DETERMINANTS OF GREAT BLUE HERON (ARDEA HERODIAS) COLONY SIZE AND LOCATION ALONG THE JAMES AND CHICKAHOMINY RIVERS IN VIRGINIA

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APPROVAL SHEET

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DEDICATION

I would like to dedicate this work to my husband, Ralph D. Clements, who has given me tremendous support and encouragement throughout this project and throughout my tenure at William and Mary.

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ABSTRACT

The factors influencing colony sizes and colony locations of Great Blue Heron colonies on the James and Chickahominy Rivers in Virginia were investigated. Three questions were examined: 1) Can variables measured off of maps and photographs be used to distinguish between sites with heron colonies and randomly selected (null) sites, and which variables are the best predictors of a heron colony site, 2) How does the area of surrounding wetlands influence colony size?, and 3) How are colonies spaced on the two rivers, and how does the location of one colony influence the location of another? I located 34 colonies by aerial survey in the watershed of these two rivers. Thirty-four null sites within the watershed were randomly chosen for comparison with active colony sites. For each active and null site, I measured 83 variables pertaining to topographic features and human disturbance factors from USGS topographic maps and recent aerial photographs. Variables were quantified within distances of 250m, 500m, and 1000m. Discriminant analysis was used to determine the variables with the greatest influence on colony location. Areas of wetlands were summed within distances of 3, 5, and 10 km from each colony or null site. Linear regression analysis was used to determine whether wetland area was correlated with colony size. A Multiresponse Permutation Procedure (MRPP) test and distance to nearest neighbors test were used to investigate colony spacing within the watersheds. Twenty-six of the variables used to compare active sites to null sites showed significant differences. Shoreline habitat and swamp habitat positively influence colony location within 500 and 1000m respectively. Cleared land, rural development, lengths of secondary roads, lengths of light roads, numbers of buildings, and agricultural fields all negatively influence colony location within 500m or 1000m of a colony site. Discriminant analysis classified 77.9% of the cases correctly, but when used to classify unknown sites, the classification rates were much lower, 52.4% overall, and 29,7% for null sites. These low classification rates show that the discriminant model could not accurately predict which of these variables was most important to colony location. Wetlands within 3 km and 5 km of a colony site were positively correlated with colony size (r^2 =0.43), but other factors are probably contributing to colony size in this study area. Results of the MRPP test and distance to nearest neighbors test show no significant difference between colonies and null sites. It is not clear at this time which factors have the most influence on spacing of the colonies, but the data suggest that colonies are spaced to allow sufficient wetland foraging area within a 5 km vicinity to reduce feeding competition for foraging sites from birds from other colonies. The data from this study could be used to develop a model for state and federal agencies to help predict locations in the coastal plain of Virginia for Great Blue Heron colonies, as well as to make management recommendations for development of land in this area.

DETERMINANTS OF GREAT BLUE HERON (ARDEA HERODIAS) COLONY SIZE AND LOCATION ALONG THE JAMES AND CHICKAHOMINY RIVERS IN VIRGINIA

Introduction

The focus of this study is the Great Blue Heron (*Ardea herodias*), North America's largest heron and a colonial breeder. Colonial nesting is a strategy where many pairs of birds nest in close proximity to each other, instead of nesting solitarily. A colony is defined as a group of two or more pairs of nesting birds.

The purpose of this study was to examine factors influencing colony size and colony location of Great Blue Herons in Virginia. The Great Blue Heron breeds in North America from southern Canada throughout the entire United States (except in the mountains), and well into Mexico (Erwin and Spendelow 1991). This species usually breeds in single species colonies, using tall trees with adequate structures to hold their large nests. Because of its wide range, the Great Blue Heron will nest in a variety of species of trees, including spruces, birches, cottonwoods, pines, cypress, sycamore and ashes, depending on the part of the continent surveyed. Occasionally, the species has been known to nest on the ground, in shrubs, or on artificial structures (e.g., DesGranges 1979). Heronries are usually located near water because of the species' preference for shallow water for foraging (Short and Cooper 1985).

The Chesapeake Bay region of Maryland and Virginia contained more than half of the estimated population of Great Blue Herons along the Atlantic coast in the mid 1970s (Erwin and Spendelow 1991). Drainages of four large rivers in the lower Chesapeake

Bay, the Potomac, Rappahannock, York, and the James, provide suitable habitat for nesting Great Blue Herons. Great Blue Herons in Virginia nest in pine stands and in bottomland hardwood swamps. Their colonies are usually located near water, but it is not known what specific local factors are most important in directly influencing colony location and size.

Pragmatic reasons exist to investigate the habitat requirements of this species. The coastal plain of Virginia is under constant development pressures. Land along the same riverbanks which provide habitat for Great Blue Herons is valuable and in demand. Shoreline developments such as housing communities and golf courses continue to encroach upon heron colony sites. Human activities along shorelines can affect both whole ecosystems and local populations of species. Although Great Blue Herons are increasing in most areas (M. Erwin, pers. comm.), this is a vulnerable species at the top of the food chain, and therefore a potential bioindicator of wetland habitat quality. More specific information on what influences colony location and size is needed to help the state of Virginia and the U.S. Fish and Wildlife Service develop a strategy for managing areas which currently have heronries, and areas that may be suitable for Great Blue Heron colonization in the future.

Because the lifespan of a Great Blue Heron colony is limited (guano from a heronry will eventually kill vegetation and nesting trees at a colony site, Weseloh *et. al.* 1971, Wiese 1978) and because development is reducing the options for this species when colonizing new locations, we need a better understanding of the habitat conditions that influence colony size and location if the Great Blue Heron is to continue to thrive in Virginia.

Studies in this area in the past have focused on a various aspects related to colony locations and sizes, such as human disturbance effects (e.g. Werschkul 1976, Grubb 1978, Vos *et. al.* 1985, Bratton 1990), and locations, sizes, and status of colonies in certain states (e.g. Vermeer 1969, 1970, 1972; Pitts 1977, Kelsall and Simpson 1979, Gray *et. al.* 1980, McCrimmon 1981, 1982; Findholt 1984, Dusi and Dusi, 1987). Most of the studies that have focused on large numbers of colonies have restricted their emphasis to describing the locations, sizes, and possible sources of food and/or disturbance to the sites (e.g. English 1978, etc.). Many of these studies were descriptive in nature, and were important because they helped determine the status of Great Blue Herons in North America. Few studies, however, have focused quantitatively on determining specific factors that influence the sizes and locations of large numbers of breeding colonies within a certain geographic location.

Studies that have investigated the influences on sizes and locations of colonies have concentrated on factors such as food availability and human disturbance. Several studies have proposed that food availability may limit colony size in ardeids. A study by Werschkul *et. al.*(1977) found a relationship between estuary area and the number of nests in heron colonies in Oregon. At a gross (state) scale, Custer and Osborn (1977) found that the abundance of wetlands correlated with numbers of herons for Atlantic coastal states. Burger (1981a) showed a correlation between the size of mixed species heron colonies and the length of shoreline around colonies. On the other hand, Erwin *et.*

al.(1987) found that size of heron colonies (but not including Great Blue Heron colonies) was not related to size of wetlands within 5 km. Fasola and Barbieri (1978) found that Grey Heron (*Ardea cinerea*) heronries in Italy were spaced closer together where rice fields (which provide flooded feeding sites) were more abundant. In addition, each heronry was spaced so as to include the same area of rice fields.

Human disturbance has also been shown to influence many species of colonially nesting birds, such as cormorants (Kury and Gochfeld 1975, Ellison and Cleary 1978, DesGranges and Reed 1981), charadriiformes (Robert and Ralph 1975, Conover and Miller 1979, Hand 1980, Burger 1981b), and ardeids (Parsons and Burger 1982, Erwin 1989). Great Blue Herons seem to be particularly sensitive to human activity. Miller (1943) suggested that distance from human activity was the most important factor in selection of a colony site by Great Blue Herons. Human disturbance has been linked to population declines of Great Blue Herons in the United States (Graber *et. al.* 1978, Thompson 1979a) and in Canada (Markham and Brechtel 1979, Kelsall and Simpson 1980). Parker (1980) found that the number of nests in a colony correlated with distance from roads. Vos *et. al.* (1985) found that people walking toward a heronry and motorcycle traffic caused the most disturbance. In addition, the Vos study found that Great Blue Herons are more sensitive to disturbance early in the breeding season. Werschkul *et. al.* (1976) showed that colony size, density, and nest occupancy were all greater in undisturbed heronries.

Other factors that may influence colony size and location are the numbers of conspecifics in nearby colonies (e.g. Furness and Birkhead 1984), island size (Greer *et. al.* 1985), and island isolation and distance from the mainland (Greer *et. al.* 1985).

Many of these studies have focused on a single factor that influences colony size or location, but one of the most comprehensive studies to date that investigated determinants of colony size and location in Great Blue Herons has been that of Gibbs *et. al.* (1987). This study described the determinants of Great Blue Heron colony distribution in coastal Maine. Nineteen colonies on coastal islands were investigated. Many different variables were tested to determine the factors that were most influential in colony size and location. The Gibbs study is important because it is very likely that many factors contribute to the size and locations of Great Blue Heron colonies on a more specific scale. Of the factors tested, distance to other colony sites and distance to towns negatively influenced colony location, and degree of forestation, and presence of hardwoods positively influenced colony location. Islands with colonies were farther than islands with no colonies ("null" sites) from other occupied islands and towns. Sites with colonies had a higher degree of forestation and presence of hardwoods than null sites. The distribution of colonies along the coast was shown to be nonrandom. The area of wetlands surrounding a colony was positively correlated with colony size. Gibbs *et.al.* (1987) hypothesized that food competition between members of the same colony probably limits the size of colonies, but food competition between members of adjacent colonies may determine colony distribution.

Given that the Gibbs study found specific factors that directly influence colony size and location in Maine, I wanted to test whether the same factors that were important in Maine, where colonies were located on coastal islands, were relevant in Virginia, where colonies are found along rivers. I focused on three factors which were most important to colony size and location in Maine, area of wetlands around a site, amount of human disturbance around a site, and the influence of the nearest colonies to a site. In addition, a concurrent goal of the study was to determine whether variables measured from maps and photographs provide enough information to be able to explain heron colony locations in the study site. Therefore, wetlands variables, attributes of human activities, and general topographic habitat variables were measured from topographic maps and from aerial photographs. Three questions will be investigated to address that influence on Great Blue Heron colony size and location in the coastal plain of Virginia:

1) Can variables easily quantified from maps and photographs be used to explain heron colony locations in the coastal plain, and which of these variables are the best predictors?

2) Do the areas of certain types of wetlands around a colony site influence the size of the colony?

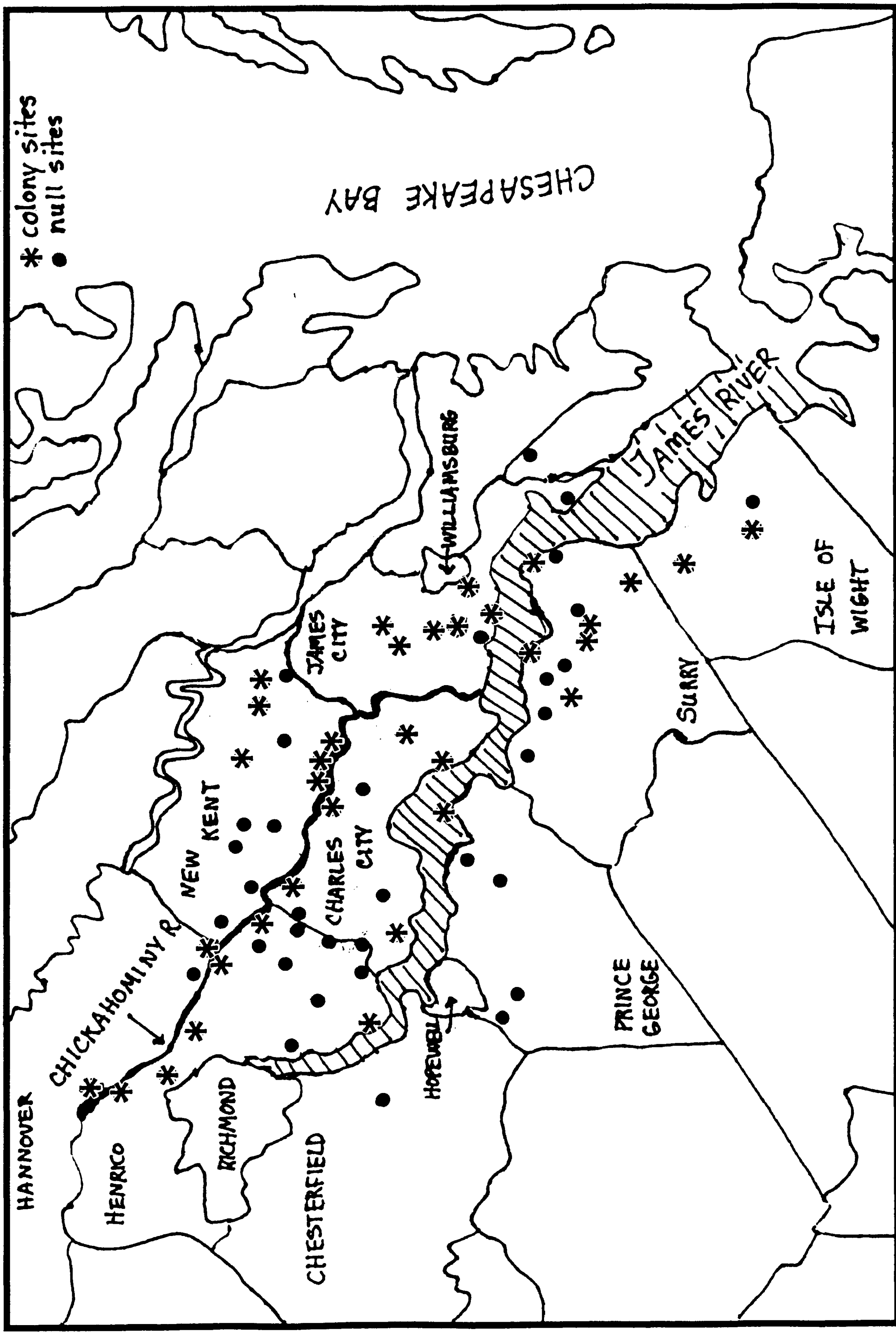
3) Is there a pattern to the spacing of Great Blue Heron colonies along the James and Chickahominy Rivers, and how does the location of one colony influence the location of another colony?

METHODS

Location of Colonies and Null Sites

The James and Chickahominy Rivers in Virginia were chosen as the study sites for the project (Figure 1.) The study area was comprised of the watershed area of the rivers from Richmond to Norfolk, Virginia. Almost all of the study area lies within the coastal plain physiographic province of Virginia. All Great Blue Heron colonies that could be found within the study area were included. The James River originates in the Allegheny Mountains of Virginia (Woodward and Hoffman 1991), and empties into the Chesapeake Bay. Below the Fall Line near Richmond, the river becomes estuarine. The Chickahominy River is a third-order tributary of the James River; it originates northwest of Richmond and meets the James River in the coastal plain, at the line dividing James City County and Charles City County. The topography of this river changes as it flows downstream. At Richmond, the river flows through a bottomland hardwood swamp, but where the river empties into the James it is an estuarine river bordered by freshwater marshes. The entire Chickahominy River watershed is approximately 777 km^2 in size (D.Eckels, USFWS, pers.comm.). This area of Virginia is characterized by hardwood and pine forests, agriculture, and moderate human development. Much land is owned by timber companies and is planted in monotypic loblolly pine (*Pinus taeda*) plantations.

