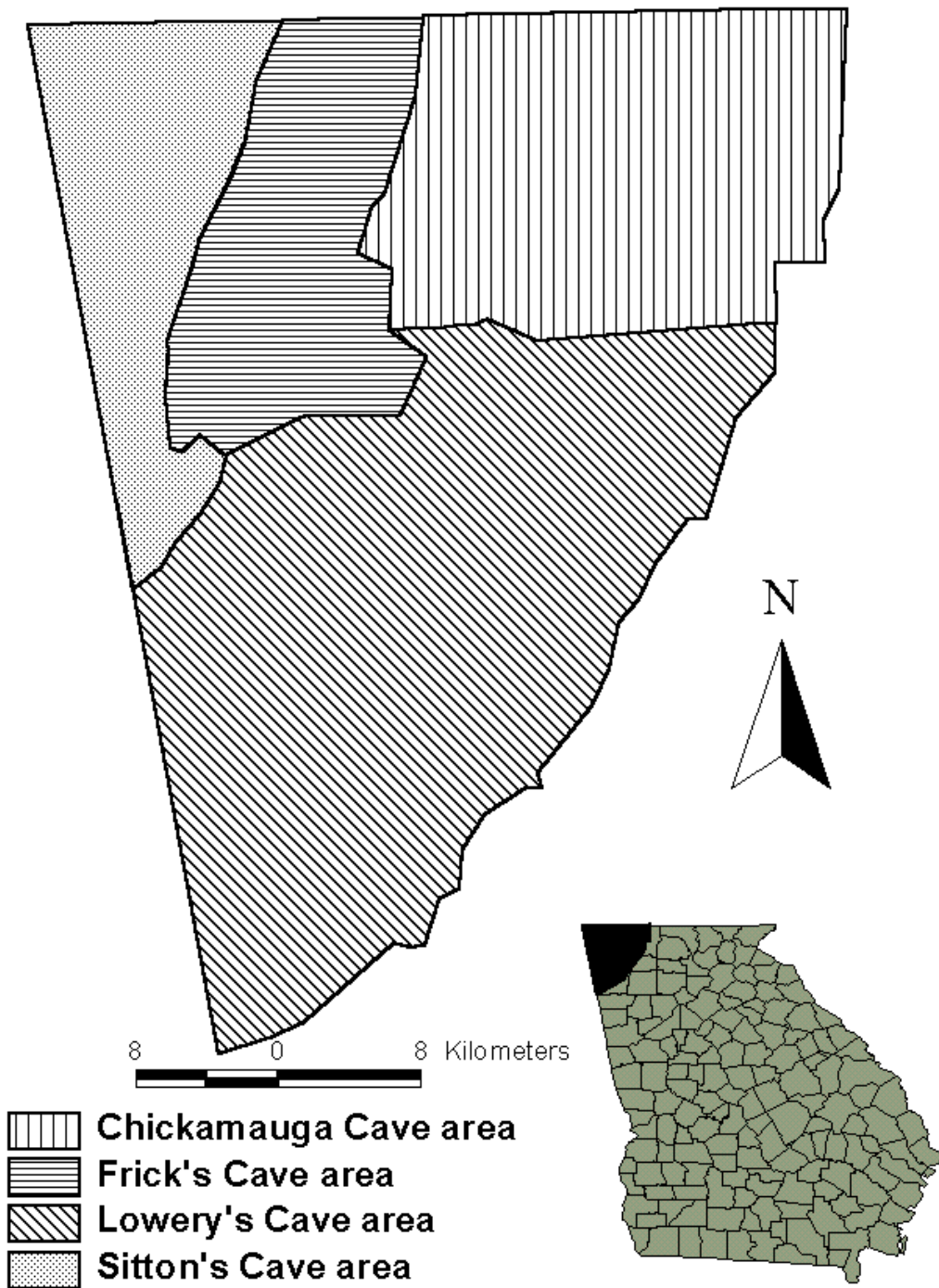
Figure 1-3. Study area divided into 4 areas; one for each gray bat colony in northwest Georgia, 2000.
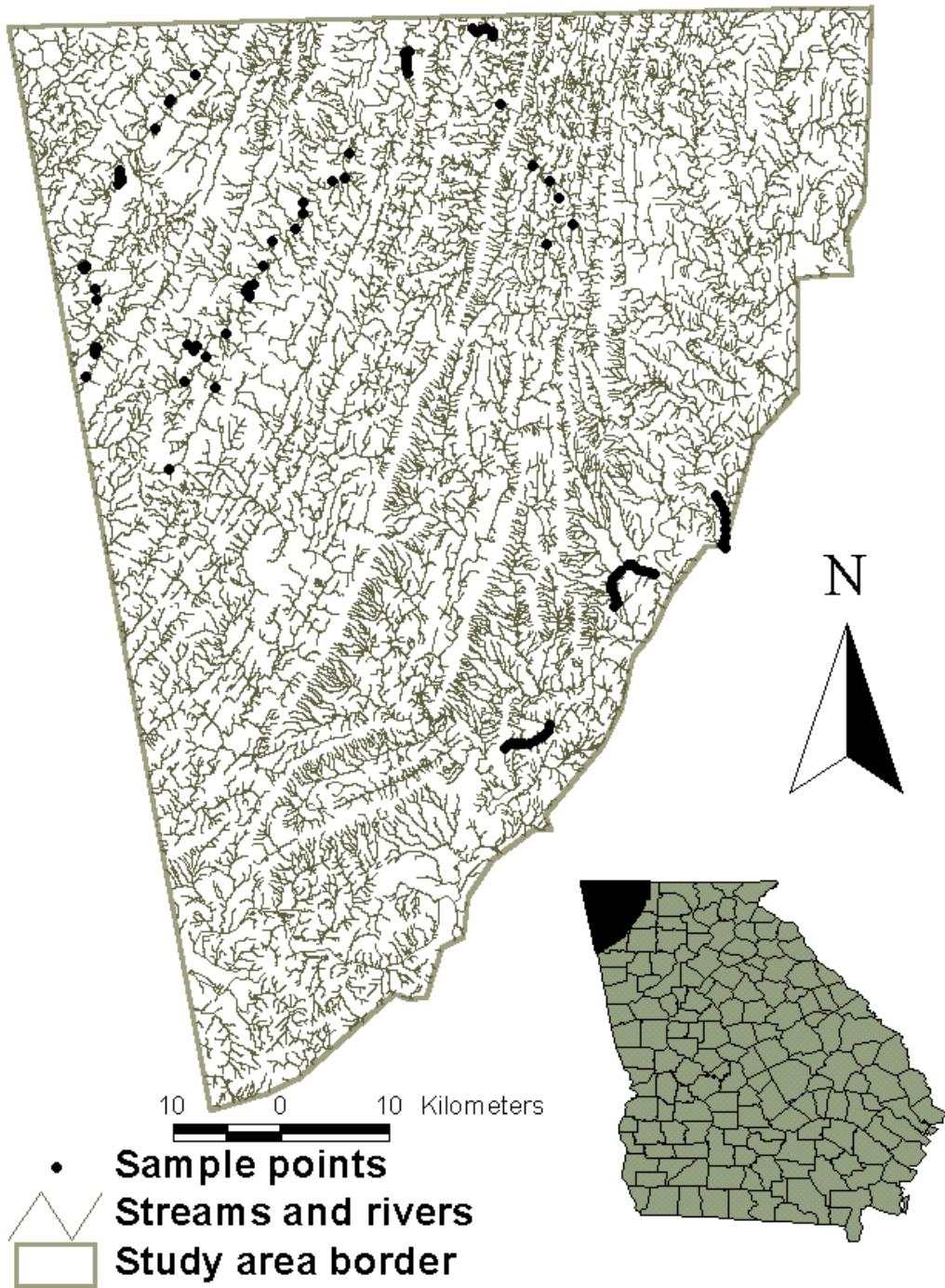
