Wildlife

AUTUMN ROOSTING HABITAT OF MALE INDIANA BATS (*MYOTIS SODALIS*) IN A MANAGED FOREST SETTING IN KENTUCKY

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Abstract—In early October 1996 and in late August and late September 1997, during the autumn pre-hibernation swarming period, a total of 22 male Indiana bats (*Myotis sodalis*) were captured by the use of a portable harp trap at the entrance to a cave hibernaculum located on the Daniel Boone National Forest in Pulaski County, Kentucky. Each bat was fitted in the field with a lightweight (0.52 g) transmitter (Holohil Systems Ltd, model LB-2) attached between the scapulae with surgical adhesive (Skin-bond), released at the point of capture within 4 hours after being caught, and subsequently tracked daily to roost trees by the use of a three-element Yagi antenna and receiver (Wildlife Materials, Model TRX-1000), during daylight hours, until its transmitter failed or it entered the hibernaculum for the winter. Each roost tree that was used by a transmittered Indiana bat was marked in the field with paint and/or plastic flagging and its location was plotted on a topographic map. Information that was collected for each tree included tree species, condition (live/dead), diameter at breast height (dbh), and (if available) the past management of the stand in which the tree was located. During 1997, percent canopy closure was measured at each roost tree by means of a concave spherical densiometer (Robert E Lemmon Forest Densiometers, Model-C). Habitat use in response to past management was evaluated by: (a) defining the analysis area to include all land (5740 ha) located within the smallest circle that could be drawn, with the bat hibernaculum as the center, that would include all known roost trees (N = 102); (b) determining the relative proportions of each type of managed habitat available to the bats within the analysis area; and (c) comparing habitat use versus availability with respect to past management practices that had taken place within each stand where known roost trees were located. The analysis area as defined above was virtually 100 percent forested, with various oak-pine, oak, yellow pine, and pine-oak forest types on the ridgetops and upper slopes and cove hardwood forest types on the lower slopes and in the stream valleys. Nearly 74 percent (4001 ha) of the analysis area was in public ownership (U. S. Forest Service); the remaining 26 percent (1445 ha) was privately owned. An impounded section of the Cumberland River, forming a 294 ha strip which extended through the northern portion of the circle, was excluded from the analysis.

During both years combined, roosting Indiana bats were located a total of 212 times in 102 different roost trees. Dead trees (snags) accounted for 86 percent (N = 88) of all roost trees found and 92 percent (N = 194) of all bat days (each day that a bat was tracked to a roost tree was defined as 1 bat day regardless of whether or not a bat had previously been found roosting in that particular tree); live trees accounted for 14 percent of all roost trees (N = 14) and 8 percent of all bat days (N = 18). Although Indiana bats were found roosting in 13 species of trees, the majority of these (79 percent) were pines (*Pinus* sp.) and oaks (*Quercus* spp.). Pine snags made up 43 percent of all roost trees (N = 44) and nearly 50 percent of all bat days (N = 105); no bats were found roosting in live pines. Oak snags (N = 25) and living oaks (N = 12) comprised 36 percent of the roost tree sample and 27 percent (N = 57) of all bat days. The most frequently used roost tree species were shortleaf pine, *Pinus echinata* (33 roost trees, 83 bat days), Virginia pine (*P. virginiana*) (11 roost trees, 21 bat days), scarlet oak, *Quercus coccinea* (15 roost trees, 19 bat days), and white oak, *Q. alba* (12 roost trees, 16 bat days).

Roost trees used by male Indiana bats during this study ranged in size from 8.4 cm to 86.6 cm (mean = 30.8 cm) dbh. Although no evening emergence counts were conducted at the individual trees, 3 different snags (2 shortleaf pines, 1 hardwood) were used simultaneously by 2 transmittered bats on a total of 8 different days, and 1 shortleaf pine snag was used simultaneously by 3 transmittered bats on 2 different days a week apart. Another shortleaf pine snag was used by different transmittered bats during successive years. These observations indicate that certain trees may be locally important as autumn roosting sites to Indiana bats that hibernate in nearby caves.

Roost tree switching was frequent for most individual Indiana bats that were monitored. In 1996, 10 bats used 1-8 different roost trees each during the 1-18 days that they were found, switching roosts a total of 46 times (including some returns to previously used trees) at an average of once every 2.0 days. In 1997, 12 bats used 2-11 roost trees each during 4-15 days of tracking, changing trees a total of 75 times for an average of once every 1.6 days. Several switched roost trees virtually every day, while others returned repeatedly to 2 or 3 particular trees. Although frequent roost tree switching was normal for most bats, in many cases all of the trees used by any individual Indiana bat during its tracking period were relatively close to one another. For the 20 bats that were found 4 times or more during both years combined, distances between roost

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trees ranged from 48 m to 2688 m, and the area of the smallest circle that could be drawn to include all roost trees used by an individual bat ranged from 0.4 ha to 568 ha. The most sedentary Indiana bats (N = 6) used 2-7 different roost trees each within a total area of 4.5 ha or less; an additional set of bats (N = 11) used 3-11 different roost trees each within a total area of 10 ha to 105 ha; and the most nomadic bats (N = 3) used 3-5 roost trees scattered over areas ranging from 518 ha to 568 ha. There did not appear to be any direct relationship between the number of times that a bat was found during a tracking period and the total area within which all of its documented roost trees were located.

As measured from the ground, canopy closure (cc) at all roost trees (N = 70) used by transmittered Indiana bats during the 1997 fall season ranged from 20 percent to 93 percent (mean = 80 percent), with 19 trees (34 bat days) located in fairly open canopy forest (<60 percent cc), 17 trees (27 bat days) in an intermediate canopy range (60-80 percent cc), and 34 trees (61 bat days) in closed canopy situations (>80 percent cc). Since most of the bats were roosting beneath loose bark in the upper portions of snags, however, there was no reasonable method available which would allow canopy closure to be measured at the actual roosts. An attempt was made to remedy this situation by using only the most open measurement that was made at each roost tree. This resulted in a canopy closure range from 0 percent (for roost trees located at the edges of large openings) to 92 percent, with 44 bat days spent in open canopy roosts (<60 percent cc), 35 bat days in intermediate canopy roosts (60-80 percent cc), and 43 bat days in closed canopy roosts (>80 percent cc).

Two separate tracts within the study area had been managed under a prescribed burning regime designed to control hardwood regeneration and maintain an open forest dominated by shortleaf pine - conditions geared toward the restoration of habitat for the federal endangered red-cockaded woodpecker (*Picoides borealis*). These tracts totaled 8 percent (436 ha) of the total amount of habitat within the analysis area, and harbored 12 of the 102 Indiana bat roost trees that were documented during both years combined. Roost tree use in prescribed burns (6 of 33 roost trees) was double the expected level (based upon the total amount of that habitat type available) during the 1996 tracking period, and equal to the expected level (6 of 70 roost trees) during the 1997 tracking period.

Although 26 percent (1445 ha) of the potential Indiana bat habitat within the study area was under private ownership, nearly all (100 of 102) of the roost trees documented were on National Forest System lands, some of which included stands where some form of timber management had taken place in recent years. During the 1996 and 1997 fall telemetry periods, approximately 17 percent of the study area (897 ha) that had been clearcut during the past 35 years yielded 0 roost trees and 0 bat days during both years combined; this was much lower than the expected level of use (16 roost trees, 35 bat days) based upon the total amount of that habitat available. Forested habitat which had not been actively managed during the past 50 years made up 44 percent of the study area (2367 ha) in 1996 and harbored 28 roost trees with 82 bat days of use as compared to an expected 15 roost trees and 39 bat days; this habitat was thus used at about twice the expected level based on its availability. This habitat type covered about 42 percent (2299 ha) of the study area in 1997, yielding 47 roost trees and 76 bat days, about 1.5 times the expected 30 roost trees and 51 bat days. Two-age shelterwood cuts (harvested during the past 5 years) and high-graded stands (up to 10 years old) comprised about 2.6 percent of the study area (143 ha) in 1996 and held 5 Indiana bat roost trees with 8 bat days of use, 4-5 times the expected level based on availability. In 1997, additional 2-age shelterwood cutting had increased the proportion of this habitat type to nearly 4 percent of the study area (211 ha), with 18 roost trees and 36 bat days documented here (6-7 times the expected levels). During both years combined, uninventoried habitats (including privately-held tracts and portions of a designated Forest Service wilderness) made up about 37 percent of the study area (2039 ha) and harbored 5 documented roost trees (of 38 expected) and 10 bat days (of 80 expected).