Figure 1. Map of study area showing locations of active colony sites and null sites



* colony sites
● null sites
CHESAPEAKE BAY
JAMES RIVER
WILLIAMSBURG
JAMES CITY
ISLE OF WIGHT
SURRY
NEW KENT
CHARLES CITY
CHICKAHOMINY R
HANNOVER
HENRICO
RICHMOND
CHESTERFIELD
HOPEWELL
PRINCE GEORGE

The locations of Great Blue Heron colonies fluctuate little from year to year (Beck 1991). Most locations of colonies on the two river systems were known from previous fixed-wing aircraft surveys (Beck 1989, 1990). The number of nests per colony was obtained from surveys done on May 3 and May 7, 1993. (B.D. Watts and M.A. Byrd, College of William and Mary, pers. comm.). In addition, sites previously unknown were obtained from these 1993 flights (see Appendix B). Colony sites were plotted on USGS 7.5 minute topographic maps. Later, in the fall of 1993, another aerial survey was flown in order to obtain more precise locations with a hand-held Global Positioning System (GPS) unit. The purpose of using the GPS unit was to obtain a latitude-longitude fix for the center of each colony. This point would be used as the reference point from which other measurements could be taken. The approximate center of the colony was flown over twice, and an average of the two readings was taken. After latitude-longitude coordinates were obtained with the GPS, specific locations were plotted on the topographic maps.

After all colonies were located, an equal number of "null" or random sites were chosen in order to compare variables at these sites with those at active sites. Random latitude and longitude coordinates were generated by computer. These coordinates were plotted on USGS 7.5 minute topographic maps. Coordinates were accepted into the null data set if they met 3 criteria: (1) they fell within the watershed of the two rivers; (2) they were within a forested area (as designated by topographic map) and; (3) they were farther than 1 km from another colony or null site (see Custer and Osborn 1977). No other restrictions, such as proximity to wetlands, were put on random sites, since colonies in other areas are known to be in upland and even suburban habitats (Erwin and Korschgen 1979).

Topographic and Map Variables

A large number of variables was chosen in order to determine whether or not variables measured from maps and photographs can be used to explain the locations of heron colonies, and which of these variables are the best predictors. These variables were divided into two general groups: general topographic habitat variables and human disturbance variables.

General Habitat Variables.- The area within 1 km of a colony or null site was investigated with reference to general topographic variables (see Appendix A). Gibbs *et.al.* (1987) compared 7 variables for colonies and null sites found on coastal Maine islands. Within the areas of the islands, he found that active sites had significantly more degree of forestation and greater presence of hardwoods than null sites. Other variables compared by Gibbs *et.al.* (1987) between active and null sites do not apply as well to my study area, because these Virginia colonies are non-insular. Accordingly, concentric circles at radii of 250m, 500m, and 1000m were drawn around each site in order to compare topographic variables in the vicinity of a site. Within each of these circles, four categories of variables were chosen that, based on other studies (e.g., Burger 1981a, Gibbs *et.al.* 1987) seem to represent important determinants of colony location. These variables were measured directly from USGS topographic maps (7.5 minute series): (1) Marsh area- This designation follows the designation for marsh on USGS topographic maps. These areas consist of tidal and nontidal marshes; (2) Swamp area- This designation follows the USGS map designation of wooded wetland; (3) Shoreline length- The shorelines of all channels greater than 10m wide were measured, and; (4) Total forested area- This variable was designated by forest on the topographic maps. All areas were measured in hectares, and all distances were measured in meters. Areas and distances were measured using a Summa Sketch digitizing tablet and SigmaScan Software by Jandel Scientific. In order to determine whether the amount of wetlands at greater distances from active and null sites could explain colony location, shoreline length was converted to area, and three additional variables summing areas of shoreline, swamp, and marsh at 3 km, 5 km, and 10 km were included.

Human Disturbance Variables- Nine categories of variables that represent potential disturbances to heron colonies were chosen to be compared between null sites and active colony sites (Appendix A). Short and Cooper (1985) recommended that a 250-m buffer zone around a Great Blue Heron colony be kept free from human activity. To test the validity of this 250m distance, variables were compared up to four times this distance. Concentric circles were drawn around sites at radii of 250m, 500m ,and 1000m, and all human disturbance variables were quantified within these circles. Recent aerial photographs from the Agricultural Stabilization and Conservation Service (ASCS) at a scale of 1 centimeter to 79.2 meters (1 inch to 660 feet) were used to measure human disturbance variables. Photographs dated from 1989-1991, with the exception of photos from James City County, which dated from 1980. Variables were traced from photographs onto mylar sheets, and were later measured with the SigmaScan program and a digitizing tablet. The following variables were measured: (1) Area of pine forests- Virginia has an active timber industry, which focuses on loblolly pine growth and harvesting. Any monotypic stand of pines in the coastal plain may present a source of future and/or past disturbance. All forest stands that seemed to be exclusively pine were included in this category, since the potential for logging is present; (2) Length of primary roads- these roads are designated as heavy use on USGS topographic maps; (3) Secondary roads- roads designated as medium use on topographic maps; (4) Light roads- all other roads seen on photographs, including logging roads and dirt roads; (5) Number of buildings- all buildings within the radii measured; (6) Rural development- these are areas of primarily cleared land, usually with one or more buildings, associated with agriculture or rural housing; (7) Urban development- these areas are concentrated human development, such as housing communities, industrial sites, schools, etc.; (8) Agriculture- agricultural fields only, and; (9) Cleared land- land that is completely cleared, exclusive of agricultural fields, or recently logged land. All areas were measured in hectares and all distances were measured in meters.

In addition, the distance from each colony site or null site to the nearest of each of these human disturbance variables was measured. Distances were classified into five categories: (1) 0-250m, (2) 251-500m, (3) 501-750m, (4) 751-1000m, and (5) >1000m. The mean distances of active sites and null sites were compared.

A total of 83 variables was measured. I chose a large number of variables during an exploratory phase, knowing that a reduced set of uncorrelated variables would emerge. Later, univariate tests for differences in means, and correlation matrices were run to eliminate variables for the final analysis. A discriminant analysis model was used on the final set of variables to determine which variables are the best predictors of colony location.

Size of Colonies and Wetland Areas

Several authors (Werschkul *et.al* 1977, Burger 1981a, Gibbs *et. al.* 1987) have found a positive relationship between area of wetlands around a colony site and the size of a colony. Others have shown that the maximum distance a Great Blue Heron will fly to forage is about 20 km (Parris and Grau 1979, Thompson 1979b, Dowd and Flake 1985). Therefore, Gibbs *et al.* (1987) used a 20 km distance from the colony site for quantifying wetlands as potential feeding habitat. Most of the authors mentioned above also found, however, that the average distance a heron flies is much less than 20 km (6.5 km- Thompson 1979b, 3.1 km- Dowd and Flake 1985). Previous surveys of Great Blue Heron colonies in the study area have shown that Great Blue Heron colonies in Virginia are close together in many instances, (Beck 1989) and a 20 km circle around one colony would certainly encompass colony sites and feeding grounds for several others. For these last two reasons, wetlands in this study have been measured out to 10 km instead of 20 km.

In order to examine whether local wetlands influenced colony size, five types of wetlands were chosen to be measured within the study area. Wetland types chosen were based on previous studies that determined what kinds of wetlands Great Blue Herons prefer for foraging (Thompson 1979b, Parris 1979, Warren 1979, Gibbs *et.al.* 1987). Wetlands to be measured by the study (see Appendix A) were designated by USGS topographic maps designations. The following wetland types were measured in the study area: (1) Area of marsh- this designation follows that of the topographic maps; (2) Area of swamp- this designation follows that of wooded wetlands on topographic maps; (3) Length of streams- only those designated as permanent streams were measured; (4) Area of mudflats- this designation follows that of topographic maps; (5) Area of shoreline habitat- all shorelines of all channels wider than 10m were measured. Since herons can only forage in relatively shallow water, a 5-m edge of all shorelines was used to calculate area. (see Gibbs *et. al.* 1987, Gibbs 1991). All areas were measured in hectares and all distances were measured in meters. I did not observe herons feeding in the field to determine where they most often forage; therefore the choice of wetland types reflects potentially available habitat only. In order to measure wetlands, each topographic map was divided into 36 rectangles, measuring 1.25 ° latitude by 1.25 ° longitude. Within each rectangle, each type of wetland was measured using a digitizing tablet and the SigmaScan program. A computer program in dbase IV was used to calculate the area of different types of wetlands within 3, 5, and 10 km of each site. If the center point of the rectangle fell within the designated radius, all of the wetlands in the rectangle were included. Each wetland type at each distance (3, 5, and 10 km) was compared to colony size using linear regression analysis. In addition, mudflat area, marsh area, swamp area, and shoreline area were summed for each distance (3, 5, and 10 km), and then these variables were compared to colony size using linear regression analysis.

Random Spacing of Colonies

Previous studies have examined the distributions of heron colonies, in order to determine what influences colony spacing (Fasola and Barbieri 1978, Gibbs *et. al.* 1987). In order to find out more about the spacing of colonies in Virginia, two different tests were performed. The first test, MRPP, (Multiresponse Permutation Procedures, Biondini *et. al.*, 1988) is nonparametric and does not require a normal distribution or equality of variance. The test determines whether there is a significant difference in the distribution of two sets of data points, in this case active and null sites. The second test which tests the distribution of colonies versus null sites is the distance to nearest neighbors test. The distance from a null site or active site to the two nearest colony sites was measured. The mean of these distances was calculated, and a one-way ANOVA was performed to determine whether if colony sites and null sites are equally spaced. These tests provide information about the spacing of the colonies on the James and Chickahominy Rivers.

RESULTS

Sites

Thirty-four colonies were located along the James and Chickahominy River watersheds (Appendix B, Figure 1.). Number of nests in a colony ranged from 3 to 460. Sixteen colonies were located on the James River watershed, and eighteen colonies were located on the Chickahominy River watershed. Each site was categorized into one of three types of habitat: forested upland, forested hummock, and swamp. Bottomland hardwood swamps in Virginia are characterized by tree species such as bald cypress (*Taxodium distichum*), red maple (*Acer rubrum*), american sycamore (*Platanus occidentalis*), and green ash (*Fraxinus pennsylvanica*). Forested upland is characterized by mostly loblolly pine (*Pinus taeda*). Forested hummock can be made up of bald cypress or loblolly pine and usually borders a river, or is surrounded by water. Appendix D shows the tree species, obtained from aerial survey (B.D. Watts and M.A. Byrd, pers. comm.), that make up each colony. This table also shows that many nests were located in dead trees or snags. Since colonies were surveyed from the air and not on foot, it was not always possible to determine all of the tree species present in a colony site, therefore a designation of "hardwoods" indicates a bottomland hardwood swamp. Twenty-eight colonies (82.4%) were located in bottomland hardwood swamp habitat. Five colonies (14.7%) were located in forested hummocks and one colony was located in forested upland.

Thirty-four null sites were chosen randomly within the watershed of the James and Chickahominy Rivers (Appendix C, Figure 1.). Random latitude-longitude coordinates were generated by computer, and sites were kept as null sites if they lay within the watershed of either of the two rivers, and if they lay within a forested area. Sites that fell in fields, cleared land, or developed areas were not used. Twenty-one null sites were located in the James River watershed, and thirteen were located in the Chickahominy River watershed. In contrast with the active sites, 26 (76.5%) of the null sites were located in forested upland, 7 (20.6%) of the null sites were located in swamp, and 1 null site was located in forested hummock (Table 1). It should be noted that, in the case of null sites, forested upland may consist of more than just loblolly pine forests. Oak-hickory and mixed pine/hardwood forests are prevalent in the coastal plain of Virginia, and since these sites were not visited, the exact composition of the sites is not known.

Topographic and map variables-General

Eighty-three variables were measured around active sites and null sites to determine which variables might explain heron colony locations and also be good predictors of Great Blue Heron colony location (Appendix A). As noted earlier, these variables were divided into two subcategories, general habitat variables and human disturbance variables. Table 2 lists the percentage of active colony sites and null sites that had greater than 0 hectares or meters of a factor within 250m, 500m, and 1000m. Each general habitat variable listed was present around a higher percentage of active colony sites than null sites, but only the variables representing swamp and shoreline showed

Table 1

Habitat characterization of colony sites and null sites

	Swamp	Forested Upland	Forested Hummock
Colonies	82.4%	2.9%	14.7%
Null Sites	20.6%	76.5%	2.9%

Table 2

Presence or absence of habitat or disturbance factors within distances of 0-250m, 0-500m, and 0-1000m of active heron colony sites and random (null) sites in the James and Chickahominy River watersheds[a]

Factor	Active within 250m (%)	Null within 250m (%)	Active within 500m (%)	Null within 500m (%)	Active within 1 km (%)	Null within 1 km (%)
Marsh	23.5	8.8	29.4	17.7	41.2	32.4
Swamp	67.7	20.6**	67.7	32.4**	79.4	44.1**
Shoreline	44.1	17.7*	55.9	26.5*	82.4	67.7
Pines (PI)	14.7	35.3	26.5	41.2	52.9	70.6
Primary Roads (PR)	2.9	5.9	8.8	14.7	26.5	32.4
Secondary Roads (SR)	2.9	17.7*	14.7	35.3*	41.2	58.8
Light Roads (LR)	26.5	58.8**	73.5	79.4	100	97.1
Buildings (BU)	2.9	41.2**	41.2	64.7	88.2	94.1
Rural Development (RD)	2.9	26.5**	20.6	50.0*	73.5	91.2
Urban Development (UD)	2.9	11.8	11.8	17.7	26.5	38.2
Agriculture (AG)	14.7	32.4	47.1	52.9	82.4	79.4
Cleared Land (CL)	5.9	32.4**	29.4	52.9*	64.7	79.4

* = $P<0.05$, ** = $P<0.01$, values from chi-square tests, comparing active and null sites at each distance interval

a : all chi-square values and significance values are shown in Appendix G significant differences (Table 2, Appendix G). Swamp habitat and shoreline habitat were more prevalent around active sites than marsh habitat. Within 250m, 67.7% of active sites had some swamp present, while only 23.5% of active sites had marsh habitat. Within 1000m, 79.4% of active sites had swamp habitat, while only 41.2% of active sites had marsh habitat. Within 1000m, shoreline habitat was present around 82.4% of active sites. All general habitat variables listed (Table 2) were consistently present around more active sites than null sites.

Human disturbance factors were present around a greater number of null sites than active sites for all factors within 250m and 500m, but those variables representing pines, primary roads, urban development and agriculture did not show significant differences (Table 2, Appendix G). Within 1000m, light roads and area of agriculture were present around more active sites than null sites. The factors of primary roads, secondary roads, buildings, rural development, and urban development were present around only one colony site in each case within 250m. Light-duty roads were present more than any other factor within 250m of a colony (Table 2).

In order to determine which variables were most important in explaining colony location, univariate tests for significance and a multivariate discriminant analysis were performed. Because the sample size consisted of 68 sites, the number of variables had to be reduced in order to run a multivariate test. The first step in reducing the number of variables is to run normality tests on the variables, since an assumption of a discriminant analysis is that the variables be normally distributed.

Using both the Shapiro-Wilks and Lillifors tests for normality, I found that most variables had a non-normal distribution, with the exception of variables FO3, FO5, LR3, and SL8 (see Appendix A for explanation of variables). Natural log and square root transformations were run on the non-normal variables, but only 14 variables achieved a normal distribution (AG3, AG5, BU3, BU5, LR2, LR4, LR5, RD3, RD5, SW6, SW7, SW8, SL6, and SL7) Most of the variables that achieved normality were human disturbance variables. From the general habitat category, only those variables which summed swamp area and shoreline habitat area at farther distances (3, 5, and 10 km) achieved normality.

Univariate Tests

A series of univariate tests was run to determine whether the means of null sites were different than those of active sites. Mann-Whitney U tests were run on the non-normal variables and t-tests were run on the normally distributed variables. The means, standard deviations, and p-values for all variables are shown in Appendix E. Twenty-six of the 83 variables tested showed a significant difference between active and null sites. These univariate tests show that none of the marsh area, forested area, pine area, primary road length, or urban development area variables demonstrated a difference between active sites and null sites. Within 1000m, active sites had significantly more swamp area and less rural development area than null sites. For distances of 500m or less, active sites contained more shoreline length, fewer buildings, less area of cleared land, less length of light roads, and less length of secondary roads. For these variables at distances greater than 500m, there is no difference between active and null sites. At a distance of 250m, null sites had significantly more area of agricultural fields than did active sites. Figures 2-14 (pp. 35-62) show the comparison of means for active sites and null sites for all variables measured. The univariate tests highlight those categories of disturbance and habitat variables which are more important to heron colony location than others. Univariate tests cannot identify which of the significant variables can be used to best discriminate between active and null sites; therefore a discriminant analysis test is required.