Figure 1-4. Study area with 114 sampling locations in northwest Georgia, 2001.
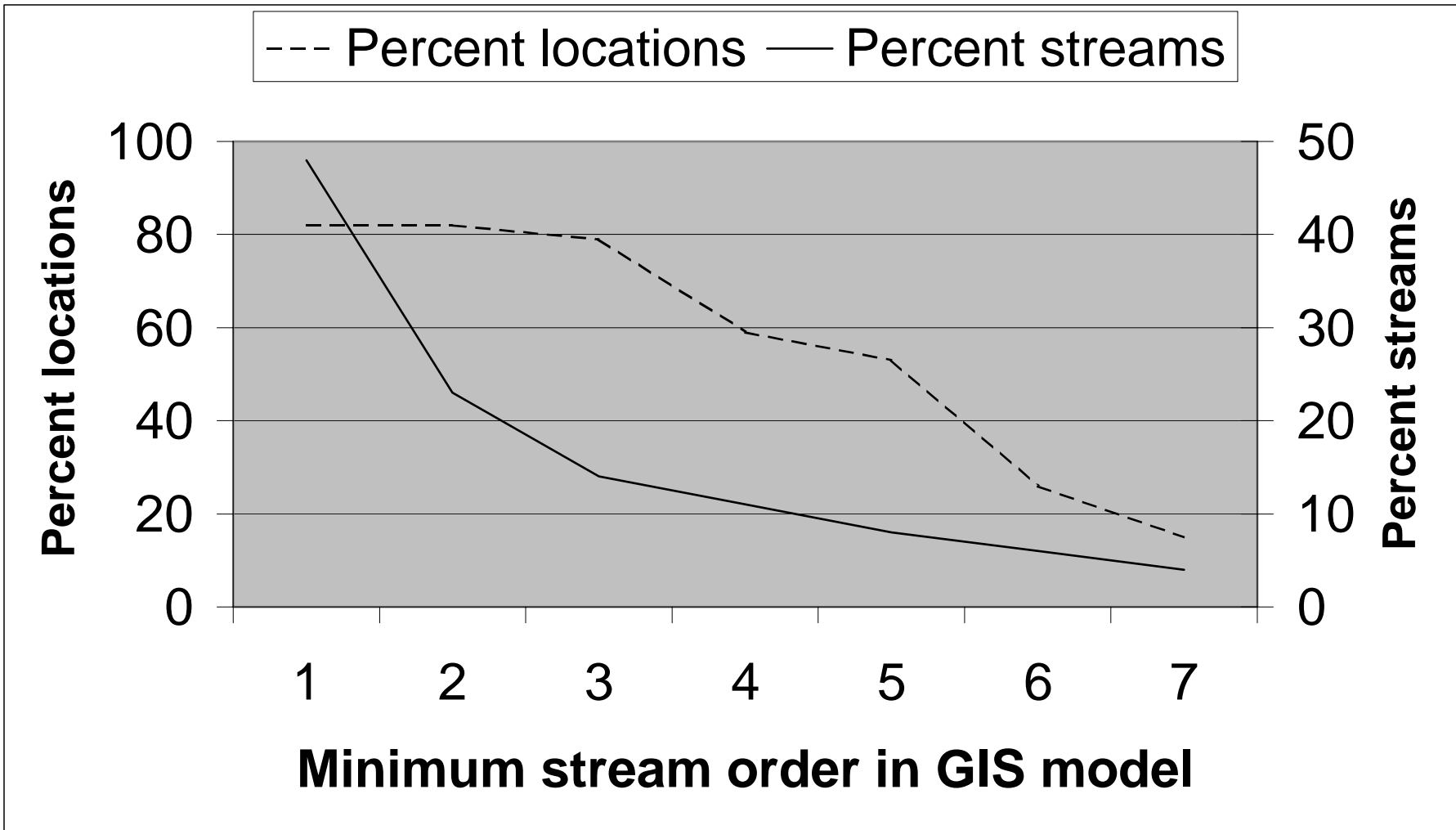
Figure 1-5. Percent locations where gray bats were detected and percent