2002

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Recommended Citation

Wilson, M. D., B. D. Watts, and B. J. Paxton. 2002. An investigation of Whip-poor-will activity, habitat use, and home range using radio telemetry within a managed landscape. CCBTR-02-11. Center for Conservation Biology Technical Report Series. College of William and Mary, Williamsburg, VA. 50 pp.

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CENTER FOR CONSERVATION BIOLOGY
COLLEGE OF WILLIAM AND MARY

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Cover Photo by Bart Paxton

Project Funded By:

The Weyerhaeuser Company
Center for Conservation Biology

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EXECUTIVE SUMMARY

The Whip-poor-will (Caprimulgus vociferus) is a nocturnal insectivore that is declining throughout many parts of its breeding range. Like several other Caprimulgid species, Whip-poor-wills have been suggested to utilize forested areas for nesting and open areas for foraging. The fact that Whip-poor-wills require resources that occur within distinctly different habitat types implies that their distribution and abundance may be influenced by the spatial association of required patches within a broader landscape. Within Weyerhaeuser forestlands in 1999 Wilson and Watts showed that Whip-poor-wills were detected within forest stands that were adjacent to plantations more frequently than forest stands adjacent to other forest stands. From a management perspective, this result suggests that targeted management should focus on a landscape scale and include the spatial and temporal orchestration of management activities. The objective of this study was to use radio telemetry to investigate the influence of landscape configuration and lunar illumination on home range size, activity patterns, and habitat use within a managed forest system.

Twenty-seven Whip-poor-wills were fitted with radio transmitters and tracked in homogenous (forest stands bordered by other forest stands) and heterogeneous landscapes (forest stands bordered by open stands) of Weyerhaeuser’s J&W management tract. Home range size and activity patterns were shown to be similar between landscape types. The habitat composition of home ranges for Whip-poor-wills in heterogeneous landscapes was equally divided between forested and open stands. Overall, Whip-poor-wills showed a strong tendency to use areas near forest openings such as open plantations and logging roads. The use of habitat openings present in both landscape types may be responsible, in part, for observed patterns of home range size and activity. Large habitat openings created by regeneration practices and extensive linear openings created by logging roads and row thinning appear to enhance landscape quality and provide Whip-poor-wills with foraging opportunities not likely present in non-managed forests.

BACKGROUND

Context

The Whip-poor-will (*Caprimulgus vociferus*) belongs to a small group of nocturnal insectivorous birds, including the Chuck-will's widow (*C. carolinensis*) and the Common Nighthawk (*Chordeiles minor*), that are commonly known as "nightjars" or "goatsuckers" (Family Caprimulgidae). Results from the annual USFWS Breeding Bird Survey indicate that the Whip-poor-will is declining throughout many parts of its breeding range. Despite these results, very little information is currently available on the breeding requirements and ecology of this neotropical migrant. This lack of information is due, in part, to the difficulty of studying the nocturnal habits of this species. Most published accounts of habitat use are based on anecdotal information (Bent 1940, Brewer et al. 1991, Peterjohn and Rice 1991, Robbins 1996). These reports have associated Whip-poor-wills with a broad gradient of pine to hardwood-dominated forests that are characterized by dense understory and midstory vegetation. In general, Whip-poor-wills and other caprimulgids require forested habitat for nesting but open habitats such as forest edges, forest clear-cuts (Wilson and Watts 2000), scrub, and agricultural areas (Cooper 1981) for foraging.

During the 1999 breeding season, the Weyerhaeuser Company and the College of William and Mary conducted a joint research project to investigate the influence of stand and landscape management on the distribution and abundance of Whip-poor-wills within a managed forest system (managed forest holdings within coastal N.C.). Based on call-count surveys, both stand condition and landscape context were determined to have a significant influence on Whip-poor-will abundance. Forested stands bordered by similar habitat supported lower bird densities compared to forested stands bordered by open (1-5 year old stands) stands. This result suggests that the orchestration of forest management on a landscape scale may be important to the maintenance of Whip-poor-will populations within extensive forest tracts. However, the underlying causes of such differences remain unclear.

One limitation inherent in the use of call counts is that information collected includes vocalizing individuals only. Whip-poor-will's are known to decrease calling frequency during periods of dim lunar illumination (Cooper 1981, Mills 1986, Watts and Wilson 2000) creating temporal gaps in collecting spatial data. Since variation in illumination may actually contribute to spatial distribution patterns, it is important to separate calling patterns from patterns of movement and space use.

Objectives

It remains unclear why Whip-poor-wills reach higher densities in forest patches associated with open patches compared to those only associated with other forest patches. The primary objective of this study was to determine patterns of space use and activity within these two different landscape settings. Specific objectives include:

1. To examine the influence of landscape configuration (i.e., the spatial arrangement of different habitat types) on activity patterns and the size of home ranges.

2. To determine the influence of habitat type and context on activity patterns and space use.

3. To determine how lunar illumination modifies space use and activity patterns.

METHODS

Study Area

This study was conducted on the Weyerhaeuser Company J&W management tract located in eastern North Carolina (approximately 35 30 N lat., 76 60 W long.) (Figure 1). Historically, much of this landscape was dominated by natural tall pocosins and hardwood swamps before being ditched, drained, and cleared for agriculture and other land uses. Currently, the land area of the Weyerhaeuser Company J&W management tract dominates a local region of agricultural fields, residential areas, and other managed forests.

Most of the acreage of the J&W tract is managed in loblolly pine (*Pinus taeda*) plantation on a 30 to 35 year rotation schedule. Pine plantations are planted as seedlings in parallel rows with relatively low stocking levels (< 1,200 pines/ha). After a period of stand maturation, plantations are normally thinned twice (at about 12-15 years and 19-21 years after planting) before the final harvest. Commercial thinning activities create alternating strips of sheared (treeless) and non-sheared lanes. The harvesting of a fully mature stand is completed by clearing all pine and hardwood stems. The staggered regime of harvesting and thinning creates a spatial mosaic of hard boundaries between adjacent forest stands. In addition, a network of logging roads and drainage ditches permeate the plantation landscape creating linear forest openings.

The vegetation structure of pine plantations varies between stand ages (Wilson and Watts 1999a, Wilson and Watts 1999b). Young pine plantations (1-6 years after planting) are characterized by a dense cover of shrubby plants and a high percentage of ground cover of grasses and forbs. Dominant plant types include switch cane (*Arundinaria gigantea*), sweet pepperbush (*Clethra anifolia*), highbush blueberry (*Vaccinium corymbosum*), and blackberry (*Rubus sp.*). Mid-rotation plantations (7-12 years after planting and before thinning) are dominated by a dense, closed canopy of pine trees and sparse understory vegetation. Commercial thinning reduces the number of trees, and opens the canopy and midstory to allow re-growth of understory vegetation. Pine stands have a distinct open appearance after the first commercial thinning. Understory regrowth may take 1-2 growing seasons after thinning before forming dense impermeable thickets. Dominant understory plants of thinned plantations include cane, sweet pepperbush, highbush blueberry, fetterbush (*Lyonia lucida*), and gallberry (*Ilex glabra*). Significant midstory regrowth takes from 3-6 growing seasons after the first thin. During this period, pine

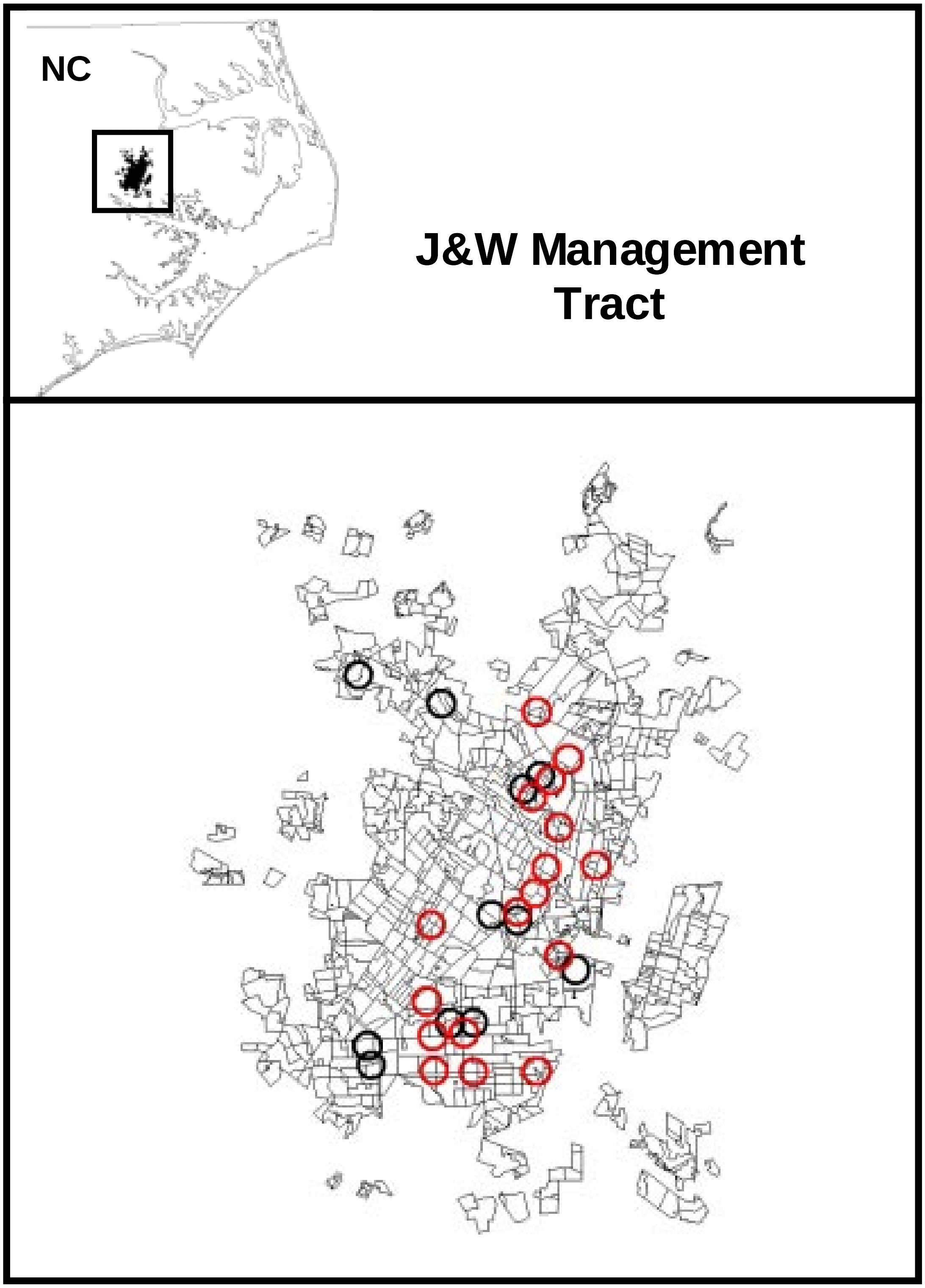


Figure 1. *Map of study area used for Whip-poor-will telemetry study. Black circles indicate general locations of birds with transmitters during the 2000 breeding season. Red circles indicate general locations of birds with transmitters during the 2001 breeding season.*

stands begin to develop increased vertical stratification associated with understory, midstory, and canopy growth. Maximal hardwood density (average of 150 trees/ha) within a mature stand is not typically reached until 3-4 years after the second thin. Dominant hardwood trees include red maple (*Acer rubrum*), sweet bay (*Magnolia virginiana*), and tulip poplar (*Lirodendron tulipifera*).

Study Design

The influence of landscape structure was examined by comparing the effects of matrix habitats (the immediate habitat that is adjacent to a given forest patch) and forest habitats on space use and activity patterns of Whip-poor-wills. Two landscape types were chosen to represent edge conditions between adjacent stands. Categories included; 1) homogenous landscape (forest stands adjacent to similar, forested matrix habitat) and 2) heterogeneous landscape (forest stands adjacent to open stands). Open stands included regeneration stands that were 1-3 years old and forest stands included stands that have been commercially thinned. Other criteria for stand selection included stand size, shape, and position. Small, narrow stands were avoided to reduce contagious effects from edges of other stands not selected for study. Similarly, stands selected within homogenous landscapes were positioned so there was no direct access to any open stands.

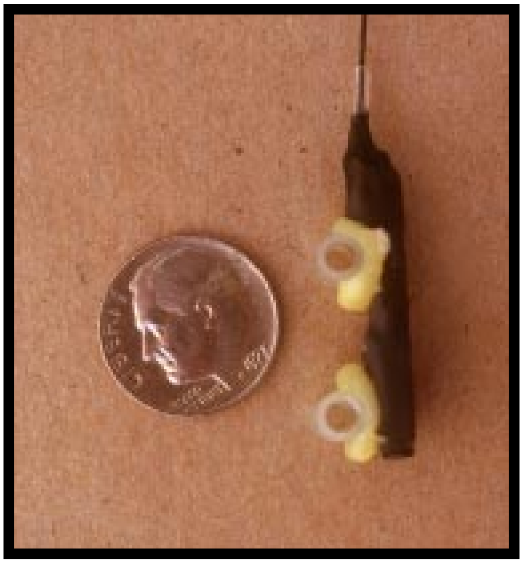
A spatial replicate consisted of one bird that was captured, fitted with a radio transmitter, and tracked during selected periods of the study. The final number of replicates representing each landscape type reflects the number of birds that were captured and tracked within each landscape condition (Table 1). At three locations, two birds relocated after the initial capture and transmitter placement to use opposing forest edges that bordered the same open stand. However, each of these birds was treated as an independent replicate within the heterogeneous landscape cell.

Radio Telemetry

Radio telemetry was used to determine home range, space use, and activity patterns of Whip-poor-wills. Whip-poor-wills were initially captured using 61mm mesh mist-nets that were 12m long and 2m high. A series of mist-nets were erected within selected landscape settings. An audio lure consisting of a continuous loop tape that broadcasted the onomatopoetic, male “whip-poor-will” call by means of a cassette player, amplifier, bell horn speaker, and car battery as a power source, was played continuously until a bird was captured or until it became apparent that there was no response (after 2-3 hours). Captured birds were banded with a U.S. Fish and Wildlife Service aluminum tarsal band, aged and sexed according to plumage characteristics, and affixed with a LTM single stage radio transmitter (Titley Electronics, New South Wales, Australia) using a modified backpack harness. The transmitter unit was 22 x 11 x 4 mm with a 23 cm wire whip antenna to transmit a radio signal. Mass of the transmitter and backpack harness was approximately 2.6 gm (less than 5 % of any captured bird’s body mass). Transmitters were fastened to backpack harnesses by gluing two lugs to the dorsal side of the transmitter. One end of a 1mm elastic cord with a black polyester cover was inserted through one lug, passed underneath the transmitter and inserted in the opposite end of the lug. The process was repeated with the other end of the cord to fashion a criss-cross harness with the transmitter

Table 1. List of stands and birds selected for study. Stands included represent the primary areas of bird distributions. Open stands (1-3 years old) are marked with an asterisk.

Landscape Type	Bird Identification #	Stand management #
Homogenous	105	42521
	109	42537, 42543, 44013, 44714
	114	42705, 42710, 44036, 44013
	118	40015, 42153
	121	42336, 42338, 42343
	122	42715, 44070, 44251,
	123	42198, 42478
	128	42154, 42157
	133	42344, 45305
	134	45340, 45343
	135	42482,45111, 46091
Heterogeneous	103	46060*, 42478
	106	42261*, 44305, 44180
	107	44381*, 44276
	108	45156*, 44135, 44304
	110	42095*, 42455
	111	44379*, 42462
	112	45156*, 42351
	113	42261*, 40714
	115	44013*, 44714
	116	42479, 42563, 42564, 44381*
	119	42521, 42757*,42762*
	126	42351, 45156*
	127	45266*,45005
	129	42532*,42548,44215*
	131	42785*, 44630*,44093
	132	42059*,42226,



Relative size of Whip-poor-will transmitter. Note harness lugs attached. Photo by Bart Paxton.

Seating of transmitter on back of Whip-poor-will. Photo by Bart Paxton.

Side view of transmitter on back of Whip-poor-will. Photo by Bart Paxton.

positioned between the wings on a bird’s dorsum and held in place by tension of the cord around the breast and abdomen. Transmitters were also glued to a bird’s scapular feathers to maintain its position before the cord was pulled taut across the breast.

Data Collection

Nocturnal locations of Whip-poor-wills were determined from two stationary observation points between 8 June through 31 July 2000 and from 3 stationary observation points between 13 May and 1 August 2001. Observation points were positioned along logging roads so that they were between the focal and matrix stands. The position of each bird was sampled on three nights of each quarterly lunar phase during each year (Table 2). During the first year of study, three to four relocations were collected over a 15-min period whereas five to ten relocations were collected over a 20-min period during 2001. Each station had one observer that used a radio-tracking receiver (Wildlife Materials Inc.) equipped with a three-element folding yagi antenna and radio headphones to obtain transmitter signals. Observers at each station registered simultaneous compass bearings to the position of the bird determined from the intensity of the radio signal. Additional information collected with each sample included the percent of lunar illumination, height of the moon (degrees above the horizon), cloud cover, air temperature, and wind speed. The order in which birds were sampled varied between nights to collect information at different periods of moon height.

Table 2. Dates of lunar phases during the study period.

Year	New Moon	First Quarter	Full Moon	Last Quarter
2000				
	2 June	9 June	16 June	25 June
	1 July	8 July	16 July	24 July
	31 July			
2001				
	23 May	29 May	6 June	15 May
	21 June	28 June	5 July	14 June
	20 July	27 July		13 July

The diurnal roost locations for each bird were sampled one time during three different days of each lunar phase in both years. Diurnal samples were collected using the same methods as above. However, because it was assumed that the birds’ locations were stationary during the daylight hours, one observer obtained compass bearings by moving between observation points.

Transmitters were equipped with mercury switches that increased the tempo of an auditory pulse signal when the angle of the transmitter inclined between 0 and 45 °. Thus, a bird's relative activity state could be distinguished between a resting horizontal position (slow pulse rate) and the vertically directed movement (fast pulse rate) of flight. "Slow" transmitter signals were broadcasted at an interval rate > 1.2 s while "fast" transmitter signals were broadcasted at an interval rate < 0.8 s. Data on bird activity rates were collected by recording the auditory signals received from the transmitter. Signals from each bird were recorded on one night for a 60-min duration during each quarterly lunar phase in 2000 and on two nights for the same duration during each quarterly lunar phase in 2001. Audio signals were registered using a cassette recorder, tracking receiver, and a non-directional base station antenna.

Data Summary and Analysis

Home Range and Spatial Patterns

Geographic locations of stationary observation points were determined using a Trimble Geoexplorer geographic positioning system unit and Pathfinder Office Software. Coordinates for these positions were corrected by comparing coordinates taken from a fixed base station. Whip-poor-will geographic locations were then calculated from compass bearings and observation points using LOAS software (Ecological Software Solutions) to produce a series of x and y geographic coordinates.

The accuracy of determining Whip-poor-will geographic locations increases with the number of observation points used to collect telemetry data. This is due to the fact that additional observation points eliminate observer errors when determining compass bearings to bird locations. Because of this, data collected from three observation points during the second year of study were used to eliminate errors in calculating geographic locations associated with using only two observation points in the first year of study. Inspection of data collected during the second year of study revealed that the deviation between locations determined with three observation points and two observation points was positively influenced by decreasing the interbearing angle (i.e., the angle formed by triangulation of two observer points to a bird's spatial location). Residual analysis of a log-log regression of the effect of interbearing angle on deviation distance (log [interbearing angle] = - .61 log [deviation distance] + 0.19, $r^2 = 0.37$, $p < 0.001$) showed that interbearing angles less than 45° produced the greatest deviation between locations. Based on this relationship, Whip-poor-will locations determined by interbearing angles less than 45° were eliminated from the analyses of data collected in the first year.

Adaptive kernel home ranges (Worton 1989) were determined using Movement, Animal Movement Analysis Arcview Extension (United States Geologic Survey, Alaska Science Center) and ArcView 3.2 software (Ecological System Research Institute). Least-squares cross validation (LSCV) (Silverman 1986) was used to select smoothing parameters to calculate utilization distributions (i.e., the number of sample locations needed to adequately determine home range and eliminate outliers) for each replicate. Adaptive kernel home ranges were calculated for 50, 75, and 95 % of the total utilization distributions. The effect of landscape type and year of study on home range size were examined using two-way analysis of variance (ANOVA) on 50 % and 75 % probability distributions. The effects of lunar illumination (two levels: moonface < 50 % and moonface > 50 % illuminated) on home range size were examined using the 95 % probability distribution.