Discriminant Model

Even though all variables are not normally distributed, if a discriminant model classifies the majority of the cases correctly, the assumption of normality may be justifiably violated. Because only 20 of the original set of 83 variables achieved normality, I considered all 83 original variables to be applicable for the discriminant analysis procedure. Twenty-six variables showed significance between active and null sites (see Appendix E). With a sample size of only 68 sites, the final discriminant model should have no more than 12-15 variables (G. Pendleton and J. Hatfield, NBS, pers. comm.). In order to eliminate more variables, the 26 significant variables were entered into a correlation matrix (Appendix F). Of the variables that were highly correlated (>0.40), the variable with the most significant difference between active sites and null sites was chosen to be included. Eight variables passed these criteria and were chosen for a discriminant analysis procedure (see Table 3).

Table 3

Variables used in discriminant analysis procedure

Variable Name	Variable Description
SW1	area of swamp within 250m
SL1	length of shoreline within 250m
AG1	area of shoreline within 250m
CL1	area of cleared land within 250m
BU1	number of buildings within 250m
FO1	area of forested land within 250m
RD5	area of rural development within 1 km
SR4	length of secondary roads within 500m

In order to test the validity of the model and the predictive value of the included variables, a discriminant function was run on 50 randomly selected sets of sites, each consisting of approximately 75% of the cases. Two or three variables were usually included in the model, before selection stopped due to the low F-values of the remaining variables (Table 4). None of the variables entered into the model every time. SW1 (swamp area) entered 47 times, RD5A (rural development area) entered 37 times, and SL1 (shoreline length) entered 20 times. Two variables never entered the model (FO1 and AG1). Excluding the two variables that did not enter the model, the remaining 6 variables were left in the model. It was apparent from further analysis that removing any of these remaining six variables would not improve the model, and might even result in lower classification rates. To further evaluate the model with respect to the six-variable set, six additional runs were performed, each with one variable at a time left out, and the classification rates were examined from these runs (see Table 5). At this point, variables BU1 and SR4 were removed because it was apparent that they did not contribute significantly to the model.

The final discriminant model consisted of four variables: SW1, RD5, SL1, and CL1, i.e., swamp area. rural development area, shoreline length, and cleared land respectively. This analysis produced a classification rate of 77.94%. Discriminant scores ranged from -3.5911 to 1.0485 for null sites and -1.3836 to 3.7756 for active sites.

The final test of the discriminant model is to determine whether the model can accurately classify sites that are unknown. Twenty "holdout runs" were performed. In each run, a model was generated using a random sample of approximately 75% of the

Table 4

Results of a discriminant analysis of 50 randomly selected subsets: Loading frequencies and mean ranks of variables

Variable	N (freq)	Mean Rank
SW1	47	1.47
RD5A	37	1.62
SL1	20	2.40
CL1	15	2.93
SR4	9	2.11
BU1	1	1.00
FO1	0	0.00
AG1	0	0.00

Table 5

Classification rates of discriminant model when one variable is left out of each run in sequence

Variable left out	Misclassified Sites			Classification Rate
	Null	Active	Total	
--------------	7	8	15	77.94%
SW1	8	9	17	75.00%
RD5A	6	12	18	73.53%
SL1	11	10	21	69.12%
CL1	8	9	17	75.00%
BU1	7	8	15	77.94%
SR4	7	8	15	77.94%

cases. The equation from each model was used to calculate discriminant scores and classify the remaining approximately 25% of the cases. This final step showed that this model does not perform well over a wide range of cases. Classification rates ranged from 33.3%- 84.6% (see Table 6). A total of 332 cases was withheld from the 20 runs, and the model classified on average 52.4% of these cases correctly as an active or null site. There was some discrepancy in this classification rate. For all 20 runs combined, the test classified an average of 70.3% of active sites correctly and 29.7% of null sites correctly. Because the correct classification rate for null sites was so low, it appears that this discriminant model is not a stable predictor of locations that would be suitable for Great Blue Heron breeding colonies.

Distance to Nearest Factor

There were 9 variables that measured the distance to the nearest human disturbance factor from each site. These variables were not normally distributed, and could not be transformed using natural log or square-root transformations. Therefore, Mann-Whitney U tests were run on these variables to test whether there were any significant differences between active and null sites. All human disturbance factors were farther, on average, from active sites than from null sites. Buildings, areas of cleared land, light roads, rural development, and secondary roads were significantly farther from active sites than from null sites (Table 7, Figure 15., p.61). There were no significant differences between active and null sites in the distances to agriculture, areas of pines, primary roads, and urban development areas.

Table 6

Final accuracy: Classification results for the 20 holdout runs of discriminant analysis with maximum of four variables

Run	Withheld		Misclassified		Total misclassified	Classification rate (%)
	null	active	null	active		
1	10	6	4	3	7	56.25
2	7	9	6	4	10	37.50
3	8	7	8	0	8	46.67
4	11	7	4	3	7	61.11
5	6	8	5	4	9	35.71
6	14	8	14	0	14	36.36
7	7	10	6	0	6	64.71
8	11	12	12	0	12	47.83
9	4	8	0	5	5	58.33
10	5	10	3	0	3	80.00
11	2	7	2	1	3	66.67
12	9	7	8	4	12	25.00
13	8	5	1	1	2	84.62
14	6	10	5	0	5	68.75
15	9	11	1	3	4	80.00
16	10	6	9	3	12	25.00
17	9	9	1	2	3	83.33
18	11	10	9	4	13	38.10
19	10	11	8	6	14	33.33
20	5	9	5	4	9	35.71
Totals	162	170	111	47	158	52.41

Table 7

Mean distances[a] from colony sites or null sites to nearest disturbance factor

Variable	Mean Active sites	Standard deviation	Mean Null Sites	Standard deviation	P-value[b]
AG6	2.85	1.42	2.50	1.52	0.27
BU6	3.18	1.19	2.29	1.38	0.004**
CL6	3.62	1.28	2.65	1.55	0.007**
LR6	2.00	0.78	1.74	1.14	0.04*
PI6	3.74	1.58	3.00	1.71	0.06
PI6	4.41	1.10	4.27	1.26	0.60
RD6	3.59	1.16	2.53	1.26	0.001**
SR6	4.21	1.15	3.44	1.58	0.04*
UD6	4.38	1.16	4.09	1.42	0.31

a: Values: 1 = 0-250m, 2 = 251-500m, 3 = 501-750m, 4 = 751-1000m, 5 = over 1000m
b: all variables tested with Mann-Whitney-U tests; * P = <0.05, **P = <0.01

Wetland Area vs. Size of Colonies

To determine whether the area of certain types of wetlands affects the size of heron colonies, correlation and regression analysis were used. The number of nests in a colony was not highly correlated with any of the individual wetland variables ($r < 0.40$, see Appendix A for explanation of variables). There was a significantly positive correlation, however, between colony size and total area of wetlands within 3 and 5 km ($r = .52$ for Add3, and $r = .46$ for Add5). Simple linear regression was run for each wetland variable separately to see if there was a linear relationship between that variable and colony size. Several variables were natural log or square-root transformed to achieve a normal distribution. Results of these regressions indicated that none of the individual wetland variables, by themselves, could explain a major proportion of the variation in colony size. The variables that explained the most variation individually were SL6 ($r^2 = 0.17$), SL7 ($r^2 = 0.12$), SW6 ($r^2 = 0.09$), SW7 ($r^2 = 0.09$), and ST3 ($r^2 = 0.08$), representing shoreline habitat area at distances of 3 and 5 km, swamp area at distances of 3 and 5 km, and stream length at a distance of 3 km. When these variables were combined in a multiple regression, only 21% of the variation in colony size was explained. As a result, colony size was compared to the three summed variables (Add3, Add5, and Add10), and another regression was run. These three variables together explained much more variation in colony size ($r^2 = 0.43$). From beta values, it seems that the most influential variable with respect to colony size is Add3, or the summed wetlands within 3 km of a colony site.

Distribution of Colonies

In order to examine whether there was any difference in the distributions of colony sites and null sites, the latitude and longitude coordinates for each site were transformed into x and y coordinates, and an Multiresponse Permutation Procedures (MRPP) test was performed. There was no significant difference between the distribution of active sites and the distribution of null sites (Table 8).

The distance from each active site and null site to the two nearest active colony sites was measured and the mean of these distances calculated. The mean of these two measurements is the average nearest neighbor distance for each site. These mean distances were compared to see if there was any difference between active sites and null sites. The mean distance from an active site to the two nearest active sites was 5.44 km (± 2.38). The mean distance from a null site to the two nearest active sites was 6.08 km (±2.70). These variables were not normally distributed, and were transformed using a natural log transformation. After transformation, a one-way ANOVA was run, and no significant difference was found between the active and null sites (P=0.458). Not only was no difference found between active and null sites, but the mean distance to another site was somewhat greater for null sites (Table 8).

Table 8

Tests for spatial differences between heron colonies and null sites (means ±1 SD)

	Active Sites	Null Sites	Test statistic	P- value
MRPP Average Distance (km)[a]	21.50	21.18	-0.99	0.13
Distance to nearest active colony site (km)[b]	5.44± 2.38	6.08± 2.70	0.55	0.46

a: Multiresponse Permutation Procedure; (Biondini *et.al.* 1988)

b = one-way ANOVA results (f-value), using distances from colony or null sites to the two nearest colony sites

Figure 2. Mean area of pine stands for active and null sites at five distance intervals from a site

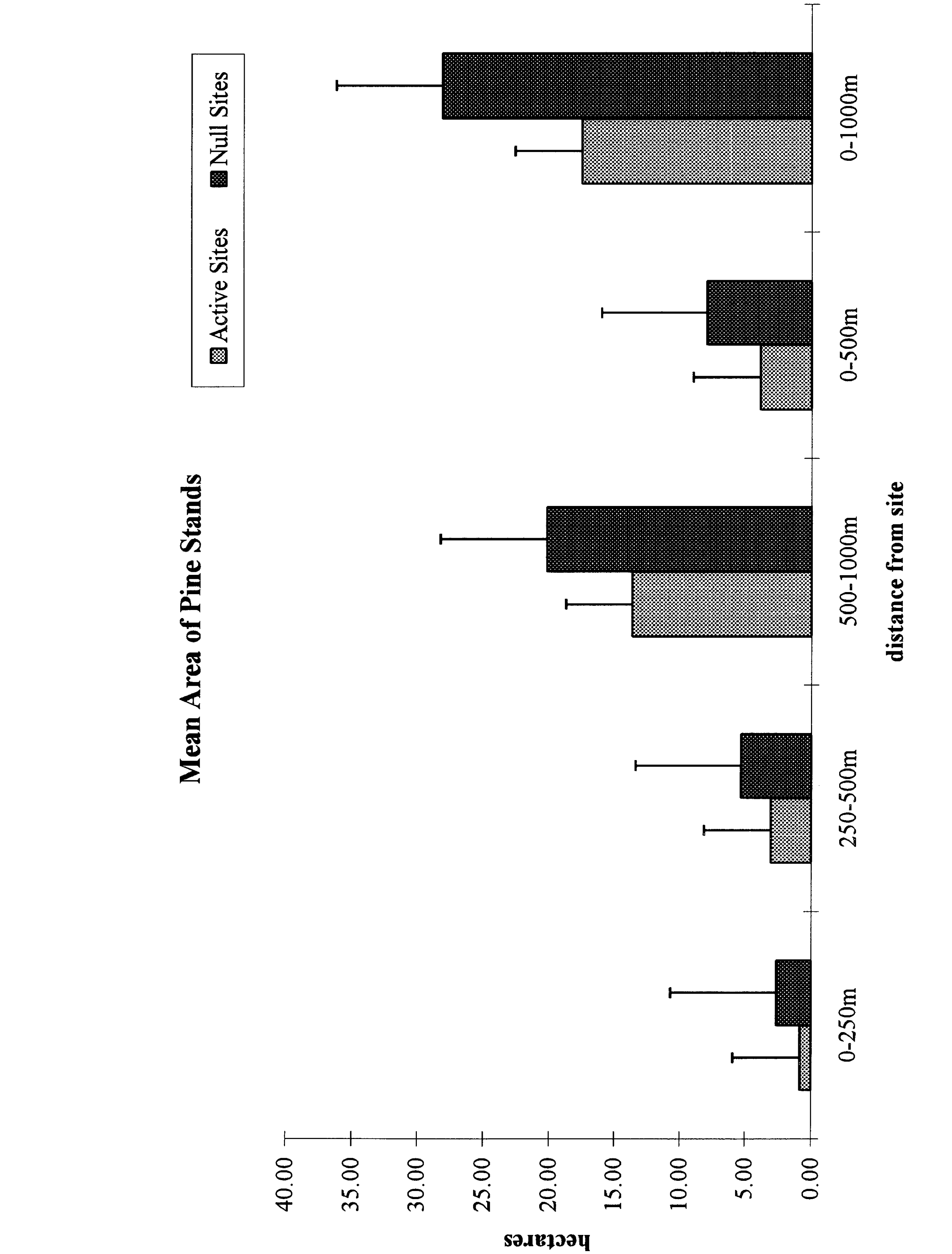

Mean Area of Pine Stands
Active Sites
Null Sites
hectares
40.00
35.00
30.00
25.00
20.00
15.00
10.00
5.00
0.00
0-250m
250-500m
500-1000m
0-500m
0-1000m
distance from site

Figure 3. Mean length of primary roads for active and null sites at five distance intervals from a site

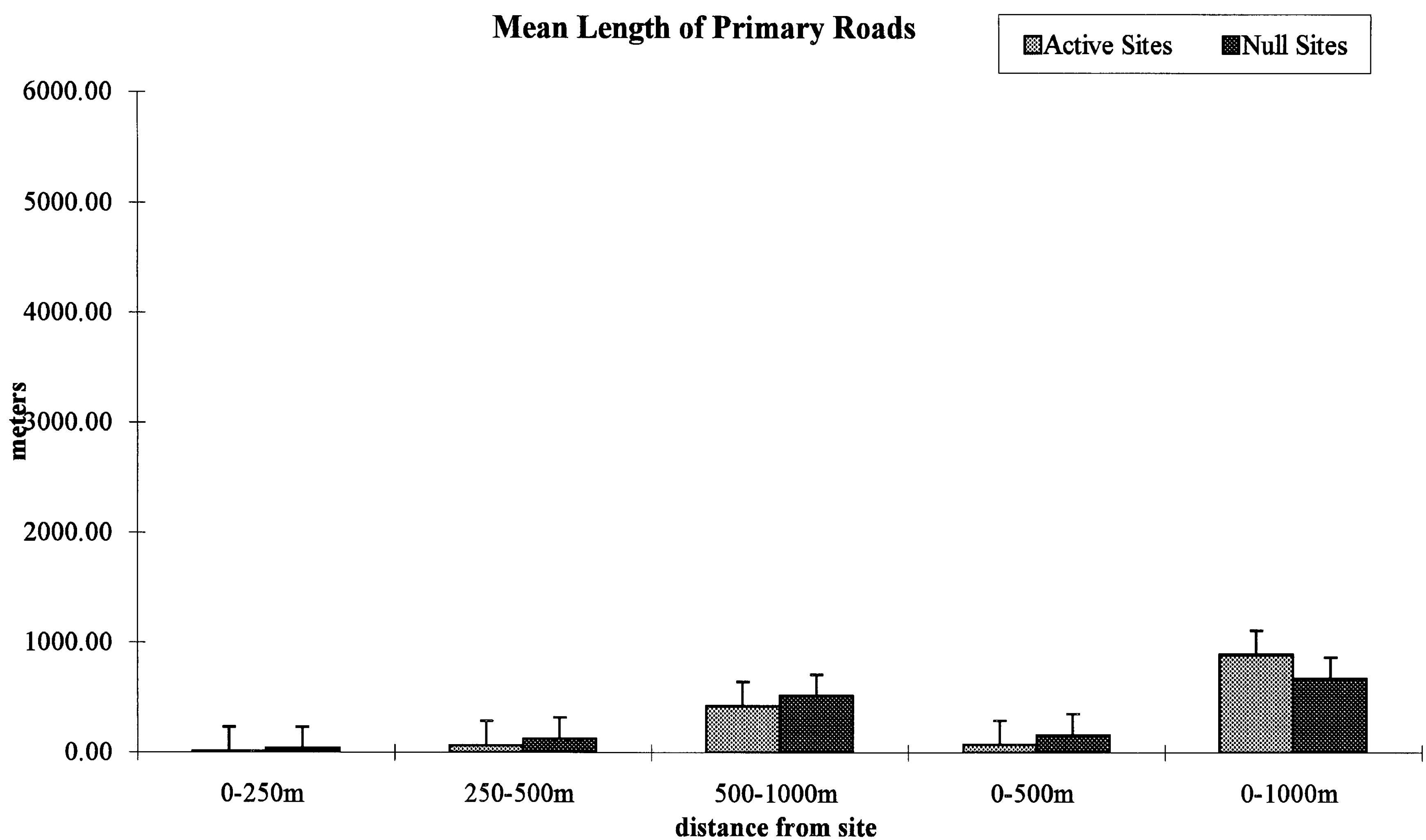

Mean Length of Primary Roads
Active Sites
Null Sites
6000.00
5000.00
4000.00
3000.00
2000.00
1000.00
0.00
meters
0-250m
250-500m
500-1000m
0-500m
0-1000m
distance from site

