

Assessing Southern Flying Squirrel, *Glaucomys volans*, Habitat Selection with Kernel Home Range Estimation and GIS

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Information on habitat selection behavior is vital to effective conservation and management of native terrestrial fauna, particularly in disturbed, fragmented habitats. Application of the kernel probability density estimation method to the description of animal home ranges, coupled with the mapping and analytical capabilities available in geographic information systems, allow researchers to gain a degree of insight into species' habitat use that has not previously been possible. This paper provides examples of habitat selection analyses performed using home range contours produced in the program KERNELHR and input into the Geographic Resources Analysis Support System (GRASS) where home range contours were overlain on habitat maps. Data for the examples were taken from a study of the Southern Flying Squirrel (*Glaucomys volans*) in fragmented forests in Arkansas, where flying squirrels were tracked by radiotelemetry on five study areas during spring and summer 1994–1996. However, the methods described here may also be applied similarly to other terrestrial vertebrates.

Key Words: kernel, KERNELHR, geographic information system, GRASS, home range, habitat selection, Arkansas.

Many native species of wildlife are being affected by habitat alteration. Effective conservation management requires information on a species' response to habitat disturbance and fragmentation. The lack of data on the effects of anthropogenic and natural disturbances on wildlife has prompted many ecologists to stress the need for autecological research in fragmented habitats (Simberloff and Abele 1982; McCoy 1983; Wilcove et al. 1986; Zimmerman and Bierregaard 1986). Recent advances in home range estimation techniques and geographic information system (GIS) technology have made new tools available to researchers seeking to better understand wildlife habitat requirements. Application of the kernel density estimator to animal home range description (Worton 1989; Worton 1995; Seaman and Powell 1996) provides a useful complement to the analysis and mapping capabilities of a geographic information system (GIS). Used together these technologies allow a more detailed and intensive examination of habitat selection than has previously been possible.

The kernel density estimator has several characteristics which make it attractive as a tool for analyzing animal location data: it is a nonparametric method applicable to multimodal distributional data, it produces a probability density estimate, and it is unaffected by grid size (Seaman and Powell 1996; Hansteen et al. 1997). However, only recently has the kernel method been used to describe home ranges (Worton 1987, 1989; Naef-Daenzer 1993; Seaman 1993; Worton 1995; Seaman and Powell 1996). The program used in this paper, KERNELHR, was first presented in the literature in 1998 (Seaman et al. 1998).

The fixed kernel home range estimator using least squares cross validation (LSCV) selection of bandwidth "h" has been shown through simulations to produce the most accurate home range estimates among five nonparametric methods, including the harmonic mean (Seaman and Powell 1996). Location data are used in the kernel method to produce an estimate of the subject animal's utilization distribution (UD, Van Winkle 1975). The UD estimates proportional usage of different areas in the home range. With a GIS, the UD can be overlain on a map of habitat types to analyze habitat use within the home range (Johnson's [1980] third-order selection) and selection in placement of the home range within a larger available area (Johnson's [1980] second-order selection).

This paper illustrates the use of the DOS-based kernel home range estimation program, KERNELHR (Seaman et al. 1998) in conjunction with the UNIX-based GIS software GRASS (Geographic Resources Analysis Support System, U.S. Army Corps of Engineers 1993) to analyze home range and habitat selection patterns. Data for examples are drawn from a study of Southern Flying Squirrel (*Glaucomys volans*) populations in managed forests (Taulman 1997). Since researchers continue to use polygon methods to describe animal home ranges (Linn and Key 1996; Stone et al. 1997) and to analyze habitat selection behaviors (Bendel and Gates 1987; Kamler and Gipson 2000), habitat selection analyses performed using the 95% minimum convex polygon (MCP, Michener 1979) and modified minimum area methods (concave polygon, Harvey and Barbour 1965) are provided for comparison.

Study Areas

A total of 94 Southern Flying Squirrels were fitted with radiotransmitter collars and tracked on five study areas in the Ouachita National Forest (ONF) of Arkansas ($34^{\circ}22'30''$ – $35^{\circ}N$, $93^{\circ}22'30''$ – $93^{\circ}45'W$) during spring and summer 1994–1996. All core study areas where squirrels were captured in nest boxes were about 15 ha in area. Forest stands were composed of mature pine and hardwood overstory trees. Three of the stands (I, II, and III) were in a relatively old-growth condition where Shortleaf Pine (*Pinus echinata*) basal area (BA) at breast height ranged from 13.8–25.3 m²/ha, hardwood BA was 4.6–11.5 m²/ha, age of overstory trees was > 70 years, and stand aspect was generally south facing. The remaining two stands had been subjected to partial harvest the summer prior to initiation of this study. One was a pine-hardwood shelterwood harvest (IV) which retained 49–99 overstory pines and hardwoods per ha (6.9–9.2 m²/ha, of which 1.1–3.4 m²/ha were hardwoods). The other was a pine-hardwood seedtree harvest (V) which left 25–37 overstory trees per ha (2.3–4.6 m²/ha, of which 1.1–2.3 m²/ha were hardwoods).