Although the total proportion of the study area that had been recently managed by the use of the 2-age shelterwood harvest method was too small to allow for a statistical verification of these preliminary results (i.e. that Indiana bats may actually be selecting this habitat type for roosting), some additional observations made during this telemetry study appear appropriate for this presentation. Stands that were harvested by the 2-age shelterwood method from 1993-1995, under Daniel Boone National Forest guidelines that called for the retention of 40 live trees and 5 snags/ha (16 live trees and 2 snags/acre), yielded 1 documented Indiana bat roost tree and 1 bat day during both years combined - slightly below expected levels of use. Stands that were harvested by the 2-age shelterwood method from 1996-1997, however, under different guidelines that called for the retention of 40 live trees/ha and additionally all snags, shagbark hickories, hollow trees, and trees with large dead limbs, harbored 15 Indiana bat roost trees and 27 bat days - well above expected levels of use. These observations and results suggest that timber harvesting by the 2-age shelterwood method, in concert with the retention of good numbers of snags and other suitable types of roost trees, can provide favorable roosting conditions for male Indiana bats during the autumn pre-hibernation period, at least over the short term.

FORAGING BEHAVIOR AND HABITAT USE OF RED BATS IN MIXED MESOPHYTIC FORESTS OF THE CUMBERLAND PLATEAU, KENTUCKY

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Abstract—Although the red bat (*Lasiurus borealis*) is a common forest-dwelling bat, limited information is available on the foraging requirements and habitat use of this species. We radiotracked red bats on the Cumberland Plateau in eastern Kentucky during July and August 1996, and May, July and August 1997. We estimated size of foraging areas and evaluated use of habitats available within foraging areas. We placed transmitters on 10 females and nine males. Size of foraging areas ranged from 113 to 850 hectares for females, and 134 to 925 hectares for males; however, most radiotagged males moved considerable distances among nights and changed foraging areas frequently. Size of foraging areas and commuting distance varied temporally, with bats exhibiting slightly larger foraging areas and longer commuting distances in late summer compared to early summer. The maximum distance bats were recorded foraging away from the day roost ranged from 1.2 to 5.5 kilometers for females, and 1.4 to 7.4 kilometers for males. Red bats were located in non-forested habitats and aquatic habitats at proportions slightly higher than the availability of these habitats. The red bat appears to be a generalist species that can tolerate a range of habitat conditions, foraging temporally and spatially over many habitats.

INTRODUCTION

Although bats represent a large percentage of the mammals in deciduous forests (Barbour and Davis 1969) and account for 25 percent of all mammal species (Altringham 1996), the importance of bats as part of forest ecosystems in North America only recently has received much attention (Barclay and Brigham 1996). Studies on the ecology of bats in forests in western North America have been completed (Brigham and others 1997, Grindal and Brigham 1998, Kalcounis and Brigham 1998, Ormsbee and McComb 1998, Rabe and others 1998), but data for only a few species of bats in eastern North America exist (Krusic and others 1996). Most studies emphasize threatened and endangered species, particularly bats that roost in caves during all or part of the year (e.g., Adam and others 1994, Humphrey and others 1977, Tuttle 1979).

Despite the general longevity (Paradiso and Greenhall 1967) and early sexual maturity (Tuttle and Stevenson 1982) of insectivorous bats in North America, most species are monestrous and raise only one young per year (Hill and Smith 1984). An exception to this general rule are the tree-dwelling bats of the genus *Lasiurus* that have litters of usually 3-4 young (Barbour and Davis 1969, Constantine 1966, Mumford 1973). The alteration of significant amounts of forest habitat could impact populations of tree-dwelling bats to where bats presumed to be common, such as the red bat (*Lasiurus borealis*), become imperiled. Red bats are known to roost and forage in habitats such as open fields or urban areas (Constantine 1966, Mumford 1973); however, research has not addressed foraging requirements of red bats in areas where large, contiguous tracts of forest exist. The objectives of this study were to determine the location, size, and habitat of foraging areas used by red bats.

METHODS

Description of Study Areas

Research took place in the Cumberland Plateau physiographic province in eastern Kentucky. The region covers ca. 28,500 square kilometers consisting of rugged, forested terrain, locally interspersed with sandstone cliffs (McGrain 1983). Research was conducted in the northeastern portion of the Cumberland province in Carter and Elliott counties (NCP), and in the southeastern corner of the province in Breathitt, Knott, and Perry counties (SCP). Forests in both areas are classified as mixed mesophytic forest (Braun 1950). Research sites represent mature, second-growth forest that largely was undisturbed by silvicultural activities and contained mature stands of timber (i.e., an average d.b.h. ≥ 25.4 centimeters; Personal communication. 1996. Paul Kalisz, Professor of Silviculture, University of Kentucky, Lexington, KY 40546-0073).

In NCP large tracts of unbroken mature, second-growth forest, 400 to 3,200 meters wide and 8 to 20 kilometers long, were present along tributaries that run into the Little Sandy River or Grayson Lake. Grayson Wildlife Management Area, adjacent to Grayson Lake, consisted of 4,190 hectares and supported a large contiguous tract of mature, second-growth forest. Upland areas of fragmented forest, agricultural lands, pastures, and residential areas surrounded the forested-tributaries and Grayson Wildlife Management Area. Dominant forest vegetation in the area consisted of yellow-poplar (*Liriodendron tulipifera*), black walnut (*Juglans nigra*), and white oak (*Quercus alba*) on the north and east slopes (Weisenberger and others 1965). Black oak (*Q. velutina*) scarlet oak (*Q. coccinea*), and hickories (*Carya* spp.) dominated the south and west slopes, and chestnut oak (*Q. prinus*), scarlet oak, and patches of shortleaf (*Pinus echinata*) and pitch (*P. rigida*) pine were common on the upper slopes and ridges

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(Weisenberger and others 1965). Mesic and riparian vegetation of the lower slopes and creek bottoms was dominated by American beech (*Fagus grandifolia*), eastern hemlock (*Tsuga canadensis*), American sycamore (*Platanus occidentalis*), sweet birch (*Betula lenta*), and thickets of rhododendron (*Rhododendron maximum*).

Robinson Forest, located in the southeastern portion of the Cumberland Plateau physiographic province (SCP), is a 5,984-hectare tract of mature, second-growth forest 70 to 80 years old, with occasional wildlife clearings 1 to 2 hectares in size (Overstreet 1984). The area surrounding Robinson Forest was almost entirely surface-mined land; thus, Robinson Forest, served as an island of forest enclosed within a disturbed landscape. Dominant tree species included yellow-poplar, scarlet oak, white oak, black oak, American beech, chestnut oak, northern red oak (*Quercus rubra*), mockernut hickory (*Carya tomentosa*), eastern hemlock, American sycamore, and pitch pine (Overstreet 1984). Upland and ridge tops were dominated by oaks, hickories, and pines. Mesic and riparian vegetation consisted primarily of American beech, American sycamore, eastern hemlock, and white oak.

Capture and Handling Procedures

Mist nets, 5.5 or 9.1 meters wide, were placed across streams, trails, road-rut ponds, and small upland ponds to capture red bats. Bats were removed from the net, their age, sex and reproductive condition was determined, and they were weighed to the nearest 0.5 gram. Age was determined based on the time of year and the closure of the cartilaginous, epiphyseal growth plates in the finger bones (Anthony 1988).

Radiotransmitters (Type LB-2, 172-173 megahertz, Holohil Syst., Ontario, Canada) weighing 0.51 gram, with whip antennae 17.5 centimeters in length, were placed on 19 red bats (10 females and nine males). Radiotransmitters were attached using surgical cement between the scapulae on the upper back of the bat. A small section of hair was clipped between the scapulae to ensure proper bonding between the transmitter and the skin, and to lengthen the period that the transmiter remained on the bat. Each bat was held with the transmitter in place for ca. 5 minutes until the cement hardened before being released. Radiotagged bats were monitored continuously for 30 minutes following release to insure that each bat was able to fly properly and to identify any complications.