Geographical information system (GIS) coverage was used to determine habitat composition within home ranges, spatial position of individual relocations, and movement distance between successive relocations within the 75 % utilization polygon. These data were also subdivided to compare space use and lunar illumination (two levels: moonface < 50 % and moonface > 50 % illuminated).

Activity Patterns

The number of samples analyzed varied between birds because data from some cassettes could not be retrieved due to inadequate sound resolution. Much of the variation in the frequency pulse rates was located between .81 and 1.19 seconds. This range represents the period when the activity state of the transmitter cannot be ascertained because it is between the “fast pulse” activated by movement (≤ .80 s) and the “slow pulse” indicative of rest (≥ 1.2 s). Because of this, activity budgets were estimated by summing the frequency in two pulse intervals; 1) ≤ 0.80 s and 2) ≥ 0.81 s. for each 60 min sample. Pulse intervals > 2.0 s were eliminated from analyses because this period most likely represents when a bird moved outside a receiver’s reception radius. Samples were then aggregated to compare the effects of landscape and lunar illumination on the percent of pulse frequencies ≤ 0.80 s.

RESULTS

A total of 4,416 nocturnal Whip-poor-will locations were recorded during the study (Appendix I). Whip-poor-wills were detected in 129 separate stands (mean = 6.3 ± 3.5 SD stands per bird) ranging from 1 through 31 years old.

Neither landscape configuration, year of study, or amount of lunar illumination were determined to have a significant influence on home range size using 50% and 75% probability distributions (Tables 3 and 4 respectively) (Figure 2). In addition, there was no significant interaction between landscape configuration and year detected. Home range size did show a considerable amount of variation within each landscape treatment. When 50 % probability distributions were considered, home ranges varied from 1.7 to 154.4 ha and from 1.1 to 94.2 ha in homogenous and heterogeneous landscapes respectively. Similarly, when 75 % probability distributions were examined, home range sizes ranged from 5.1 to 282.8 ha and from 2.3 to 165.6 ha in homogenous and heterogeneous landscapes respectively. The source and relevance of this variation remains unclear. As with landscape configuration and year, the amount of lunar illumination had no significant effect on home range size (Table 5) (Figure 3). However, mean home ranges varied between factor levels by a factor of nearly two. This difference was not statistically significant due to very high level of variation.

Table 3. Results of a two-way ANOVA for the effect of landscape type (two levels; 1) homogeneous 2) heterogeneous) and study year (two levels; 1) 2000 and 2) 2001) on variation of home range size. Home ranges were calculated based on 50 % of the total utilization distribution.

Source of variation	df	SS	MS	F	P
Landscape Type	1	1.37	1.366	0.001	> 0.90
Year of Study	1	4645.82	4645.43	3.578	> 0.05
Interaction	1	5.51	5.51	0.004	> 0.90
Error	23	29861.9	5142.9		

Table 4. Results of a two-way ANOVA for the effect of landscape type (two levels; 1) homogeneous 2) heterogeneous) and study year (two levels; 1) 2000 and 2) 2001) on variation of home range size. Home ranges were calculated based on 75 % of the total utilization distribution.

Source of variation	df	SS	MS	F	P
Landscape Type	1	0.8	0.8	0.001	> 0.90
Year of Study	1	3525.8	3525.8	0.685	> 0.50
Interaction	1	8.2	8.2	0.001	> 0.10
Error	23	118287.9	5142.9		

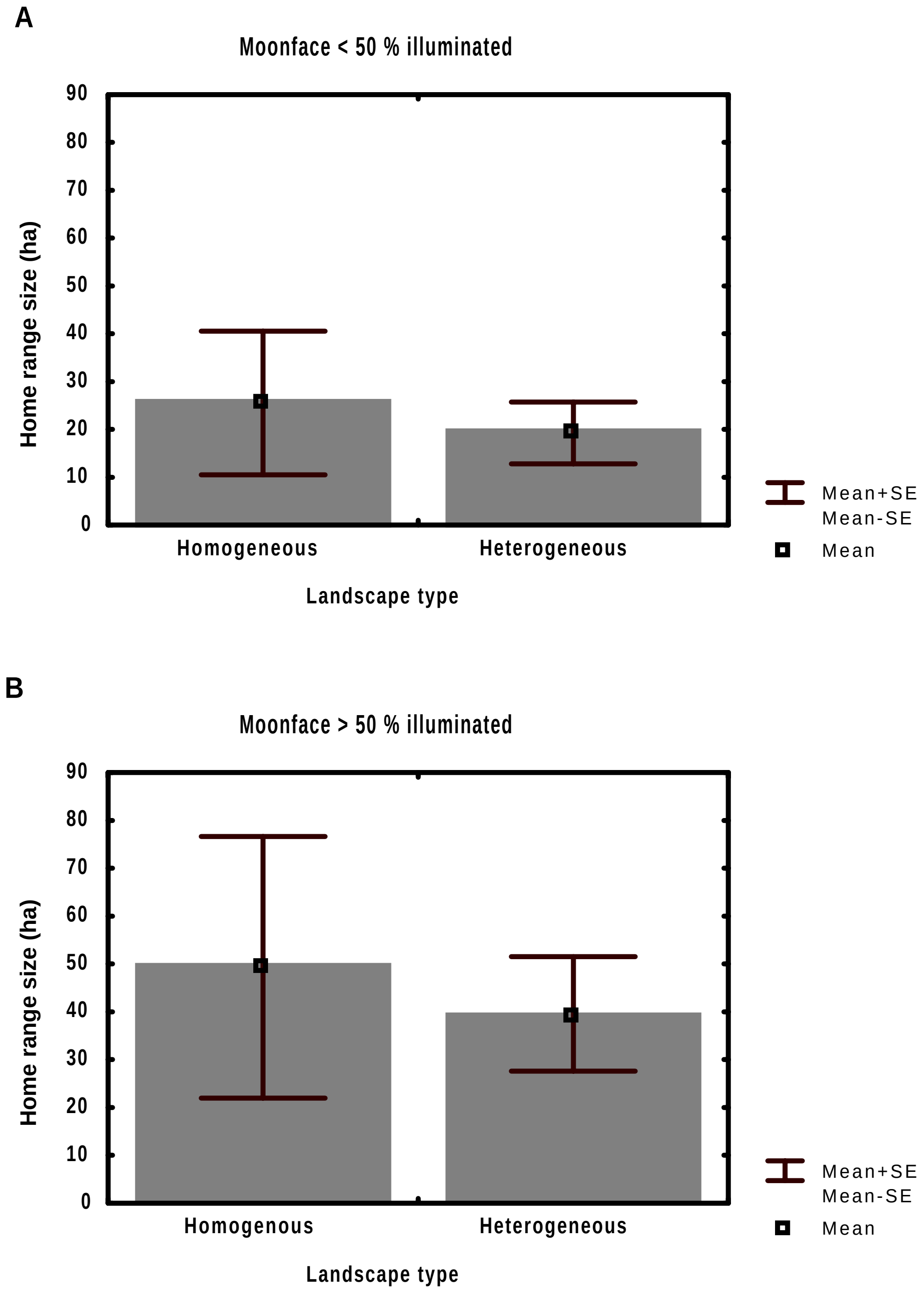


Figure 2. *Mean home range of radio-tracked Whip-poor-wills located in homogeneous (forested stands bordered by similar forested stands) and heterogeneous (forested stands bordered by open stands) landscapes: A) home range calculated based on 50 % of the total utilization distribution and B) home range calculated from 75 % of the total utilization distribution.*

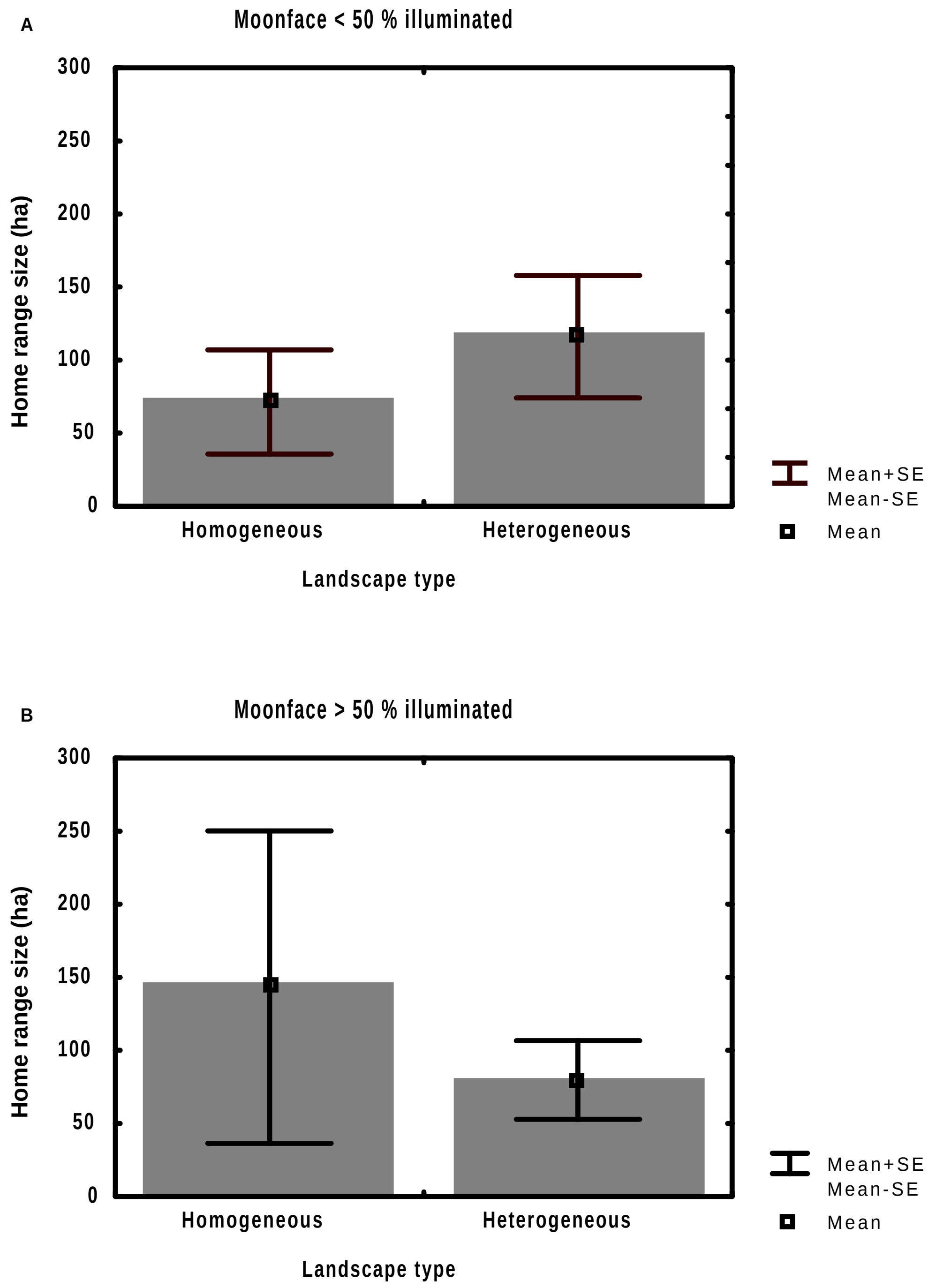


Figure 3. *Mean home range of radio-tracked Whip-poor-wills located in homogeneous (forested stands bordered by similar forested stands) and heterogeneous (forested stands bordered by open stands) landscapes when A) moonface < 50 % illuminated and B) moonface > 50 % illuminated. All home ranges calculations based on 95 % of the total utilization distribution.*

Table 5. Results of a two-way ANOVA for the effect of lunar illumination (two levels; 1) moonface < 50 % illuminated and 2) moonface > 50 % illuminated) landscape type (two levels; 1) homogeneous 2) heterogeneous) and on variation of home range size. Home ranges were calculated based on 95 % of the total utilization distribution.

Source of variation	df	SS	MS	F	P
Lunar illumination	1	4125.81	4124.81	0.11	> 0.50
Landscape type	1	1138.52	1138.52	0.28	> 0.50
Interaction	1	37719.64	37719.64	0.94	> 0.10
Error	49	189472.22	40239.89		

Habitat composition of home ranges in heterogeneous landscapes was equally distributed between forest and adjacent open stands (t-test for dependent samples, $t_8 = 0.77$, $p > 0.40$) (Figure 4). However, relocated Whip-poor-wills were detected with a significantly greater frequency in open habitat compared to adjacent forest patches ($c^2_{15} = 233.1$, $p < 0.001$). An average of 60.3 % (± 21.4 %) of all relocations were observed within the open habitats of these home ranges. The amount of lunar illumination had no significant effect on the mean percentage of open habitat composing the home range (t-test for dependent samples, $t_{10} = 0.35$, $p > 0.70$) (Figure 4) and similarly, had no significant effect on the frequency of relocated Whip-poor-wills in open habitat compared to adjacent forest patches (2x2 contingency test, $c^2_1 = 0.13$, $p > 0.70$).

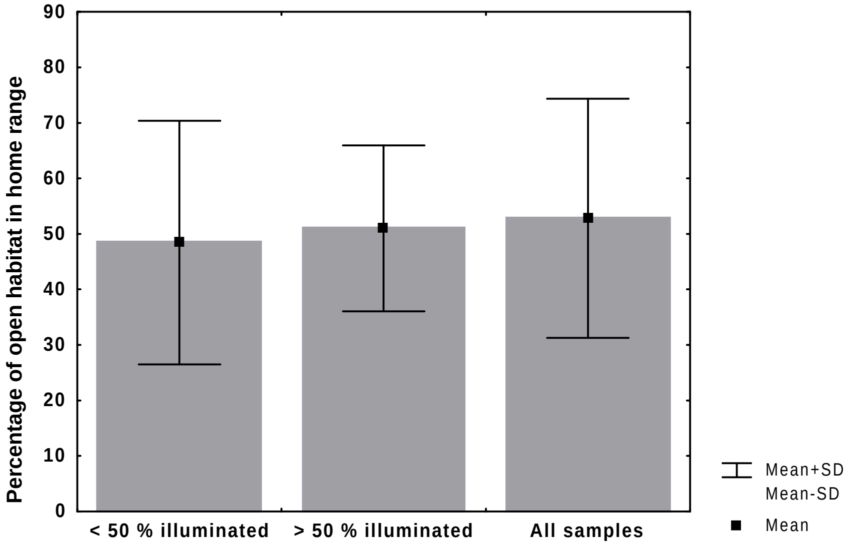


***Figure 4.** Habitat composition of home ranges for Whip-poor-wills (N = 16) occupying heterogeneous landscapes (forested stands bordered by open stands).*

Overall, Whip-poor-wills showed a strong preference for stand edges (i.e., edges created by logging roads in homogeneous landscapes and edges created by the boundary between forest stands and open clear-cuts in heterogeneous habitats) (Figure 5). Nearly 60 % of relocations in each landscape type were distributed within 100 m of a logging road or the ecotone between forested and open habitat and over 85 % of relocations were detected within 200 m of these landmarks. Overall, these distributions were significantly different from that expected based on a random distribution of points ($c^2_1 > 100.0$, $p < 0.001$ for all pairwise comparisons between observed and random distributions) (Figure 6). Landscape configuration had a significant effect on the median distance of relocations from stand edges (K-S test, $p < 0.01$). Although the difference in median distance from edges between landscape types was only 7 m (median = 87.3 m and 80.0 m for homogenous and heterogeneous landscapes respectively), Whip-poor-wills were shown to be distributed closer to edges in heterogeneous landscapes compared to homogenous landscapes. Lunar illumination also had a significant effect on relocation distance from edges in both landscape types (K-S test, $p < 0.05$ for both landscape comparisons) (Figure 7). In each landscape, Whip-poor-wills were distributed 7 m further away from edges when the moon was greater than half full compared to less than half full.

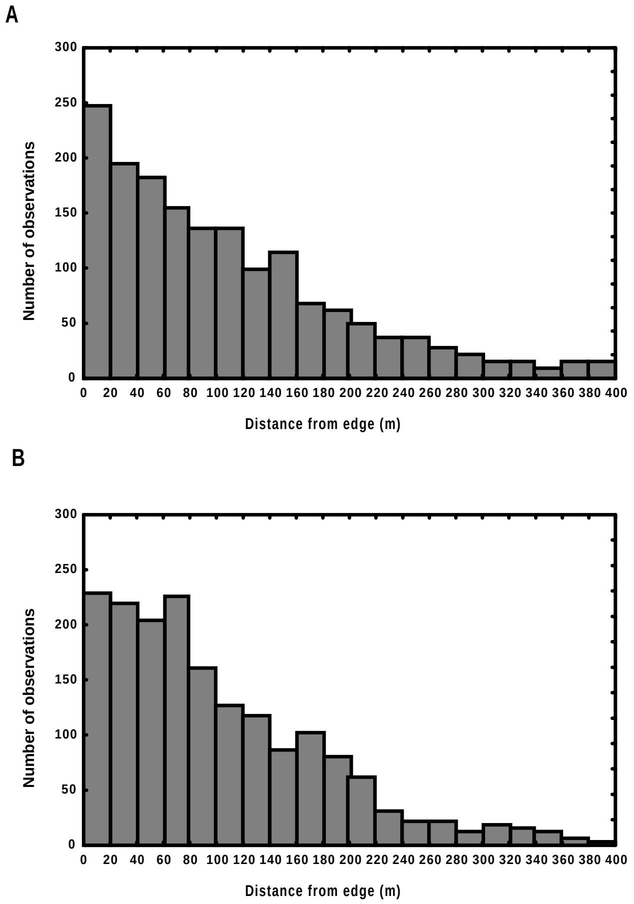


Figure 5. *Frequency distributions for the distances of relocated Whip-poor-wills from A) roadside edges in homogeneous landscapes, and B) the edge between forested stands and open stands.*

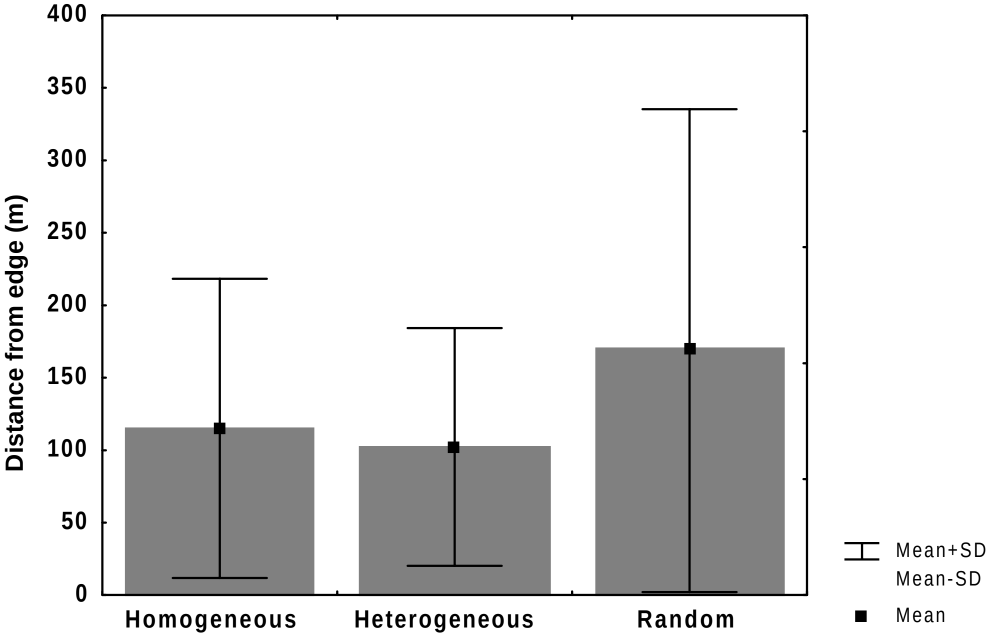


Figure 6. *Comparison for the mean distance of relocated Whip-poor-will from 1) roadside edges in homogeneous landscapes, 2) the edge between open and forested habitats in heterogeneous landscapes, and the mean distance of random points from roadside edges and and ecotone edges.*

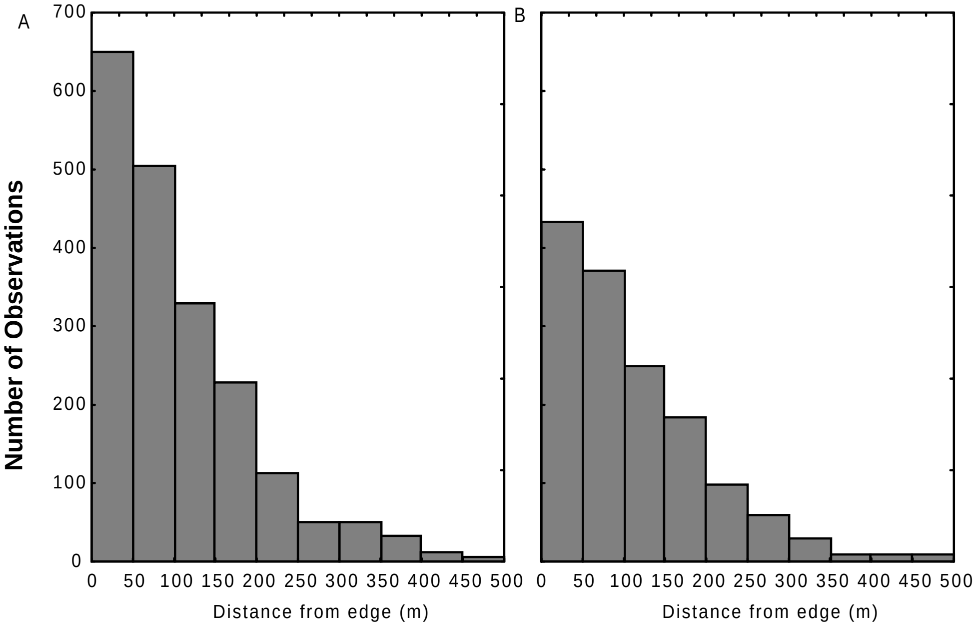


Figure 7. *Frequency distribution for the distance of relocated Whip-poor-wills from roadside edges in homogeneous landscapes and distance from edges between open and forested habitats in heterogeneous landscapes for periods when A) the moon is < 50 % illuminated, and B) the moon is > 50 % illuminated.*

Activity Patterns

Activity budgets were calculated for 414,736 s (over 6,912 min) from 116 bird-night samples. Landscape configuration had no significant influence on activity rates ($t_{25} = 0.63$, $p > 0.50$) (Table 6). However, lunar illumination did have a significant influence on activity rates in both landscape types ($t_9 = 3.5$, $p < 0.05$ and $t_{14} = 2.8$, $p < 0.05$). Overall, Whip-poor-wills showed a 20 % increase in activity when the moon was greater than half full compared to when it was less than half full.