Methods

Habitat description and mapping

Habitat types on and around each core stand were categorized and described using a set of 22 vegetative variables measured on multiple 400 m² macroplots. Variables represented shrub-layer and understory vegetative density, lower and upper mid-story tree densities, and overstory tree densities (Taulman et al. 1998). Quantitative comparisons of variables among different habitat types at each study area and among similar habitats at different study areas were used to validate habitat designations (Taulman et al. 1998). Habitat boundaries were digitized from aerial photos into GRASS, where raster maps were created. Differentially corrected global positioning system (GPS, Basic Plus and Geo-Explorer receivers, Trimble Company, Sunnyvale, California, USA) fixes of prominent landscape features and habitat edges (30–60 on each study area) were used register aerial photos and to edit and improve the accuracy of maps.

Radiotelemetry

Flying squirrels were captured during nest box surveys in March 1994–1996 and were fitted with radiotransmitter collars. Nest boxes were closed after the March survey and remained closed during telemetry activities. We located radiocollared animals by tracking on foot with a Wildlife Materials TRX-1000S receiver and an A 148-3S 2-meter FM yagi hand-held antenna (Cushcraft Corporation, Manchester, New Hampshire, USA). We began at dark, tracking an individual until either directly under the arboreal animal or in view of the squirrel

on a tree trunk or on the ground. When a GPS receiver was available, direct measurement of location coordinates was taken at the site. Otherwise, an assistant marked the position of the nearest site on which a GPS fix was known, the azimuth to that site was determined by the researcher at the squirrel position, and the distance was measured with a string hip chain. Universal Transverse Mercator coordinates were later computed trigonometrically for each telemetry location. Data collection continued for 6–8 hours; starting times were staggered to alternately include post-sunset and pre-sunrise activity patterns.

Squirrels were tracked in different order each night; normally one to two locations were obtained on each individual on a study area during a nightly shift, according to the suggested procedure of Swihart and Slade (1985a). The importance of independent data points for home range analysis is not unanimously agreed upon (Swihart and Slade 1985a; Andersen and Rongstad 1989; Reynolds and Laundre 1990; Minta 1992; Swihart and Slade 1997). Swihart and Slade (1988) described time to independence (TTI) as “the minimum time interval over which an animal could occur, in a probabilistic sense, anywhere in its home range”, and as “the time necessary for an animal to traverse its home range” (Swihart and Slade 1985b). They found that body mass in hunter species (those which utilized fruits, seeds, or mobile prey) was related to rate of home range use according to the formula $TTI \text{ in min} = 195 M^{0.49}$, M = mass in kg (Swihart and Slade 1988). Using the average mass of all adult squirrels encountered in 1993 (74 g) with the TTI formula for hunter species resulted in a calculated TTI estimate of 54 min for *G. volans*. We thus decided initially to maintain a temporal separation of at least one hour between successive locations on each animal during 1994 and 1995. This is double the minimum TTI considered sufficient for Southern Flying Squirrels by Fridell and Litvaitis (1991). In 1996, the minimum time interval between fixes was increased to two hours to observe whether statistical independence of locations would be thus improved. All sets of telemetry locations were examined with the three tests of independence (t^2/r^2 [Schoener 1981; Swihart and Slade 1985b]; Ψ [psi, Swihart and Slade 1985a]; and γ [gamma, Swihart and Slade 1986]) included in the computer program HOME RANGE (Ackerman et al. 1990).

Kernel home range calculation

Description of the kernel density estimation method as applied to animal home ranges (and comparisons with other common home range estimation methods) is given elsewhere (Silverman 1986; Seaman and Powell 1996; Seaman et al. 1998). The 95% fixed kernel density contour, computed using least squares cross validation selection of the smoothing parameter “h”, was used to describe home ranges in