Radiotelemetry Procedures

Red bats were tracked in the NCP in July and August in 1996 and 1997, and in the SCP in May and August 1997. Telemetry stations were established at various high points in close proximity, i.e., 400 to 1,000 meters, to diurnal roost sites. Field personnel, equipped with a TRX 1000s receiver (Wildlife Materials, Inc., Carbondale, IL), a 3-element yagi antenna, and a compass, maintained contact using two-way radios. Once field personnel located a signal, azimuths were obtained simultaneously from stations at 2- to 3-minute intervals until either the bat perched in a night roost or the signal was lost. Azimuths were taken simultaneously from two or three stations, depending on the location of the bat and the movement of personnel to alternate stations to improve signal reception. Azimuths were plotted immediately at a base station on laminated 7.5-minute topographic maps to determine the location of a bat.

Data Analyses

A minimum of 40 locational crosses was used to calculate a foraging area estimate of a bat, as size of foraging areas of red bats was not found to increase beyond this sample size (Hutchinson 1998). The Calhome Software package (Kie and others 1996) was used to analyze spatial resolution on bat foraging locations, with estimates of foraging area size calculated using the adaptive kernel method. We used the adaptive kernel method because it is a nonparametric technique suitable for smaller sample sizes, does not require the assumption of normality, and is robust to changes in spatial resolution (Hansteen and others 1997). The adaptive kernel method calculates the size of a foraging area based on the intensities of locational crosses within areas, and is less biased by outliers than other existing methods (Worton 1989).

Habitat use and availability were determined by placing foraging area polygons and locational crosses over 7.5-minute topographic maps. Habitats were grouped into the following categories: forested habitat, non-forested habitat, such as clearings, agricultural land and human development, and aquatic habitat, including streams, ponds and lakes. The percentage of each habitat available and the number of radiolocations in each habitat was determined within the foraging area of each red bat for which ≥ 40 locational crosses were obtained.

Statistical summaries are based on the mean and standard error of the mean. All statistical tests were made using the Mann-Whitney U test (Hollander and Wolfe 1973).

RESULTS

The mean body mass of radiotagged adults was 12.9 ± 0.59 (SE) grams, while juveniles averaged 9.83 ± 0.60 (SE) grams (table 1). Body mass of adult females (14.1 ± 0.68 (SE) grams) was significantly greater ($U = 2.0$; $P = 0.006$) than for adult males (10.9 ± 0.40 (SE) grams). Three radiotagged females were pregnant, and two other adult females were in various stages of lactation. Female #606 roosted with two non-volant young, and female #745 roosted with two volant young. The post-lactating female (#745) was observed on several occasions leaving the roost shortly after her young emerged. Four males had descended testes, and the remaining bats showed no sign of reproductive activity.

No radiotagged adult red bats appeared to exhibit difficulty with flight after release. Commonly, radiotagged bats flew a short distance (ca. 50 to 100 meters) from the processing station to roost, and remained for 5 to 20 minutes. The bats probably were adjusting to the handling process and the added burden of the transmitter. After the initial adjustment period, the bats exhibited normal foraging habits and often foraged until we left the study area for the night, usually around 0100 hours. Twelve bats were radiotracked for a

Table 1—Sex, age, body mass, reproductive status, and tracking success of radiotagged red bats

Bat no.	Sex	Age	Mass	Status	Date of attachment	No. locations
			g			
389	F	A	14.5	Not active	7/09/97	120
430	F	A	13.5	Not active	7/21/97	46
432	M	A	11.0	Testes	7/25/97	59
451	M	J	11.0	Not active	8/05/97	0
504	F	A	15.0	Not active	8/11/97	24
521	M	A	11.0	Not active	8/11/97	0
546	F	A	11.0	Not active	8/12/97	74
575	F	A	11.5	Not active	8/12/97	54
606	F	A	14.5	Lactating	7/11/96	123
622[a]	M	J	9.5	Not active	7/24/96	0
645[a]	M	J	9.0	Not active	7/24/96	0
622[a]	M	A	12.5	Testes	7/30/96	0
645[a]	M	A	10.5	Testes	8/06/96	49
745	F	A	12.5	Post-lactating	8/09/96	40
845	M	A	11.0	Testes	8/09/96	0
883	M	A	9.5	Not active	5/20/97	41
944	F	A	14.0	Pregnant	5/20/97	66
963	F	A	16.5	Pregnant	5/20/97	53
984	F	A	18.0	Pregnant	5/20/97	46

[a] Indicates transmitter used on > 1 red bat.

sufficient period (Mean = 7.75 nights) to obtain an estimate of foraging area size.

Eighty-two percent of the azimuths resulted in locational crosses. Adult females, particularly those that were pregnant, lactating or post-lactating, were easier to monitor than adult males and often used the same foraging area for five to 12 nights (table 2). If a bat remained in the area, we usually observed little variation in the location of crosses obtained after the first three to four nights. Female bats that were not reproductively active exhibited foraging patterns more typical of adult males. All red bats were difficult to monitor in August.

The shape of foraging areas typically was bivariate and there was substantial overlap in the foraging areas (fig. 1). The foraging areas of bats contained their diurnal roost sites in all but one instance (#645) and most foraging areas included a permanent water source. Two bats (#606, #645) had foraging areas that were transected by secondary or major roadways and the foraging areas of all bats contained either forested trails or seldom used gravel or paved roads. Bats #645 and #430 each had two distinct foraging areas, separated by distances of 4 kilometers and ca. 75 meters, respectively.

The overall size of foraging areas of red bats, pooling females and males, was 334 ± 82.1 (SE) hectares (table 2). No difference (U = 11.0; P = 0.29) was observed in the mean size of foraging areas for bats in the NCP and the SCP. Males (Mean = 450 ± 242 (SE) hectares) used a foraging area almost 1.5 x larger than females (Mean = 295 ± 82.1 (SE) hectares), but this difference was not significant (U = 9.0; P = 0.46).

Reproductively active females had a mean foraging area size of 176 ± 28.0 (SE) hectares compared with a mean foraging area size for non-reproductive females of 444 ± 161 (SE) hectares, but the difference was not significant (U = 5.0; P = 0.20). During late summer, foraging areas of females appeared to increase (table 2). Although females remained in the proximity of their diurnal roost sites in late summer, they occasionally made forays out of the range of receivers. These females, all non-reproductive, usually returned within 45 minutes.

The maximum distance that bats were recorded foraging away from the day roost ranged from 1.2 to 5.5 kilometers for females, and 1.4 to 7.4 kilometers for males (table 2). Bats traveled somewhat further to foraging sites in the NCP than the SCP. When the distance traveled by red bats was examined temporally, bats monitored in late summer (August) were detected an average of 5.02 kilometers from the roost, whereas remaining bats traveled an average of 1.55 kilometers from the roost.

The foraging area polygons of red bats consisted of 87.2 percent forested habitat, 11.8 percent non-forested areas,

Table 2—Estimates of foraging area size and maximum distances traveled from day roosts of radiotagged red bats[a]

Bat no.	Study area	Days monitored	Foraging area	Maximum distance
			Ha	*Km*
389	NCP	12	193	1.4
430	NCP	2	179	1.3
432	NCP	4	291	2.7
606	NCP	12	262	1.7
645	NCP	8	925	7.4
745	NCP	7	120	5.5
546	SCP	6	554	3.3
575	SCP	9	850	3.9
883	SCP	9	134	1.4
944	SCP	10	116	1.2
963	SCP	6	113	1.2
984	SCP	8	192	1.5

[a] Includes only bats for which ≥ 40 locational crosses were obtained.

and 1.0 percent aquatic habitat (table 3). The bats were recorded foraging over forested habitat 78.3 percent of the time, non-forested areas 16.0 percent of the time, and aquatic habitat 5.7 percent of the time. In the NCP where the landscape was more fragmented, 76.8 percent of the foraging area of red bats was forested and bats spent 68.6 percent of their foraging time over those habitats. The total foraging area of red bats in the SCP was 97.5 percent forested habitats and the bats used these areas 88.0 percent of the time. Aquatic habitats accounted for ≤ 1 percent of the total habitat within all foraging areas of red bats, yet accounted for 5.0 percent and 6.5 percent of the foraging locations of bats in the NCP and SCP, respectively.