Table 6. Activity budgets of birds by landscape type and lunar illumination (N = number of bird-nights used to calculate activity budgets).

Landscape Type	N	Total observation time (s)	Mean percentage of time spent active (± SD)
Homogenous	53	169,184	25.2 ± 32.1
Lunar illumination < 50 %	33	97,462	21.8 ± 25.6
Lunar illumination > 50 %	20	71,722	40.3 ± 33.4
Heterogeneous	61	245,542	35.5 ± 28.1
Lunar illumination < 50 %	32	123,505	27.7 ± 26.6
Lunar illumination > 50 %	29	122,037	46.7 ± 29.5

Both landscape configuration and lunar illumination had significant effects on the distance moved between successive relocations (K-S tests, all p values < 0.01). In general, movement distances were significantly greater in heterogeneous landscapes compared to homogenous landscapes ($t_{4103} = 2.28$, $p < 0.05$) (Table 7). However, the effect of lunar illumination on movement distances varied between landscape types. Movement distances were significantly greater when the moon was > 50 % illuminated for Whip-poor-wills in heterogeneous habitats ($t_{2130} = 2.9$, $p < 0.005$). By comparison, lunar illumination had no significant effect on movement distances in homogenous landscapes ($t_{1971} = 0.89$, $p > 0.90$).

The greater movement distances exhibited by Whip-poor-wills in heterogeneous habitats were due, in part, to significant variation in movement distances between open and forested habitats ($t_{1649} = 10.9$, $p < 0.001$). Movement distance was over two times greater when Whip-poor-will were occupying forested portions of their home range compared to when they occupied open habitats (Figure 8). This result was consistent during both periods of lunar light intensity.

Table 7. Mean distance moved between successive relocations of radio-tracked Whip-poor-wills in homogenous landscapes (forested stands bordered by similar forested stands), heterogeneous landscapes (forested stands bordered by open stands) and lunar illumination.

Landscape Type	N	Mean distance (ha) (± SD)
Homogenous	1675	102.2 ± 135.9
Lunar illumination < 50 %	1004	101.2 ± 139.4
Lunar illumination > 50 %	671	102.8 ± 130.2
Heterogeneous	1765	112.0 ± 142.5
Lunar illumination < 50 %	998	103.2 ± 132.6
Lunar illumination > 50 %	767	122.4 ± 154.1

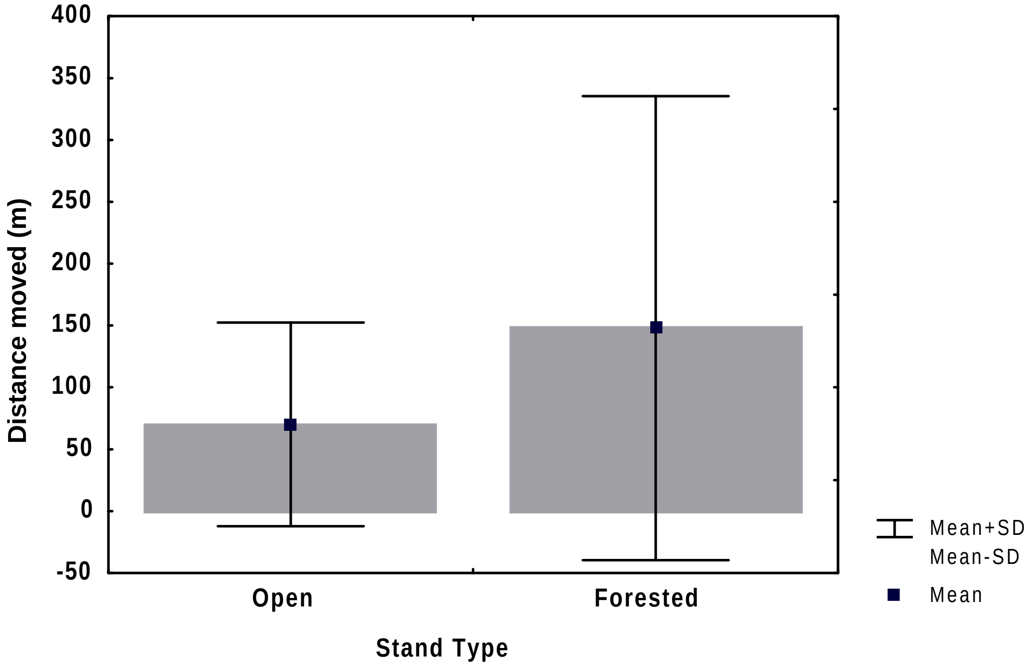


Figure 8. *Mean distance moved between successive observations of radio tracked Whip-poor-wills occupying heterogeneous landscapes. Open habitats include regeneration stands that were 1-3 years old; forested habitats include stands that have been commercially thinned one or more times.*

Diurnal Patterns

A total of 333 diurnal roosts were located during the study. Overall, Whip-poor-wills used 71 different management stands (mean = 2.7 ± 0.9 stands per bird). Diurnal stand usage was generally a subset of the stands used at night. Most birds showed the tendency to utilize one stand more than others, although all birds relocated roost sites between days. Ranges of relocated diurnal roosts were an average of 48 % of the area occupied by nocturnal home ranges.

Birds in heterogeneous landscapes were evenly distributed between open and forest stands ($c^{2}_{1} = 0.02$, $p > 0.50$) with 44 % of relocations detected in open stands. Over 80 % of diurnal roosts were within 200 m of a logging road or the boundary between open and forest stands and 96 % were within 400 meters of these landmarks.

DISCUSSION

For many species, the use of a habitat patch within a heterogeneous landscape is influenced both by the characteristics of the patch (e.g., food supply, predation risk, competitive pressure, behavioral constraints) and the characteristics of surrounding patches (Johnson et al. 1992, Foster and Gaines 1991, Hannson 1977). Species that depend on resources that are not contained within single habitats must broaden habitat use to include all areas needed to meet their requirements. For such species, the spatial association of habitat patches is an important landscape characteristic that determines distribution and abundance (Szaro and Jackle 1985, Pearson 1993, Sisk et al. 1997, Watts 1997). From a management perspective, targeted plans to consider these species should focus on a landscape scale and include the spatial and temporal orchestration of management activities.

Like several other Caprimulgid species, Whip-poor-wills have been suggested to utilize forested areas for nesting and open areas such as pine plantations, agricultural fields, and marshes for foraging (e.g. Cooper 1982, Peterjohn and Rice 1991). The fact that Whip-poor-wills require resources that occur within distinctly different habitat types implies that their distribution and abundance is influenced by the spatial association of required patches within a broader landscape. This notion is consistent with the suggestion that Whip-poor-will density is highest in areas where required habitats exist in close proximity. Within Weyerhaeuser forestlands in 1999 Wilson and Watts (2000) showed that Whip-poor-wills were detected within forest stands that were adjacent to plantations more frequently than forest stands adjacent to other forest stands. Cooper (1981) reported a similar account in Georgia, where Whip-poor-wills were found to be most abundant in areas with 90 % forested and 10 % agricultural habitats present in the landscape, but were also detected in areas that contained 50 % forested and 50 % agricultural habitat. Similarly, other accounts have briefly described the use of forest openings for foraging by Whip-poor-wills (Cooper 1982, Peterjohn and Rice 1991, Robbins 1996), Chuck-will’s-widows, (Cooper 1981, Cooper 1982, Straight and Cooper 2000) and numerous other Caprimulgiformes (Alexander and Creswell 1990, Wang and Brigham 1997).

The influence of patch context on Whip-poor-will density implies that patch complexes containing both forested and open habitats represent higher quality breeding areas when compared to forest-forest complexes. General territorial economics suggest that home range size should vary with habitat quality. In general, an inverse relationship between territory size and habitat quality has been established for a number of bird species (e.g. Wiens et. al. 1995, Smith and Shugart 1987). This relationship presumably results from the need to increase space use when faced with poor habitat patches in order to meet a variety of resource demands. This leads to the prediction that Whip-poor-will pairs within forest-plantation complexes should have smaller home ranges compared to Whip-poor-will pairs within forest-forest complexes. Within the current study, home range size was determined to vary over three orders of magnitude from 1.1 to 154.4 ha (50% ranges). The underlying source of this variation remains unclear. However, landscape type (heterogeneous vs homogeneous) was not determined to have a significant influence on home range size.

Although there are a number of factors within the current investigation that may influence home range size, it remains difficult to pinpoint those that account for discrepancies between expected and observed patterns. It is possible that the extensive system of roadways throughout the J&W tract may moderate the influence of larger openings such as young plantations on distribution by providing open habitats along roadway corridors. Birds were regularly flushed from roadbeds while driving at night throughout the site. In addition, many telemetry locations of birds within the forested landscapes were along roadways suggesting that these habitat elements may themselves provide openings used for foraging. Since radio-tracked birds were initially captured along logging roads, they may provide a somewhat biased account of overall space use. It is possible that birds positioned away from roads or in forest systems without forest openings may use the landscape differently. This possible explanation is generally compatible with the density pattern recorded in 1999 since roadways provide smaller open patches and thus could support fewer pairs than large plantations. If roadways and plantations were similar in quality in respects other than size, birds would exhibit an overall density bias without a difference in home range.

One potential complicating factor that may serve to conceal landscape effects on home range is that breeding location and disposition were not known for birds being tracked. Every effort was made to set up and capture birds early in the season to maximize the opportunity of capturing territorial males. In addition, the technique used was to broadcast male advertising calls to draw birds into nets in an attempt to capture males responding to territorial intruders. However, confirmation of breeding could not be obtained. Vegetation was too dense to locate nests even with the use of telemetry. The structure of the population in terms of birds that are mated verses unmated floaters is not known within the J&W. Because of this there is no way of determining whether or not the males tracked were actually breeding or when they were breeding. Variation between individuals in terms of their breeding status could account for the large amount of unexplained variation observed and obscure any landscape-scale effects within the breeding population.

Lunar illumination has been suggested to be a major determinant of Whip-poor-will breeding and foraging activity (Mills 1986). Whip-poor-wills primarily forage on aerial prey using short, upward-directed flights initiated from or near the ground. Foraging activity has been shown to increase with lunar light intensity and has been suggested to be an adaptation for exploiting back-lit insects (Mills 1986). Habitats that receive more lunar illumination may provide greater opportunities for visual detection of prey. The timing of breeding activity has been suggested to be arranged so that the energetic demands of young are near a peak when light conditions for foraging are optimal. Using call counts, Wilson and Watts (1999) showed that detection rates for Whip-poor-wills within the J&W were significantly higher under favorable periods of the lunar cycle. Results from the current investigation were consistent with this observation. Activity patterns increased along with lunar light illumination. Within both landscape types movement rates increased by 20% when the moon was greater than half full compared to less than half full. However, the influence of illumination on movement distances varied between landscape types. Birds within heterogeneous landscapes increased average movement distances when illumination was greater than 50%. Birds within homogeneous landscapes did not make longer movements under greater illumination. The difference in this response is further clarified by the fact that within heterogeneous landscapes, movement distances increased within open plantations but not within forest areas in response to greater illumination. The biological significance of differences in average movement distances with illumination are not clear.

Managed plantations within the J&W tract support a significant population of Whip-poor-wills. The relatively high number of habitat openings created by forest regeneration practices, and the extensive linear openings created by logging roads and commercial row thinning provide Whip-poor-wills with foraging opportunities not present in less intensively managed forest systems. Even so, the distribution of this population is influenced by the spatial pattern of forest management. Forest stands adjacent to recently harvested plantations appear to support more birds than the same forests prior to harvest. This pattern suggests that Whip-poor-will distribution and overall population size are under management control. However, information collected during the current study provides no evidence of systematic variation in home range suggesting that home range may not be under management control.

ACKNOWLEDGEMENTS

This project would not have been possible without the efforts of many people. Darren Miller and Tony Melchoirs provided the opportunity to conduct the study and administrative support. Bill Barber and Keven O’Kane were instrumental in helping to select study sites and in providing insight into the study area and forest management practices. Sonya Hylton provided GIS data layers on the J&W management tract. Catherine Markham, William Sbrega, Beau Willsey, and Ryan Deibler assisted with telemetry work. Lydia Whitaker, Carlton Adams, and Renee Peace, Anne Womack, Gloria Sciole, Mark Roberts, and Cheryl Pope provided important administrative support from the College of William and Mary. This study was funded through a cooperative agreement between the Weyerhaeuser Company and the College of William and Mary.

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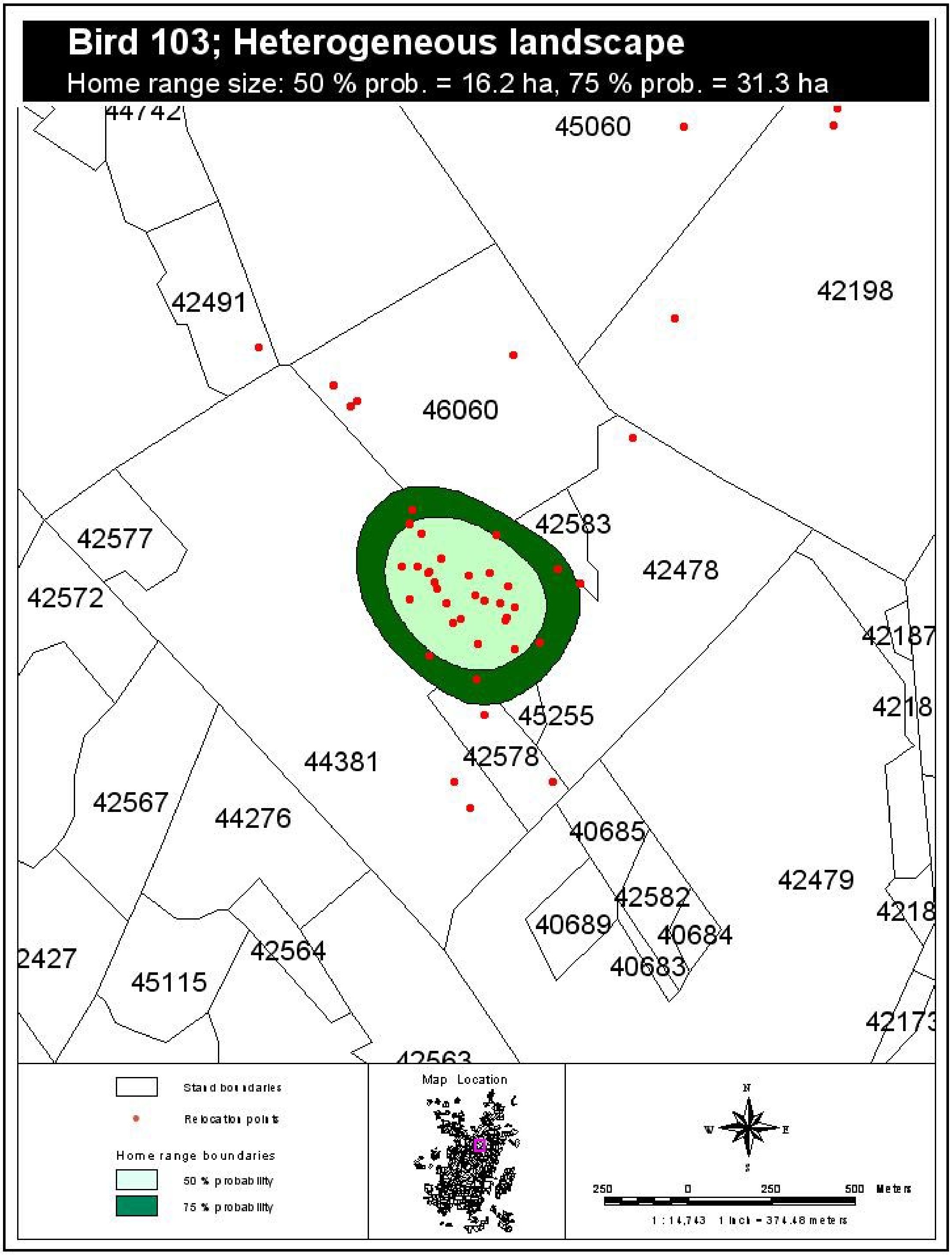
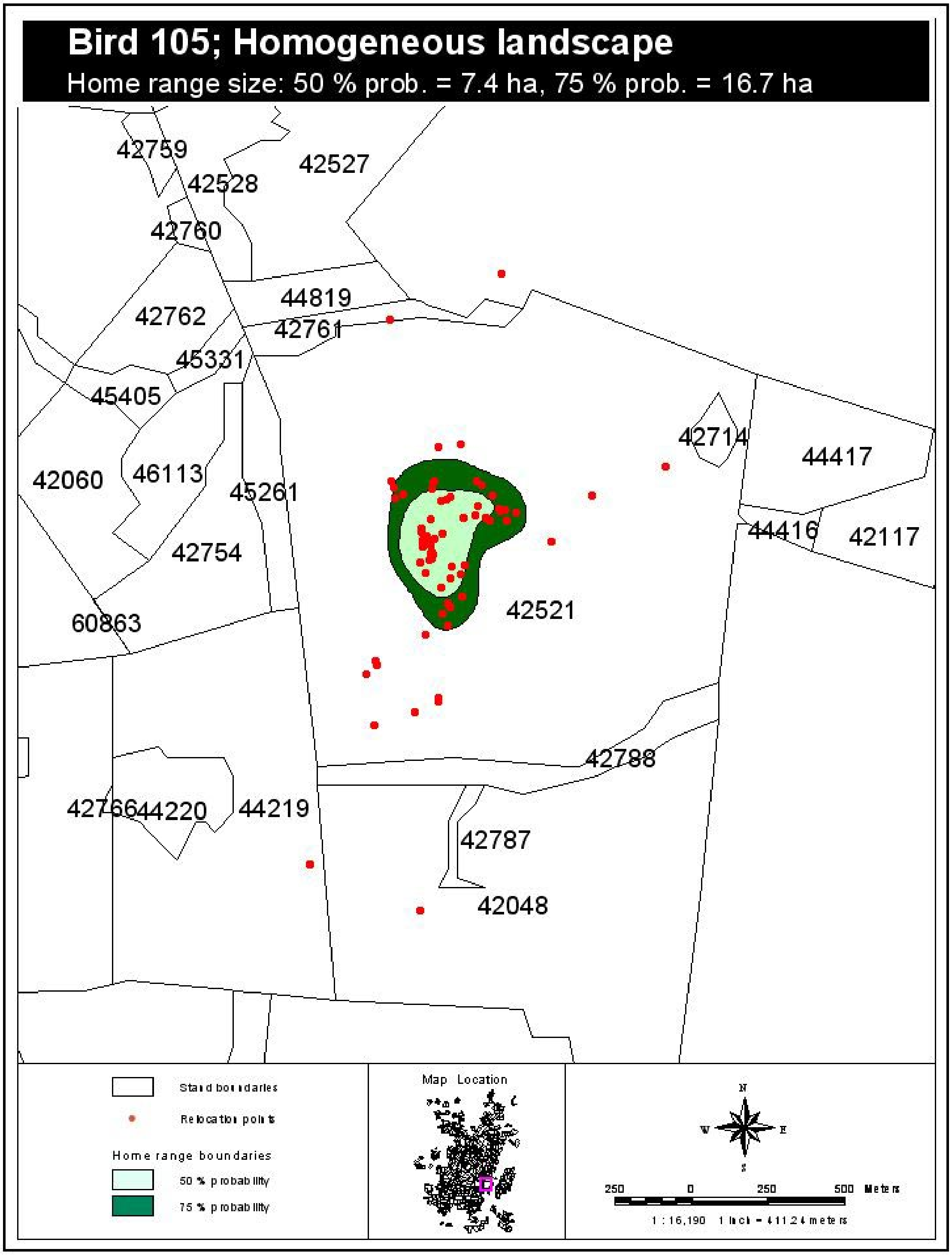
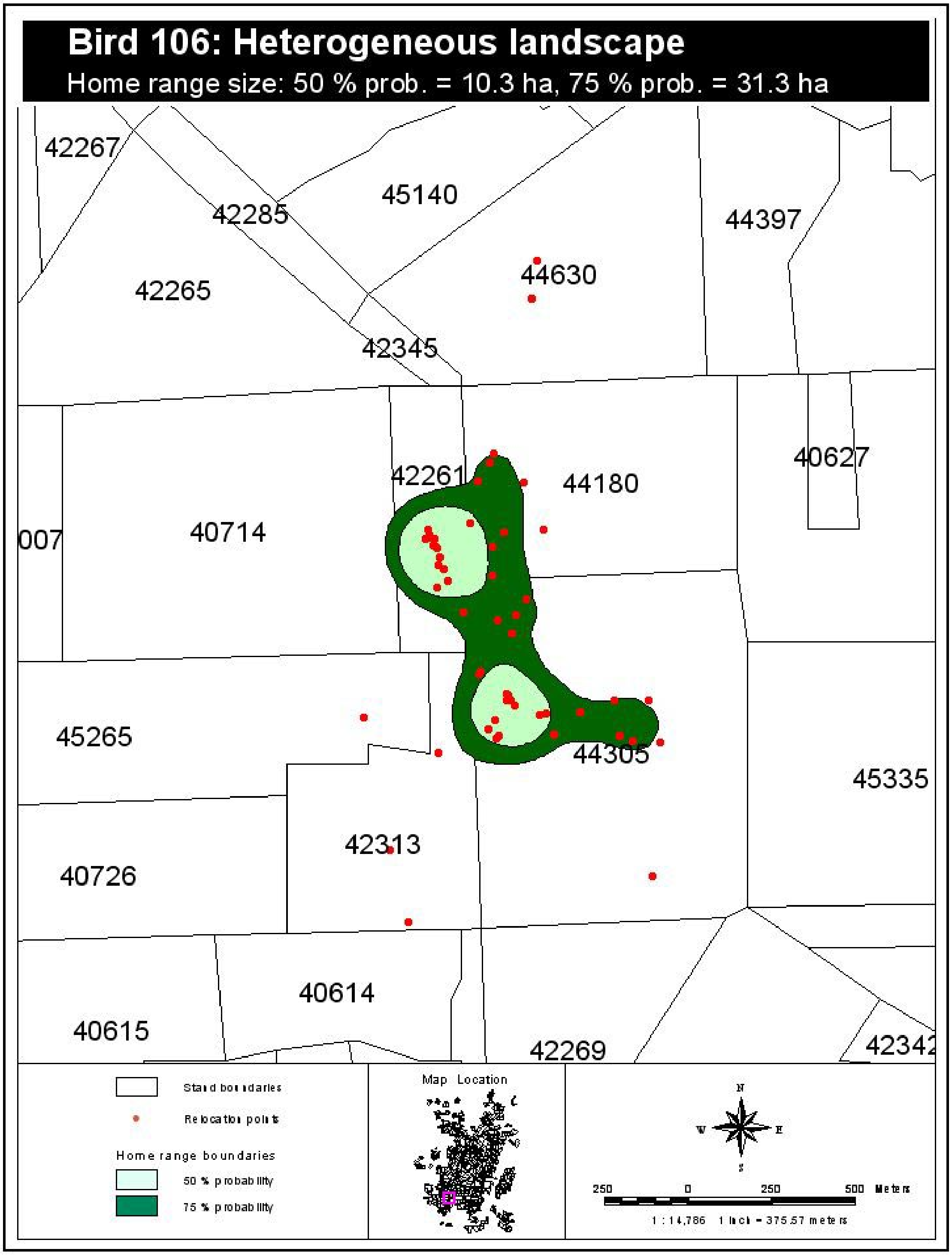
APPENDIX I: Home range maps for individual birds.