Figure 4. Mean length of secondary roads for active and null sites at five distance intervals from a site

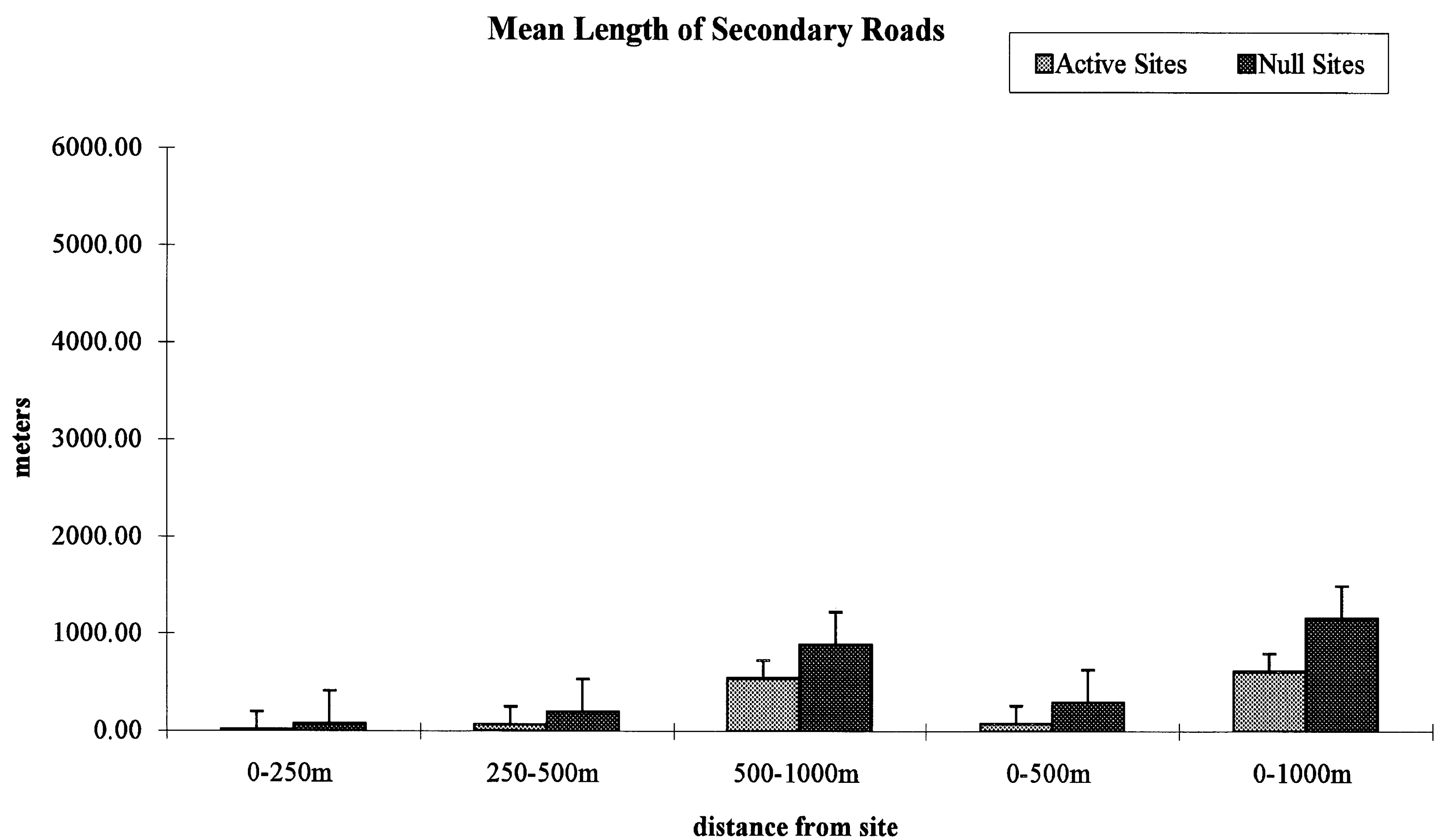

Mean Length of Secondary Roads
Active Sites
Null Sites
6000.00
5000.00
4000.00
3000.00
2000.00
1000.00
0.00
meters
0-250m
250-500m
500-1000m
0-500m
0-1000m
distance from site

Figure 5. Mean length of light duty roads for active and null sites at five distance intervals from a site

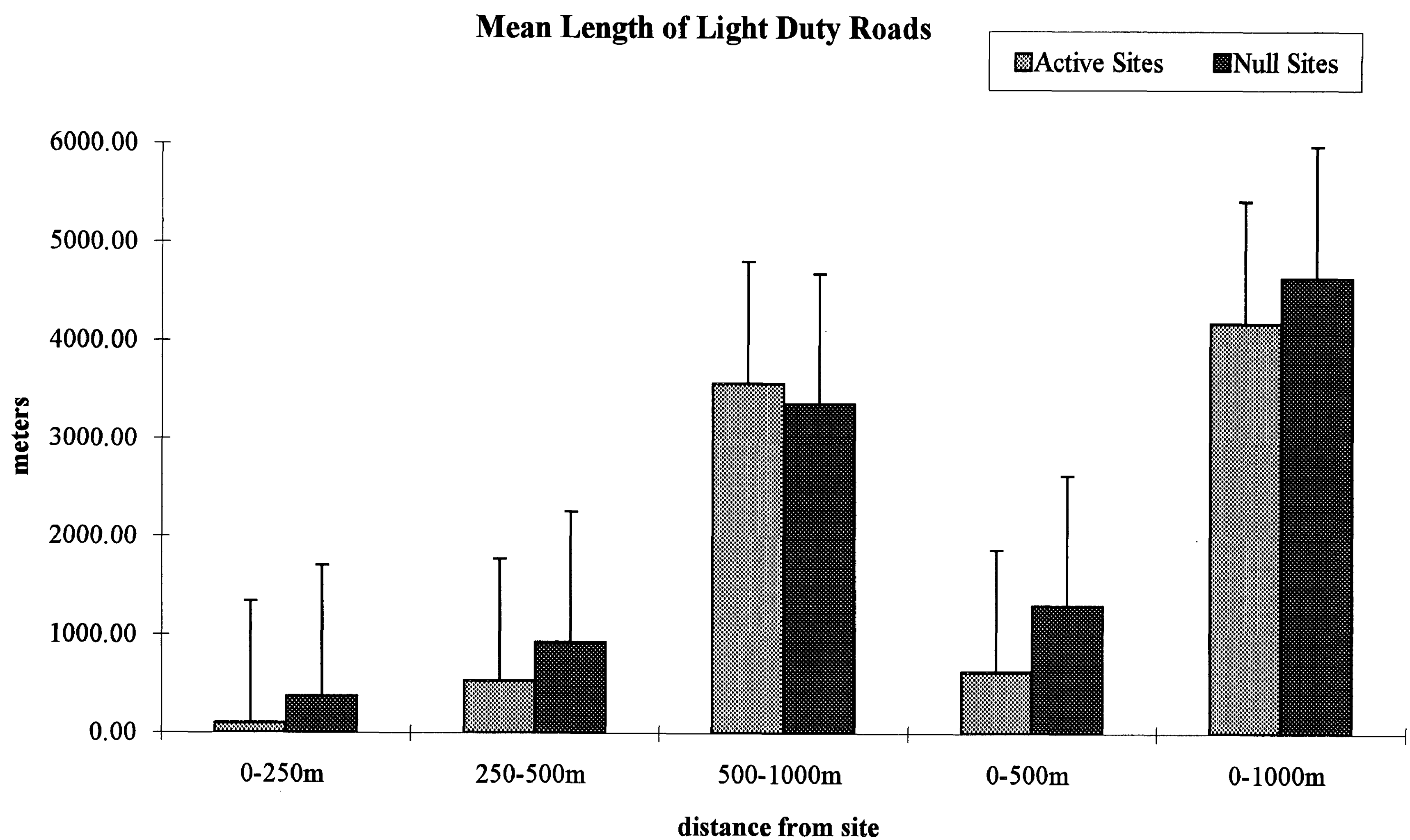

Mean Length of Light Duty Roads
Active Sites
Null Sites
meters
6000.00
5000.00
4000.00
3000.00
2000.00
1000.00
0.00
0-250m
250-500m
500-1000m
0-500m
0-1000m
distance from site

Figure 6. Mean number of buildings for active and null sites at five distance intervals from a site

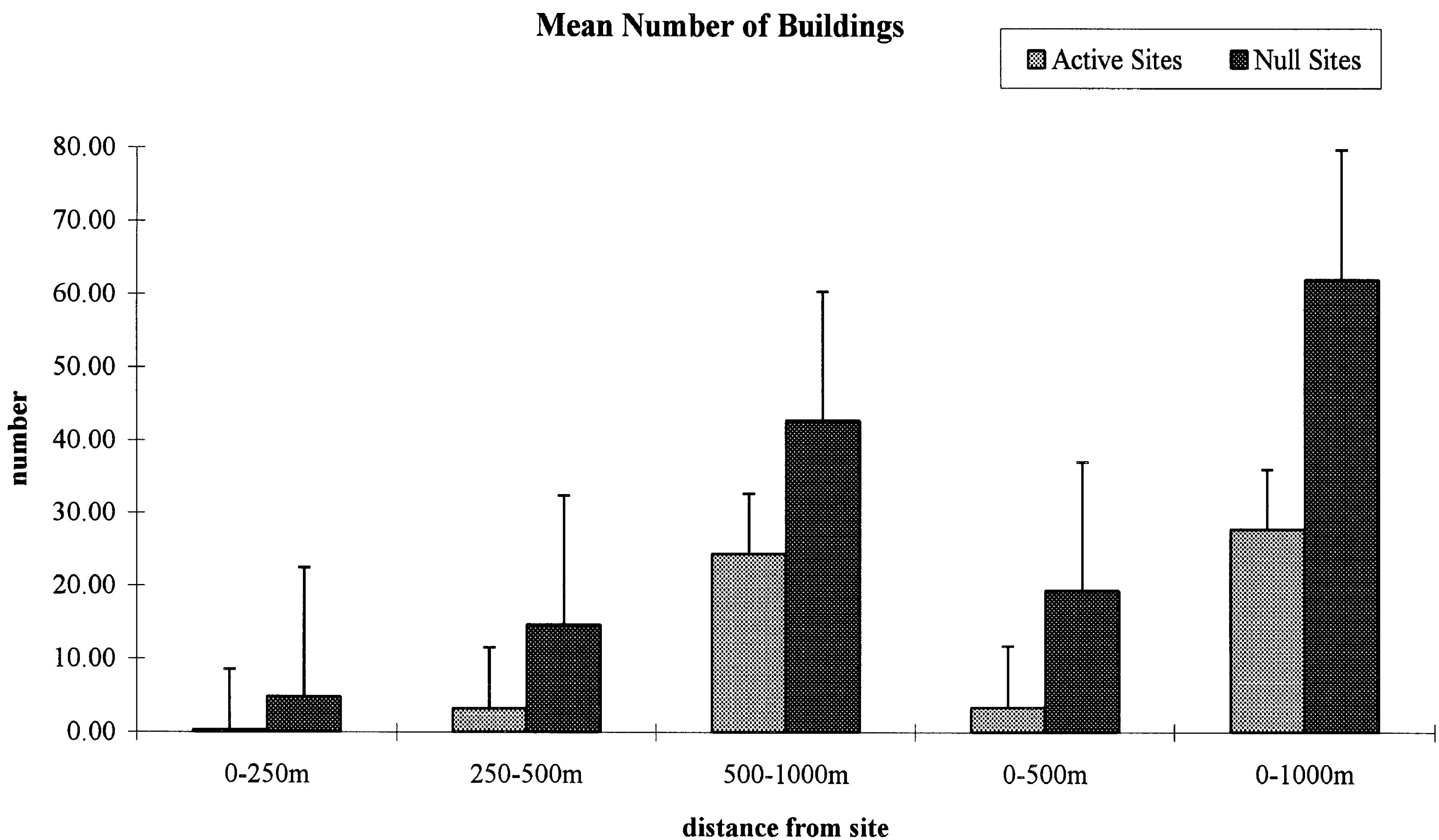
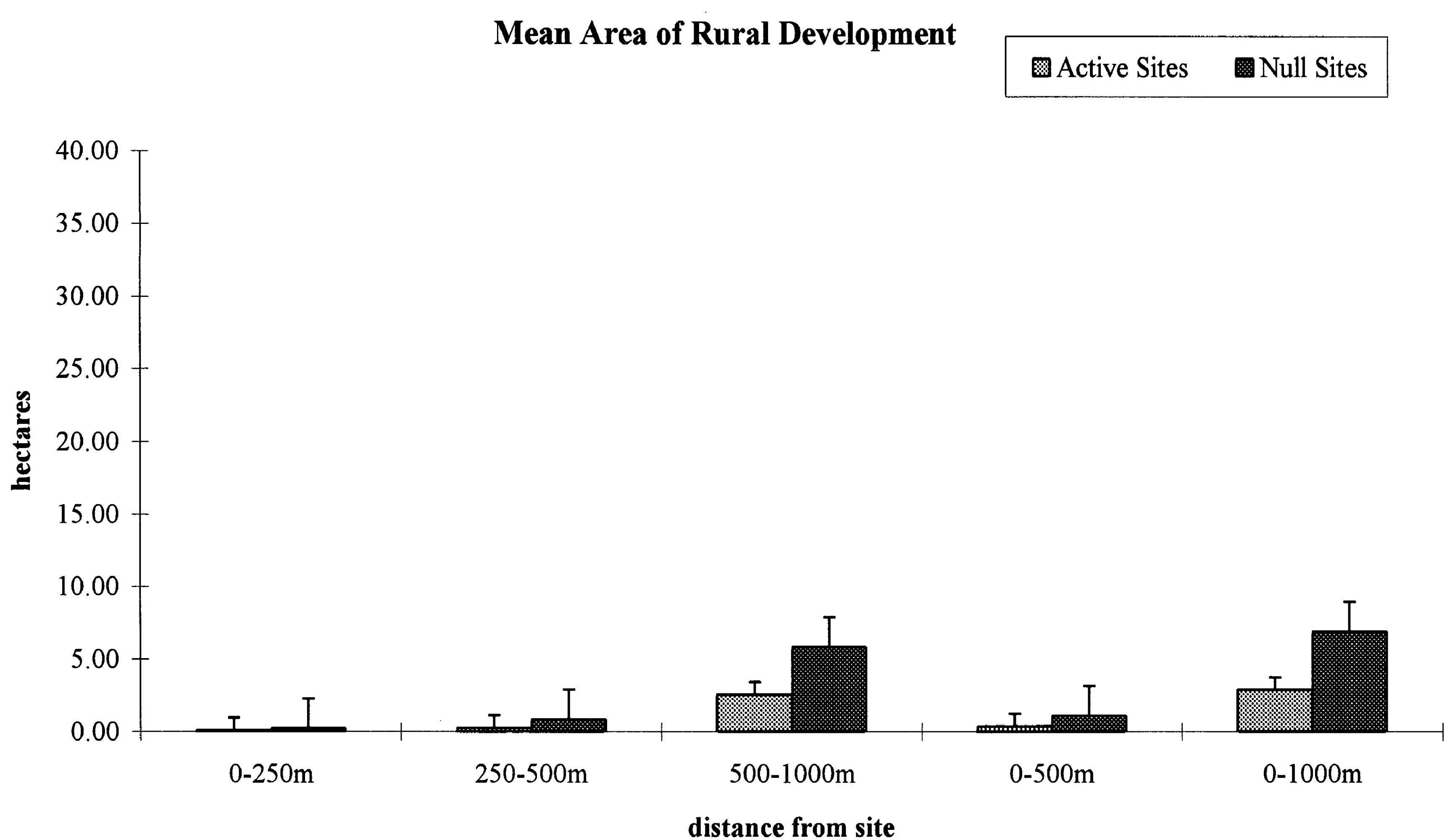