DISCUSSION

The characteristics of the landscape appeared to dictate the habitats that red bats used as foraging habitat. Although forested habitat predominated in both study areas, red bats also used other habitats such as grazing lands, agricultural fields, cemeteries, street lights and other human residential areas, especially in the more fragmented NCP. These data are consistent with those obtained for red bats in other locations where this species was frequently detected foraging in non-forested habitat (Hickey and Fenton 1990; Hickey and others 1996; McCracken and others 1997).

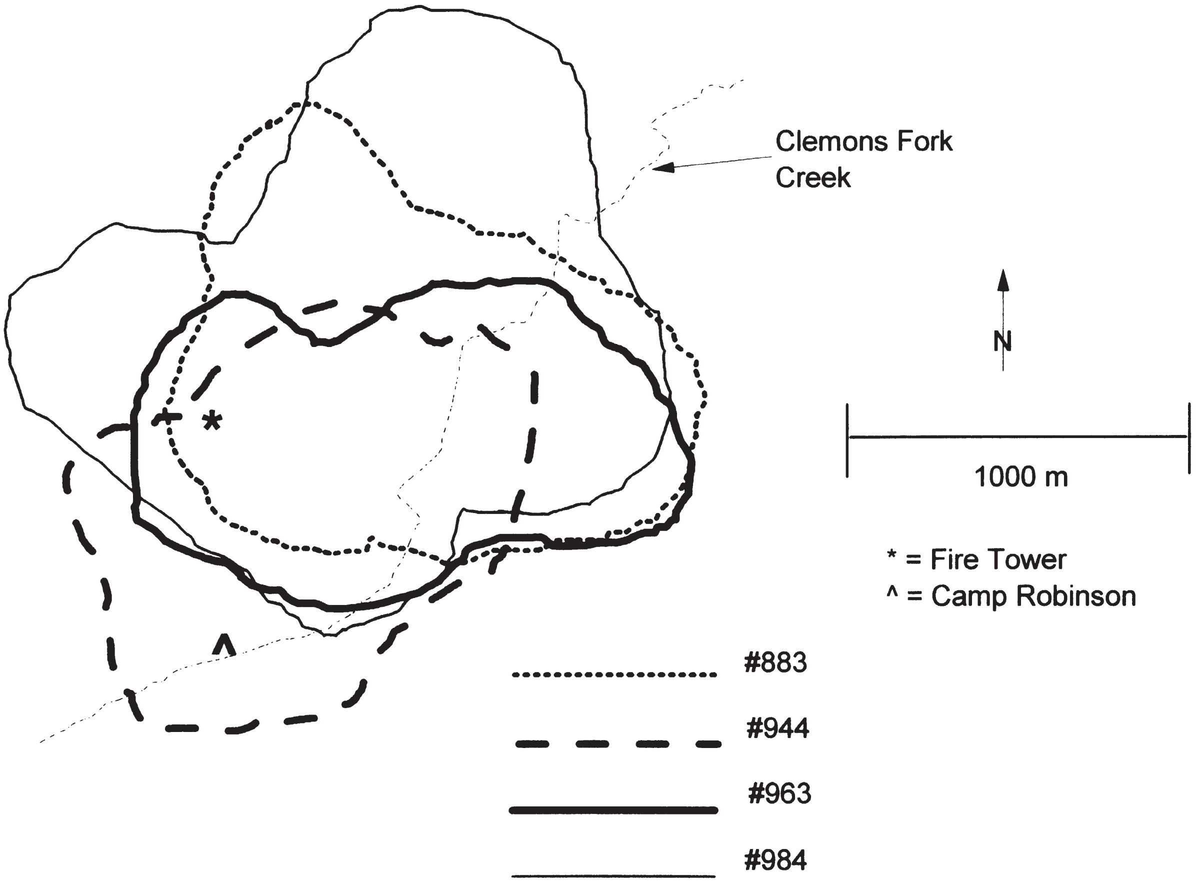

Figure 1—Foraging area polygons for four radiotagged red bats showing overlap in use of available habitat.

Table 3—Comparison of habitat available within foraging area polygons to the percentage of locational crosses by habitat (in parentheses) of radiotagged red bats in eastern Kentucky[a]

Bat no.	Study area	Forested habitat	Non-forested habitat	Aquatic[b] habitat
		- - - - - - - - - *Percent*	- - - - - - - - - -	- - - - - - - - -
389	NCP	99.0 (95.8)	0.0 (1.7)	1.0 (2.5)
430	NCP	79.0 (56.5)	20.0 (36.9)	1.0 (6.6)
432	NCP	90.0 (67.8)	9.0 (30.5)	1.0 (1.7)
606	NCP	64.0 (57.7)	35.0 (36.6)	1.0 (5.7)
645	NCP	76.0 (71.4)	23.0 (20.4)	1.0 (8.2)
745	NCP	53.0 (62.5)	46.0 (32.5)	1.0 (5.0)
546	SCP	98.0 (92.0)	1.0 (4.0)	1.0 (4.0)
575	SCP	98.0 (87.0)	1.0 (3.7)	1.0 (9.3)
883	SCP	98.0 (92.7)	1.0 (4.9)	1.0 (2.4)
944	SCP	95.0 (75.8)	4.0 (16.7)	1.0 (7.5)
963	SCP	98.0 (86.8)	1.0 (1.9)	1.0 (11.3)
984	SCP	98.0 (93.5)	1.0 (2.2)	1.0 (4.3)

[a] Includes only bats for which ≥ 40 locational crosses were obtained.
[b] Availability of water in foraging area estimated to be ≤ 1.0 percent for all red bats monitored.

Because red bats selectively foraged over water at proportions greater than the availability of this habitat in the landscape, a source of permanent water in the vicinity of roosting sites of red bats apparently is important. However, in the NCP where large bodies of water were present, i.e., Grayson Lake and the Little Sandy River, red bats were seldom detected foraging over these sites. The majority of locational crosses of red bats over water occurred while the bats were foraging over small streams during the first 30 to 45 minutes after emergence. Mumford and Whitaker (1982) reported that red bats needed bodies of water for drinking and observed this species foraging over small pools of water ca. 1.2 x 1.8 meters in size and as shallow as 2.5 centimeters in depth. A small permanent source of water transected the foraging areas of all but two of the red bats monitored.

Despite their use of aquatic and non-forested habitats, red bats foraged in forested habitat more often than the other habitats available, but used forests at proportions less than their availability in the landscape. This was especially true for bats in the SCP where large disturbed habitats in the form of reclaimed strip mines and numerous upland ponds were nearby, but were never used as foraging areas. Instead, red bats remained in contiguous forest almost 90 percent of the time. Barclay (1984) observed similar patterns for red bats in Manitoba. He found that red bats used forested ridges 75 percent of the time they were foraging and spent much less time foraging in the other habitats.

We observed substantially larger foraging areas of red bats than previously reported (Hickey and Fenton 1990; McCracken and others 1997). In these studies, red bats centered their foraging activity around street lights and, in one study, averaged 127 minutes/night foraging around lights (Hickey and Fenton 1990). The echolocation calls of red bats foraging around street lights may be homed in on by other red bats in search of prey (Hickey and Fenton 1990). Although more than one red bat was seen occasionally foraging around street lights, we never observed two radiotagged bats using street lights at the same time despite substantial overlap in the foraging areas of red bats monitored simultaneously (fig. 1). The red bats monitored in the Cumberland Plateau physiographic region of eastern Kentucky did not exploit the prey densities around street lights in rural areas to the extent hypothesized by Furlonger and others (1987).

By recording azimuths every 2 to 3 minutes, the possibility exists that our data are affected by autocorrelation (White and Garrott 1990). Autocorrelation leads to a biased underestimate of foraging area size (Hansteen and others 1997, White and Garrott 1990). Extending the length of time between azimuths will correct for autocorrelation, but will also lead to a reduction in sample size (Hansteen and others 1997). Given the length of time that the transmitters were likely to remain active (ca. 1 to 2 weeks), we felt that sample size was a more important consideration in our study. Further, our estimates of foraging area size of red bats were larger than any reported in the literature (Hickey and Fenton 1990, McCracken and others 1997); therefore, it is unlikely that autocorrelation, if present, altered the conclusions drawn from this study.