streams retained in the GIS model and corresponding minimum stream orders.
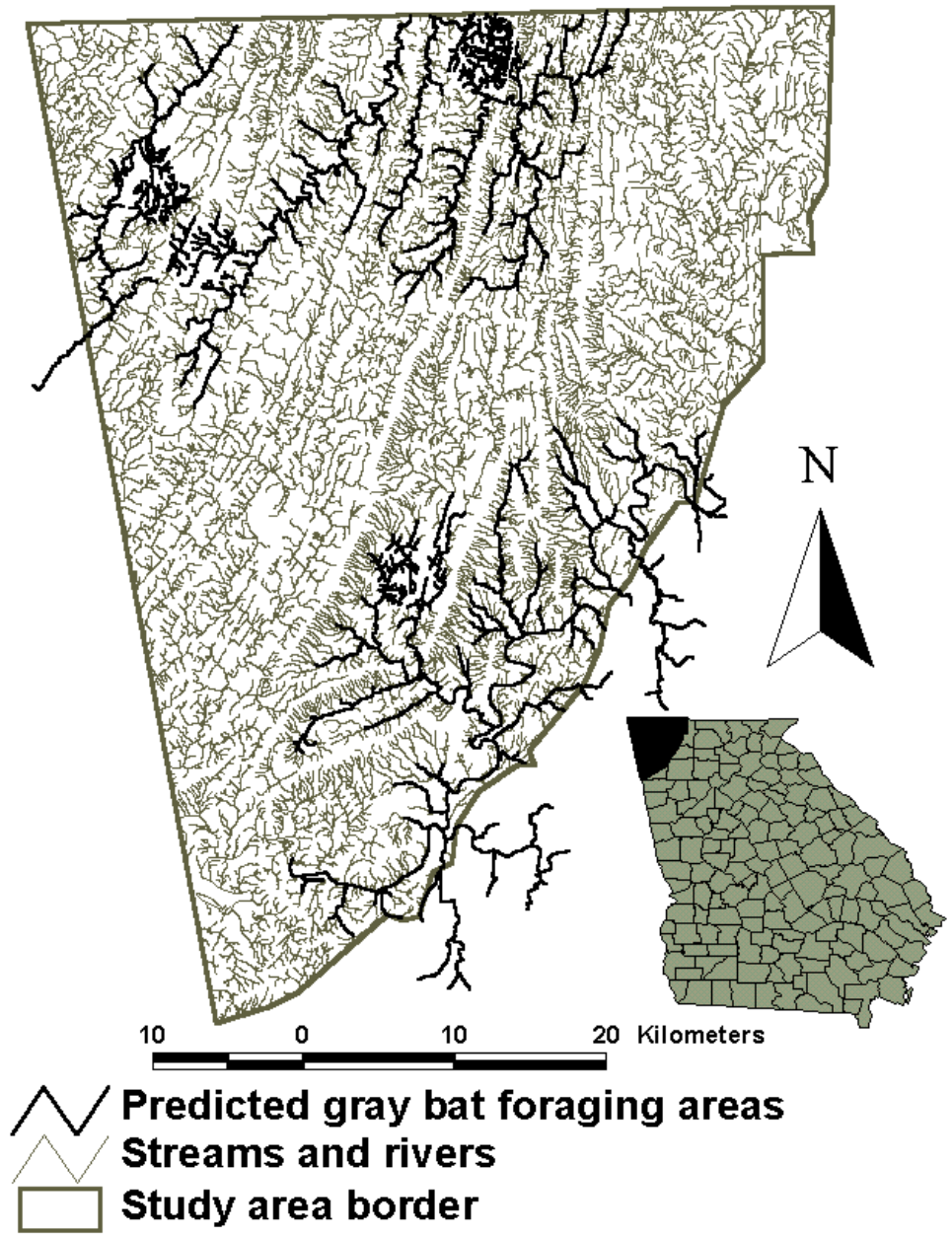
Figure 1-6. Predicted gray bat foraging areas in northwest Georgia, 2000.