Mean Number of Buildings
Active Sites
Null Sites
80.00
70.00
60.00
50.00
40.00
30.00
20.00
10.00
0.00
number
0-250m
250-500m
500-1000m
0-500m
0-1000m
distance from site

Figure 7. Mean area of rural development for active and null sites at five distance intervals from a site



Mean Area of Rural Development
Active Sites
Null Sites
hectares
40.00
35.00
30.00
25.00
20.00
15.00
10.00
5.00
0.00
0-250m
250-500m
500-1000m
0-500m
0-1000m
distance from site

Figure 8. Mean area of urban development for active and null sites at five distance intervals from a site

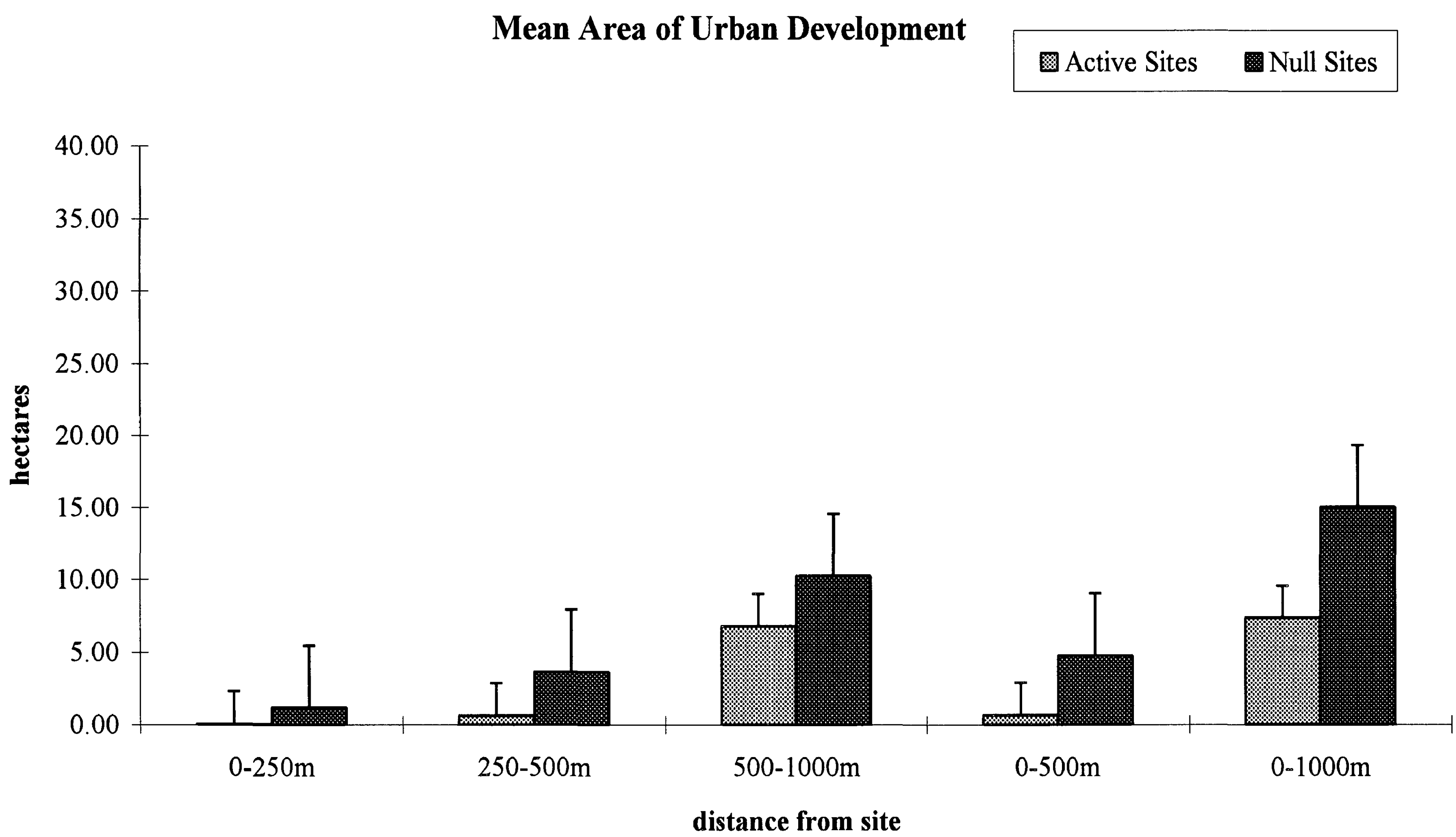
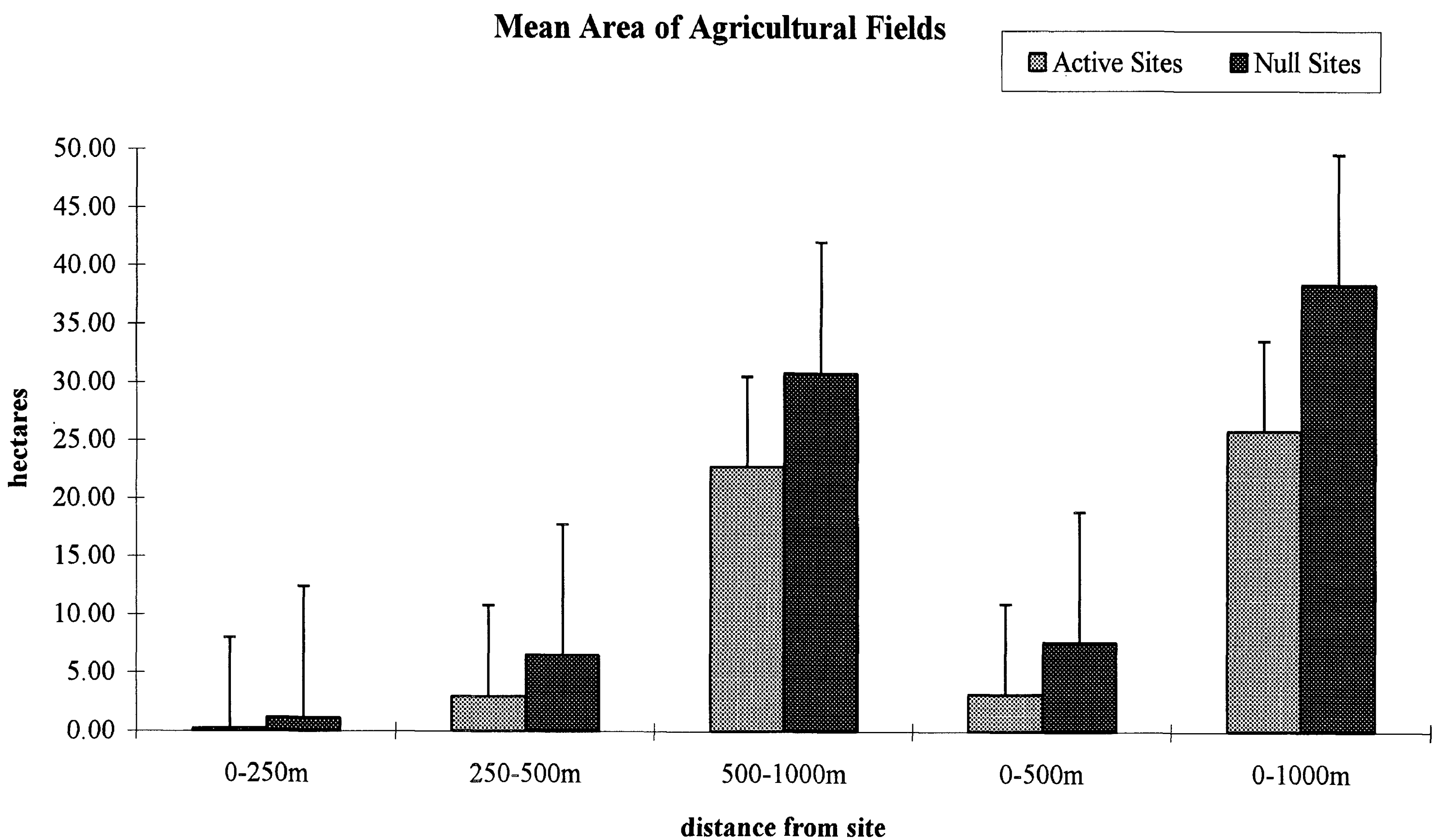
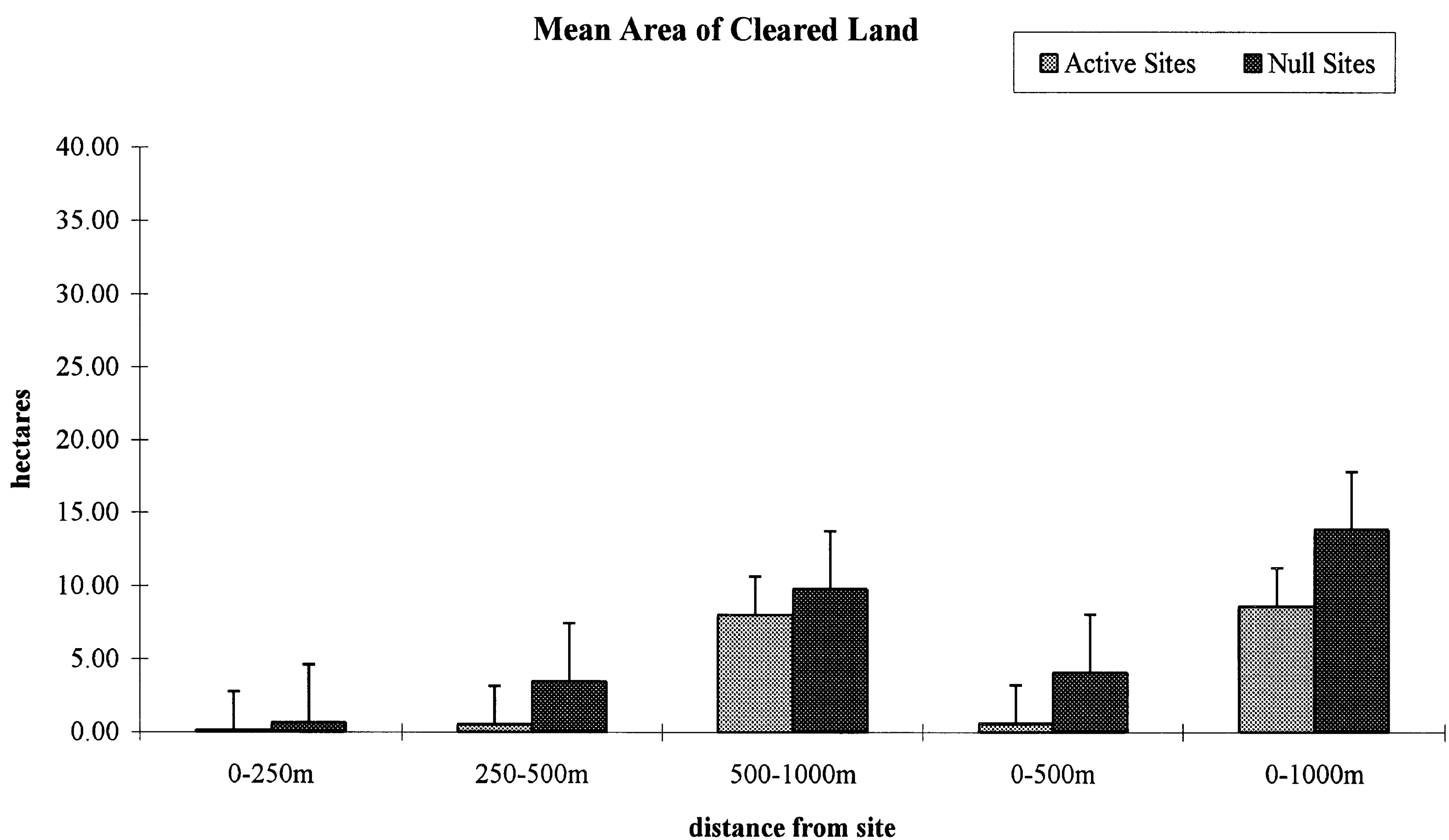

Mean Area of Urban Development
Active Sites
Null Sites
hectares
40.00
35.00
30.00
25.00
20.00
15.00
10.00
5.00
0.00
0-250m
250-500m
500-1000m
0-500m
0-1000m
distance from site

Figure 9. Mean area of agricultural fields for active and null sites at five distance intervals from a site



Mean Area of Agricultural Fields
Active Sites
Null Sites
hectares
50.00
45.00
40.00
35.00
30.00
25.00
20.00
15.00
10.00
5.00
0.00
0-250m
250-500m
500-1000m
0-500m
0-1000m
distance from site

Figure 10. Mean area of cleared land for active and null sites at five distance intervals from a site



Mean Area of Cleared Land
Active Sites
Null Sites
hectares
40.00
35.00
30.00
25.00
20.00
15.00
10.00
5.00
0.00
0-250m
250-500m
500-1000m
0-500m
0-1000m
distance from site

Figure 11. Mean area of marsh habitat for active and null sites at five distance intervals from a site