The maximum distance red bats foraged away from their roosting sites was slightly greater for bats in the fragmented landscape of the NCP than for bats inhabiting the contiguous forests of the SCP. These distances increased in late summer, likely coinciding with the breakup of family units as suggested by Constantine (1966). Kunz (1982) proposed that roost lability, especially among tree-roosting species of bats, results in decreased commuting costs to foraging areas; however, the distances that red bats were recorded traveling from roosting sites to feed were comparable in length to those recorded for cliff-roosting bats, i.e., *Corynorhinus* species, on the Cumberland Plateau of eastern Kentucky (Adam and others 1994, Hurst 1997). Based on Kunz (1982), we anticipated shorter commuting distances for red bats than were observed for cliff-roosting species, because of a higher availability of potential roosting sites for red bats. Because red bats traveled long distances to feed and often used large foraging areas, roost lability probably was not a factor influencing commuting cost or foraging area size in the red bats that we radiotracked. Instead, we propose that commuting cost and foraging area size in red bats were a function of the seasonal cycle and the reproductive status of individual bats. The location of foraging areas ultimately may be determined by the presence of preferred diurnal roosting sites.

Because all bats in which ≥ 40 locational crosses were obtained met the 5 percent load-carrying rule for transmitter mass (Aldridge and Brigham 1988), we believe that these data accurately depict the foraging behavior of red bats. All radiotagged red bats exhibited normal foraging patterns within 20 minutes after release, with the exception of two juvenile males in July 1996. We found adult males to be much more difficult to track than adult females, with increased movements for bats radiotagged after 24 July in both years. Saugey and others [In Press] reported similar problems in radiotracking male red bats back to roosting sites in Arkansas, referring to the roosting pattern of males as “vagabond.”

CONCLUSIONS

Although there is considerable plasticity in the selection and use of foraging habitat by red bats, the extensive use of forests by this species suggests that large blocks of contiguous forest provide suitable habitat. Shorter commuting distances for red bats in the less fragmented SCP and the complete absence of radiotagged bats in the heavily disturbed habitat (i.e., surface-mined lands) nearby, indicate that some deforested areas and habitat fragments may provide less than optimal habitat conditions for this species. Studies comparing the survivorship and fecundity of red bats inhabiting forested and fragmented landscapes, including agricultural and surface-mined lands, are warranted.

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WHITE-TAILED DEER IMPACT ON FOREST REGENERATION: MODELING LANDSCAPE-LEVEL DEER ACTIVITY PATTERNS

Linda S. Gribko, Michael E. Hohn, and William M. Ford[1]

Abstract—White-tailed deer (*Odocoileus virginianus*) herbivory has been identified as a major impediment to the survival and growth of forest regeneration in the northeastern United States. As a supplement to direct control of deer densities through hunting, it may be possible for land managers to manipulate habitat and browsing pressure through carefully planned timber harvest. We are developing methods to relate deer habitat use patterns to regeneration condition and complexity across large landscapes. The preliminary research presented here involved development of methodology to efficiently and effectively model deer habitat use patterns across forested landscapes using fecal pellet groups as an activity index.

Work was conducted in summer 1997 on the 3,078-hectare West Virginia University Forest (WVUF) in north-central West Virginia and the 3,413-hectare Westvaco Wildlife and Ecosystem Research Forest (WERF) in the south-central portion of the state. Fecal pellet group counts were conducted on geolocated 1.72-meter radius circular plots at an intensity of approximately 1 plot per 2.4 hectares. We used variography to investigate spatial dependence in the data. Deposition patterns were modeled using geographic information systems (GIS) technology and a spatial statistics technique known as 2-dimensional ordinary point kriging. Variography revealed spatial contagion in the WVUF data that could be accurately modeled using this methodology. The resulting interpolated probability map is of high potential value in the long-term monitoring of deer activity patterns across this forested landscape. Results on the WERF indicated that sampling intensity was too coarse to allow modeling of strong localized dependence in the data.

INTRODUCTION

Excessive white-tailed deer (*Odocoileus virginianus*) herbivory, or browsing, has been identified as a major impediment to the survival and growth of tree seedlings and herbaceous plants in the northeastern United States (Shafer and others 1961, Tierson and others 1966, Jordan 1967, Alverson and others 1988, Tilghman 1989, Trumbull and others 1989). Browsing can affect forest regeneration by reducing seedling numbers, reducing seedling height, altering species composition, delaying stand establishment, or causing complete regeneration failure (Redding 1987). Of particular concern to forest managers are conversions of woody understories to ferns and grasses (Marquis 1974, Horsely and Marquis 1983) and the elimination of highly valued commercial tree species such as northern red oak (*Quercus rubra*) from the pool of large advance regeneration under mature forest canopies (Marquis and others 1976). Severely impacted forest ecosystems are devoid of most understory plants that are palatable to deer and may exhibit an overall reduction in animal diversity (deCalesta 1994).

Deer herbivory research conducted to date suggests that deer population densities in many forested landscapes should be reduced (Behrend and others 1970, Marquis 1981, Storm and others 1989, Bowersox and others 1993, McCormick 1993). However, the public demand for deer hunting opportunity often outweighs concerns about browsing impacts; state wildlife agencies are consequently reluctant to lower deer densities to suggested levels (Sheffer 1987).

Rather than attempting to control deer densities directly through harvest, it may be possible to manage forested landscapes to reduce browsing pressure and regeneration damage. The manipulation of the spatial distribution of clearcuts has been suggested as one means of accomplishing this objective (Ford and others 1994). Deer extensively forage in recent clearcuts during spring and summer months when succulent leaves and new growth are available (Wentworth and others 1990, Ford and others 1993). In the central and southern Appalachians, the availability of clearcuts has been found to increase carrying capacity of the surrounding forest and reduce browsing pressure on forested understories during the summer months (Johnson and others 1995). Improvement of forage conditions through timber harvest has been suggested as a means of reducing relative deer densities (deCalesta and Stout 1997). Careful planning of the intensity, timing, and location of timber harvest areas may allow managers to draw deer away from forested understories while maintaining the population at a sufficient density to provide adequate hunting opportunity.

Currently, a lack of deer herbivory research conducted at the landscape level constrains the development of forest management recommendations. Most studies have considered localized, or stand-level, effects of deer browsing. Investigators have considered the impacts of deer in contiguous closed-canopy forests (Marquis 1981), in small isolated woodlots (Storm and others 1989, Bowersox and others 1993), in recently clearcut areas (Marquis and

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Grisez 1978), or after specific stand treatments such as thinnings (McCormick 1993). Typically, such research has involved comparisons of areas with varying densities of deer or the use of fencing and barriers to manipulate deer impacts. Work at larger spatial scales (200 to 400-hectare blocks) has been recently initiated in Pennsylvania (Stout and others 1995). However, the more fragmented severely browsed forests of Pennsylvania may not be comparable to the more continuous less intensively browsed forests found elsewhere in the Appalachian region.

In 1997, we initiated a study designed to relate deer habitat use patterns to woody regeneration condition and complexity across landscapes dominated by relatively continuous closed-canopy second-growth hardwood forest. This paper reports the results of the first phase of study in which we developed a method of quantifying landscape-level deer habitat use patterns using fecal pellet group counts as an activity index. Generally, pellet groups are counted on either rectangular belt transects (Bennett and others 1940, Robinette and others 1958, Fuller 1991) or circular plots of various dimensions (Eberhardt and Van Etten 1956, Robinette and others 1958, Van Etten and Bennett 1965). Counts of fecal pellet groups are widely used to census deer populations and to determine habitat use (Neff 1968). Average counts within management units or habitat types are compared as relative indices of deer abundance or are used with defecation rate to estimate population densities. Bennett and others (1940) found that deer defecate close to feeding areas, indicating that high densities of fecal pellets may be associated with high levels of herbivory.