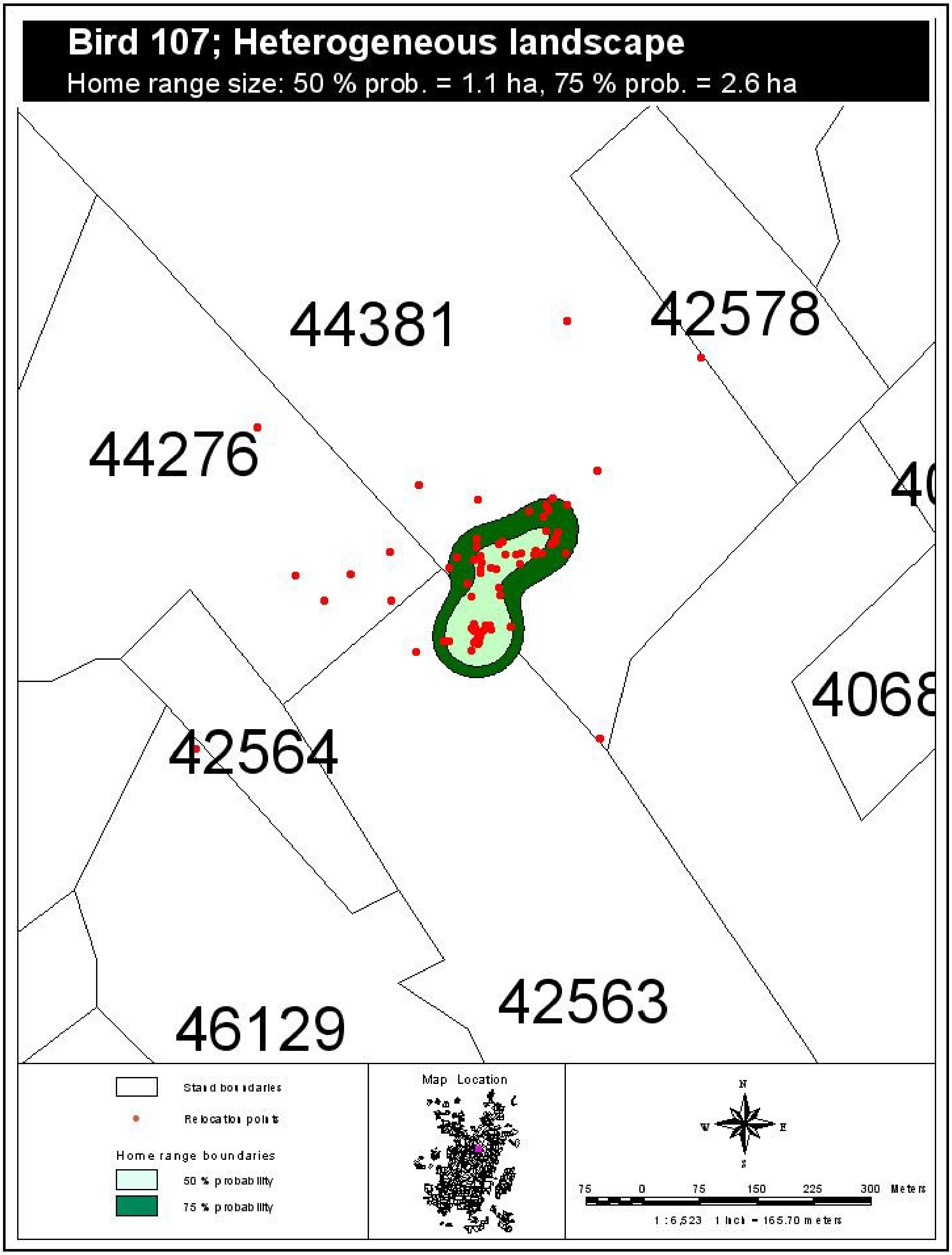

Bird 103; Heterogeneous landscape
Home range size: 50 % prob. = 16.2 ha, 75 % prob. = 31.3 ha
44742
45060
42491
42198
46060
42577
42583
42572
42478
42187
45255
4218
44381
42578
42567
44276
40685
42479
42582
40689
4218
40684
2427
42564
40683
45115
4217
42563
Stand boundaries
Relocation points
Home range boundaries
50 % probability
75 % probability
Map Location
N
W
E
S
250
0
250
500
Meters
1 : 14,743
1 inch = 374.48 meters


Bird 105; Homogeneous landscape
Home range size: 50 % prob. = 7.4 ha, 75 % prob. = 16.7 ha
42759
42528
42527
42760
44819
42762
42761
45331
45405
42714
44417
42060
46113
45261
44416
42117
42754
42521
60863
42788
42766
44220
44219
42787
42048
Stand boundaries
Relocation points
Home range boundaries
50 % probability
75 % probability
Map Location
N
W
E
S
250
0
250
500
Meters
1 : 16,190
1 inch = 411.24 meters