CHAPTER 2 — COMPARISON OF TWO ACOUSTICAL BAT SURVEY TECHNIQUES

INTRODUCTION

Previous research has illustrated the utility of using acoustical monitoring to complement capture data for improving bat survey accuracy (Kunz and Brock 1975, Mills et al. 1996, Kuenzi and Morrison 1998, O'Farrell and Gannon 1999). Many bat species that are difficult to capture in mist nets often are more readily inventoried via acoustical monitoring. Recent advances in acoustic monitoring technology have provided researchers with additional tools for surveying bat communities (Parsons et al. 2000, Fenton et al. 2001). Frequency-division detectors coupled with zero-crossing systems such as Anabat II that can be used to simultaneously monitor a range of frequencies have been widely used in acoustical bat surveys. Anabat detectors are useful for investigating bat community composition, relative activity levels, and echolocation call characteristics (Mills et al. 1996, Hayes 1997, O'Farrell et al. 1999). Other Anabat studies have recorded calls directly to audiotape and later transferred the analog calls to computer via a Zero-Crossing Analysis Interface Module (ZCAIM, Titley Electronics, Ballina, Australia; Grindal 1995, Hayes and Adam 1996, Krusic et al. 1996, Menzel et al. In press). Unfortunately, echolocation call quality may be compromised by recording calls to audiotape and later transferring them from tape to computer (O'Farrell et al. 1999, White and Gehrt 2001). A quantitative comparison of bat activity determined by passively recording to tape and to computer showed no significant differences in bat activity levels or number of identifiable calls (White and Gehrt 2001). However, they did not compare differences in species composition recorded, which is a frequent goal of surveys, between media types. Call quality degradation caused by recording to audiotape and later transferring to computer may potentially lead to an under estimation of bat species richness.

In Europe, bat researchers commonly employ active monitoring techniques when surveying for bats. These techniques typically involve acoustical monitoring while walking (Gjerde and Kovacic 1999), riding bicycles (Walsh et al. 1993), or driving along survey transects (de Wijs 1999). Other active monitoring studies have used point-count methods similar to bird survey methods (Ralph et al. 1993) where researchers remain stationary at a point and move the bat detector in a sweeping motion to focus the sample volume in areas of concentrated bat activity (Dietz et al. 1999, Harbusch 1999, Menzel et al. In press). Rarely used in the United States, however, most acoustical monitoring studies have employed passive monitoring protocols (Hayes and Hounihan 1994, Hayes and Adam 1996, Krusic et al. 1996, Perdue and Steventon 1996). No research has quantitatively compared the results of simultaneously conducted passive and active surveys.

My objective was to compare bat surveys conducted by actively monitoring with an Anabat detector linked to a laptop computer and by passively monitoring with an Anabat detector linked to a tape recorder. I examined differences in number of calls recorded, proportion of unidentifiable calls, number of species detected/site, number of calls of each bat species, and number of sites where each bat species was detected between the 2 techniques.

STUDY AREA

I conducted my study in the Cumberland Plateau and Ridge and Valley physiographic provinces in northwest Georgia. This area was characterized by long, linear ridges and plateaus with sharp escarpments rising 300-400 m above valley floors. River valleys were wide and flat in the ridge and valley to the east, with water courses forming deeply cut, narrow gorges to the northwest on the Cumberland Plateau. Oak (*Quercus* spp.) -pine (*Pinus* spp.) forests dominated the uplands whereas in riparian areas, communities with sweetgum (*Liquidambar styraciflua*),

sycamore (*Platanus occidentalis*), yellow-poplar (*Liriodendron tulipifera*) or shrub wetlands with buttonbush (*Cephalanthus occidentalis*) and black willow (*Salix nigra*) occurred. Much of the valley area in the ridge and valley was cleared for pasture and row crops. Limestone geology occurred throughout and the area is unique to Georgia for its abundance of caves. Eight species of bats are confirmed in the area and 4 others also may occur (Menzel et al. 2000a). Daily summer (June-August) temperatures averaged 26.1° C in 2000 and 25.2° C in 2001; average precipitation was 19.9 cm in 2000 and 26.2 cm in 2001 (http://www.nndc.noaa.gov).

METHODS

I surveyed the bat community at 213 sites near water sources (e.g. rivers and streams), by simultaneously recording bat activity passively with an Anabat II detector linked to a tape recorder and actively with an Anabat II detector linked directly to a laptop computer. I used an ultrasonic pest control device (Trasonic 200, Weitech, Sisters, Oregon, USA) with an output frequency of 40 kHz to equilibrate the sensitivities of each Anabat detector (Menzel et al. In press). An 8.3 $\times$ 9.4 km sampling grid was established over a 5,100 km^2 study area in the northwestern corner of Georgia. Each grid crossing ($n = 69$) was sampled by locating 3-4 water sources within 4 km of each grid intersection. Sampling was conducted between 2115 and 0200 hours. I monitored bat activity at each site for 20 minutes. Areas with high levels of ultrasonic background noise (e.g. rapids) were avoided. I surveyed only open areas to reduce clutter-induced variations in echolocation call structure (Obrist 1995). Sampling was not conducted during periods of high wind or rain to avoid biased behavioral responses.