Traditionally, spatial patterns of pellet group deposition are not considered. However, if the spatial dependency among fecal pellet counts made at a large number of discreet points throughout a forested landscape is strong enough to be modeled, the relationship could be used to estimate pellet count densities at unsampled locations. A map, or data layer, of predetermined spatial resolution would result. The field of geology offers techniques, termed geostatistics, that can be used to quantify the inherent spatial dependencies in data and use them to create interpolated data coverages. Although developed to model petroleum and mineral reserves, geostatistics have also been used in the modeling of ecological data (Robertson 1987, Rossi and others 1992, Pelletier and Parma 1994, Villard and Maurer 1996). One of these techniques, *kriging*, has been applied outside of the geological sciences to model insect outbreaks (Kemp and others 1989, Liebhold and others 1991, Hohn and others 1993, Gribko and others 1995), forest biomass and nutrient cycles (Pauly and others 1996), and old-growth forest characteristics (Biondi and others 1994).

The purpose of this study was to determine if fecal pellet group counts made at discreet points could be used to model deer activity patterns across a forested landscape. Specific objectives included: 1) quantifying the spatial dependence inherent in deer fecal group deposition, and 2) determining the suitability of geostatistical techniques, specifically 2-dimensional ordinary point kriging, in mapping white-tailed deer use of forested landscapes.

METHODS

Study Areas

The study was conducted on two sites: the 3,078-hectare West Virginia University Forest (WVUF) in Monongalia and Preston Counties, WV, and the 3,413-hectare Westvaco Wildlife and Ecosystem Research Forest (WERF) located in Randolph County, WV. The WVUF is located on the western-most anticline of the Allegheny Mountains. Elevations range from 318 to 796 meters. The tract is covered by closed-canopy 70-80 year old hardwood forest; no more than 200 hectares have been impacted by timber harvest or major canopy disturbance in the past 20 years. Four forest types as classified by SAF (Eyre 1980) have been identified on the WVUF: yellow-poplar (*Liriodendron tulipifera*)—white oak (*Quercus alba*)—northern red oak, white oak—black oak (*Quercus velutina*)—northern red oak, chestnut oak (*Quercus prinus*), and yellow-poplar. The two types containing yellow-poplar components are found in protected coves, on north and east aspects, and at shaded mid-slope positions. The oak-dominated types are found on the drier, less protected sites; the chestnut oak type is constrained primarily to ridgetops and upper slope positions.

Elevations on the WERF range from 699 to 1176 meters. The topography is dominated by a series of ridges oriented northeast to southwest. Ninety-seven percent of the forested area is comprised of 60 to 70-year-old stands of mature hardwoods. However, the majority of the mature stands have been partially harvested at least once in the past decade and canopy cover is not continuous. The WERF includes 3 forest types in addition to 140 hectares of open or non-forested land. Ninety percent of the forest cover is classified as the sugar maple (*Acer saccharum*)-beech (*Fagus grandifolia*)-yellow birch (*Betula allegheniensis*) SAF type; associated species include white ash (*Fraxinus americana)*, American basswood (*Tilia americana*), black cherry (*Prunus serrotina*), yellow-poplar, and northern red oak. The yellow-poplar—white oak—northern red oak type is found on 195 hectares of protected coves. The remaining 21 hectares are classified as the white oak SAF type; associated species include chestnut oak, scarlet oak (*Quercus coccinea*), black oak, and hickory (*Carya* spp.).

Field Methods

Data was collected in summer 1997. Sample points were established in an approximately square-grid pattern at an intensity of approximately 1 per 2.4 hectares; points were approximately 240 meters apart. A total of 1,400 points were located on the WVUF; 1,445 points were located on the WERF. The points were georeferenced using a hand-held GPS unit and fixed base station which allowed differential correction of the satellite locations. Each point was the center of a 1.72-meter (9.29 square meters) radius circular plot on which fecal pellet surveys were conducted (Robinette and others 1958, Van Etten and Bennett 1965). Pellet groups on each of the plots were counted once from June to July on the WVUF and from August to September on the WERF. All pellets were destroyed by crushing. The counts provided baseline data and were not assumed to represent deer activity during any specific season.

Data Analysis

Topographic variables—It was first necessary to examine the relationships between pellet group densities and possibly confounding variables related to topography. Digital elevation models (DEMs) were available for both experimental forests. The model for the WERF was developed by Westvaco personnel at a resolution of slightly over 15 meters. The 30-meter resolution USGS DEM was used to describe the topography of the WVUF. We calculated percent slope and aspect in degrees azimuth using the elevation data and the raster-based geographic information system (GIS), IDRISI (Eastman 1997). We then standardized the aspect data by subtracting 180 degrees and taking the absolute value of the difference; effectively lumping the data collected on approximately eastern and western aspects (intermediate site quality) while segregating data collected on approximately northern (highest site quality) and southern (lowest site quality) aspects. For each experimental forest, pellet group data were plotted against elevation, slope, and aspect and relationships were examined.

Variography—Spatial dependence on each experimental forest was quantified with the variogram, a graph that illustrates the relationship between the distance separating pairs of data points (*h*) and half the average squared deviation of a regionalized variable ($\gamma(h)$). In this case, the variogram statistic at each given distance *h* represents half the average squared difference between paired fecal pellet group counts separated by that particular distance (Hohn 1988, Isaaks and Srivastava 1989, Liebhold and others 1991, Rossi and others 1992). The variogram statistic is defined as

$$\gamma(h) = \frac{1}{2n}\sum_{k=1}^{n_h}[z(x_k) - z(x_k + h)]^2$$

where n_h is the number of pairs of cells separated by a distance of *h* (expressed in meters in this study), $z(x_k)$ is the observed pellet group count at location x_k, and $z(x_k + h)$ is the observed count at a location *h* meters from x_k. In the absence of spatial dependence, the variogram is constant with distance *h*. In the presence of strong spatial dependence, the difference between $z(x_k)$ and $z(x_k + h)$ is relatively small when *h* is small and increases with separation distance. At some distance, the difference between counts fails to increase further and the variogram levels off. This distance is referred to as the *range* of the variogram. The value of $\gamma(h)$ at the range is called the *sill*. In general, one would expect the variogram to originate at the origin; however, variograms manifest a non-zero y-intercept when some component of the variability is non-spatial or on a smaller scale than sample spacing.

For each experimental forest, VARIOWIN version 2.2 (Pannatier 1996) was used to calculate the variogram statistic in 120-meter lags with a 60-meter tolerance to a maximum separation distance of 1200 meters. The first lag included pairs having a separation distance smaller than the tolerance; in other words, all pairs separated by less than 60 meters. The few pairs in this lag were retained rather than disregarded. The relationship between pairs separated by more than 1200 meters was not considered. Surface plots of the variogram statistics calculated in the east-west direction versus those calculated in the north-south direction were examined for indications of directionality in the data (Figure 1-2). In the presence of strong directional trends, several individual models are required to accurately describe the spatial dependence in the data. In its absence, a single omnidirectional model is sufficient. In neither data set was there discernible directionality.

Omnidirectional variograms for each forest were plotted using VARIOWIN and models were fit iteritively by eye (Hohn 1988). Single and nested linear, exponential, gaussian, and spherical model forms were tested for

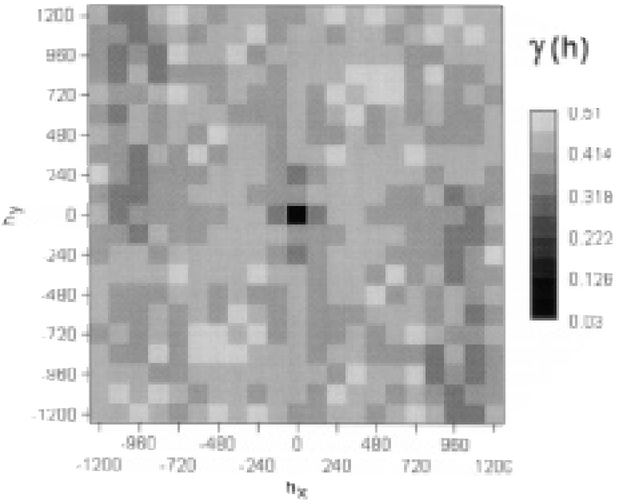

Figure 1—Variogram surface for the West Virginia University Forest (WVUF).