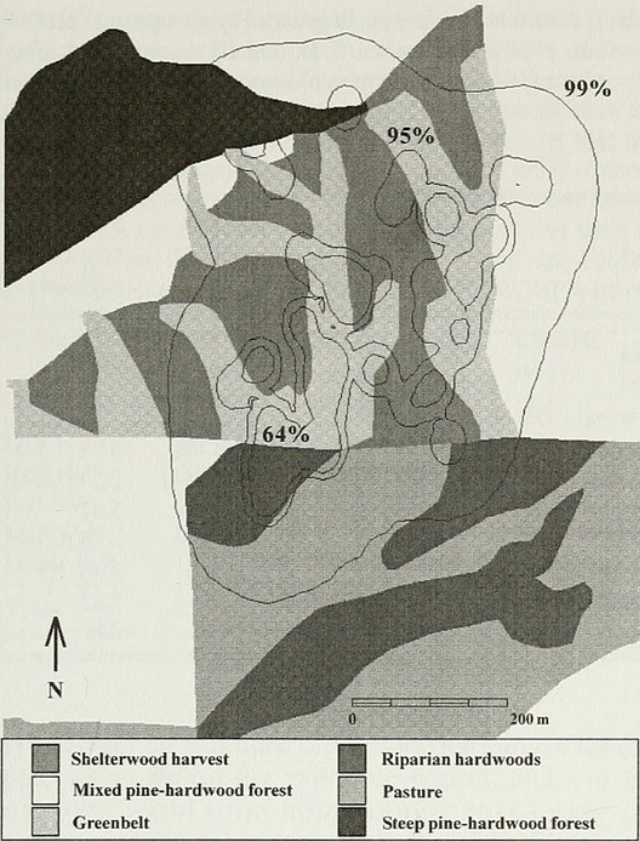


FIGURE 1. Home range, core activity area, and available area contours for a single adult female Southern Flying Squirrel on study area IV in 1995. The contour data were computed in the KERNELHR home range program, then input into GRASS, where maps of habitats had been digitized from aerial photos. Fixed kernel 95% home range and core contours are shown, calculated using least squares cross validation procedures for selection of the smoothing parameter “h”, and limiting “h” to the range 0.25–1.0 (as suggested by Seaman 1993). The 99% contour was computed from the same location data set, selecting the 99% level and using the “reference” smoothing parameter optimized by the program KERNELHR for bivariate normal data; it is used as an estimation of the habitats available for the placement of the home range.

this study. We limited the program’s selection range for “h” to 0.25–1.0 times the reference value, as suggested by Seaman (1993). We follow Burt’s (1940) definition of home range as “that area traversed by the individual during its normal activities of food gathering, mating, and caring for young” As computed by the program KERNELHR, home ranges in this study comprise the smallest area containing 95% of the utilization distribution, as suggested by Seaman and Powell (1996). The core activity area computed by KERNELHR is that area enclosed by a contour within which locations are closer together than would be expected under the assumption of a uniform use of the home range area (Worton 1987), commonly from 60–75% of the utilization distribution.

Previous studies of habitat selection have presented what sometimes seem to be rather arbitrary and inconsistent methods for estimating available areas for habitat selection analyses (Neu et al. 1974; Byers et al. 1984; Rolley and Warde 1985; Gese et al. 1988). The accurate estimation of available habitats is essential to a valid habitat selection analysis which compares used and available areas (Johnson 1980; Porter and Church 1987). In order to arrive at a systematic method for estimating available area for an animal’s placement of its home range, we used each animal’s location data set to create a 99% contour using the “reference” h smoothing parameter value (without least squares cross validation), which is appropriate for bivariate normal data (Silverman 1986; Worton 1995; Seaman and Powell 1996). This contour is positively biased for multimodal, nonnormal data, typical of animal utilization distributions

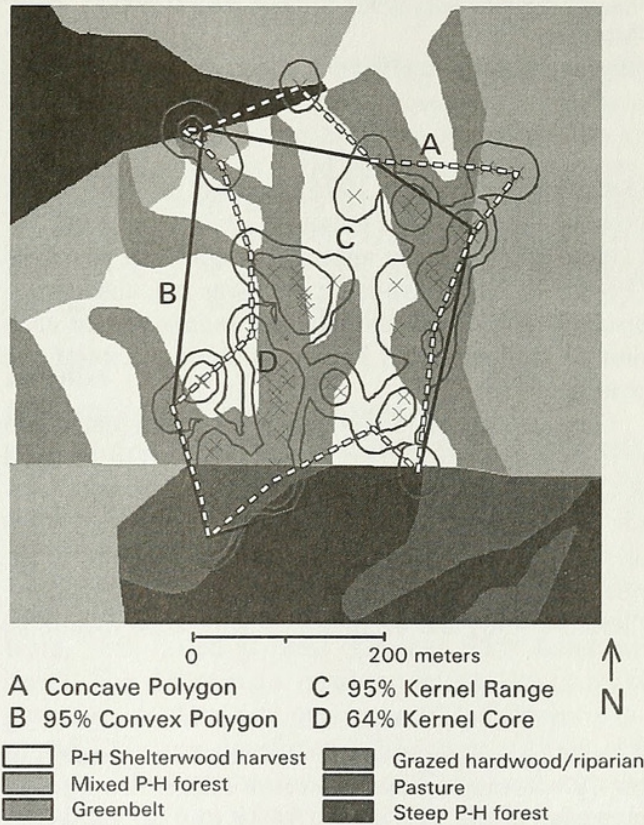


FIGURE 2. A comparison of the utilization distribution shapes and areas of habitats enclosed in home ranges estimated using the fixed kernel method with least squares cross validation selection of the smoothing parameter (program KERNELHR, Seaman and Powell 1995) to compute the 95% (C) and core activity area contours (D), the 95% minimum convex polygon (B, Michener’s [1979] method in program HOME RANGE, Ackerman et al. 1990), and the modified minimum area method (A, Harvey and Barbour’s [1965] method in program Telem88, Coleman and Jones 1988). All contours were computed using the same location data set from the adult female squirrel depicted in Figure 1. The 69 locations used to compute these ranges are denoted by Xs.