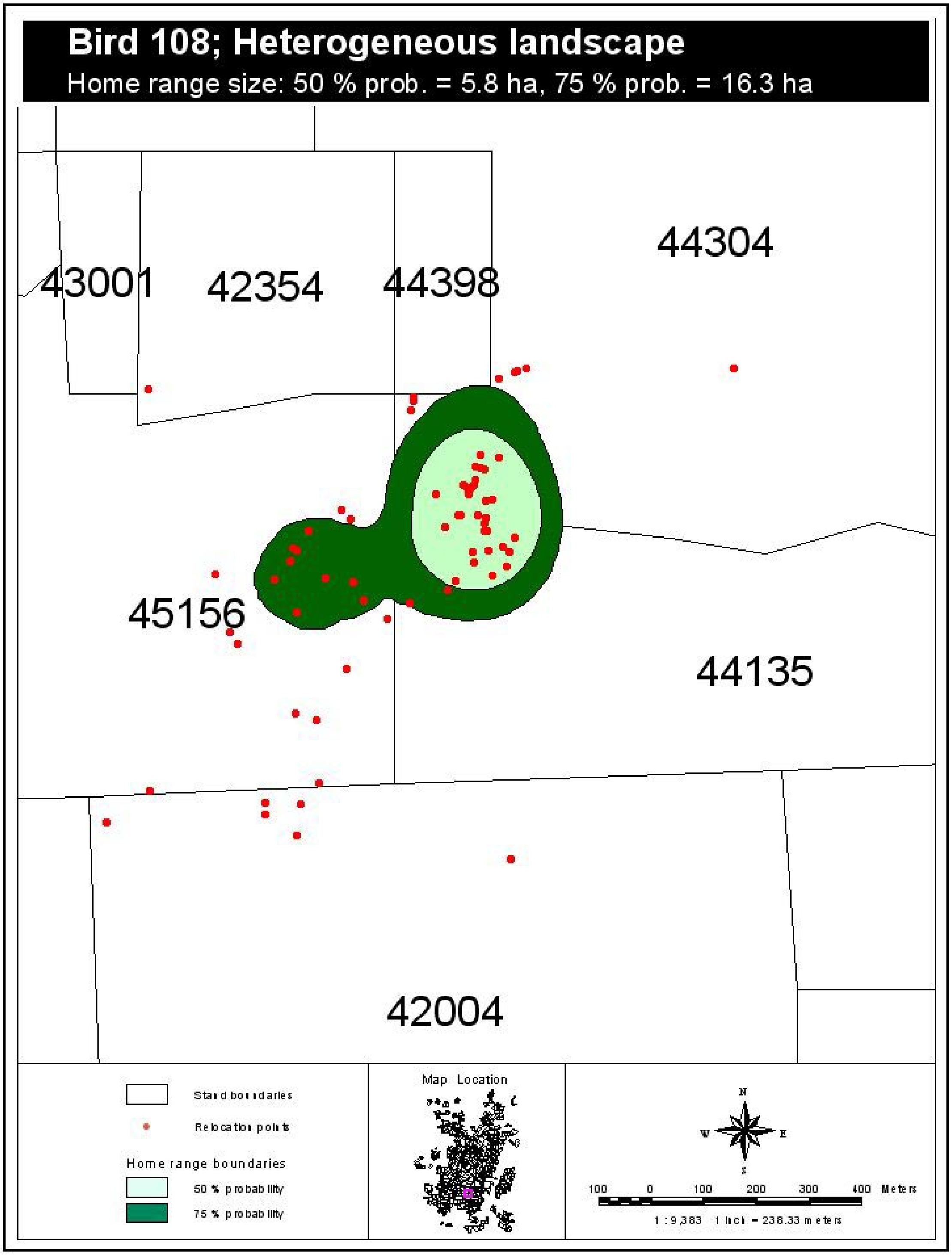
Bird 106: Heterogeneous landscape

Home range size: 50 % prob. = 10.3 ha, 75 % prob. = 31.3 ha

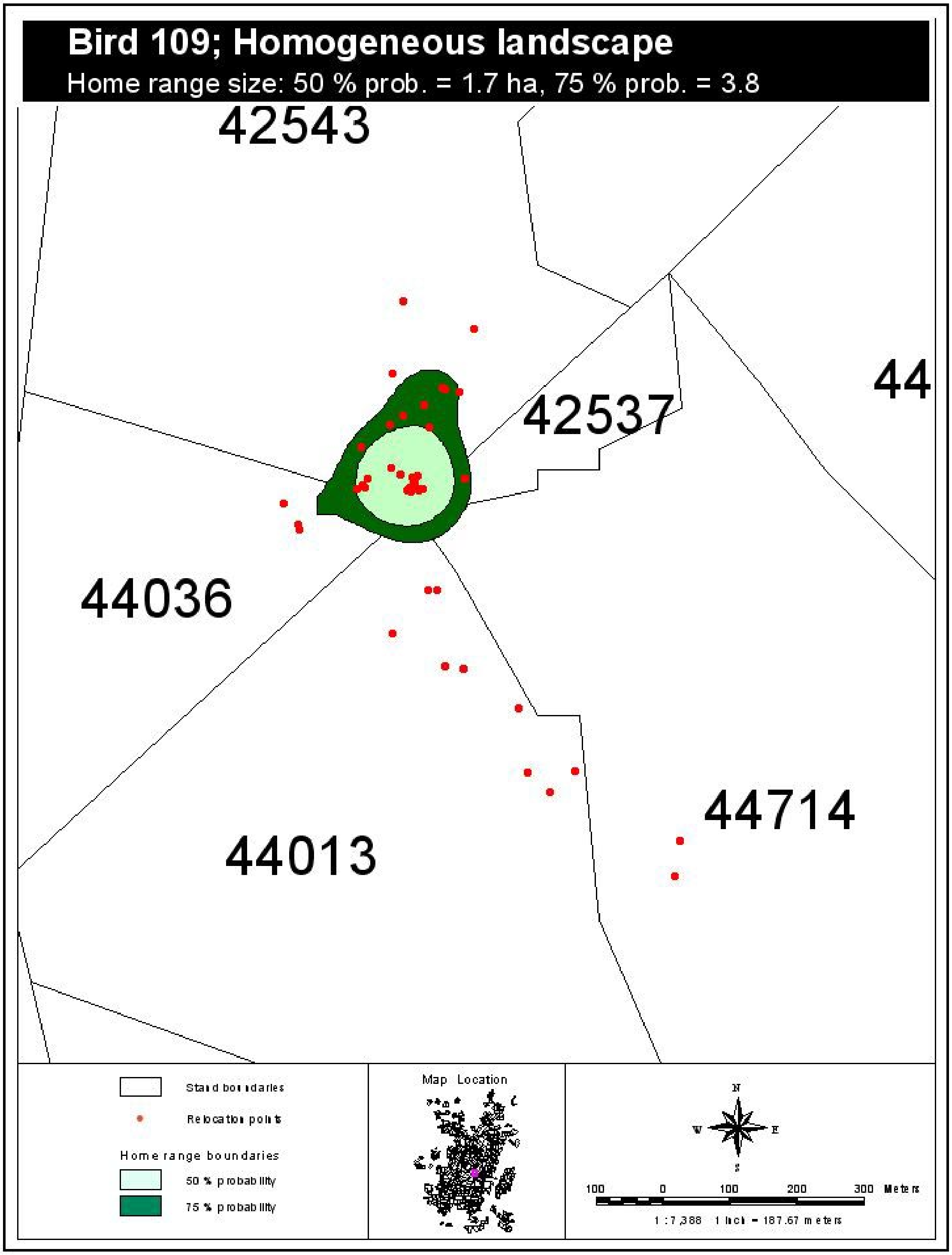


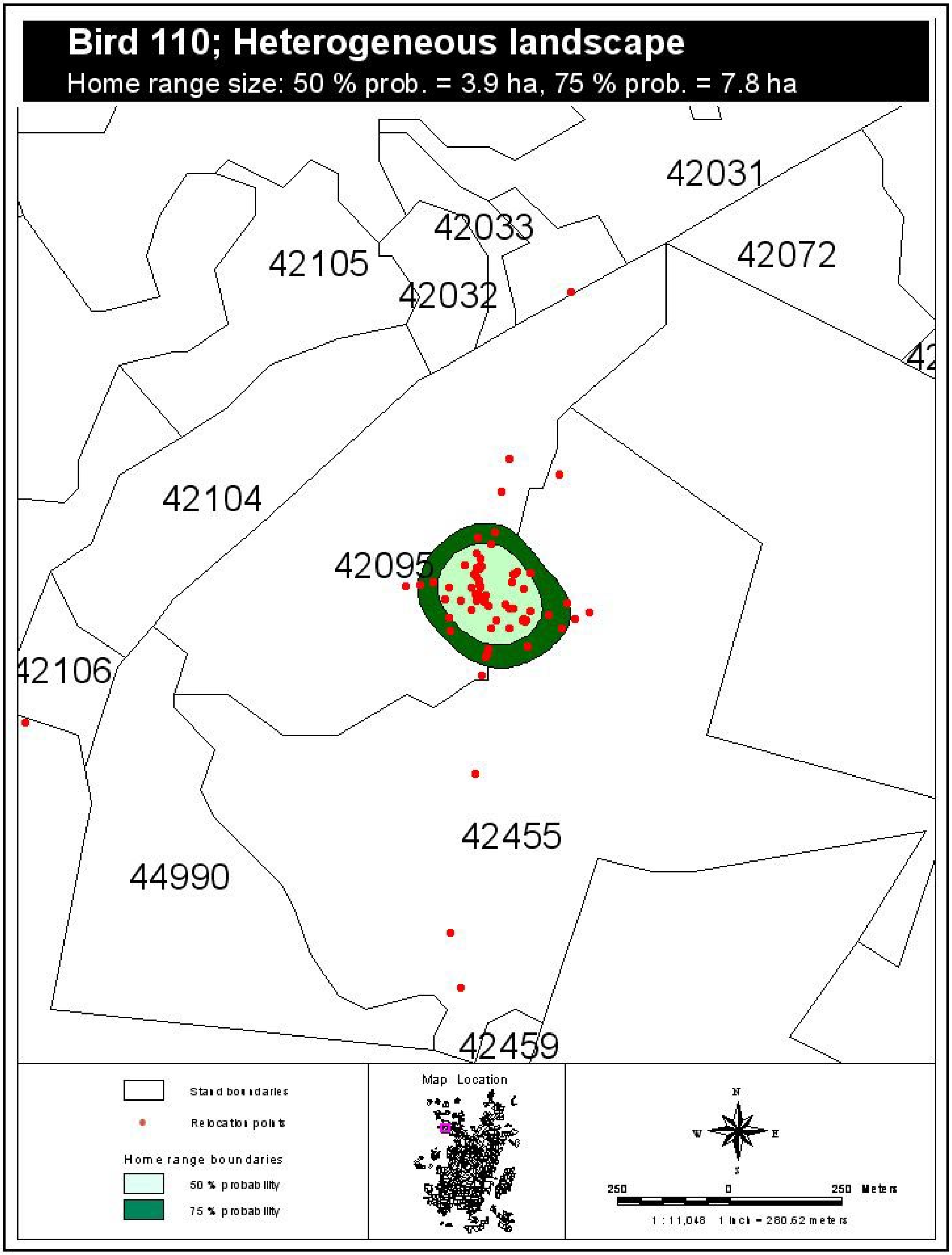
Bird 107; Heterogeneous landscape

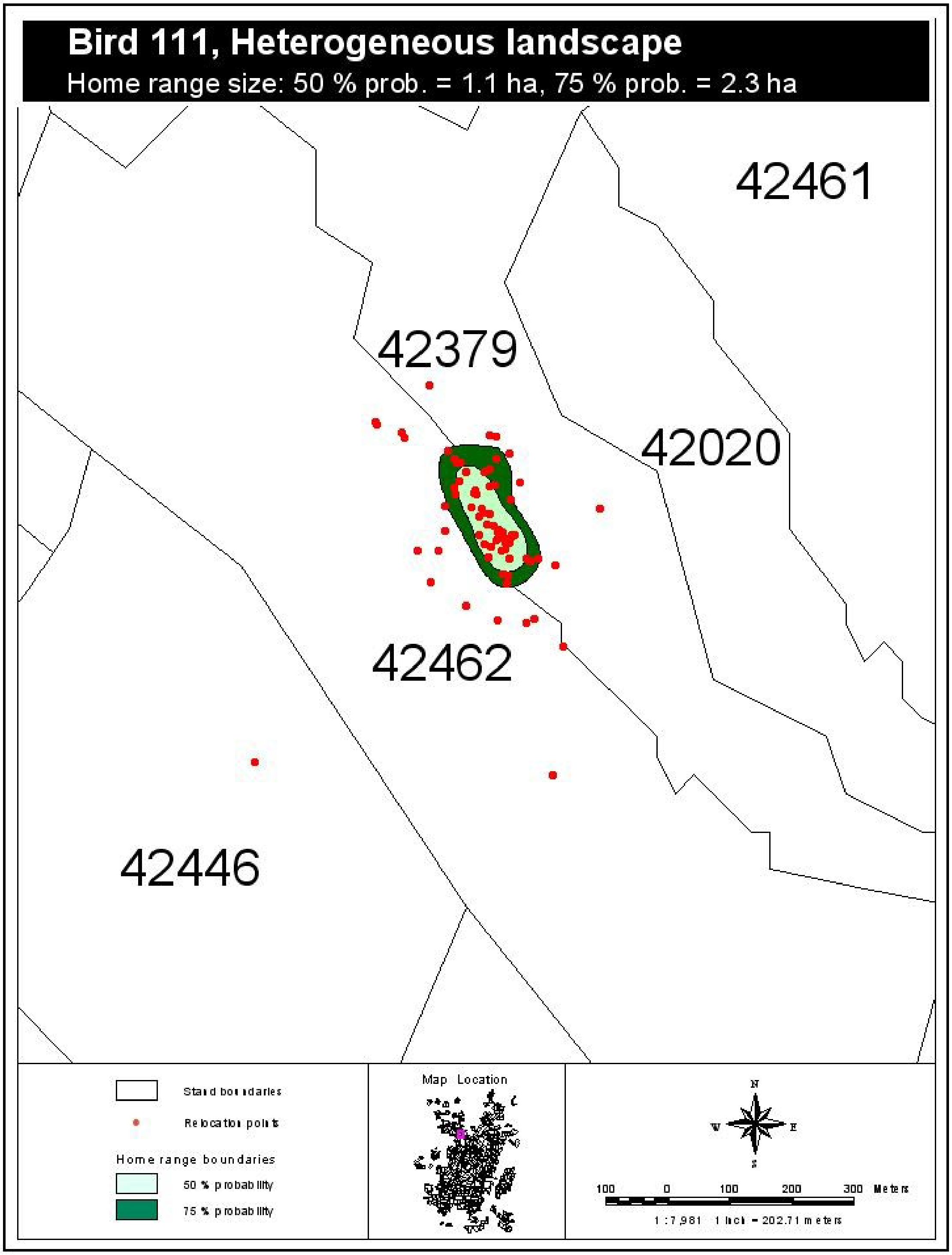
Home range size: 50 % prob. = 1.1 ha, 75 % prob. = 2.6 ha

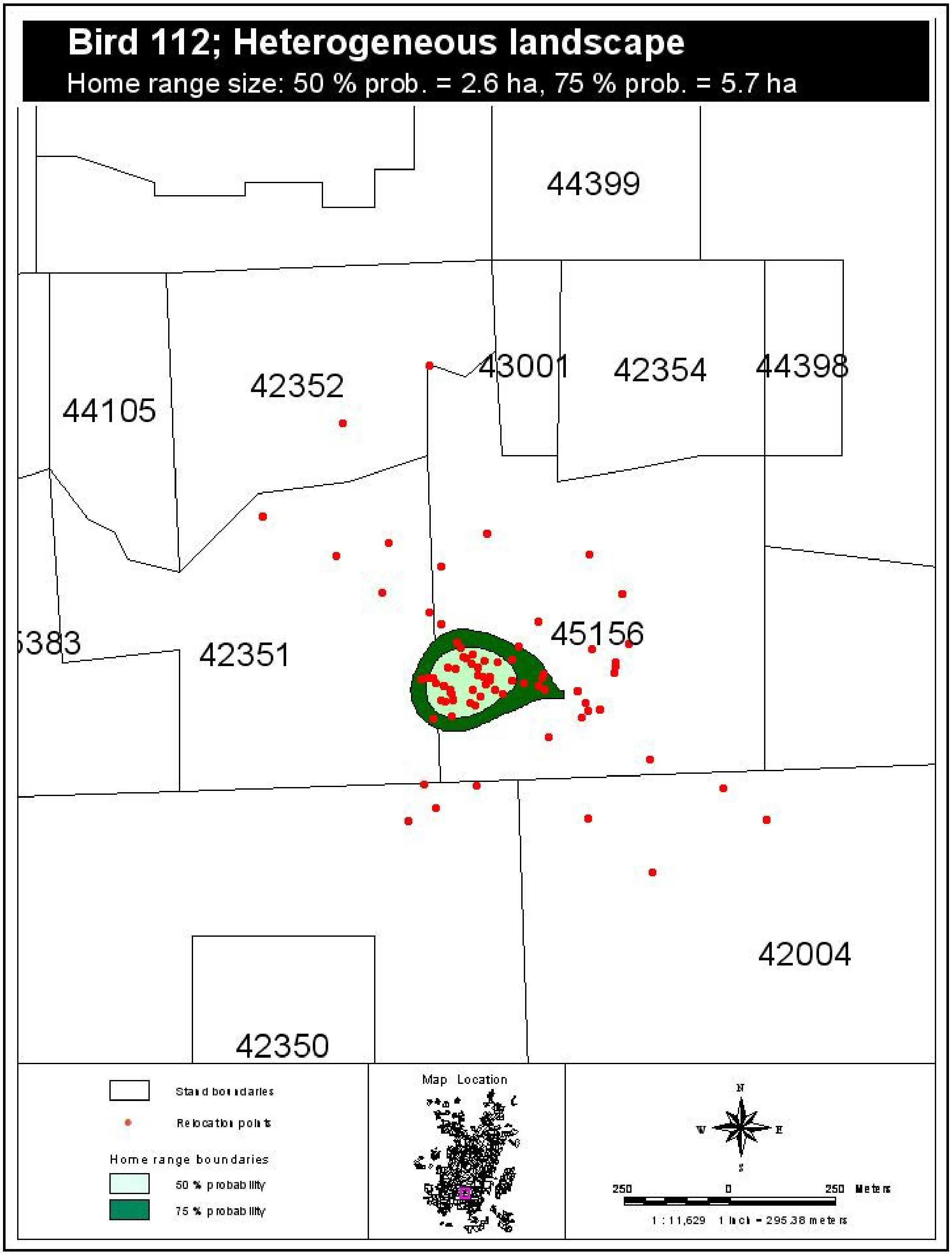

Bird 108; Heterogeneous landscape

Home range size: 50 % prob. = 5.8 ha, 75 % prob. = 16.3 ha


Bird 109; Homogeneous landscape
Home range size: 50 % prob. = 1.7 ha, 75 % prob. = 3.8
42543
42537
44
44036
44013
44714
Stand boundaries
Relocation points
Home range boundaries
50 % probability
75 % probability
Map Location
N
W
E
S
100
0
100
200
300
Meters
1 : 7,388 1 inch = 187.67 meters

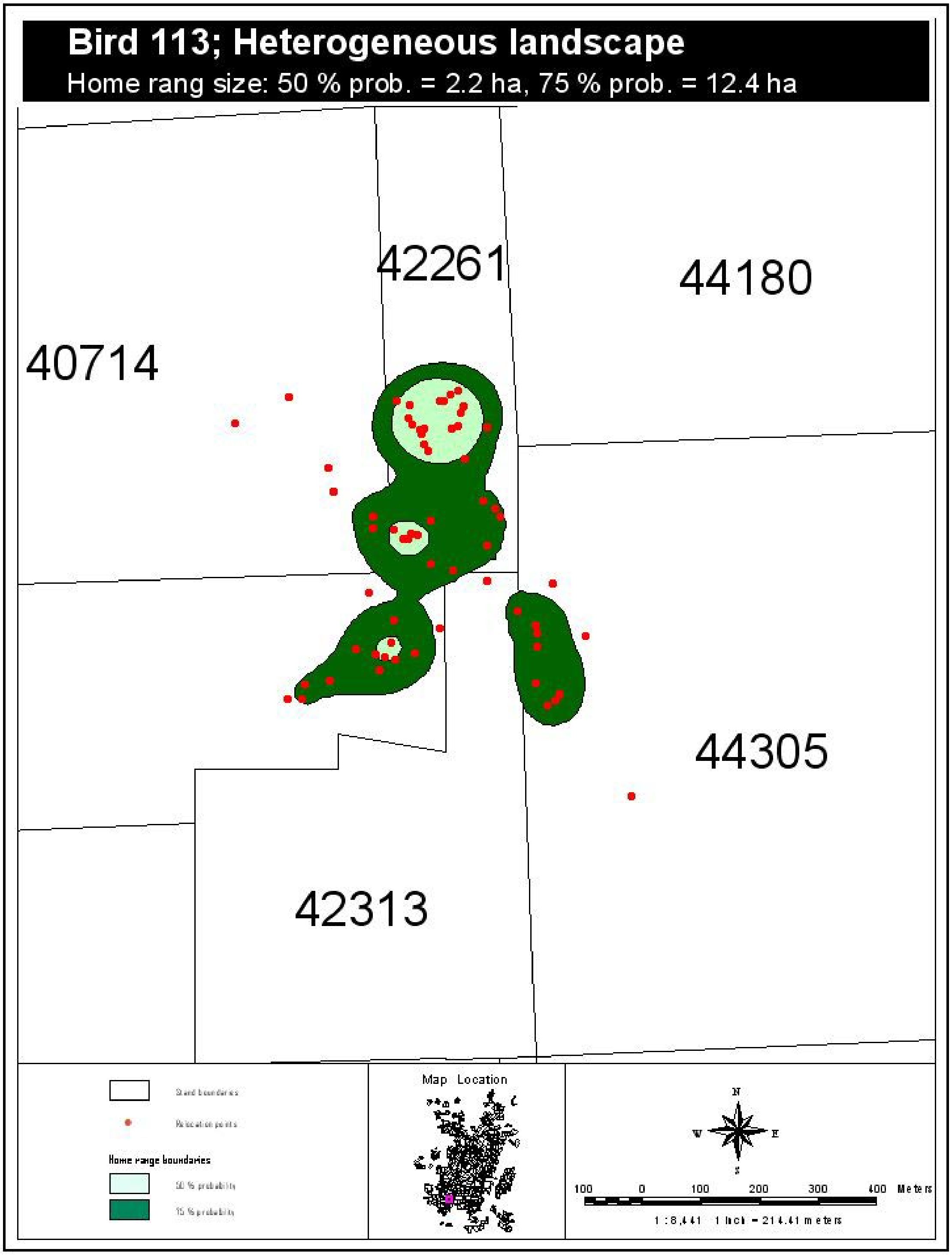

Bird 110; Heterogeneous landscape
Home range size: 50 % prob. = 3.9 ha, 75 % prob. = 7.8 ha
42031
42033
42105
42072
42032
42104
42095
42106
42455
44990
42459
Stand boundaries
Relocation points
Home range boundaries
50 % probability
75 % probability
Map Location
N
W
E
S
250
0
250 Meters
1 : 11,048 1 inch = 280.62 meters

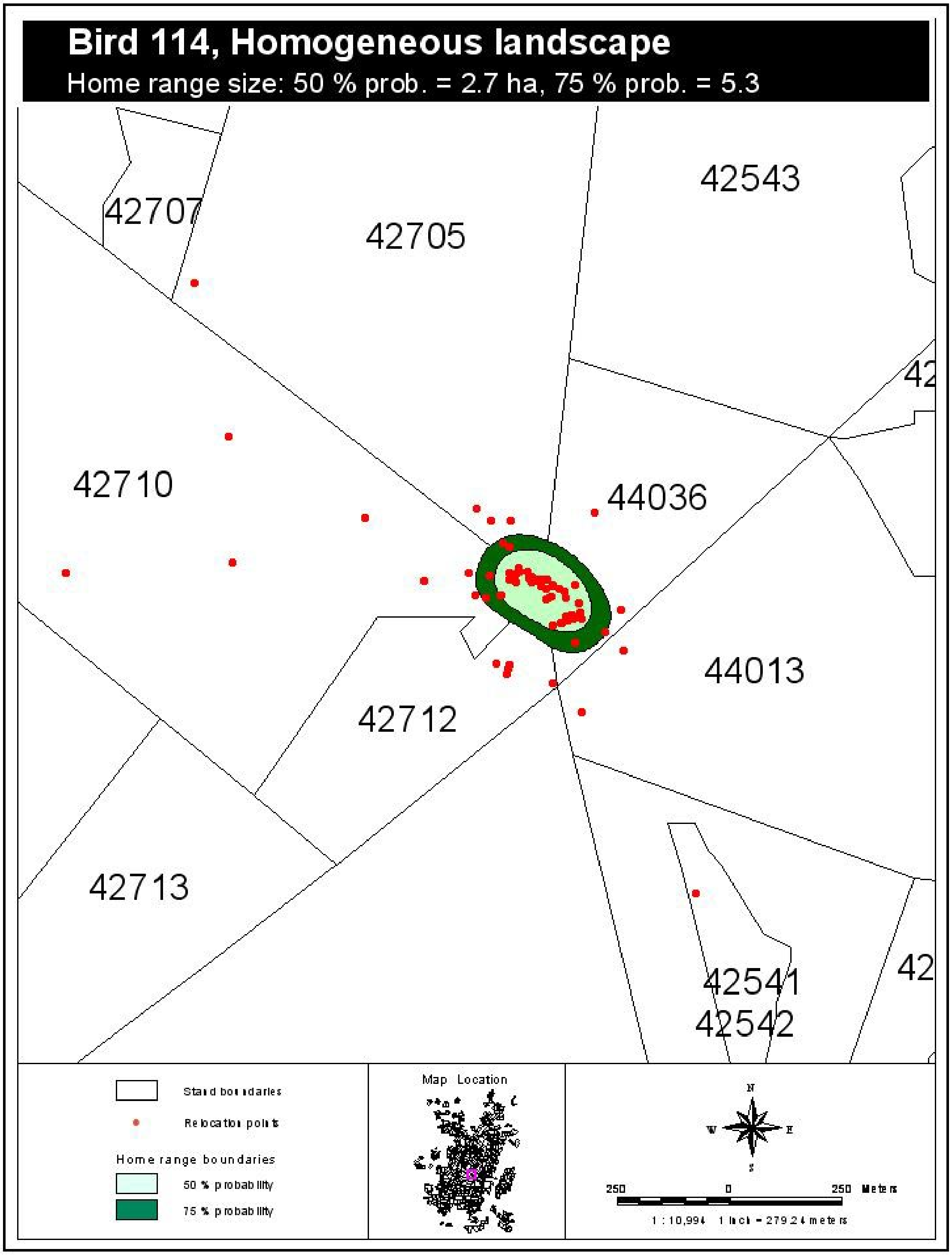

Bird 111, Heterogeneous landscape
Home range size: 50 % prob. = 1.1 ha, 75 % prob. = 2.3 ha
42461
42379
42020
42462
42446
Stand boundaries
Relocation points
Home range boundaries
50 % probability
75 % probability
Map Location
N
W
E
S
100
0
100
200
300
Meters
1 : 7,981 1 inch = 202.71 meters