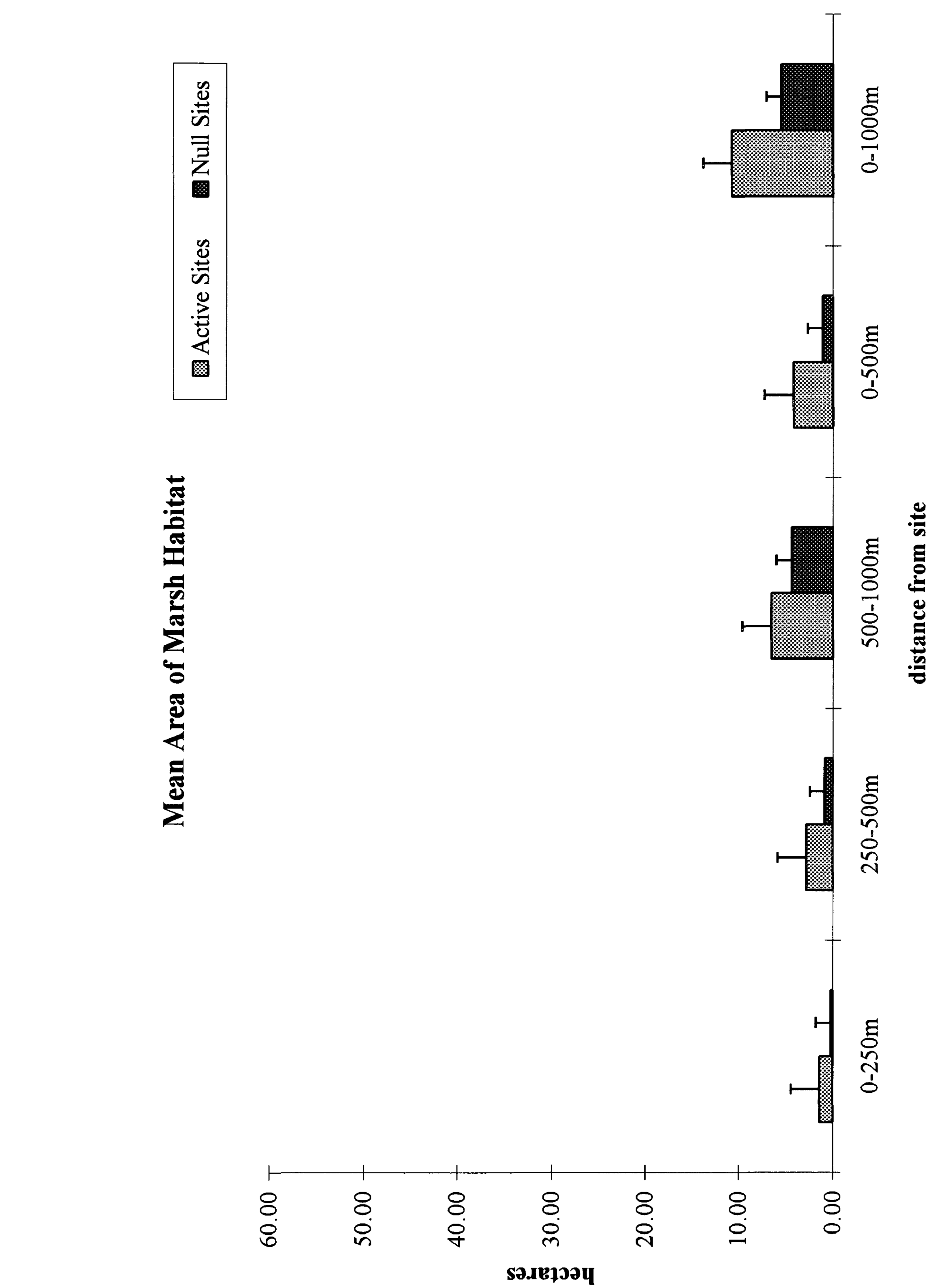

Mean Area of Marsh Habitat
Active Sites
Null Sites
hectares
60.00
50.00
40.00
30.00
20.00
10.00
0.00
0-250m
250-500m
500-1000m
0-500m
0-1000m
distance from site

Figure 12. Mean area of swamp habitat for active and null sites at five distance intervals from a site

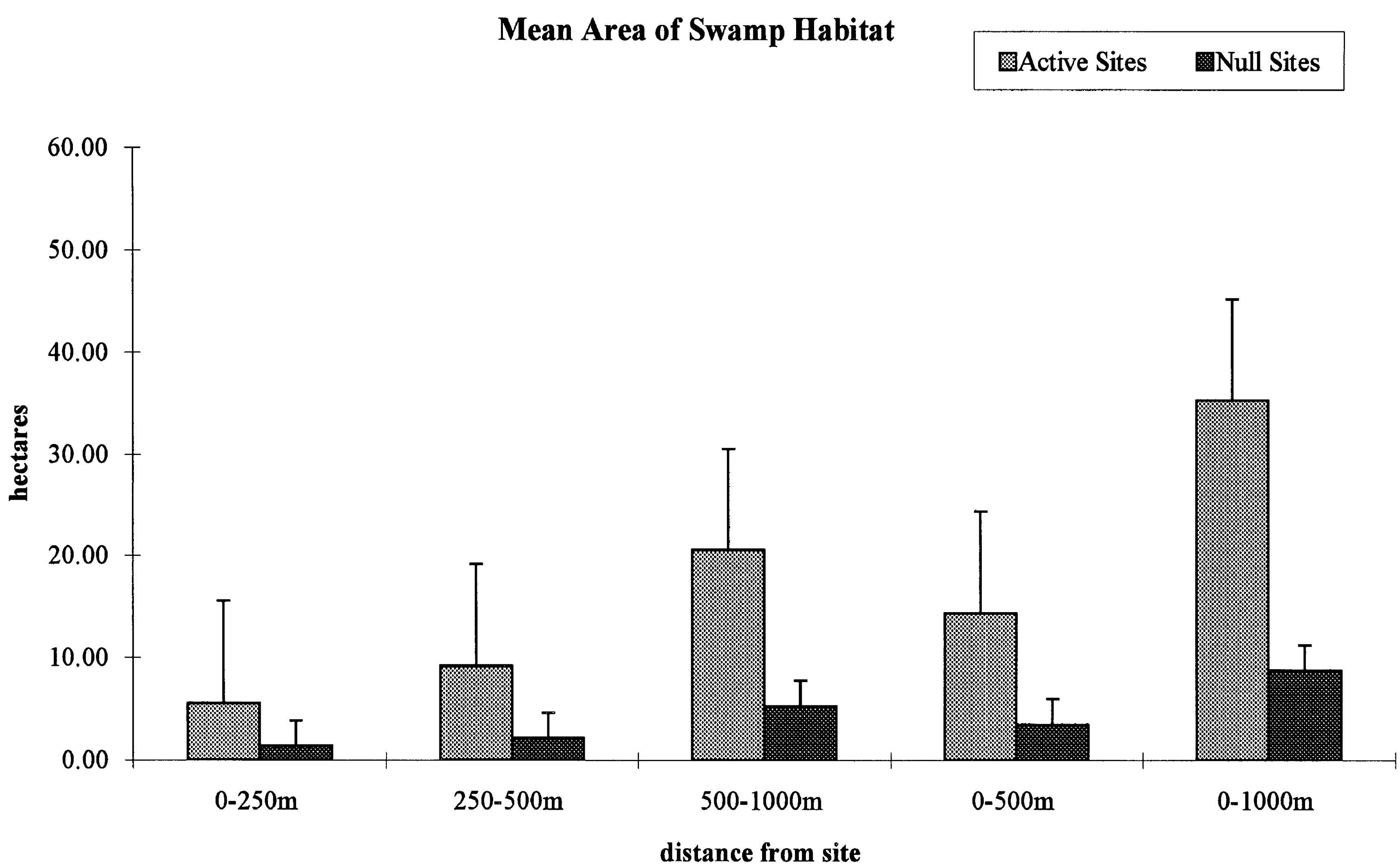

Mean Area of Swamp Habitat
Active Sites
Null Sites
hectares
60.00
50.00
40.00
30.00
20.00
10.00
0.00
0-250m
250-500m
500-1000m
0-500m
0-1000m
distance from site

Figure 13. Mean length of shoreline habitat for active and null sites at five distance intervals from a site

Mean Length of Shoreline Habitat

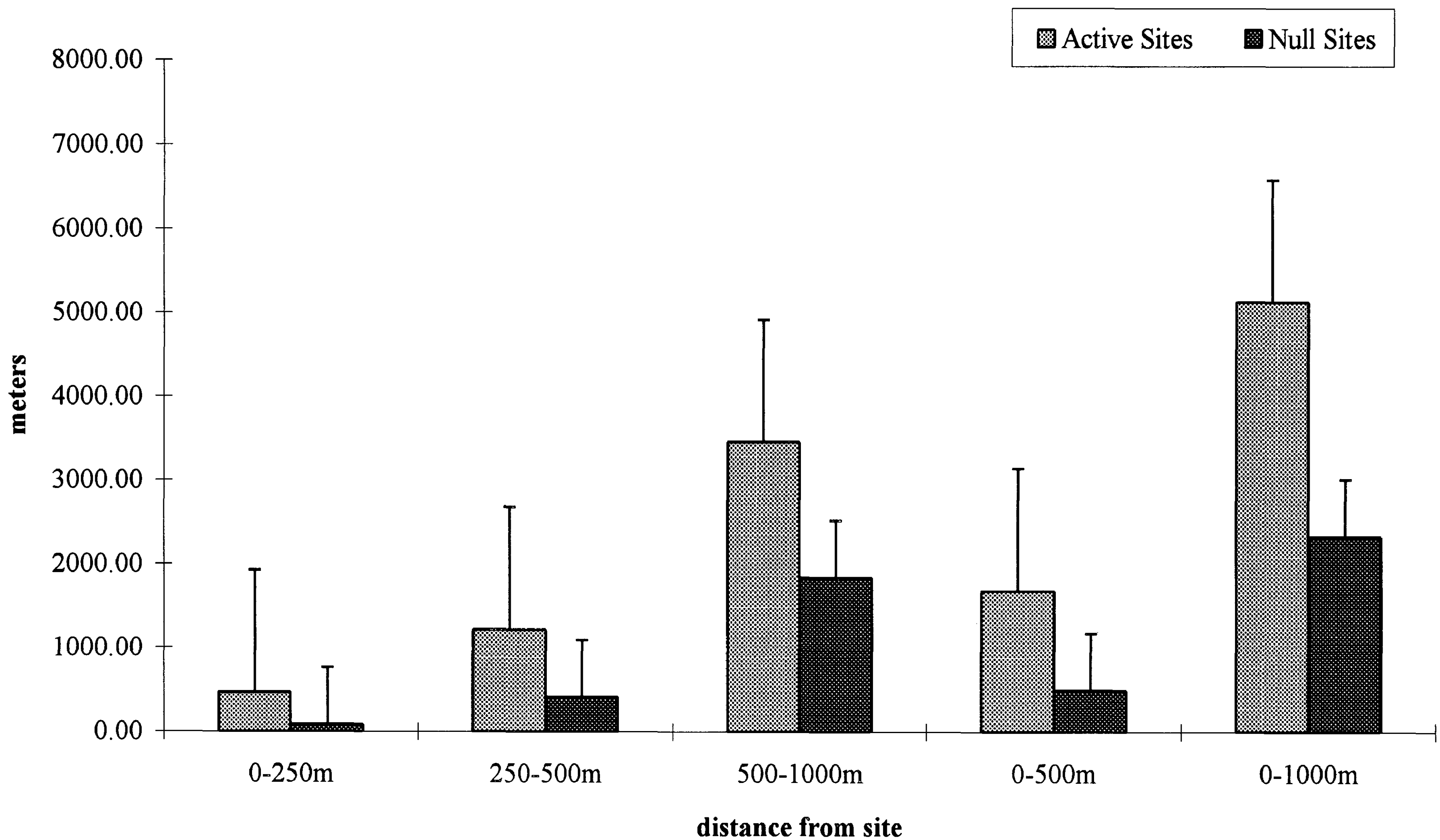


Figure 14. Mean area of forested habitat for active and null sites at five distance intervals from a site

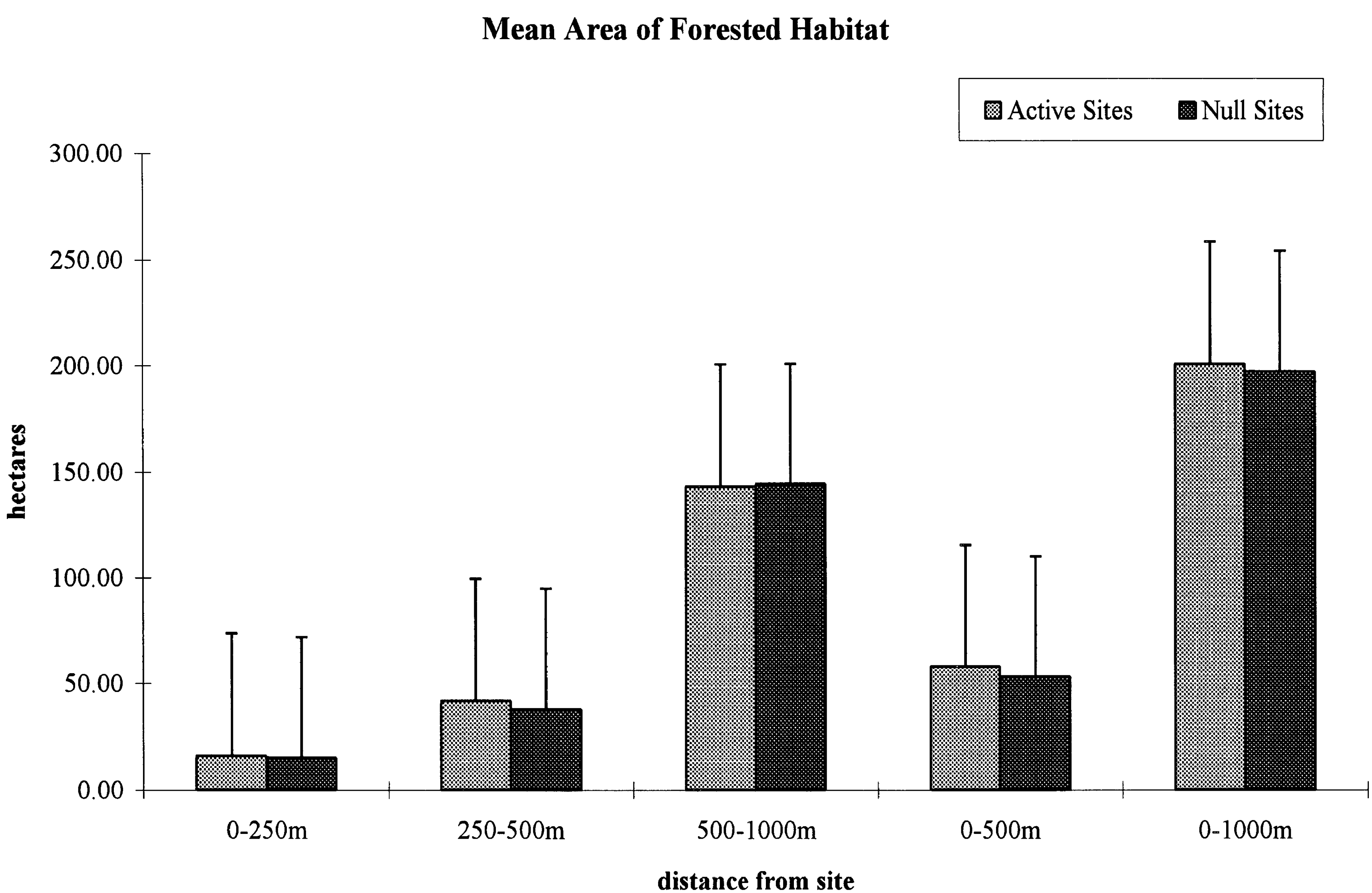
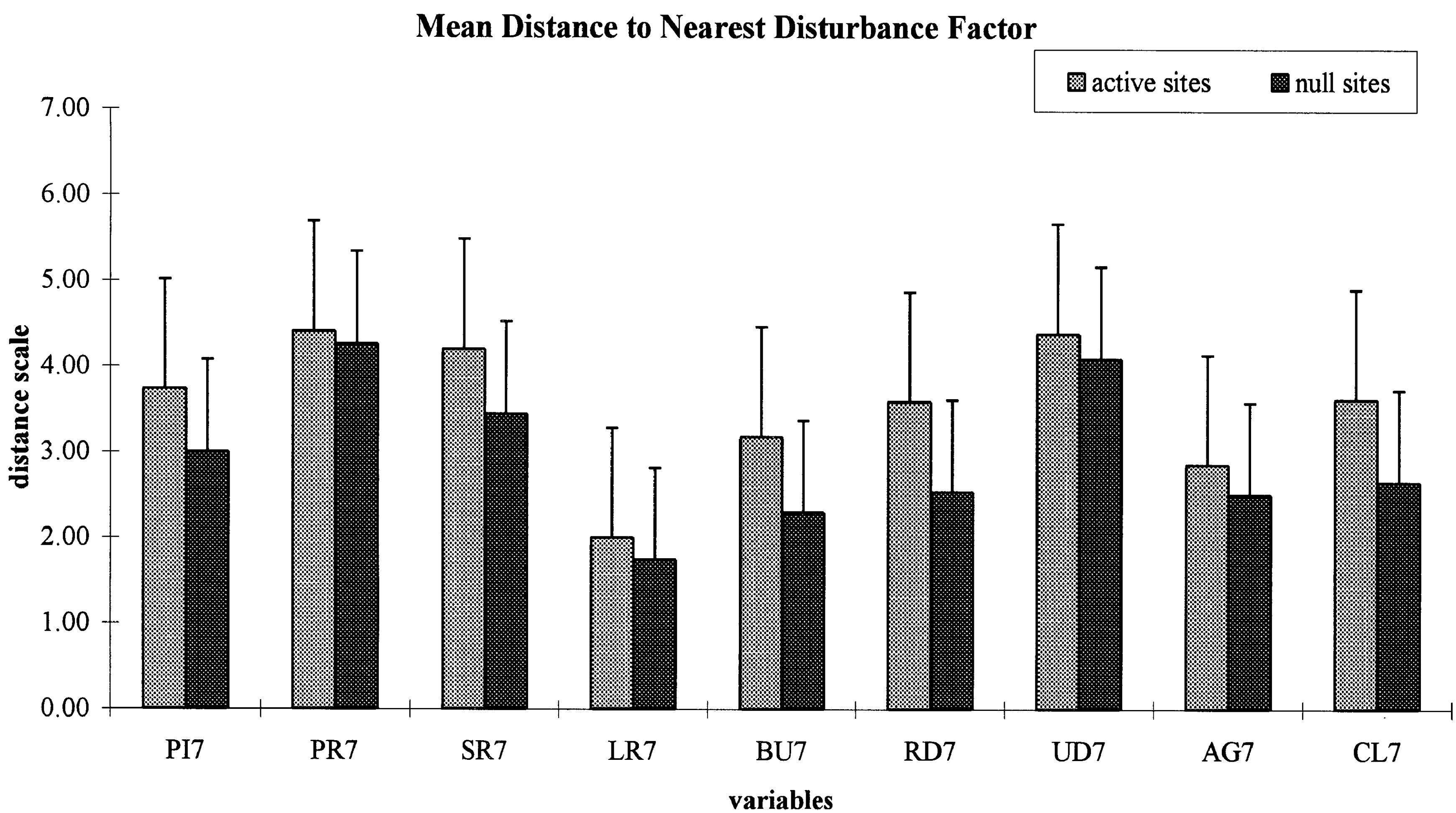