TABLE 1. Mean 95% kernel home range areas (with 1 standard error) for male and female Southern Flying squirrels on five study areas, computed with the program KERNELHR (Seaman et al. 1998). Study areas I, II, and III were mature pine-hardwood forest study areas, IV was a shelterwood harvest study area, and V was a seedtree harvest study area. Data were collected on study areas I and V in 1994, II in 1994 and 1995, III in 1995, and IV in 1995 and 1996. For comparison, home range areas computed with the 95% minimum convex polygon (MCP) and modified minimum area (concave polygon) methods are also given.

Study area	Gender	N	Mean locations	Mean time between observations (hr)	Inclusive dates	Mean (SE) 95% Kernel area (ha) ¹	Mean (SE) 95% MCP area (ha) ²	Mean (SE) concave polygon area (ha) ³
I	M	2	45.5	53.0	4/16 - 8/23, 1994	14.3	21.56	11.45
	F	6	47.3	55.9	3/23 - 8/23, 1994	6.43 (1.57)	5.08 (1.06)	3.27 (0.52)
II	M	6	47.9	49.8	4/12 - 8/18, 1994 and 1995	19.09 (5.65)	24.58 (8.45)	13.04 (3.57)
	F	8	57.5	42.4	4/12 - 8/19, 1994 and 1995	6.09 (1.87)	11.24 (5.59)	4.98 (1.56)
III	M	3	36.3	21.5	5/3 - 8/8, 1995	44.00 (15.16)	46.23 (11.60)	22.33 (8.90)
	F	2	60.5	36.0	4/23 - 8/8, 1995	6.04	4.62	5.41
IV	M	5	75.4	21.9	3/27 - 6/19, 1995 and 1996	4.80 (0.82)	5.84 (0.92)	3.96 (0.74)
	F	9	64.9	32.8	3/27 - 8/4, 1995 and 1996	5.57 (0.81)	6.97 (1.07)	5.30 (0.99)
V	M	2	38.0	80.4	3/28 - 7/23, 1994	2.76	3.26	1.85
	F	1	41.0	65.8	3/21 - 6/8, 1994	3.38	7.50	2.85

¹Seaman and Powell (1996), Seaman et al. (1998).

²Michener (1979)

³Harvey and Barbour (1965).

(Seaman and Powell 1996). It also includes areas beyond the observed locations, a “buffer zone” of habitats in which the animal has not been observed (Figure 1). Thus, available area was calculated consistently among all animals, but separately for each animal, and reflected known individual habitat use patterns.

Only location data sets which reached a plateau on a location-area curve (Cain 1938; Odum and Kuenzler 1955) were used for home range and habitat selection analyses (50 of 94). Worton (1987) advised that a minimum of about 30 locations are needed for nonparametric home range estimators; therefore, only the 42 data sets with ≥ 30 locations,

were used in comparisons of home range size among study areas. However, available area and home range should be biased proportionately for each individual, and habitat selection analyses are considered valid for each animal whose location data showed a plateau on the location-area curve, including the eight with fewer than 30 (14–29) total locations.

Home ranges of all 50 squirrels were also estimated using the 95% minimum convex polygon method and the modified minimum area method (Figure 2).

Habitat selection analysis

We analyzed two levels of habitat selection for squirrels during their nightly activities [Johnson’s

TABLE 2. A sample of nesting habitat selection results on study area II in 1995. Available area of different habitat types (m_i), proportion of available areas of each habitat type ($\pi_i = m_i / m_+$), number of diurnal nest trees in each type (u_i), used proportion of nest trees in each habitat ($o_i = u_i / u_+$), habitat selection ratios ($\hat{w}_i = o_i / \pi_i$), and Bonferroni confidence intervals (after Manly et al. 1993). Each interval represents a 99% confidence limit, total confidence for all intervals approximately 95% (confidence intervals for habitats with less than five trees not conclusive). A + indicates significant selection for a habitat type, - against. MAT P-H = mature pine-hardwood forest, YNG PLA = young pine plantation (< 15 years old), IMM PLA = immature pine plantation (15 - 40 years old), STP P-H = steep pine-hardwood forest, GB = greenbelt.

Habitat type	Area in home ranges (ha) (m_i)	Available proportion (π_i)	Diurnal nests (u_i)	Used proportion (o_i)	Selection ratio ($\hat{w}_i$)	Standard error	Lower C.I.	Upper C.I.
MAT P-H	108.38	0.758	49	0.875	1.154	0.034	1.07	1.24 +
YNG PLA	13.90	0.097	1	0.018	0.184	0.002	0.18	0.19 -
IMM PLA	1.99	0.014	0	0	0	0		-
STP H-P	3.46	0.024	0	0	0	0		-
GB	15.22	0.106	6	0.107	1.006	0.004	0.99	1.02
Total	142.95	1.000	56	1.00				