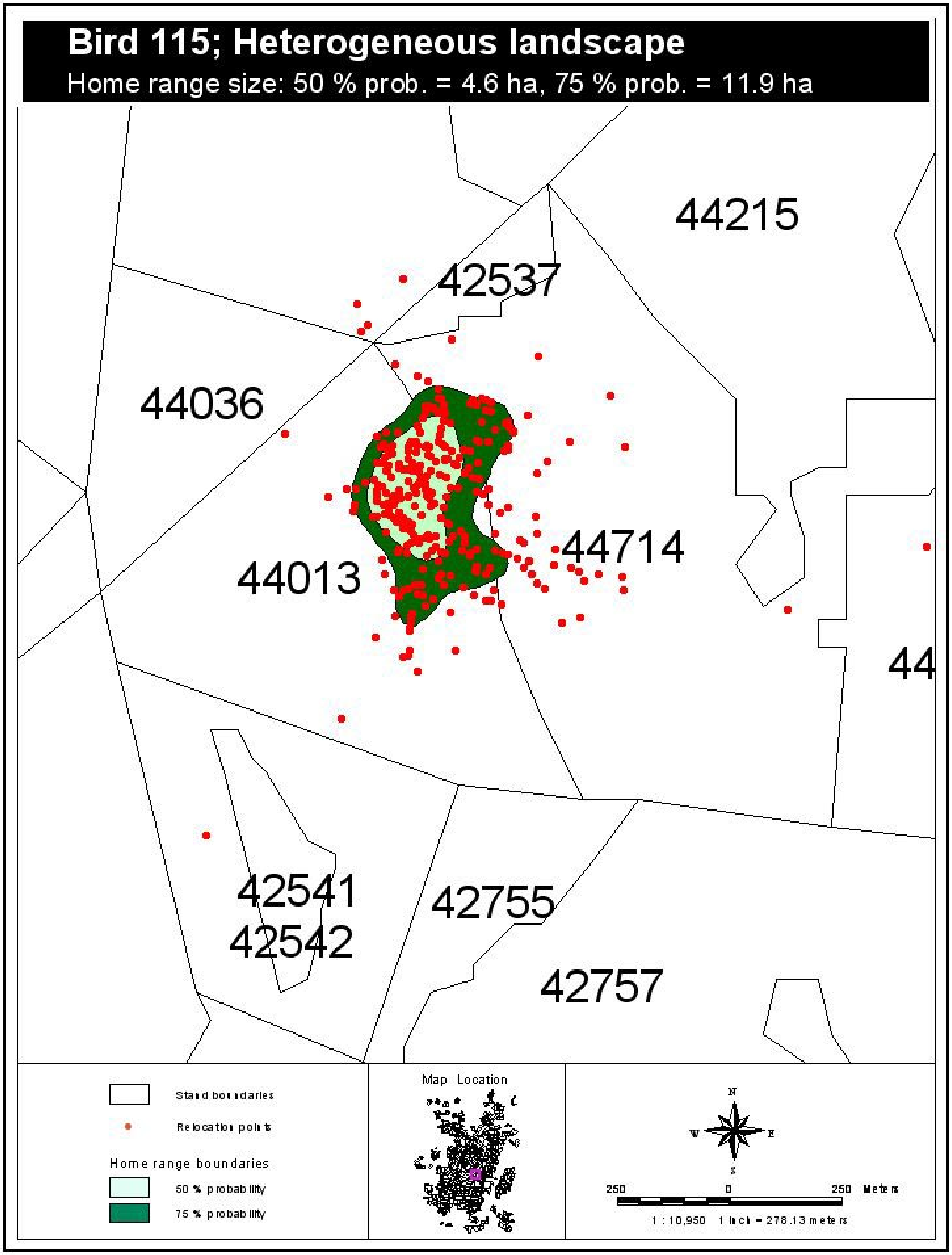


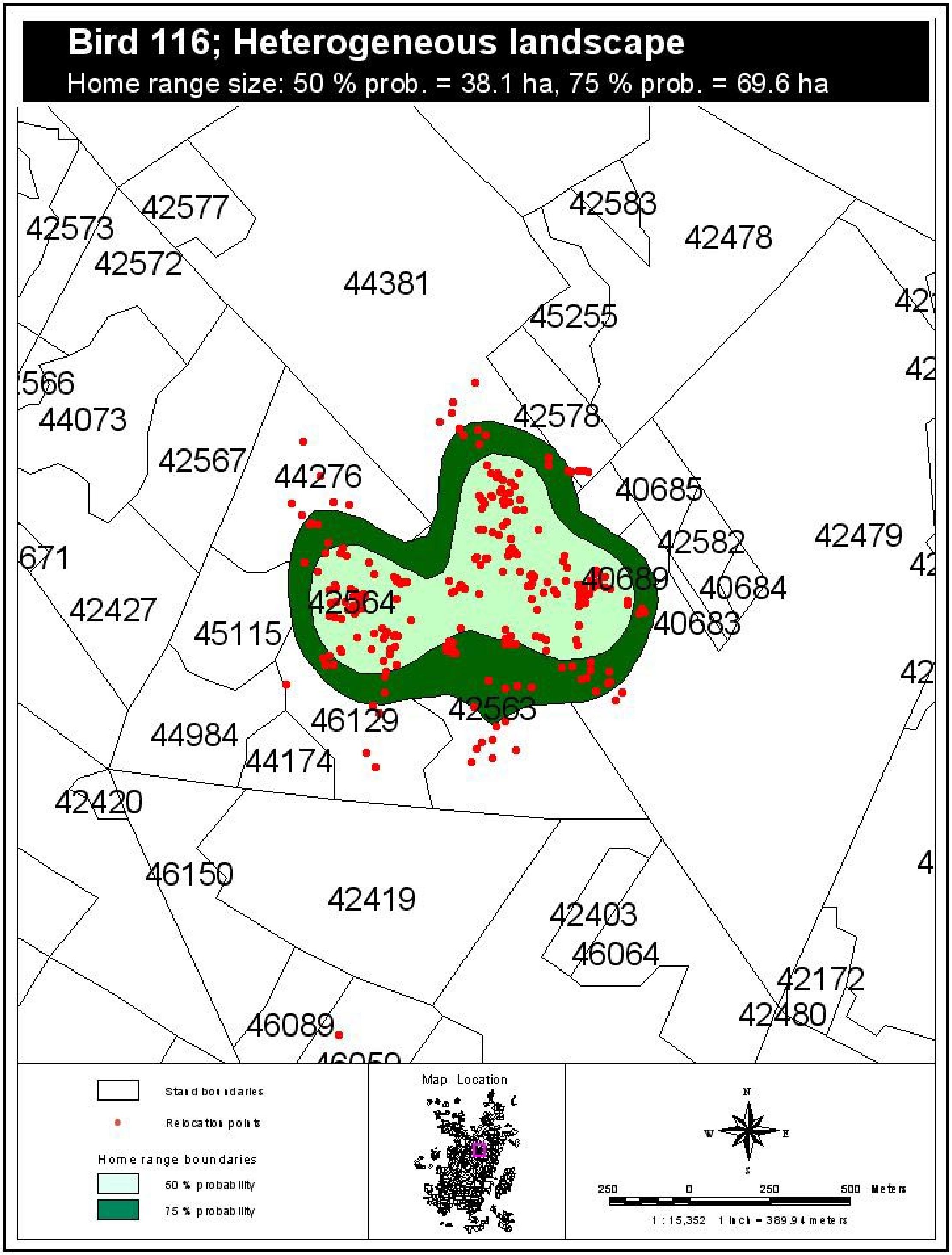
Bird 112; Heterogeneous landscape

Home range size: 50 % prob. = 2.6 ha, 75 % prob. = 5.7 ha


Bird 113; Heterogeneous landscape
Home rang size: 50 % prob. = 2.2 ha, 75 % prob. = 12.4 ha
42261
44180
40714
44305
42313
Stand boundaries
Relocation points
Home range boundaries
50 % probability
75 % probability
Map Location
N
W
E
S
100
0
100
200
300
400
Meters
1 : 8,441 1 inch = 214.41 meters

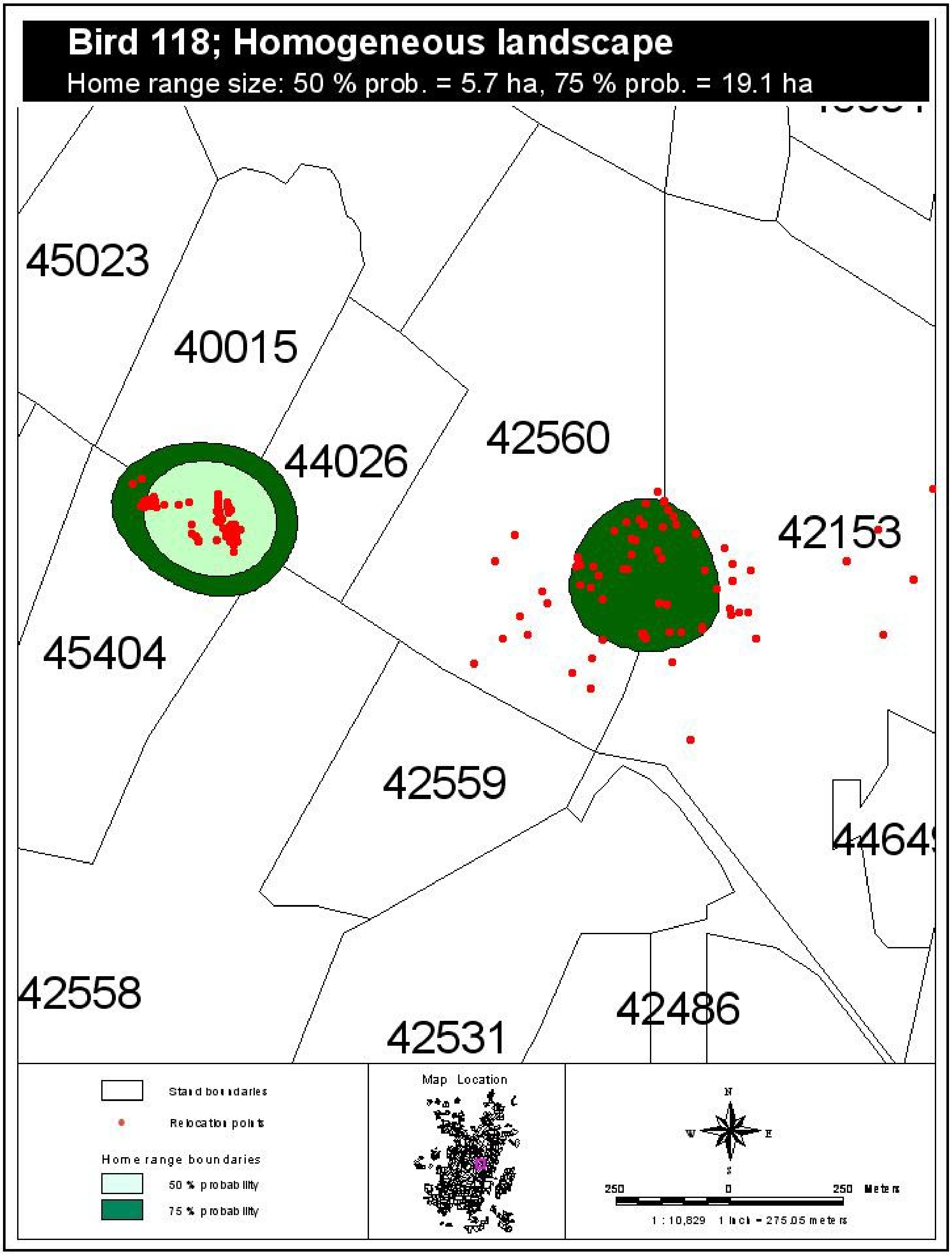

Bird 114, Homogeneous landscape
Home range size: 50 % prob. = 2.7 ha, 75 % prob. = 5.3
42707
42705
42543
42
42710
44036
44013
42712
42713
42541
42542
42
Stand boundaries
Relocation points
Home range boundaries
50 % probability
75 % probability
Map Location
N
W
E
S
250
0
250 Meters
1 : 10,994 1 inch = 279.24 meters

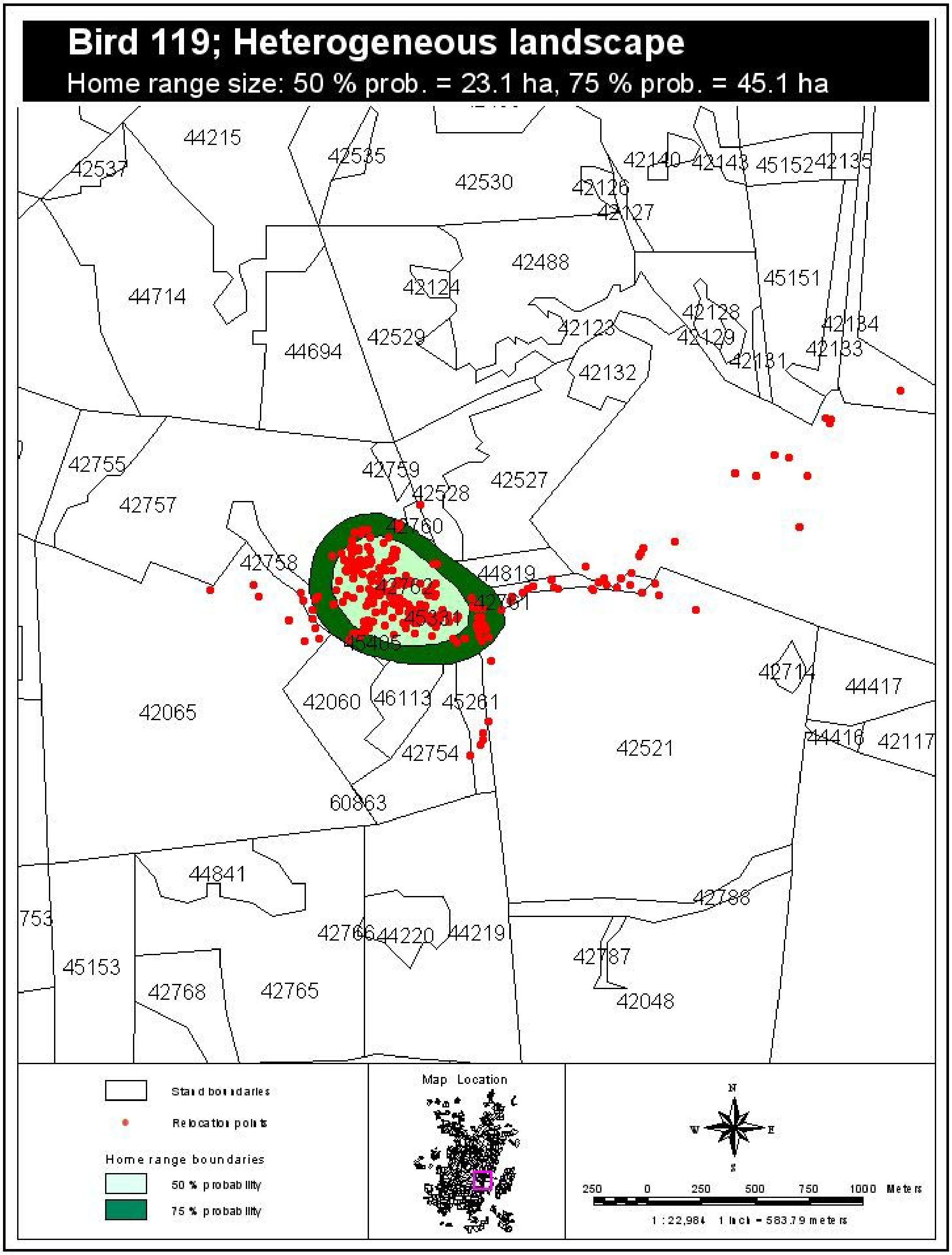

Bird 115; Heterogeneous landscape
Home range size: 50 % prob. = 4.6 ha, 75 % prob. = 11.9 ha
44215
42537
44036
44714
44013
44
42541
42542
42755
42757
Stand boundaries
Relocation points
Home range boundaries
50 % probability
75 % probability
Map Location
N
W
E
S
250
0
250 Meters
1 : 10,950 1 Inch = 278.13 meters



Bird 116; Heterogeneous landscape

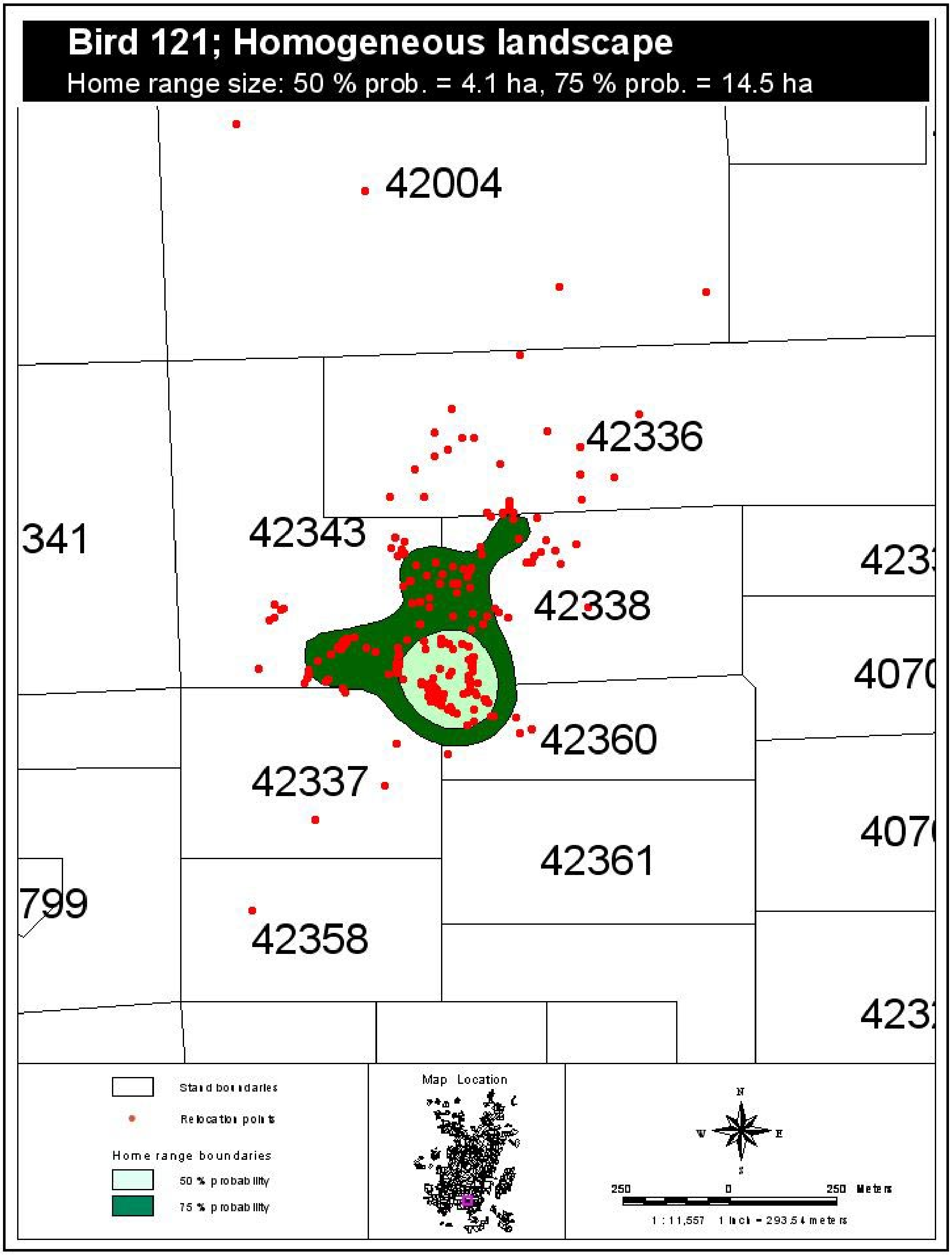
Home range size: 50 % prob. = 38.1 ha, 75 % prob. = 69.6 ha

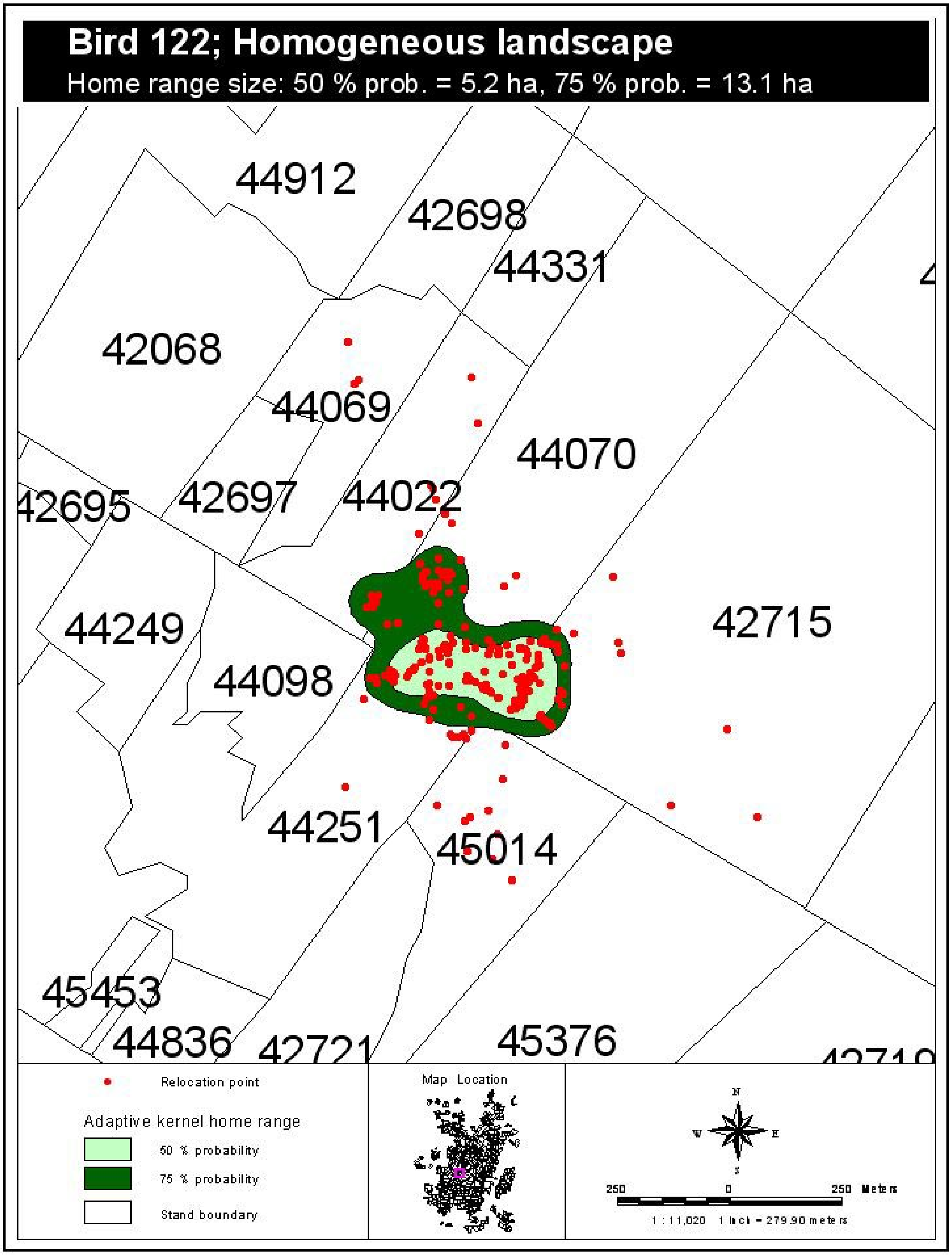

Bird 118; Homogeneous landscape
Home range size: 50 % prob. = 5.7 ha, 75 % prob. = 19.1 ha
45023
40015
44026
42560
42153
45404
42559
4464
42558
42531
42486
Stand boundaries
Relocation points
Home range boundaries
50 % probability
75 % probability
Map Location
N
W
E
S
250
0
250 Meters
1 : 10,829 1 inch = 275.05 meters