Mean Area of Forested Habitat
Active Sites
Null Sites
300.00
250.00
200.00
150.00
100.00
50.00
0.00
hectares
0-250m
250-500m
500-1000m
0-500m
0-1000m
distance from site

Figure 15. Mean distance to the nearest disturbance factor measured for all active sites and null sites; variables represent each type of disturbance measured; distance scale: (1) 0-250m; (2) 251-500m; (3) 501-750m; (4) 751-1000m; (5) over 1000m


Mean Distance to Nearest Disturbance Factor
active sites
null sites
7.00
6.00
5.00
4.00
3.00
2.00
1.00
0.00
distance scale
PI7
PR7
SR7
LR7
BU7
RD7
UD7
AG7
CL7
variables

DISCUSSION

The overall goal of this study was to investigate what determines Great Blue Heron colony size and colony locations in the coastal plain of Virginia. I attempted to focus on factors that have been shown to influence colony size and location in other areas. Studies that have investigated influences on heron colony size and location have many times focused exclusively on microhabitat measurements taken in the colonies themselves, such as tree species, tree height, diameter of tree, etc. (e.g. Gray *et.al.* 1980, Gibbs *et. al.* 1987). I wanted to determine whether variables measured on topographic maps and aerial photographs, instead of field-oriented measurements, can be used to distinguish heron colony sites from random (or null) sites, and whether these variables can be used to predict if a site would be suitable for a Great Blue Heron colony.

From the measurements taken on the maps and photographs, it is clear that several types of factors found within 1000m of a site are important to heron colony location in the coastal plain of Virginia. Of the general habitat variables measured, swamp habitat was the most important to colony location, given that the mean area of swamp was significantly greater around colony sites than null sites up to distances of 1000m from a site. Shoreline habitat is also important in distinguishing colony sites from null sites, but only out to 500m from a site. The amount of forested land measured around active and null sites was essentially equal, but this may be because there is an abundance of forested land in the study area. The lack of significance in this variable does not mean that forested area is not important to colony location. Gibbs *et. al.* (1987) found that degree of forestation was important in distinguishing null sites from colony sites in Maine.

The only general habitat variable that did not affect colony location was area of marsh habitat. Null sites had less marsh area within all distances when compared to active sites, but these differences were not significant. Although tidal and estuarine area has been shown to influence the size of colonies (Werschkul *et. al.* 1977, Gibbs *et. al.* 1987), it is not clear that the presence of marsh habitat within 1000m or less of a site is necessarily an influence on colony location on these two river systems in Virginia. Most colonies located on the Chickahominy River have no marsh habitat in their vicinity, and only 41.2% (see Table 2) of all colonies located have marsh habitat present within 1000m of the site. In contrast, 79.4% of all colonies located on the two rivers have some amount of swamp habitat present within 1000m of the site.

While swamp and shoreline habitat within close proximity to a colony affect colony location, the same is not true at greater distances. Within 3, 5, and 10 km of a site, colony sites had slightly greater (not significantly) areas of marsh, swamp, and shoreline habitat, and greater lengths of streams than null sites. At a distance of 10 km, null sites had a slightly greater (not significantly) area of mudflats than active sites. It is evident from these results that these types of topographic factors are important to Great Blue Heron colony locations only within 1000m of a site. The results of the univariate tests show that swamp habitat and shoreline habitat variables measured from topographic maps can be used to distinguish heron colony sites from null sites in the coastal plain of Virginia, and thus predict what is unsuitable habitat, but not necessarily to predict which sites would serve as suitable habitat for Great Blue Herons.

Human disturbance can affect the locations of Great Blue Heron colonies (Werschkul *et. al.* 1976, Parker 1980), and several human disturbance factors appear to affect colony location in Virginia. Disturbance variables measured from aerial photographs can be used to distinguish active colony sites from null sites. Forty-five human disturbance variables were measured for active and null sites, and for 43 of these variables, colony sites were less "disturbed" than were null sites. However, not all of these differences were significant. Within 500m of a site, numbers of buildings, area of cleared land, and lengths of secondary and light roads showed significant differences between active and null sites, and therefore are important to colony location. Differences in rural development area were significant and important to colony location out to 1000m from a site. Differences in area of agricultural fields were significant and important out to 250m from a site.

Even though null sites were surrounded by greater areas of urban development and greater lengths of primary roads, these differences were not statistically significant. Urban development and primary roads rarely were present around either active or null sites, and therefore the power to test for differences was minuscule. It is clear from other studies (e.g., Parker 1980) that these factors can affect Great Blue Heron colonies.

Areas of pine stands were slightly higher (not significantly) around null sites than active sites. The reason that areas of pines were measured in this study was because Virginia has a substantial timber industry and pine stands represent possible future logging disturbances. Other studies have shown that logging presents a threat to Great Blue Heron colonies (e.g. Werschkul *et. al.* 1976). Specifically in Virginia, eight years of monitoring Great Blue Heron colonies has shown that logging activity can decrease colony size or cause complete colony abandonment (Beck 1991). Since it was difficult to determine from photographs how old the trees in these areas were, it is not known whether these pine stand areas had any influence on colony location at the time of colony establishment. For the purposes of this study, area of pine (without knowledge of recency of disturbance) is not a useful variable in distinguishing heron colony sites from those without herons.

Swamp habitat, shoreline habitat, buildings, secondary and light roads, rural development, cleared land, and agriculture appear to be important to Great Blue Heron colony location in the coastal plain of Virginia. Although these variables can be used to distinguish active sites from null sites, it is not clear which of these variables has the most influence on colony location, and which (if any) can be used as predictors of a good potential future colony site. Discriminant analysis was used to determine this information, and the final model identified four variables as the best predictors. These variables were swamp habitat within 250m (SW1), shoreline habitat within 250m (SL1), rural development area within 1000m (RD5), and cleared land area within 250m (CL1). Unfortunately, the model was unstable over a wide range of cases and cannot be used to predict whether or not a site would be a suitable location for a Great Blue Heron colony.

There are several reasons that might explain the model's failure to perform well. The accuracy of multivariate tests depends on a number of assumptions that the data must meet, such as equality of variances and normally distributed variables. The variables used in this model were not normally distributed, and could not be transformed due to being so highly skewed. As with many statistical tests, the larger the sample size, the more accurate the results. There were 34 active sites and 34 null sites used in this study, and this number may be too small to avoid errors in determining which factors can consistently be used to distinguish one type of site from the other. A similar study on Bald Eagle (*Haliaeetus leucocephalus*) habitat in Virginia (Watts *et. al.* 1994), which also used a discriminant model to classify suitable Eagle habitat, used a total of 254 cases. This eagle model performed well and was useful in predicting which sites might support eagles in the future.

The lack of accuracy of my model might also be due to the nature of the variables chosen to be measured or the nature of the sites themselves. In particular, the model classified a large percentage (70.3%) of null sites as active sites. It may be that the variables used in the model (swamp, shoreline, cleared land, and rural development) do not provide enough information by themselves to rule out a site that would not be suitable for a heron colony. Even if there is sufficient area of swamp habitat in the vicinity, the trees may not be mature enough to hold Great Blue Heron nests, and this factor was not measured. This information could be determined by visiting the null sites and looking at the forest composition, dbh, height of trees, etc. Alternatively, it is possible that the sites picked as null sites in some cases may be suitable for herons, and the habitat is simply not saturated. It is also possible that some sites picked as null sites were too close to occupied sites, and would not support another heron colony.

In order for this type of model to be used in the future to help determine whether or not a site may be a suitable location for a Great Blue Heron colony, the model would have to be reworked. If all Great Blue Heron colonies located on inland rivers in the state of Virginia were used, the sample size would increase significantly. Great Blue Heron colonies can be found on the Potomac, Rappahannock, York, Blackwater, and other rivers in Virginia in addition to the James and Chickahominy. In addition, individual measurement and discrimination of variables might be improved by using National Wetland Inventory maps instead of USGS topographic maps to measure areas of marsh and swamp habitat.

A second purpose of this study was to investigate the influence of nearby wetlands on Great Blue Heron colony size. Other studies (Werschkul *et.al.* 1977, Burger 1981a, Gibbs *et.al.* 1987) have found a positive correlation between colony size and the abundance of wetlands within foraging ranges of a colony. In this study, the summed area of four wetland types (swamp, marsh, mudflat, and shoreline habitat) within 3 km and 5 km of a Great Blue Heron colony site was found to be positively correlated with colony size, and explained 43% of the variation in colony size ($r^2 = 0.43$). Wetland areas beyond 5 km from a colony site were not correlated significantly with colony size. This result differs from Gibbs *et.al.* (1987), who found a positive correlation ($r^2 = 0.67$) between colony size and area of wetlands within 20 km of a site. Even though Great Blue Herons will fly as far as 20 km to forage, colonies in the coastal plain of Virginia are much closer together than colonies in Maine (5.4 km, as opposed to 16.1 km). It is clear that the area of these wetlands within 3 and 5 km of Great Blue Heron colonies has an influence on the size of the colony, but there are most likely additional factors which are also operating to determine colony size, such as social interaction and human disturbance (Werschkul *et.al.* 1976, Parker 1980).

The final purpose of this study was to investigate colony spacing on these two rivers in Virginia. Other studies that have investigated colony spacing have shown that different influences are at work in different areas. Fasola and Barbieri (1978) determined that colonies in Italy were arrayed in such a manner that each site had approximately the same area of wetlands (rice fields) around it. The study in Italy did not take colony size into account. Gibbs *et.al.* (1987) found colonies in Maine to be evenly spaced, despite variability of local feeding grounds and variation in colony size. Heron colonies in this area of Virginia do not have the same amounts of wetlands around each colony. In addition, it is unclear whether colonies along these two rivers are evenly spaced, like those in Maine, because this was not determined from the information collected. The MRPP test shows that the overall distribution of the null sites is not different from the distribution of the active sites within the watershed of these two rivers.

Gibbs *et. al.* (1987) found that, on average, the distance between colonies was significantly farther than the distance from null site to colony site. Average between-colony distance in Maine was 16.1 km, whereas colony-to-null distance was 10.4 km. It was hypothesized that colonies in Maine were farther from null sites because Great Blue Herons in Maine are spacing themselves to avoid competition with birds from other colonies for foraging sites. I did not find this difference in my study area, where between-colony distance averaged 5.4 km and colony-to-null distance averaged 6.1 km. The fact that the null sites in Virginia are just as far from colony sites on average as between-colony distances could suggest that the habitat is not saturated and some of the null sites may be good candidates for heron colonies in the future. It would be premature to make this conclusion, however, because there are probably other reasons for this result. There were a limited number of sites that could be used as null sites in Maine, because null sites were located on islands. In the watershed of the James and Chickahominy Rivers, forested habitat is abundant, and null sites may need to be defined more precisely to exclude areas of forested habitat that for other reasons are not selected by herons.

In order to understand their true influences on heron colonies, colony spacing and influences of wetlands on colony size need to be considered together. The size of Great Blue Heron colonies and their spacing in coastal Virginia are probably related to one another, and the areas of wetlands surrounding colonies probably has an influence on both of these factors. Area of wetlands surrounding colonies influences colony size, but the data show that this is probably not the only factor influencing colony size. The spacing of colonies on these two rivers does not appear to follow patterns shown for herons in other locations (Fasola and Barbieri 1978, Gibbs *et. al.* 1987). In order to comprehend the situation in Virginia, colony size and colony spacing must be considered along with the influence of neighboring wetlands, the foraging habits of Great Blue Herons, and the history of colonization of each site.

The largest colonies in the study area ($\geq$ 100 pairs) were located in areas that either directly bordered the James or Chickahominy Rivers, and subsequently had large amounts of wetlands within a close vicinity, or were located in areas that were protected from human intrusion, such as preserves, national parks, or in large bottomland hardwood swamps. These observations suggest that the size of colonies in Virginia's coastal plain is influenced not only by size of wetland area within close proximity, but probably also by human disturbance.

Given the data from this study, Great Blue Herons in coastal Virginia seem to follow the some of the predictions made by Gibbs *et. al.* (1987) for the patterns of colony distribution in Maine. Based on the results of that study, a model was formed to explain how the distribution of colonies arose, and what predictions about general heron colony distribution could be made. It was hypothesized that in Maine new colonies formed far from old colonies, perhaps as a mechanism to avoid competition for foraging sites with birds from other colonies. Great Blue Herons have been shown to be territorial foragers where resources could be defended (e.g. Krebs 1974, Bayer 1978, Mock 1978). Gibbs *et. al.* (1987) hypothesized that when all areas with non-overlapping foraging territories were settled, birds formed colonies halfway between existing colonies, because competition would be minimal in these areas. It was predicted that this distribution of colonies remained stable. From this model, three predictions were made: (1) Colony distribution will be at some interval which is related to foraging distances; (2) There should be a correlation between colony size and wetland foraging area within a similar interval, and; (3) There should be maximum usage of the foraging habitat.

Based on the information learned in this study, the data suggest that Great Blue Heron colonies on these two rivers in Virginia follow at least the first two predictions of the Gibbs model. Colonies are spaced approximately 5.4 km apart in coastal Virginia, and there is a positive correlation between colony size and wetland availability within 5 km. It could be hypothesized that this distance is a common distance for the birds to fly to forage in order to avoid competition from birds from other colonies. This information is hypothetical, because birds from neighboring colonies have not actually been followed to foraging sites in Virginia, and it is not known how long foraging flights are, and to what degree birds from neighboring colonies use the same foraging sites. It would be necessary to gain information about lengths of foraging flights, exact locations of foraging sites, and common use of sites by birds from more than one colony in order to determine whether the third prediction of the Gibbs model is applicable in Virginia. Given the information found in this study, however, the Gibbs model is a logical hypothesis to explain how spacing of colonies and size of colonies are related to nearby wetlands.