TABLE 3. A sample of nesting habitat selection results on a harvested stand, study area IV, in 1995. Available area of different habitat types (m_i), proportion of available areas of each habitat type ($\pi_i = m_i / m_+$), number of diurnal nest trees in each type (u_i), used proportion of nest trees in each habitat ($o_i = u_i / u_+$), habitat selection ratios ($\hat{w}_i = o_i / \pi_i$), and Bonferroni confidence intervals (after Manly et al. 1993). Available area for nesting determined by summing all habitat areas from squirrel home ranges and combining total number of diurnal nest trees. It is assumed that squirrels are able to independently select nesting sites in areas overlapping the ranges of other squirrels; nesting aggregations common for *Glaucomys volans* support this assumption. Each interval represents a 99% confidence limit, total confidence for all intervals approximately 95% (confidence intervals for habitats with less than five trees not conclusive). A + indicates significant selection for a habitat type, - against. GB = greenbelt, STP P-H = steep pine-hardwood forest, P-H SW = pine-hardwood shelterwood harvest, MIX P-H = uneven aged pine-hardwood forest, HDW RIP = private, grazed hardwood riparian zone.

Habitat type	Area in home ranges (ha) (m_i)	Available proportion (π_i)	Diurnal nests (u_i)	Used proportion (o_i)	Selection ratio ($\hat{w}_i$)	Standard error	Lower C.I.	Upper C.I.
GB	14.36	0.400	23	0.511	1.276	0.030	1.198	1.355 +
STP H-P	2.85	0.079	1	0.022	0.280	0.002	0.275	0.284 -
P-H SW	8.26	0.230	4	0.089	0.386	0.010	0.360	0.412 -
MIX P-H	8.82	0.246	16	0.356	1.446	0.018	1.399	1.492 +
HDW RIP	1.57	0.044	1	0.022	0.508	0.001	0.505	0.510 -
Total	35.86	1.00	45	1.00				

(1980) second and third order selection]: home range placement within the available region, and use of habitats within the home range, respectively. Selection ratios represented: (1) the proportion of a habitat in the home range vs. the proportion of that habitat in the available area; and (2) the percentage of locations in each habitat within the 95% home range vs. the proportion of that habitat type available in the home range. Selection ratios were calculated for each habitat category for each squirrel using that habitat. At each study area mean selection ratios were computed for each habitat type using all individual selection ratios. Bonferroni 95% confidence intervals (Manly et al. 1993) were computed for selection ratio means; an entire 95% confidence interval > 1 was interpreted as indicating significant selection for a particular habitat type; < 1 indicated significant avoidance of a habitat type.

To evaluate diurnal nest-site habitat selection we defined available habitat as the area enclosed by the 95% kernel home range contours for all squirrels on a study area. Percentages of all nesting trees on a study area in each habitat type during a given year were compared with summed proportions of habitat areas within 95% kernel home range contours for all squirrels on a study area. This method acknowledges that home ranges may overlap and assumes that squirrels are able to independently select nesting sites within areas of overlap. Communal nesting, commonly seen in Southern Flying Squirrels (Muul 1974; Taulman et al. 1998), confirms that nesting sites are not mutually exclusive among individuals. The combined number of nest trees within all home ranges is thus proportional to available habitats in those ranges summed for all squirrels.

Since we know of no logical and defensible paradigm for estimating available area for the place-

ment of a home range described by the polygon method, we did not attempt a second-order habitat selection analysis using MCP or concave polygon range estimators. We did perform the third-order analysis of use of habitats within the polygon home ranges, comparing the percentage of locations in a habitat type in the home range with the proportion of that habitat area within the range polygon.

Results

Independence of telemetry locations

In tests of the independence of location data sets, 36% percent of data sets in 1994 and 1995 showed no autocorrelation, 50% failed at least one of the significance tests, and 14% of sets failed all three tests. Examining data from 1996, with a two-hour minimum time between observations, 38% passed all tests, 38% failed at least one, and 25% failed all three. The differences in observed statistical independence of data sets under the two different estimated TTI were significant (Chi-square = 11.63, d.f. = 2, $p = 0.003$), but inconclusive. Compared with the one-hour TTI in 1994 and 1995, more data sets passed one or two independence tests, but more data sets failed all three tests, under the two-hour minimum TTI in 1996.

Home ranges

Kernel 95% home range areas of males among all three years were marginally larger than those for females (Mann-Whitney $U = 153.5$, $p = 0.055$). Kernel range areas for males were different among years 1994 to 1996 (Kruskal-Wallis $H = 6.44$, $p = 0.04$), but not among study areas (Table 1). The multiple comparisons test (Siegel and Castellan 1988) indicated that male ranges were significantly larger in 1995 compared with 1996, reflecting large ranges