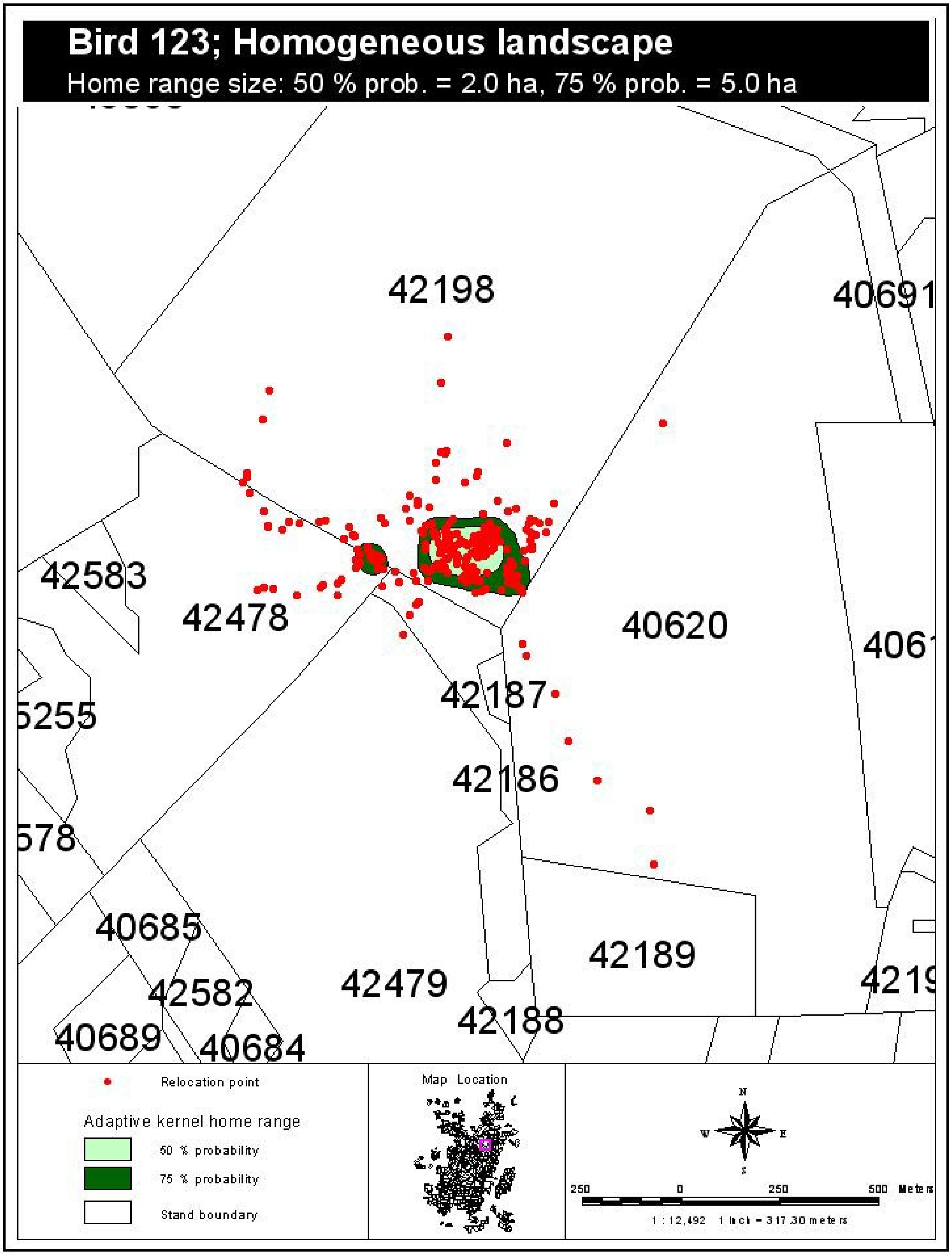


Bird 119; Heterogeneous landscape

Home range size: 50 % prob. = 23.1 ha, 75 % prob. = 45.1 ha

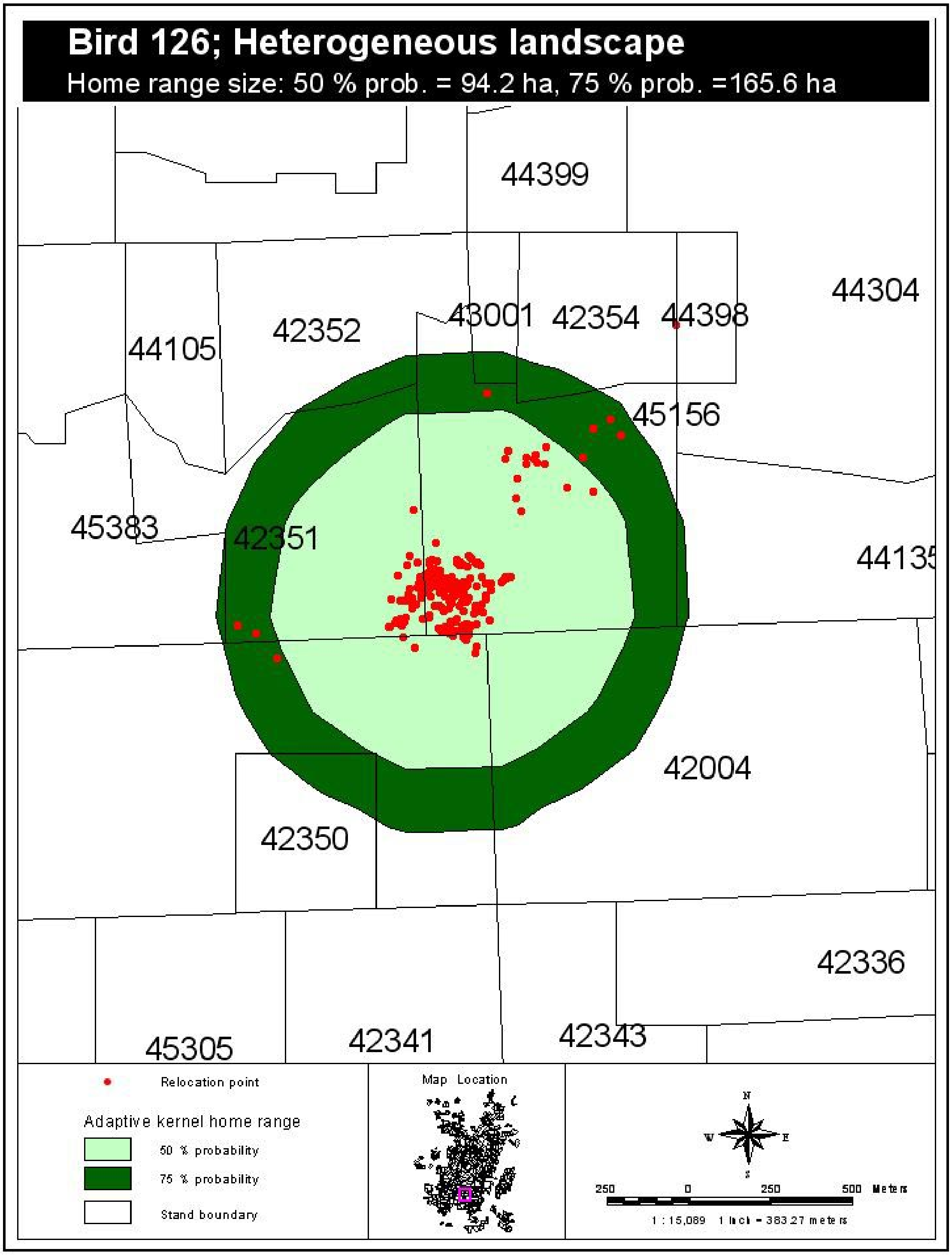

Bird 121; Homogeneous landscape
Home range size: 50 % prob. = 4.1 ha, 75 % prob. = 14.5 ha
42004
42336
341
42343
4233
42338
4070
42360
42337
4070
42361
799
42358
4232
Stand boundaries
Relocation points
Home range boundaries
50 % probability
75 % probability
Map Location
N
W
E
S
250
0
250 Meters
1 : 11,557 1 inch = 293.54 meters

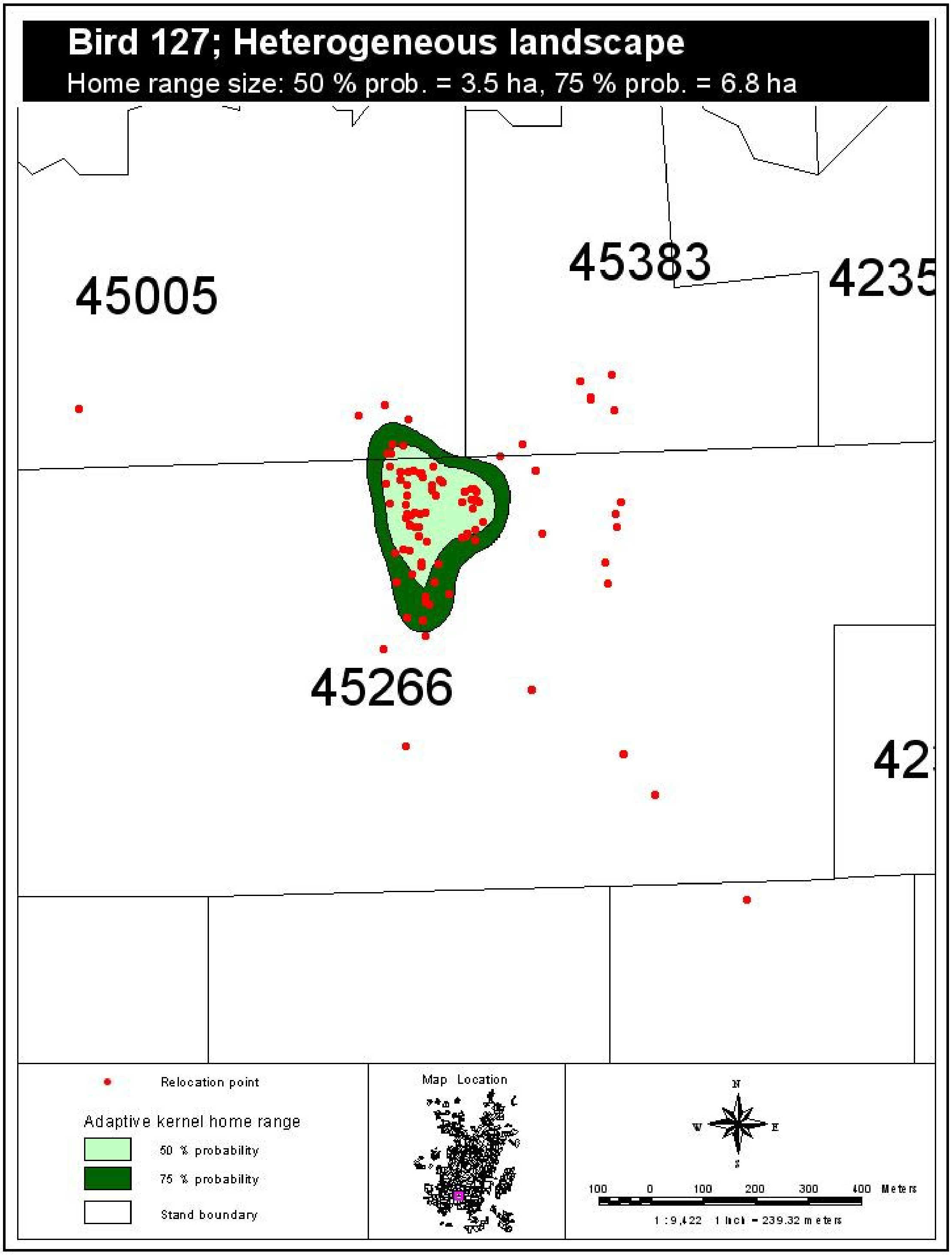

Bird 122; Homogeneous landscape
Home range size: 50 % prob. = 5.2 ha, 75 % prob. = 13.1 ha
44912
42698
44331
42068
44069
44070
42695
42697
44022
42715
44249
44098
44251
45014
45453
44836
42721
45376
Relocation point
Adaptive kernel home range
50 % probability
75 % probability
Stand boundary
Map Location
N
W
E
S
250
0
250 Meters
1 : 11,020 1 inch = 279.90 meters

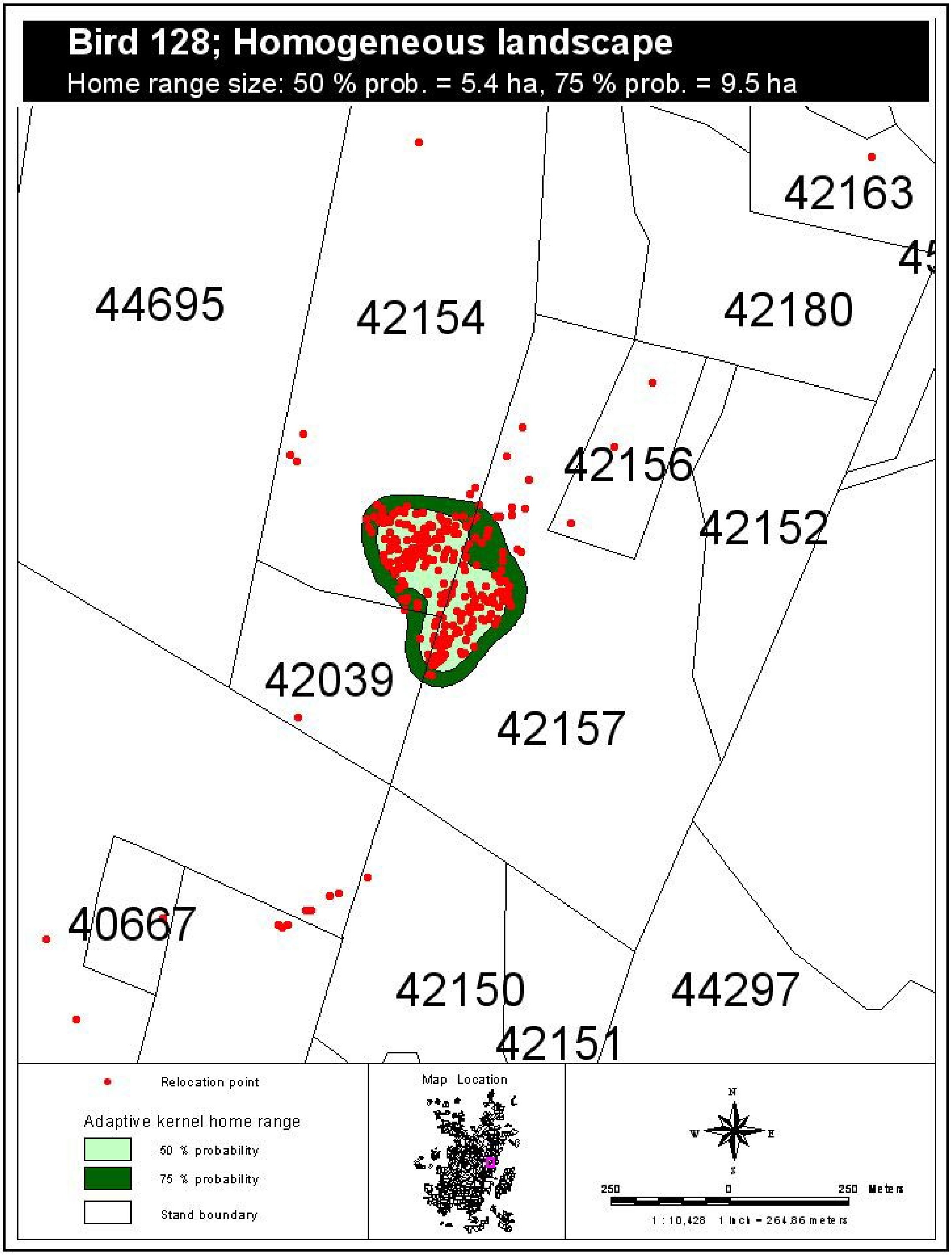


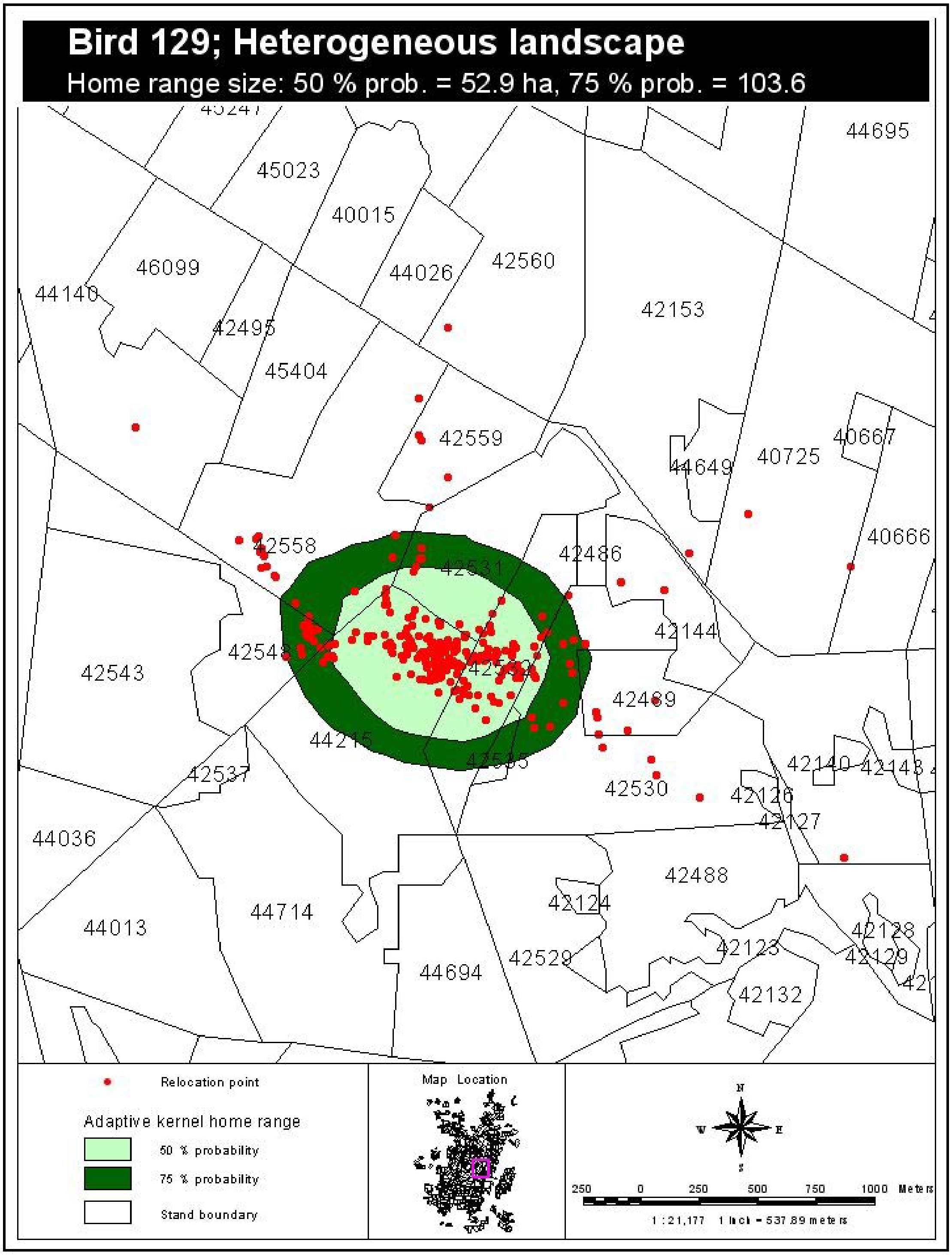
Bird 123; Homogeneous landscape

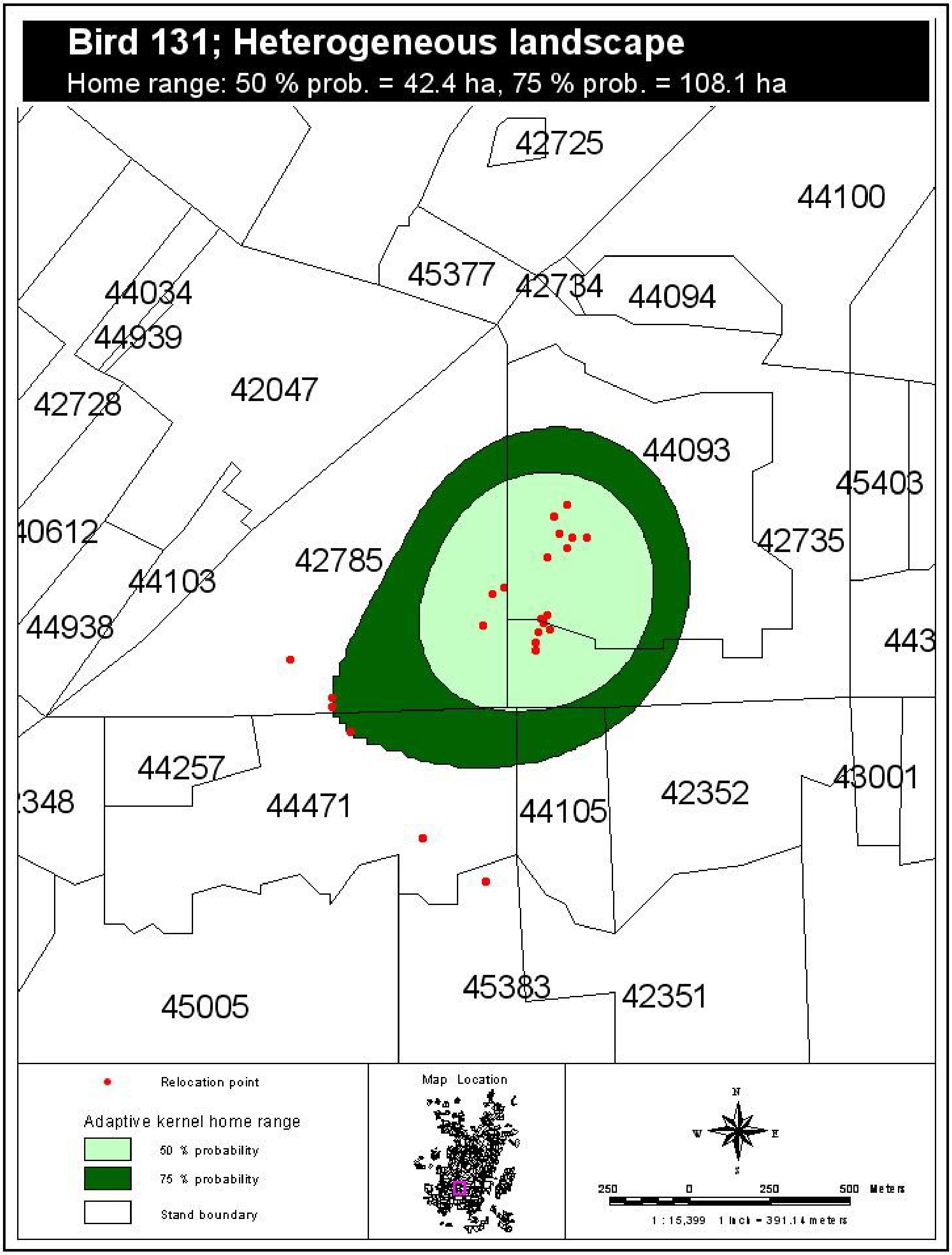
Home range size: 50 % prob. = 2.0 ha, 75 % prob. = 5.0 ha