The tape recorder system was placed approximately 1 m above the ground on the stream bank or lakeshore and oriented at a 45° angle relative to the water surface. Calls detected by tape recorder were recorded using a CTR-116 Tandy tape recorder (Tandy Corporation, Fort Worth,

Texas, USA) and Sony HF 90-minute tapes (Sony Corporation of America, New York, New York, USA). I later downloaded echolocation calls collected on tape to computer via an Anabat V ZCAIM using Anabat 6.2d software (Corben 1999). The laptop system's detector was held approximately 1 m above the ground and was slowly swept back and forth to scan for activity over the water. When activity was detected, I attempted to orient the detector to capture as much of the call sequence as possible (O'Farrell et al. 1999). Calls detected using the laptop were recorded to a Compaq Presario 1200 computer (Compaq Computer Corporation, Houston, Texas, USA) via an Anabat V ZCAIM using Anabat 6.2d software. I analyzed all calls using Analook 4.7j software (Corben 1999).

To identify calls, I used qualitative and quantitative methods. I only identified call sequences containing ≥3 pulses. Calls were examined with filter parameters similar to those described by Britzke and Murray (2000) using Analook. Filters were necessary to preserve the diagnostic portion of the echolocation calls, while screening out the unnecessary portions that would interfere with the quantitative techniques used for identification, particularly the slope of the Myotid calls. I qualitatively identified calls of non-Myotids by comparing structures and frequencies of unknown calls to known calls of hand-released bats marked with chemiluminescent tags (Fenton and Bell 1981). The library of known calls was comprised of calls from bats across the southeast United States (Menzel et al. In press). I quantitatively identified Myotids based on frequency and slope characteristics of calls (O'Farrell 1999, Britzke and Murray 2000). I identified all calls to reduce bias and increase identification precision (O'Farrell et al. 1999).

Data were not normally distributed and unresponsive to transformation. Therefore, I used a Wilcoxon-Mann-Whitney two-sample test (Proc Npar1way; SAS Institute Inc.1990) to test for

differences between techniques in number of calls recorded, proportion of the total calls that were unidentifiable, number of species detected at each site, and number of calls of each bat species (Steel and Torrie 1980). I used McNemar's test (Proc Freq; SAS Institute inc. 1990) to compare the number of sites where each species was detected (McNemar 1947).

RESULTS

I collected 8,905 call sequences, 2,633 by tape recorder and 6,272 by laptop. I identified calls of big brown bats (*Eptesicus fuscus*, $n = 19$), eastern red bats (*Lasiurus borealis*, $n = 129$), hoary bats (*L. cinereus*, $n = 6$), gray bats (*Myotis grisescens*, $n = 3$), eastern pipistrelles (*Pipistrellus subflavus*, $n = 589$) and unidentified Myotids (*Myotis* spp., $n = 38$) from tape recordings. From laptop recordings, I identified calls of big brown bats ($n = 49$), eastern red bats ($n = 307$), hoary bats ($n = 5$), gray bats ($n = 230$), little brown bats (*M. lucifugus*, $n = 55$), northern long-eared myotis (*M. septentrionalis*, $n = 23$), Indiana bats (*M. sodalis*, $n = 2$), eastern pipistrelles ($n = 2,612$), and unidentified Myotids ($n = 156$),

Mean number of calls recorded at each site with the laptop was significantly greater than by tape recorder (Table 2-1). The laptop recorded significantly greater numbers of big brown bat, gray bat, little brown bat, northern long-eared myotis, and eastern pipistrelle calls at each site, on average, than did the tape recorder. Mean numbers of eastern red bat, hoary bat, and Indiana bat calls recorded at each site were similar between laptop and tape recorder systems (Table 2-1). The percentage of unidentifiable calls was lower for the laptop than for the tape recorder (Table 2-1). Mean number of bat species detected at each location was significantly greater for the laptop than for the tape recorder (Table 2-1). Big brown bats, gray bats, little brown bats, northern long-eared myotis, Indiana bats, *Myotis* spp., red bats, and eastern pipistrelles were

44

detected at more locations by laptop alone than by tape recorder alone. The number of locations where hoary bats were detected was similar between laptop and tape recorder (Table 2-2).

DISCUSSION

Active monitoring with an Anabat linked to a laptop computer resulted in a more complete survey of the bat community in my study area. My results suggest that more calls can be collected/unit of time using active monitoring techniques than passive techniques (2.4× as many in my study) and active monitoring to laptop may be as much as 4× as efficient at recording identifiable calls sequences as passively monitoring to tape recorder (4.5× in my study). Moreover, data collected via actively monitoring to a laptop presented a more accurate representation of relative activity levels of each species than did passive monitoring with an Anabat linked to a tape recorder. Active monitoring to laptop produced higher species richness than passively monitoring to tape recorder (>2× more species). I was able to identify the calls of 3 species (i.e. little brown, northern long-eared, and Indiana bats) from laptop data that were not detected from tape recordings. Most of the echolocation calls of these Myotids recorded by tape recorder were either eliminated by the software filter or were of such low quality that they could not be identified beyond genus.