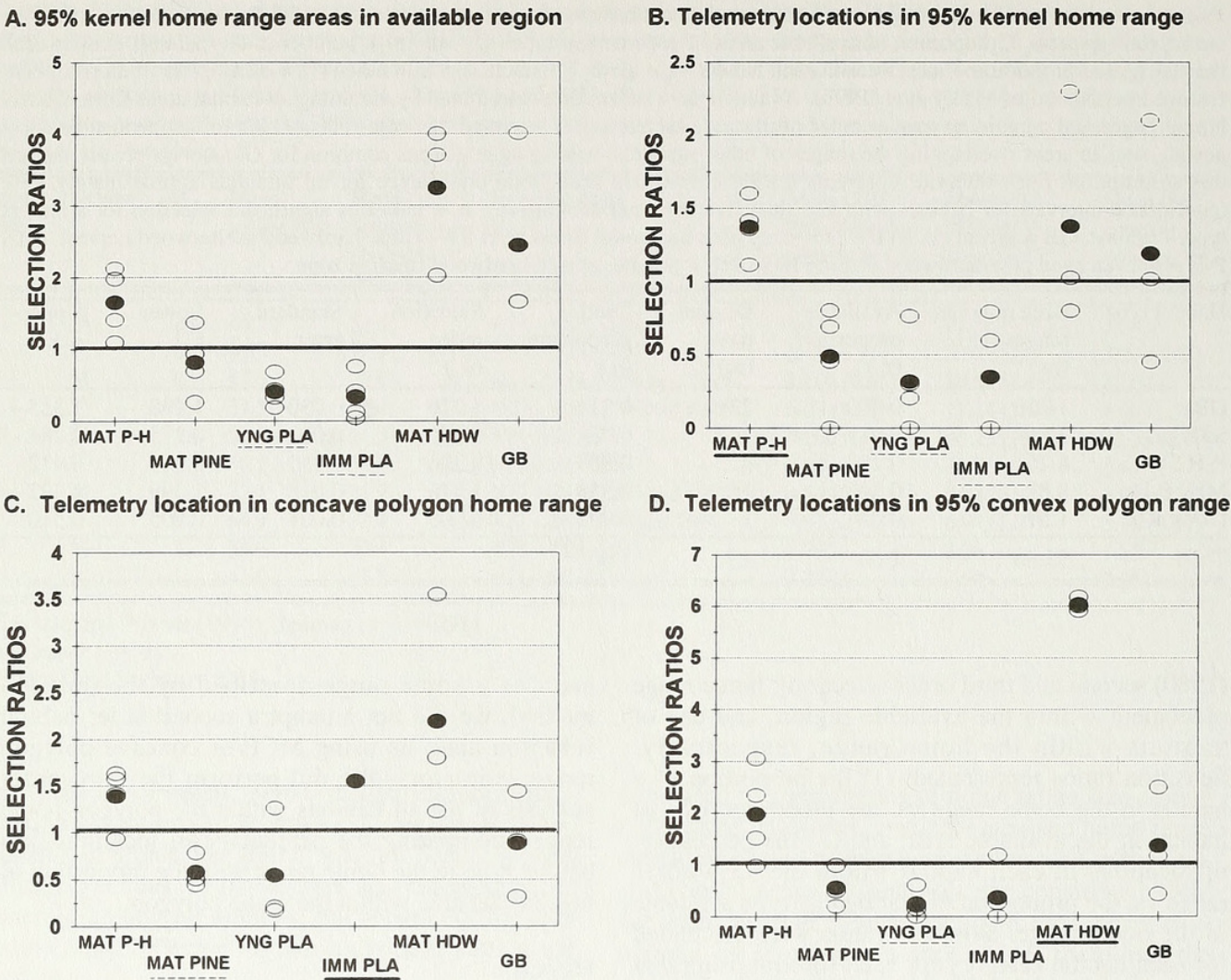


FIGURE 3. A sample of habitat selection results for nightly activities of five squirrels on an unmanaged mature forest stand. Selection ratios are shown for study area III in 1995. A. Proportions of habitats in the 95% kernel home range divided by proportions of habitats within the available region. B. Proportions of telemetry locations in each habitat type divided by habitat area proportions in the 95% kernel home range. C. Proportions of telemetry locations divided by habitat proportions in the concave polygon home range estimate. D. Proportions of telemetry locations divided by habitat proportions in the 95% minimum convex polygon home range estimate. Selection ratios equal to 1 indicate no selection, > 1 indicate selection for a habitat type, < 1 against that habitat type. Mean selection ratios for each habitat type denoted by filled black ovals. Significant selection for a habitat type indicated by solid underscore, significant selection against a habitat shown with a dashed line underscore. Significance of selection against or for each habitat determined by 95% Bonferroni confidence intervals falling completely below or above 1, respectively. MAT P-H = mature pine-hardwood forest, MAT PINE = mature pine plantation, YNG PLA = young pine plantation (< 15 years old), IMM PLA = immature pine plantation (15–40 years old), MAT HDW = mature mixed hardwood forest, GB = greenbelt, mature forest riparian strips through harvested habitat.

on two study areas sampled in 1995 but not in 1996. Kernel 95% range areas of female squirrels did not differ among years or among the five study areas (Table 1). Ranges on study area III were largest and those on study area V were the smallest.

Both the MCP and minimum area methods produced range estimates which enclosed proportionately large areas where radiocollared squirrels had not been observed (Figure 2). The size of the polygon ranges is generally larger than the kernel range estimate due to the inclusion of unused habitats. The shape of ranges created by both polygon methods does not reflect intensity of use of areas

within the home range, as does the kernel function (Figure 2).