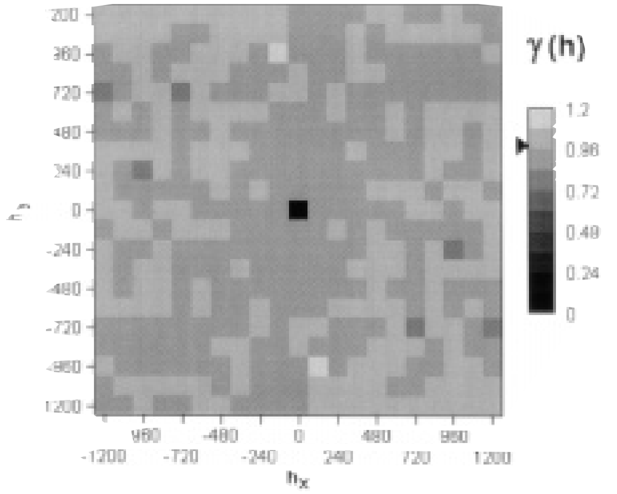

Figure 2—Variogram surface for the Westvaco Wildlife and Ecosystem Research Forest (WERF).

general fit to the shape of the variograms and the models were fine-tuned by alternately adjusting the *sill* and the *range*. Special care was taken to fit the first few lags accurately, so the final models may or may not have exhibited the best overall goodness of fit. In both cases, the origin was forced through zero.

Kriging—Results of the variogram analysis were used to calculate weights employed in the 2-dimensional ordinary point kriging of the pellet count data. Kriged estimates are weighted averages of values at nearby locations

$$z^* = \sum_{j=0}^{n} w_j \cdot z_j$$

where z^* is the interpolated value being estimated, $z = [z_1, z_2, z_3, \ldots, z_n]$ is the vector of values at nearby locations and $w = [w_1, w_2, w_3, \ldots, w_n]$ is the vector of corresponding weights to be used in averaging the values. Because the *kriging* procedure minimizes the variance of the errors, the weight matrix can be estimated as

$$w = C^{-1} \bullet D$$

where C is the (n+1) by (n+1) covariance matrix and all the z values from nearby samples and D is the n+1 vector of covariances of z values between the point being estimated and the nearby samples. The covariances can be computed directly from the variogram as

$$\mathrm{cov}(h) = c - \lambda(h)$$

where c is the variogram sill.

GSLIB version 2.0 was used to krige the data (Deutsch and Journel 1998). Kriged estimates were made at a 30-meter resolution and were based on at last 2, but no more than 36, values collected within 500 meters of each unsampled location. Estimates made near the boundaries of the experimental forests were based necessarily on fewer samples than those made in the interior.

RESULTS

There were no strong identifiable relationships between the topographic variables and pellet group counts on either of the experimental forests. Aspect may have some effect on the WERF as evidenced by somewhat depressed, but statistically insignificant, pellet group counts on the more southerly aspects. It appears that elevation possibly may be related to counts on the WVUF; however, high pellet group densities at elevations over 600 meters were clustered on a portion of the forest that was heavily impacted by overstory mortality in 1990-91. Higher counts in these areas were likely related to browse availability rather than elevation. Linear regressions through these data were all essentially horizontal with R^2 values less than 0.01. No attempt was made to transform the data.

Variogram surface plots revealed no directional dependence in the WVUF data (Figure 1). Weakly elevated dependence was suggested among pellet plots oriented in a northeast to southwest direction on the WERF (Figure 2). However, the trend was not strong enough to necessitate calculation of directional variograms. The majority of the cells in the variogram surface had values of approximately 0.72 - 0.96; had the values been appreciably lower in the northeast-southwest direction (perhaps in the range of 0.24 – 0.48), a pair of directional variograms may have improved our ability to model the data.

Omnidirectional variograms and the final fitted models for both forests are shown in Figures 3-4. The variogram calculated for the WVUF data was fit with the nested exponential model:

$$\gamma(h) = 0.015\left[1 - e^{\frac{-3|h|}{156}}\right] + 0.415\left[1 - e^{\frac{-3|h|}{231}}\right].$$

The omnidirectional variogram for the WERF was fit with the nested model:

$$\gamma(h) = 0.75\left[1.5\frac{|h|}{92} - 0.5\left(\frac{|h|}{92}\right)^3\right] + 0.20\left[1 - e^{\frac{-3|h|}{485.48}}\right] \quad \text{if } |h| \leq 92,$$

else,

$$\gamma(h) = 0.75 + 0.20\left[1 - e^{\frac{-3|h|}{485.48}}\right].$$

The first structure in this model is spherical; the second is exponential.

Maps of the kriged estimates are displayed in Figures 5-6.

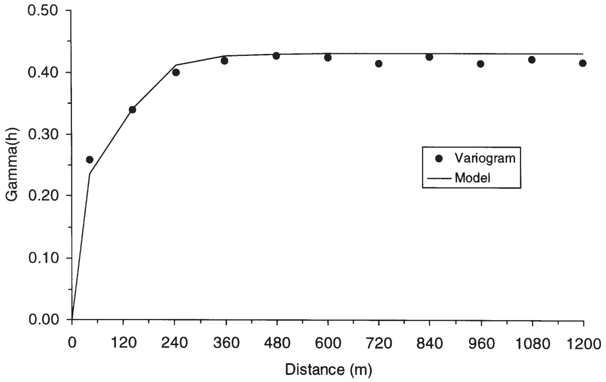

Figure 3—Variogram and fitted model for the WVUF.

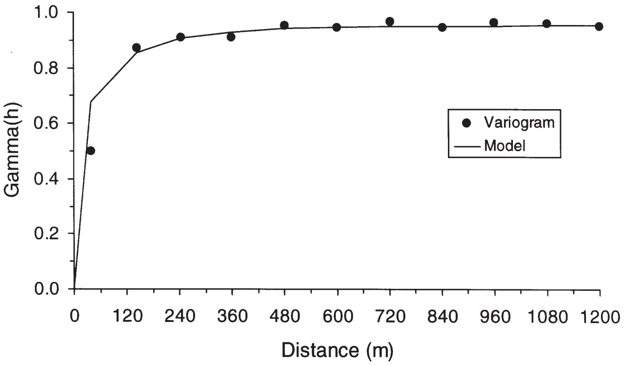

Figure 4—Variogram and fitted model for the WERF.