The higher quality of Myotid calls recorded directly to the laptop allowed more calls to be identified to species. For example, gray bat calls accounted for 0.11% of all calls recorded to tape, whereas this species accounted for 3.67% of all calls recorded to laptop. Little brown bats, Indiana bats, and northern long-eared bats were never recorded as an identifiable call using the tape recorder system. Call degradation effects on identification of bat species using tape recorders may result in a biased picture of relative activity levels of bats in a community, and may not be suitable for clearly detecting presence or absence of the genus *Myotis*. Because of

low sample sizes of hoary bats, Indiana bats, and northern long-eared bats, I could not make reliable comparisons between techniques on the basis of these species .

White and Gehrt (2001) found that the laptop system recorded more, although not significantly more, calls than the tape recorder system when passively monitoring with both techniques. My finding that the laptop system recorded significantly more calls than the tape recorder system may be due to my increased sample size (i.e. $n = 12$ vs. $n = 213$). Additionally, active monitoring allows for increased number and quality of calls by focusing survey efforts precisely in areas of concentrated bat activity. Passive monitoring with the tape recorder recorded fewer calls because the sampling cone of the detector was stationary. Bats often flew quickly through the tape recorder sampling cone resulting in only 1-2 individual call pulses recorded. Accurate call sequence identification is extremely difficult if <3 pulses are recorded. Active monitoring allows collection of longer sequences by following bat flight paths.

For researchers and managers wanting to more completely survey bat communities, my findings suggest that active monitoring techniques are superior to passive techniques. Passively monitoring to a tape recorder not only collects less data, but data of lower quality. Such deficiencies require an increased sampling intensity with passive units using tape recorders than with active units using computers to record the equivalent number of identifiable call sequences. Moreover, monitoring efforts using Anabats linked directly to computers may be more effective in detecting bat species with less distinct calls (e.g. Myotids) than units using tape recorders. A survey conducted via active monitoring is more efficient in terms of improved call quality and a higher assurance of assessing the full richness of the bat community. Where research questions focus on attributes other than species richness (e.g. habitat use), which may require a more

rigorous sampling design, passive monitoring may be necessary to reduce bias. Future research is

needed to address issues of observer and analytical bias using active survey techniques for bats.

Table 2-1. Comparison of number of calls recorded, percentage of unidentifiable calls, bat species richness, and number of calls by bat species per collection site ($n = 213$) between active monitoring with Anabat detectors directly linked to laptop computers (Computer) and passive monitoring with Anabat detectors linked to tape recorders (Tape) in northwest Georgia, June-August, 2000.

Variable	Computer		Tape		Z	P
	Mean	SE	Mean	SE		
No. calls	30.01	2.75	12.60	1.76	7.06	<0.001
% calls unidentifiable	46.80	1.80	72.00	2.11	8.53	<0.001
Species richness	1.60	0.07	0.71	0.06	8.88	<0.001
Big brown bat	0.23	0.05	0.09	0.03	2.30	0.021
Eastern red bat	1.47	0.42	0.62	0.23	1.79	0.075
Hoary bat	0.02	0.01	0.03	0.01	0.28	0.780
Gray bat	1.10	0.28	0.01	0.01	5.50	<0.001
Little brown bat	0.26	0.06	0.00	0.00	4.08	<0.001
Northern long-eared bat	0.11	0.04	0.00	0.00	2.70	0.008
Indiana bat	0.01	0.01	0.00	0.00	1.41	0.159
Eastern pipistrelle	12.50	1.47	2.82	0.53	7.13	<0.001
Unidentified Myotids	0.75	0.12	0.18	0.05	4.42	<0.001

Table 2-2. Number of sites where each bat species was detected by active monitoring with an Anabat linked directly to a laptop computer (Computer), by passive monitoring with an Anabat linked to a tape recorder (Tape), by both techniques (Both), and with neither technique (Neither) in northwest Georgia, June-August, 2000.

Species	Computer	Tape	Both	Neither	S [a]	P
Big brown bat	17	3	12	181	9.80	0.002
Eastern red bat	46	6	27	134	30.77	<0.001
Hoary bat	1	1	4	207	0.00	1.000
Gray bat	31	0	2	180	31.00	<0.001
Little brown bat	27	0	0	186	186.00	<0.001
Northern long-eared bat	13	0	0	200	200.00	<0.001
Indiana bat	2	0	0	211	211.00	<0.001
Eastern pipistrelle	64	4	89	56	52.94	<0.001
Unidentified Myotids	57	10	8	138	32.97	<0.001

[a] S-statistic in McNemar's test; approximates χ^2 distribution with 1 degree of freedom

Table A-1. List of landscape and macro-habitat variables collected in northwest Georgia in summer 2000-2001 for use in logistic analysis for prediction of gray bat presence.