Habitat selection patterns

Habitat selection analyses were performed for squirrels on study areas I (8), V (5), and II (6) in 1994; II (12), III (5), and IV (6) in 1995; and IV (8) in 1996. As illustrative examples, overall habitat selection results for nightly activity periods are presented for study areas III and IV in 1995 (Figures 3 and 4, respectively, including selection analyses using polygon methods for range estimation). Diurnal nesting habitat selection results are shown

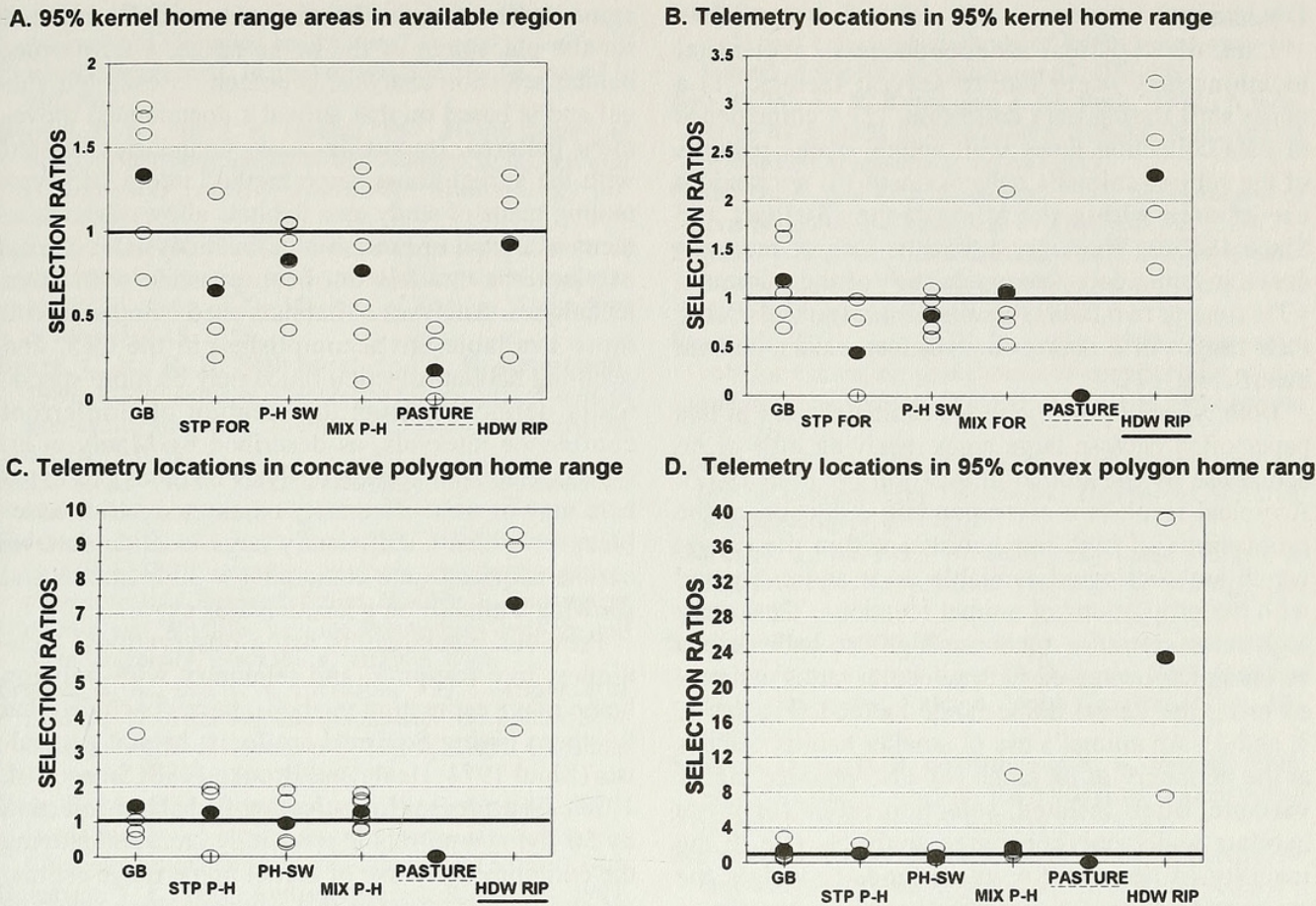


FIGURE 4. A sample of habitat selection results nightly activities of five squirrels on study area IV in 1995. A. Proportions of habitats in the 95% kernel home range divided by proportions of habitats within the available region. B. Proportions of telemetry locations divided by habitat proportions in the 95% kernel home range. C. Proportions of telemetry locations divided by habitat proportions in the concave polygon home range estimate. D. Proportions of telemetry locations divided by habitat proportions in the 95% minimum convex polygon home range estimate. For interpretation, see Figure 3 caption. GB = greenbelt, mature forest riparian strips through harvested habitat, STP FOR = steep mixed pine-hardwood forest, P-H SW = pine-hardwood shelterwood harvest area, MIX P-H = mixed aged pine-hardwood forest, PASTURE = grazed pasture on private land, HDW RIP = mature hardwood riparian forest on private land.