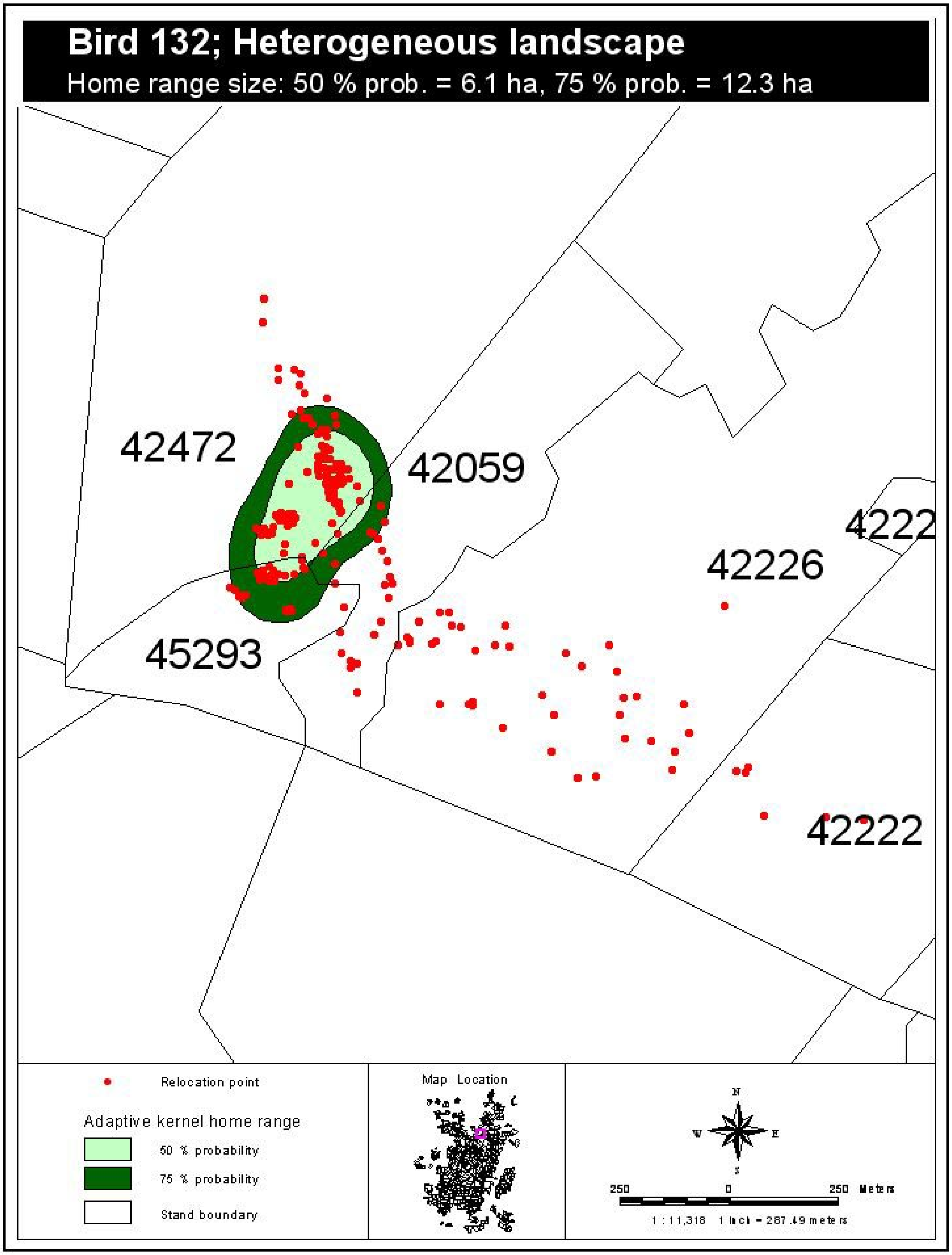

Bird 126; Heterogeneous landscape
Home range size: 50 % prob. = 94.2 ha, 75 % prob. =165.6 ha
44399
44304
42352
43001
42354
44398
44105
45156
45383
42351
4413
42004
42350
42336
45305
42341
42343
Relocation point
Adaptive kernel home range
50 % probability
75 % probability
Stand boundary
Map Location
N
W
E
S
250
0
250
500 Meters
1 : 15,089 1 inch = 383.27 meters

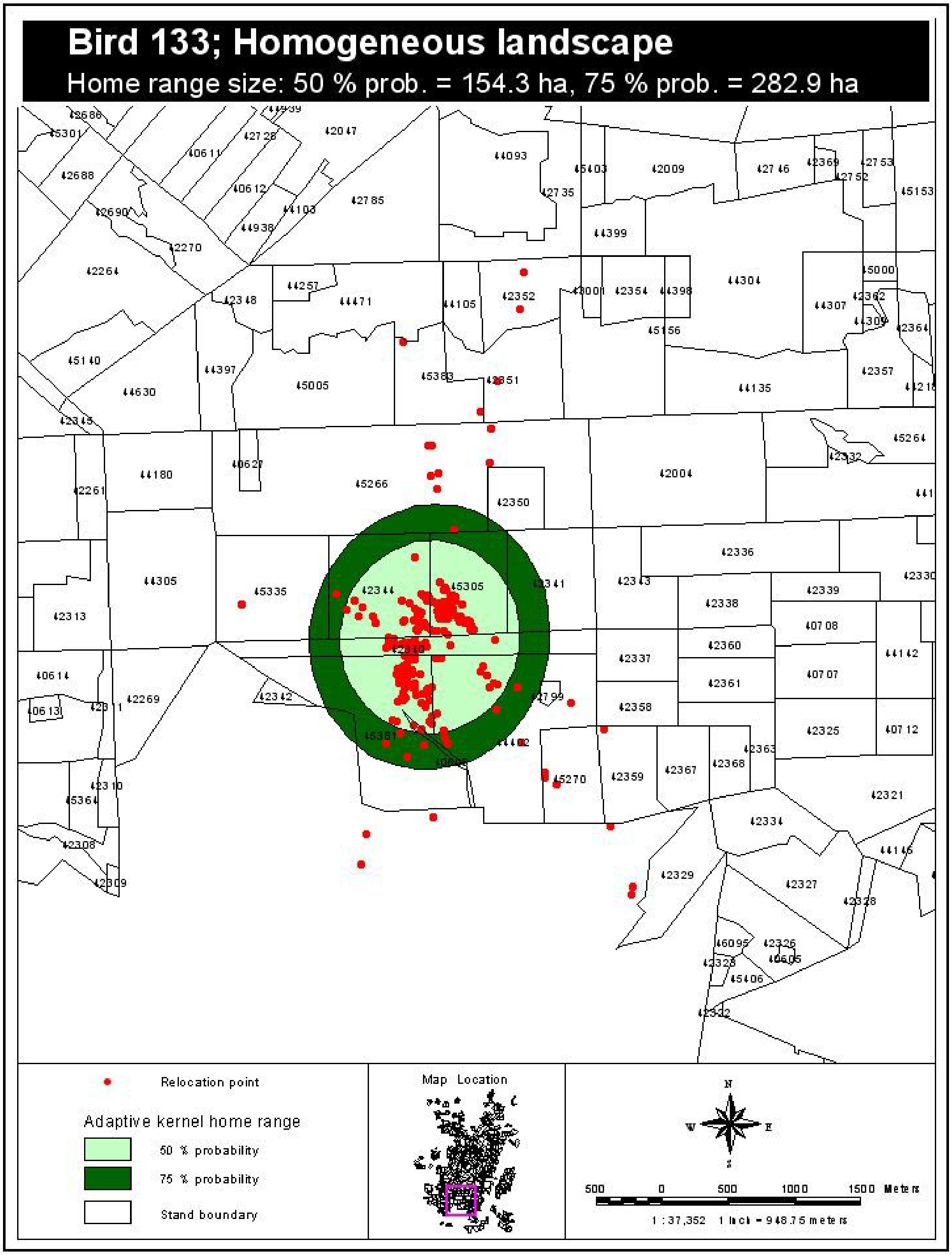

Bird 127; Heterogeneous landscape
Home range size: 50 % prob. = 3.5 ha, 75 % prob. = 6.8 ha
45005
45383
4235
45266
42
● Relocation point
Adaptive kernel home range
🟩 50 % probability
🟩 75 % probability
☐ Stand boundary
Map Location
N
W
E
S
100 0 100 200 300 400 Meters
1 : 9,422 1 inch = 239.32 meters


Bird 128; Homogeneous landscape
Home range size: 50 % prob. = 5.4 ha, 75 % prob. = 9.5 ha
42163
4
44695
42154
42180
42156
42152
42039
42157
40667
42150
44297
42151
Relocation point
Adaptive kernel home range
50 % probability
75 % probability
Stand boundary
Map Location
N
W
E
S
250
0
250 Meters
1 : 10,428 1 Inch = 264.86 meters


Bird 129; Heterogeneous landscape
Home range size: 50 % prob. = 52.9 ha, 75 % prob. = 103.6
45023
40015
44695
46099
44026
42560
44140
42153
42495
45404
42559
40667
44649
40725
42558
42486
40666
42531
42144
42543
42548
42532
42489
44215
42140
42143
42537
42535
42530
42126
42127
44036
42488
44714
42124
44013
42128
42123
42129
42529
44694
42132
Relocation point
Adaptive kernel home range
50 % probability
75 % probability
Stand boundary
Map Location
N
W
E
S
250
0
250
500
750
1000 Meters
1 : 21,177 1 Inch = 537.89 meters


Bird 131; Heterogeneous landscape
Home range: 50 % prob. = 42.4 ha, 75 % prob. = 108.1 ha
42725
44100
45377
42734
44094
44034
44939
42728
42047
44093
45403
40612
42735
42785
44103
44938
443
44257
43001
348
44471
44105
42352
45005
45383
42351
Relocation point
Adaptive kernel home range
50 % probability
75 % probability
Stand boundary
Map Location
N
W
E
S
250
0
250
500 Meters
1 : 15,399 1 Inch = 391.14 meters


Bird 132; Heterogeneous landscape
Home range size: 50 % prob. = 6.1 ha, 75 % prob. = 12.3 ha
42472
42059
4222
42226
45293
42222
Relocation point
Adaptive kernel home range
50 % probability
75 % probability
Stand boundary
Map Location
N
W
E
S
250
0
250 Meters
1 : 11,318 1 inch = 287.49 meters

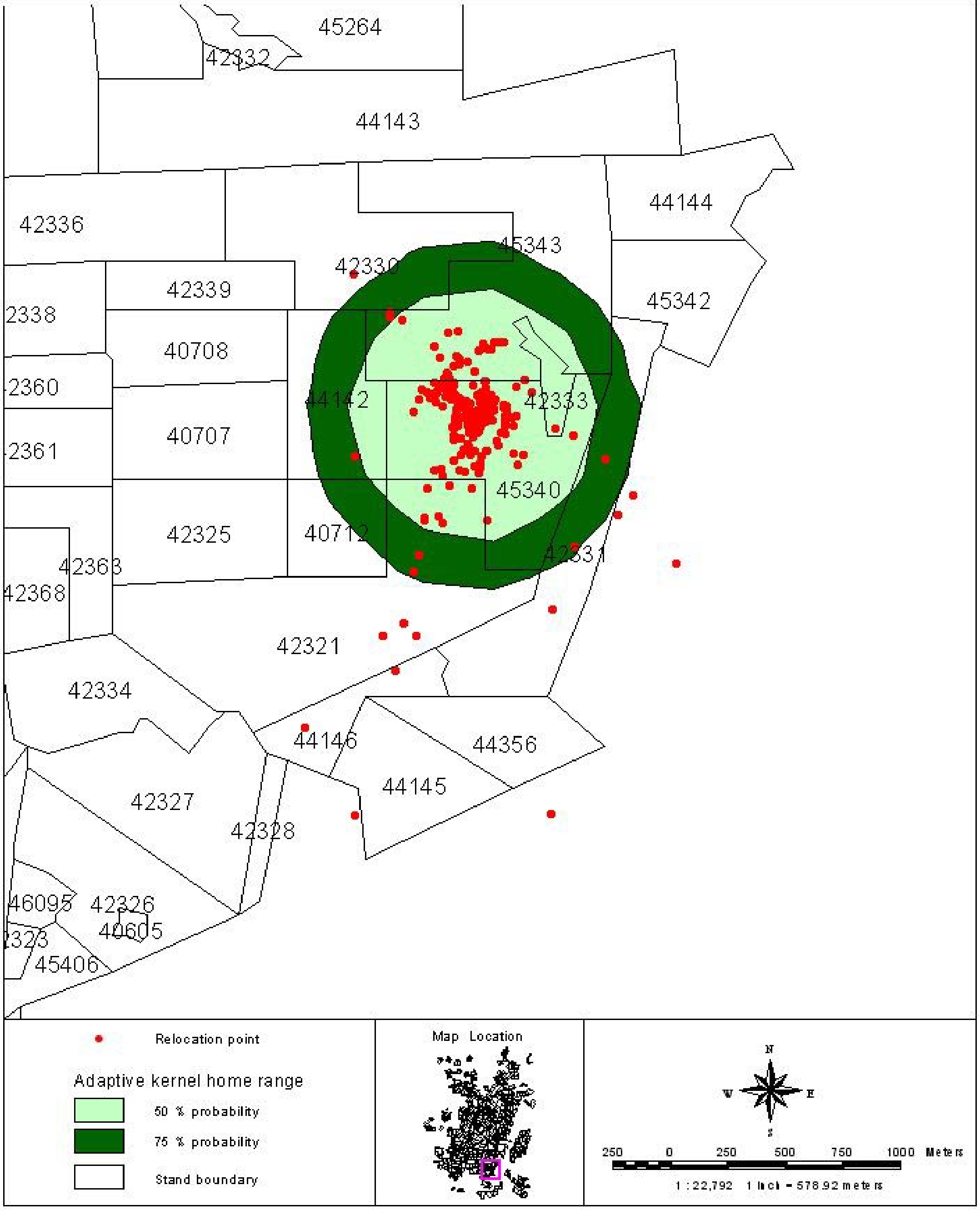


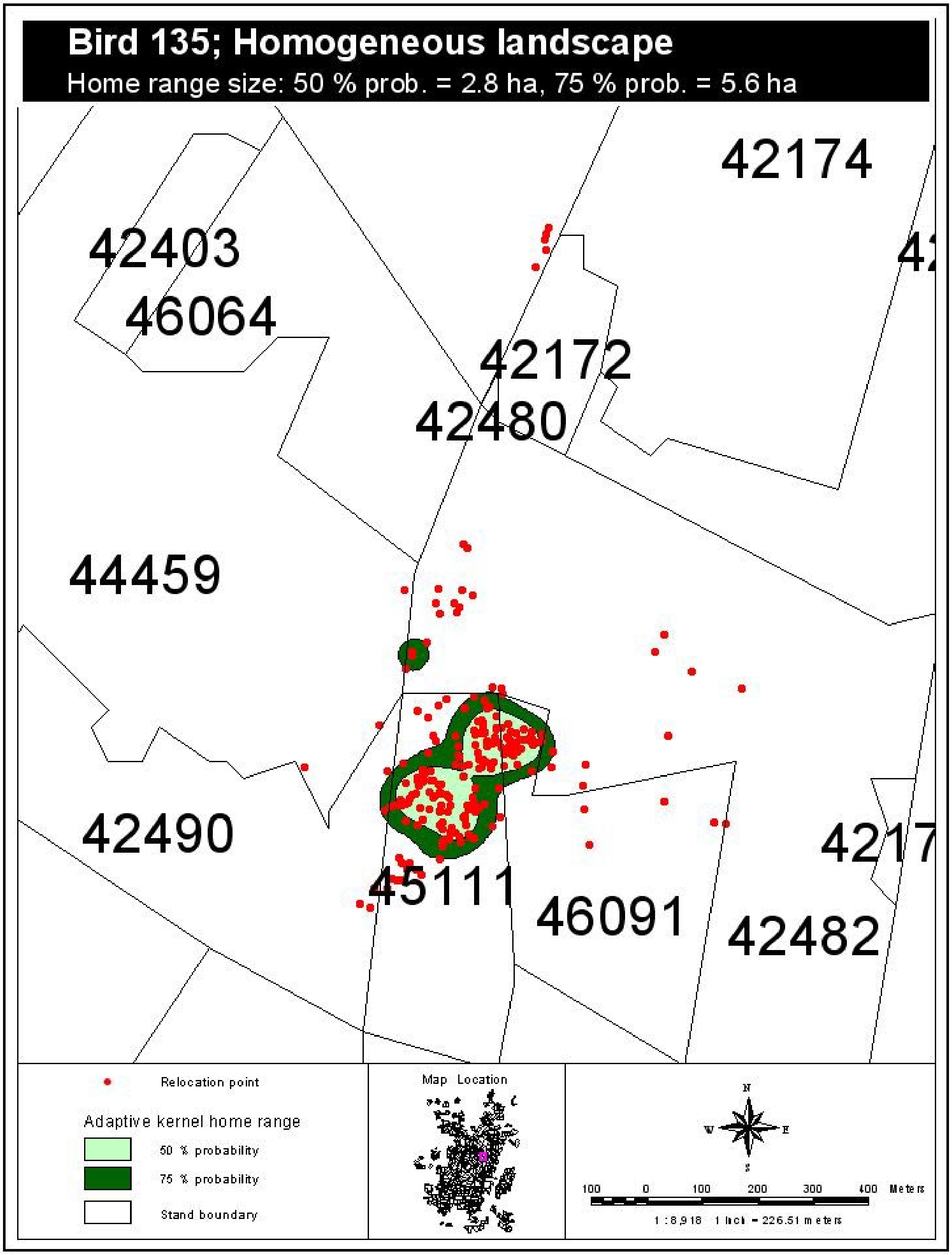
Bird 133; Homogeneous landscape

Home range size: 50 % prob. = 154.3 ha, 75 % prob. = 282.9 ha

Bird 135; Homogeneous landscape

Home range size: 50 % prob. = 89.3 ha, 75 % prob. = 166.8 ha




Bird 135; Homogeneous landscape
Home range size: 50 % prob. = 2.8 ha, 75 % prob. = 5.6 ha
42174
42403
46064
42
42172
42480
44459
42490
4217
45111
46091
42482
Relocation point
Adaptive kernel home range
50 % probability
75 % probability
Stand boundary
Map Location
N
W
E
S
100 0 100 200 300 400 Meters
1 : 8,918 1 Inch = 226.51 meters