Variable[a]	Abbreviation	Model	Data Type	Notes
Immediate landclass	Immland	Landscape	Categorical	1-wide alluvial bottom, 2-narrow bottom, 3-terraced bottom, 4-incised stream
Surrounding landclass	Surrland			1-flat peneplain, 2-rolling hills, 3-knobs, 4-linear ridges, 5-mountains
Elevation	Elev		Continuous	
Distance to nearest cave	Distnear			
GIS model	GISmodel		Binary	0-outside of GIS buffer, 1-inside GIS buffer
Actual stream width	Actwid	Macro-habitat	Continuous	
Actual current flow	Actflow		Categorical	1-pool, 2-run, 3-riffle, 4-rapid
Stream width, bankfull	Bankfull		Continuous	
Depth at bank	Dbank		Categorical	1-0-15 cm, 2-16-90 cm, 3->90 cm
Depth at center	Dcent			1-0-15 cm, 2-16-90 cm, 3->90 cm
Substrate	Substr			1-clays/mud, 2-sand, 3-gravel, 4-cobble, 5-bedrock
Stream speed	Sspeed			1-still, 2-slow current, 3-fast current
Waterfall/plunge pool	Wfall		Binary	0-no waterfall present, 1-waterfall present
Water clarity/turbidity	Clarity		Categorical	1-clear, 2-semi-turbid, 3-turbid
Water temperature	Wtemp		Continuous	
Bridge	Bridge		Categorical	0-no bridge present, 1-unimproved bridge,2-gravel bridge, 3-single-lane bridge, 4-double-lane bridge, 5-expressway

Table A-1.(continued)

Variable	Abbreviation	Model	Data Type	Notes
Streambank undercut	Undercut		Binary	0-neither bank undercut, 1-both banks undercut
Streambank vegetated	Veg			0-neither bank vegetated, 1-both banks vegetated
Streambank forested	Forest	Macro-habitat	Binary	0-neither bank forested, 1-both banks forested
Percent canopy cover	%Canopy		Categorical	
Streamside width, side 1	Sside1		Continuous	
Streamside width, side 2	Sside2			
Shrub, clutter over stream	Shrub		Categorical	0-no shrubs or limbs 20-complete obstruction by shrubs and limbs
Average forest height	ForestHt		Continuous	
Number of snags within 50 m	Snags			
Number of trees with exfoliating bark within 50 m	Exfobark			
Percent open water within 56.4 m	%11		Discrete	0-100%
Percent low-intensity residential within 56.4 m	%21			
Percent high-intensity residential within 56.4 m	%22			
Percent commercial/industrial within 56.4 m	%23			
Percent quarries/strip mines within 56.4 m	%32			
Percent transitional within 56.4 m	%33			
Percent deciduous forest within 56.4 m	%41			
Percent coniferous forest within 56.4 m	%42			
Percent mixed forest within 56.4 m	%43			
Percent pasture/hayfield within 56.4 m	%81			
Percent row crops within 56.4 m	%82			
Percent urban grasses within 56.4 m	%85			
Percent woody wetlands within 56.4 m	%91			
Stream order	Sorder		Discrete	1-7

[a]Variables including the word 'stream' also were measured for sampling locations at lakes and ponds except stream order.

Table A-2. Landuse/landcover types in northwest Georgia, 2000, based on 30-m resolution Landsat thematic mapper data.

Metadata Code	Landuse/Landcover
0	No data
11	Open water
21	Low intensity residential
22	High intensity residential
23	Commercial/Industrial/Transportation
31	Bare rock/Sand/Clay
32	Quarries/Strip mines/Gravel pits
33	Transitional
41	Deciduous forest
42	Coniferous forest
43	Mixed forest
81	Pasture/Hay
82	Row crops
85	Urban/Recreation grasses
91	Woody wetlands
95	Emergent Herbaceous Wetlands

Table A-3. Details of logistic analysis using stepwise variable selection of landscape-level data collected in northwest Georgia, 2000 to predict gray bat presence.

Variable	Step	Score χ^2	$P > \chi^2$
Elev	1	1.2940	0.2553
Immland		0.8992	0.3430
Surrland		4.1975	0.0405
GISmodel*a		26.9112	0.0001
Distnear		10.7724	0.0010
Elev	2	0.1859	0.6663
Immland		0.0853	0.7702
Surrland*		4.7787	0.0288
Distnear		1.8798	0.1704
Elev	3	0.0000	0.9974
Immland		0.0020	0.9643
Distnear		3.0185	0.0823

[a] Asterisks indicate the variable entered into the model in each step.

Table A-4. Details of logistic analysis using stepwise variable selection of macro-habitat-level data collected in northwest Georgia, 2000 and 2001 to predict gray bat presence.

Variable	Step	Score χ^2	$P > \chi^2$
Actwid	1	4.4809	0.0343
Actflow		0.7467	0.3875
Bankfull		4.3582	0.0368
Dbank		1.2285	0.2677
Dcent		7.3817	0.0066
Substr		1.0790	0.2989
Sspeed		0.4626	0.4964
Wfall		5.9098	0.0151
Clarity		0.2992	0.5844
Wtemp		4.6496	0.0311
Bridge		2.5727	0.1087
Undercut		0.0326	0.8566
Veg		0.0007	0.9784
Forest		2.3562	0.1248
%Canopy		2.1356	0.1439
Sside1		2.0479	0.1524
Sside2		0.3839	0.5355
ForestHt		3.8182	0.0507
Snags		1.4888	0.2224
Exfobark		0.3812	0.5369
Shrub		11.4924	0.0007
%11		0.1648	0.6848
%21		2.5745	0.1086
%22		0.2132	0.6443
%23		2.8268	0.0927
%32		0.3464	0.5561
%33		0.3464	0.5561
%41		0.0334	0.8550
%42		1.7832	0.1818
%43		0.9241	0.3364
%81		3.1203	0.0773
%82		0.9890	0.3200
%85		0.6363	0.4251
%91		0.9691	0.3249
Sorder[*a]		11.9083	0.0006
Actwid	2	0.3987	0.5278
Actflow		1.4250	0.2326
Bankfull		0.3667	0.5448
Dbank		0.4883	0.4847
Dcent		1.2348	0.2665
Substr		0.0181	0.8930

Table A-4 (continued).