for study areas II and IV in 1995 (Tables 2 and 3, respectively). Mean selection ratios for squirrels in individual habitat types on each study area showed selectivity in the placement of the home range within the available habitats, in use of habitats within the home range, and in nest site location. Unmanaged mature pine-hardwood and hardwood forests were selected for nesting and foraging where available (Figure 3); on harvested stands protected forests in riparian greenbelt (GB) zones were highly selected for nesting, and GB and adjacent mature forests were used for foraging (Figure 4, Table 3). During nightly activity periods, some male squirrels made long forays to distant hardwood stands on mature pine-hardwood study areas in which both densities of overstory hardwoods, and actual mast production measured during fall 1994 and 1995 surveys, were low. Home range shapes showed elongation where valued habitats were narrow or widely separated. Home ranges overlain on habitat

maps, and habitat selection ratio results, showed that young and immature pine plantations were generally avoided, except for infrequent forays to exploit soft mast resources at study areas with low hard mast availability in mature forests. Corridors of mature pines and hardwoods along riparian zones were used to travel through pine plantations. Due to the lack of a correlation between the area of a habitat type in an individual squirrel's polygon range and the intensity of use of that habitat by the squirrel, habitat selection ratios calculated using 95% MCP and modified minimum area (concave polygon) range estimators gave results which sometimes showed significant habitat selection for a type that was actually avoided by squirrels (such as the significant selection indicated for immature pine plantation habitat in the concave polygon analysis at study area III, Figure 3). Such spurious results did not occur with selection results from the kernel range estimation method (Figures 3 and 4).

Discussion

Lack of statistical independence in sequential locations may occur due to several factors: (1) a range shift during data collection, (2) a coincidence of data collection times with natural cyclic patterns of the subject animal's behavior, and (3) nonrandom use of area within the home range (Swihart and Slade 1985b). We suggest that the lack of independence in some data sets under each of the minimum TTIs (one or two hours) resulted from squirrels using their ranges in a nonrandom manner, rather than an insufficient TTI.

Both types of polygon range estimates used in this paper often enclose large areas receiving little or no actual use by the animal in question (Worton 1987). A typical result is a corresponding reduction in the proportions of high-use habitats within the range, which are considered available areas and compared with the proportions of animal locations. Thus, very high selection ratios for those high-use habitats can be obtained, compared with selection ratios computed using the kernel home range method (Figures 2, 3, and 4). An animal's use of smaller habitat patches at the periphery of its range can also produce highly variable, often inflated, selection ratios for those habitats under polygon range analyses, due to the inability of perimeter point methods to weight the range and add area to peripheral sections containing clusters of locations (see Figure 2). These differences in selection ratio results between kernel and polygon methods were less pronounced in analyses of nesting habitat than those seen in analyses of overall use (Tables 3 and 4).

Researchers continue to use polygon methods, such as the minimum convex polygon and modified minimum area method, to describe animal home ranges (Linn and Key 1996; Stone et al. 1997) and to analyze habitat selection behaviors (Bendel and Gates 1987; Smith et al. 1999). However, polygon home range estimates give no information on the relative intensity of use of habitats within the home range, and are therefore of little value in examining habitat use patterns. Polygon home range methods also provide no logical method for defining an available area which the researcher can use to investigate habitat selection in an animal's placement of its home range.

The kernel home range estimation method provides additional information over polygon methods about individual variation in habitat use and avoids the problems associated with the harmonic mean method, such as the lack of a probability density estimate, sensitivity to grid cell size, and inconsistent results depending upon distance of observations from grid intersections (Worton 1989). In addition, the kernel home range estimation method may be used to create a contour from a location data set which encompasses unused habitats surrounding an

animal's home range. This estimate of available area for the placement of the home range, a third-order habitat selection analysis, is unique for each individual and is based on that animal's documented movement patterns. Importing range boundaries created with the kernel home range method into a GIS containing maps of study area habitats allows the attainment of a level of precision in the analysis of habitat use patterns that has not been possible with other techniques. Analyses of habitats used compared with those available are accomplished in the GIS, and resulting habitat selection ratios may be more specifically defined through the creation of Bonferroni confidence intervals, as described by Manly et al. (1993). Habitat selection analysis methods presented here may be used effectively on any terrestrial vertebrate for which a sufficiently large location data set can be acquired (one containing > 30 locations and showing a plateau on a location/area curve).

Previous investigators using observational techniques, live trapping, and telemetry with polygon home range estimation methods, have concluded that Southern Flying Squirrels are forest habitat generalists (Muul 1974; Healy and Brooks 1988; Stone et al. 1997). The present investigation of habitat selection by 50 flying squirrels at five study areas, employing the complimentary use of kernel home range estimator and a GIS, revealed that squirrels were selective in habitats used during both their nocturnal activity periods and for natural diurnal nesting sites.

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