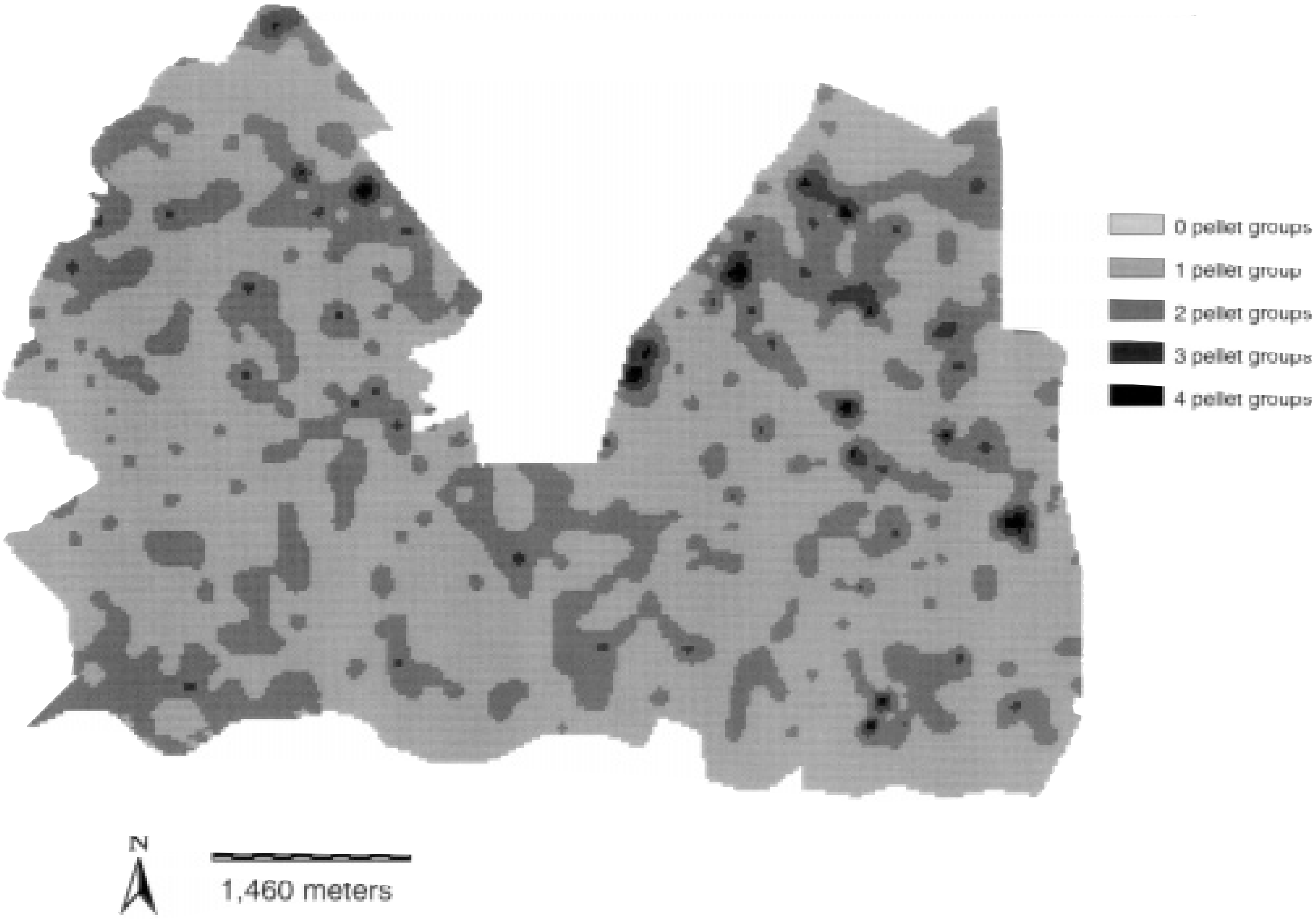

Figure 5—Kriged estimate map for the WVUF. Cells are 15 by 15 meters.

DISCUSSION

Absence of both strong directional trends and strong associations with topographic variables simplifies the modeling process and suggests that differences in pellet group densities are likely related to differences in habitat quality. On both study sites, a single omnidirectional model can be used to describe spatial contagion in the data. In addition, there is no apparent need to incorporate additional independent variables through the use of more complex geostatistical techniques such as cokriging or kriging with external drift (Goovaerts 1997, Deutsh and Journel 1998). This will allow us to monitor the response of deer populations to timber management activities across the study sites without the added complication of confounding variables.

Because the exact location and orientation of the sample plots were not critical in this initial exploratory study, we used temporary locations with the distance between plots paced, rather than measured. This facilitated more rapid data collection but also resulted in less uniformity in the sample design; some plots were installed in closer proximity to adjacent plots than was actually planned. These data could have been omitted; however, we chose to retain them because they provide important information about spatial dependencies in the data at smaller separation distances. The WVUF data included 132 pairs of plots that were separated by an average distance of 42.31 meters and 5,832 pairs separated by an average distance of 142.76 meters. Numbers of additional pairs ranged from 9,928 at a separation distance of 244.40 meters to 37,576 at the maximum separation distance of 1,200.19 meters. The WERF data included 78 pairs separated by an average distance of 40.25 meters and 5,426 separated by an average distance of 144.03 meters. Numbers of pairs ranged from 9,946 at 244.76 meters to 39,144 at approximately 1,200 meters.

The variogram models for both forests included two nested structures; indicating that on both sites there existed local and regional trends in the data. Both structures used in the construction of the WVUF variogram model were of exponential form. The first had a range of 156 meters and sill of 0.015, whereas the second had a range of 231 meters and sill of 0.415. The model used to describe the variogram of the WERF data was more complex. The first structure had a spherical form that described the steep increase in variability between separation distances of less than approximately 100 meters. The second structure, of exponential form, had a range of 485.48 and sill of 0.20. It is important to note that the fit of this model is heavily

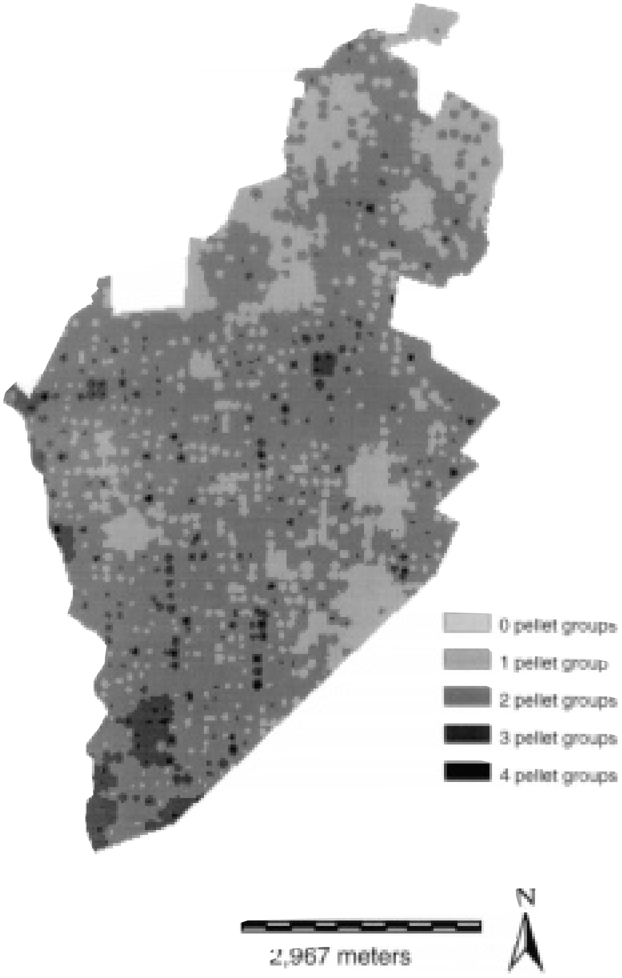

Figure 6—Kriged estimate map for the WERF. Cells are 15 by 15 meters.

influenced by the 78 pairs at very close separation distances.

Overall, pellet group counts made on the WERF were more spatially variable than those made on the WVUF. The combined sill of 0.95 for the WERF data was more than double the 0.43 sill for the WVUF data. This was expected given the differences in the sites. The WVUF is relatively uniform and continuous with harvest units clustered along a rudimentary road system. The majority of the site has not been actively managed for 80 years and little of the total area is in early successional stages. In addition, the forest is heavily hunted and deer populations are not excessive (no quantitative estimate of deer densities are available at this time). In contrast, the WERF has been heavily impacted by both partial timber harvest and dispersed regeneration harvests. The habitat is more variable and more of the total area is covered by young forest. The area is also heavily bisected by a well-developed road system; however, the WERF is gated and hunting is prohibited. Deer populations are consequently much higher on the WERF; the excessive browsing of woody understory vegetation and paucity of herbaceous vegetation indicate that the site is saturated with deer.

The relative lack of sample data at small separation distances combined with the strong localized trend in the WERF data appears in the kriged estimate map as an “egg crate” effect; the overwhelming influence of the most proximal samples caused localized depressions and peaks in the kriged estimates. This problem apparently could be rectified through more intensive sampling. Based on the results of the variography, sampling intensity may have to be more than doubled.

In contrast, the kriged estimates for the WVUF reveal clearly defined areas of heightened deer activity. Less overall variability, a weaker local trend, and a stronger regional trend enabled us to produce an apparently useful predictive map of baseline deer activity patterns. In general, the peaks in estimated pellet counts correspond quite well with known canopy disturbances. For example, peak deer activity occurred in the northeastern lobe of the forest, which was impacted by high overstory mortality in 1990-91 followed by timber salvage operations. The spike of activity at the tip of the northwestern lobe corresponds with a gas pipeline right-of-way. Peaks in the southeastern corner correspond with recent timber harvest operations.

CONCLUSIONS

In general, pellet group data appears to contain enough spatial contagion to allow the production of estimate maps using 2-dimensional ordinary point kriging. Although the estimates have not yet been validated, it appears that spikes in pellet group densities on the WVUF correspond to overstory disturbances and resultant increased availability of woody browse. The results on the WERF were less conclusive and generally indicate that the technique may be less useful in areas of extremely high deer population and variable habitat. However, based on the presence of localized spatial dependence in the small number of samples collected at less than 240 meters, it appears that a follow-up study at higher sampling intensity is warranted before concluding that the technique cannot be used on the WERF or similarly impacted sites.

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