Variable	Step	Score χ^2	$P > \chi^2$
Sspeed	2	1.6556	0.1982
Wfall		5.3130	0.0212
Clarity*		5.3972	0.0202
Wtemp		1.2113	0.2711
Bridge		0.1701	0.6800
Undercut		0.4309	0.5115
Veg		0.3139	0.5753
Forest		0.9014	0.3424
%Canopy		0.0902	0.7640
Sside1		2.2644	0.1324
Sside2		0.7125	0.3986
ForestHt		1.2909	0.2559
Snags		0.6173	0.4321
Exfobark		0.9880	0.3202
Shrub		2.9596	0.0854
%11		0.3220	0.5704
%21		1.4786	0.2240
%22		0.3461	0.5563
%23		2.7394	0.0979
%32		0.2921	0.5889
%33		0.2921	0.5889
%41		0.1163	0.7331
%42		1.0291	0.3104
%43		0.3382	0.5609
%81		4.0401	0.0444
%82		1.5561	0.2122
%85		0.0715	0.7892
%91		0.3537	0.5520
Actwid	3	0.5215	0.4702
Actflow		2.2913	0.1301
Bankfull		0.5373	0.4636
Dbank		0.0049	0.9445
Dcent		3.6131	0.0573
Substr		0.6393	0.4240
Sspeed		2.5483	0.1104
Wfall		5.4151	0.0200
Wtemp		2.8481	0.0915
Bridge		0.4840	0.4866
Undercut		0.6616	0.4160
Veg		0.1454	0.7030
Forest		0.5911	0.4420
%Canopy		0.1328	0.7155

Table A-4. (continued).

Variable	Step	Score χ^2	$P > \chi^2$
Sside1	3	2.2485	0.1337
Sside2		0.5342	0.4649
ForestHt		1.0606	0.3031
Snags		0.7390	0.3900
Exfobark		0.9904	0.3196
Shrub*		6.5110	0.0107
%11		0.0020	0.9646
%21		1.0972	0.2949
%22		0.1702	0.6800
%23		3.5376	0.0600
%32		0.2322	0.6299
%33		0.0787	0.7791
%41		0.6842	0.4081
%42		1.2317	0.2671
%43		0.0721	0.7883
%81		4.1530	0.0416
%82		1.4840	0.2231
%85		0.1342	0.7141
%91		0.5717	0.4496
Actwid	4	0.4080	0.5230
Actflow		2.2965	0.1297
Bankfull		0.4191	0.5174
Dbank		0.1191	0.7300
Dcent		4.0538	0.0441
Substr		1.4985	0.2209
Sspeed		2.3632	0.1242
Wfall		4.5615	0.0327
Wtemp		2.9412	0.0863
Bridge		1.0612	0.3030
Undercut		0.1556	0.6932
Veg		1.6597	0.1977
Forest		0.8273	0.3630
%Canopy		0.0002	0.9902
Sside1		2.0557	0.1516
Sside2		0.7800	0.3772
ForestHt		2.1477	0.1428
Snags		0.9433	0.3314
Exfobark		0.7694	0.3804
%11		0.0046	0.9462
%21		3.2653	0.0708
%22		0.0114	0.9148
%23		2.9568	0.0855

Table A-4. (continued).

Variable	Step	Score χ^2	$P > \chi^2$
%32	4	0.1257	0.7229
%33		0.0279	0.8674
%41		0.8267	0.3632
%42		1.1249	0.2889
%43		0.0325	0.8569
%81[*]		4.5810	0.0323
%82		1.7490	0.1860
%85		0.3474	0.5556
%91		0.3342	0.5632
Actwid	5	0.9037	0.3418
Actflow		2.7391	0.0979
Bankfull		0.8333	0.3613
Dbank		0.0942	0.7589
Dcent		3.4717	0.0624
Substr		0.8107	0.3679
Sspeed		2.7620	0.0965
Wfall		3.0408	0.0812
Wtemp		2.4117	0.1204
Bridge		1.4940	0.2216
Undercut		0.6417	0.4231
Veg		1.5037	0.2201
Forest		0.9313	0.3345
%Canopy		0.0624	0.8028
Sside1		3.8824	0.0488
Sside2		1.6269	0.2021
ForestHt		2.7087	0.0998
Snags		0.8371	0.3602
Exfobark		0.2911	0.5895
%11		0.2591	0.6107
%21		1.9449	0.1631
%22		0.0046	0.9461
%23		2.7193	0.0991
%32		0.1786	0.6726
%33		0.0361	0.8494
%41		0.0001	0.9921
%42		0.1670	0.6828
%43		1.7123	0.1907
%82		1.5128	0.2187
%85		0.2541	0.6142
%91		0.8108	0.3679

[a] Asterisks indicate the variable entered into the model in each step.

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