Summary and Recommendations

In summary, the locations of Great Blue Herons colonies in the coastal plain of Virginia are influenced negatively by the abundance and proximity of buildings, roads, rural development, cleared land, and agriculture, and positively by the abundance and proximity of swamp habitat, forested habitat, and shoreline habitat. The size of a particular colony seems to be related to the areas of wetlands within a close (3-5 km) foraging distance, and possibly to human disturbance factors. It has been shown that variables measured from maps and photographs can be used to gain information about the quality of a particular habitat for Great Blue Herons, but in order to gain predictive value, modifications would have to be made. With some adjustment, a model could be developed to test potential sites that may be suitable for heron colonies in the future. Variables such as area of swamp habitat, area of shoreline habitat, amount of various disturbance factors, etc. could be measured and then entered into a flow chart or other model. If these variables "passed the test", field studies of the area could be made in order to further determine whether the site could be suitable. Field studies on six colonies in coastal Virginia have been completed, and this information would be useful in complementing any model that could be developed (R.A. Beck, pers. comm.).

Even if a model such as this were developed, users of the model would have to be careful in predicting whether a site would be suitable for a Great Blue Heron colony in the future. Habitat selection is a complex process involving many levels of selection, and anyone trying to make predictions about the quality of a site for herons would have to consider many factors. Nesting habitat or feeding habitat selection may be thought to occur at three levels, (1) selection of a general area to nest; (2) selection of a specific colony site, and; (3) selection of a nest site or tree (Erwin 1983). These selections may be influenced not only by habitat factors measured in this study, such as swamp or proximity to human activity, but also by social factors involving other conspecifics. The number of birds already at a site might influence more birds to settle there. In addition to social and selection factors, information about the size and longevity of existing colonies could provide insight on what makes a good colony site. Colonies that persist for 20 years are probably better sites than colonies that diminish in 5 years. All of these factors involving habitat selection must be considered when making predictions about the quality of a potential heron colony site.

This study has several implications for management of Great Blue Heron colonies in this area of Virginia. Data from this study could be used to make management decisions about how close to allow development to existing heron colonies in Virginia. Based on the results of this study, the recommended distance from disturbance given by the Great Blue Heron Habitat Suitability Index (Short and Cooper 1985) of 250m should be extended to 500m. Greater distances might be needed depending on the type of disturbance. In addition, when colonies are located near large loblolly pine stands, efforts should be made to gain information on the landowners' intentions for the property, in order to prevent colony abandonment due to logging activities.

This study introduces additional questions, whose investigation would yield more information on Great Blue Heron colonies in Virginia, and the factors which influence their size and distribution. A study in which birds were followed from colony sites to foraging sites would be valuable in determining the degree to which birds from neighboring colonies compete for foraging sites. This information in turn would help decipher the pattern of colony spacing in Virginia, and measure the influence wetlands have. This and future studies will not only help the biological community learn more about the ecology of Great Blue Herons, but should also help state and federal agencies and private landowners determine what can be done to protect habitat and reduce disturbance to Great Blue Herons and other wildlife species.

Appendix A

Variables measured for active and null sites

Variable Name	Variable Description
Human Disturbance Variables:	
PI1 (ha)	area of pines within a 250m radius of site
PI2 (ha)	area of pines from 250-500m
PI3 (ha)	area of pines from 500m-1km
PI4 (ha)	area of pines within 500m
PI5 (ha)	total area of pines within 1 km of a site
PI6 (m)	distance to nearest pine stand
PR1 (m)	length of primary roads within a 250m radius of a site
PR2 (m)	length of primary roads from 250-500m
PR3 (m)	length of primary roads from 500m- 1km
PR4 (m)	length of primary roads within 500m
PR5 (m)	total length of primary roads within 1km of a site
PR6 (m)	distance to nearest primary road
SR1 (m)	length of secondary roads within a 250m radius of a site
SR2 (m)	length of secondary roads from 250-500m
SR3 (m)	length of secondary roads from 500m- 1 km
SR4 (m)	length of secondary roads within 500m
SR5 (m)	total length of secondary roads within 1 km of a site
SR6 (m)	distance to nearest secondary road
LR1 (m)	length of light roads within a 250m radius of a site
LR2 (m)	length of light roads from 250-500m
LR3 (m)	length of light roads from 500m - 1km
LR4 (m)	length of light roads within 500m
LR5 (m)	total length of light roads within 1 km of a site
LR6 (m)	distance to nearest light road
BU1 (#)	number of buildings within a 250m radius of a site
BU2 (#)	number of buildings from 250-500m
BU3 (#)	number of buildings from 500m- 1km
BU4 (#)	number of buildings within 500m
BU5 (#)	total number of buildings within a 1 km radius of a site
BU6 (m)	distance to nearest building

Appendix A - continued

Variable Name	Variable Description
RD1 (ha)	area of rural development within a 250m radius of a site
RD2 (ha)	area of rural development from 250-500m
RD3 (ha)	area of rural development from 500m - 1km
RD4 (ha)	area of rural development within 500m
RD5 (ha)	total area of rural development within 1km of a site
RD6 (m)	distance to nearest rural development
UD1 (ha)	area of urban development within a 250m radius of a site
UD2 (ha)	area of urban development from 250-500m
UD3 (ha)	area of urban development from 500m - 1km
UD4 (ha)	area of urban development within 500m
UD5 (ha)	total area of urban development within 1 km of a site
UD6 (m)	distance to nearest urban development
AG1 (ha)	area of agriculture within a 250m radius of a site
AG2 (ha)	area of agriculture from 250-500m
AG3 (ha)	area of agriculture from 500m - 1 km
AG4 (ha)	area of agriculture within 500m
AG5 (ha)	total area of agriculture within 1 km of a site
AG6 (m)	distance to nearest agriculture
CL1 (ha)	area of cleared land within a 250m radius of a site
CL2 (ha)	area of cleared land from 250-500m
CL3 (ha)	area of cleared land from 500m - 1 km
CL4 (ha)	area of cleared land within 500m
CL5 (ha)	total area of cleared land within 1 km of a site
CL6 (m)	distance to nearest cleared land
General Habitat Variables:	
TM1 (ha)	Area of marsh within a 250m radius of a site
TM2 (ha)	Area of marsh from 250-500m
TM3 (ha)	Area of marsh from 500m - 1 km
TM4 (ha)	Area of marsh within 500m
TM5 (ha)	Total area of marsh within 1 km of a site
TM6 (ha)	Total area of marsh within 3 km of a site
TM7 (ha)	Total area of marsh within 5 km of a site
TM8 (ha)	Total area of marsh within 10 km of a site

Appendix A - continued

Variable Name	Variable Description
SW1 (ha)	Area of swamp within a 250m radius of a site
SW2 (ha)	Area of swamp from 250-500m
SW3 (ha)	Area of swamp from 500m - 1 km
SW4 (ha)	Area of swamp within 500m
SW5 (ha)	Total area of swamp within 1 km of a site
SW6 (ha)	Total area of swamp within 3 km of a site
SW7 (ha)	Total area of swamp within 5 km of a site
SW8 (ha)	Total area of swamp within 10 km of a site
SL1 (m)	Length of shoreline within a 250m radius of a site
SL2 (m)	Length of shoreline from 250-500m
SL3 (m)	Length of shoreline from 500m - 1 km
SL4 (m)	Length of shoreline within 500m
SL5 (m)	Total length of shoreline within 1 km of a site
SL6 (ha)	Total area of shoreline within 3 km of a site
SL7 (ha)	Total area of shoreline within 5 km of a site
SL8 (ha)	Total area of shoreline within 10 km of a site
FO1 (ha)	Forested area within a 250m radius of a site
FO2 (ha)	Forested area from 250-500m
FO3 (ha)	Forested area from 500m - 1 km
FO4 (ha)	Forested area within 500m
FO5 (ha)	Total forested area within 1 km of a site
Wetland Variables:	
TM6 (ha)	area of marsh within a 3 km radius of a site
TM7 (ha)	area of marsh within a 5 km radius of a site
TM8 (ha)	area of marsh within a 10 km radius of a site
SW6 (ha)	area of swamp within a 3 km radius of a site
SW7 (ha)	area of swamp within a 5 km radius of a site
SW8 (ha)	area of swamp within a 10 km radius of a site
SL6 (ha)	area of shoreline habitat within a 3 km radius of a site
SL7 (ha)	area of shoreline habitat within a 5 km radius of a site
SL8 (ha)	area of shoreline habitat within a 10 km radius of a site
MF3 (ha)	area of mudflat within a 3 km radius of a site
MF52 (ha)	area of mudflat within a 5 km radius of a site
MF10 (ha)	area of mudflat within a 10km radius of a site

Appendix A - continued

Variable Name	Variable Description
ST3 (m)	length of permanant streams within a 3 km radius of a site
ST5 (m)	length of permanent streams within a 5 km radius of a site
ST10 (m)	length of permanent streams within a 10 km radius of a site
Add3 (ha)	Sum of marsh, swamp, mudflat, and shoreline area within 3 km
Add5 (ha)	Sum of marsh, swamp, mudflat, and shoreline habiata within 5 km
Add10 (ha)	Sum of marsh, swamp, mudflat, and shoreline habitat within 10 km

Appendix B

Locations of Great Blue Heron colonies

Site Name	Latitude	Longitude	Nests
Bacon's Castle NW*	37 5.00	76 41.84	5
Bacon's Castle SE*	37 1.94	76 40.62	30
Brandon NW#	37 19.23	76 56.35	3
Brandon SW*	37 17.65	76 58.80	100
Charles City#	37 18.04	77 0.73	125
Dutch Gap SW*	37 22.54	77 22.40	160
Hog Island SE#	37 10.88	76 40.24	180
Hog Island SW#	37 8.18	76 44.96	7
Norge NE	37 19.28	76 46.39	13
Norge SE I*	37 15.17	76 46.58	7
Norge SW*	37 18.53	76 48.97	95
Norge SE II*	37 16.39	76 47.25	33
Providence Forge SE#	37 15.59	77 1.69	45
Quinton SW#	37 32.42	77 14.03	19
Richmond NE#	37 35.78	77 23.38	220
Roxbury NE I#	37 29.67	77 10.98	460
Roxbury NE II#	37 28.17	77 7.55	24
Seven Pines NW	37 34.90	77 21.12	90
Seven Pines SE#	37 32.55	77 15.05	20
Smithfield NE*	36 56.25	76 37.88	6
Surry NE I#	37 12.26	76 48.35	90
Surry NE II#	37 11.79	76 45.57	155
Surry SE*	37 7.98	76 45.83	17
Surry SW*	37 10.13	76 51.93	38
Toano*	37 27.61	76 51.76	12
Walkers NE*	37 28.20	76 54.44	14
Walkers NW I*	37 28.59	76 58.00	3
Walkers SW I*	37 24.49	76 56.50	250
Walkers SW III	37 24.64	76 59.62	13
Walkers SW II*	37 24.55	76 57.53	22
Westover NW*	37 20.90	77 12.75	3
Williamsburg SW*	37 15.70	76 43.28	3
Yellow Tavern SE I*	37 39.46	77 25.82	18
Yellow Tavern SE II*	37 37.68	77 24.73	23

* Indicates that general location of colony (not GPS reading) and 1993 numbers of nests were obtained from Watts/Byrd

# Indicates that only 1993 numbers of nests were obtained from B.D.Watts/ M.A.Byrd

Appendix C

Locations of null sites

Site Name	Latitude	Longitude
NS1 Charles City SW	37 16.45	77 7.46
NS2 Westover NE	37 22.42	77 8.27
NS3 Claremont NW	37 12.34	76 56.30
NS4 Hog Island SW	37 8.37	76 44.20
NS5 Seven Pines NE	37 34.49	77 17.55
NS6 Hopewell SW	37 16.16	77 22.07
NS7 Quinton SW	37 32.08	77 11.56
NS8 Tunstall SE	37 34.41	77 3.07
NS9 Walkers NE	37 26.51	76 56.16
NS10 Claremont SE	37 11.03	76 53.31
NS11 Surry SW	37 11.08	76 50.27
NS12 Hopewell SE	37 15.54	77 18.44
NS13 Toano NW	37 26.53	76 57.56
NS14 Dutch Gap SE	37 24.30	77 15.57
NS15 Tunstall SW	37 30.02	77 7.28
NS16 Roxbury SW I	37 25.27	77 12.13
NS17 Roxbury NW	37 29.19	77 13.15
NS18 Roxbury SW II	37 24.06	77 13.33
NS19 Roxbury NE	37 26.47	77 10.35
NS20 Providence Forge NE	37 29.24	77 1.49
NS21 Surry NE	37 14.40	76 47.27
NS22 Yorktown SE	37 9.27	76 31.31
NS23 Dutch Gap NE	37 28.39	77 15.00
NS24 Providence Forge SE	37 23.47	77 0.43
NS25 Surry SE	37 10.22	76 48.51
NS26 Mulberry Island NW	37 7.24	76 36.01
NS27 Tunstall SE II	37 31.41	77 2.09
NS28 Hog Island SE	37 9.13	76 40.36
NS29 Chester NW	37 21.53	77 28.56
NS30 Dutch Gap SW	37 26.03	77 19.03
NS31 Benns Church SW	36 56.03	76 36.56
NS32 Roxbury NE II	37 26.39	77 9.33
NS33 Disputanta North NE	37 14.58	77 9.30
NS34 Drewry's Bluff NE	37 28.35	77 24.42

Appendix D

Types of primary nest trees found in each of the colonies located along the James and Chickahominy Rivers

Colony Site	Location	dead snags	Cypress	Poplar	LL Pine	dead LL Pine	hardwoods*	Red Maple	Sycamore
Bacon's Castle NW			X						
Bacon's Castle SE		X		X					
Brandon NW							X		
Brandon SW		X							
Charles City			X						
Dutch Gap SW		X							
Hog Island SE					X	X			
Hog Island SW		X							
Norge NE							X		
Norge SE I								X	
Norge SW			X						
Norge SE II		X	X					X	
Providence Forge SE		X			X				
Quinton SW							X		
Richmond NE							X		
Roxbury NE I			X						
Roxbury NE II			X				X		

Appendix D - continued

Colony Site	Location	dead snags	Cypress	Poplar	LL Pine	dead LL Pine	hardwoods*	Red Maple	Sycamore
Seven Pines NW							X		
Seven Pines SE							X		
Smithfield NE			X						
Surry NE I					X				
Surry NE II					X				
Surry SE		X	X						
Surry SW			X						
Toano		X							
Walkers NE		X							
Walkers NW I									X
Walkers SW I			X						
Walkers SW III			X						
Walkers SW II			X						
Westover NW		X							
Williamsburg SW		X							
Yellow Tavern SE I		X			X				
Yellow Tavern SEII		X						X	

Appendix E

Descriptive statistics for all variables measured

Variable	Mean-Active Sites	Stdev	Standard Error	Mean-Null Sites	Stdev	Standard Error	P-value
TM1 (ha)	1.39	3.06	0.52	0.22	0.83	0.14	0.08a
TM2	2.78	6.44	1.10	0.84	3.54	0.61	0.10a
TM3	6.54	14.88	2.55	4.37	13.70	2.35	0.43a
TM4	4.16	9.30	1.59	1.06	4.35	0.75	0.16a
TM5	10.71	23.84	4.09	5.43	17.18	2.95	0.31a
SW1 (ha)	5.54	6.09	1.04	1.35	3.38	0.58	0.0001a**
SW2	9.16	10.73	1.84	2.11	4.68	0.80	0.0006a**
SW3	20.57	25.05	0.30	5.27	10.52	1.80	0.001a**
SW4	14.35	16.13	2.77	3.47	7.63	1.31	0.0007a**
SW5	35.27	39.77	6.82	8.73	17.09	2.93	0.0004a**
SL1 (m)	463.67	734.71	126.00	83.60	228.62	39.21	0.01a**
SL2	1215.19	1849.45	317.18	409.14	989.88	169.76	0.02a*
SL3	3455.80	4935.95	846.51	1838.31	3149.29	540.10	0.11a
SL4	1678.86	2530.76	434.02	492.74	1194.10	204.79	0.01a**
SL5	5134.66	7190.57	1233.17	2331.06	4133.64	708.91	0.06a
FO1 (ha)	15.92	5.42	0.93	15.12	4.33	0.74	0.03a*
FO2	41.91	16.74	2.87	38.01	14.10	2.42	0.12a
FO3	143.26	56.80	9.74	144.47	42.24	7.24	0.92t
FO4	57.83	21.91	3.76	53.13	17.76	3.05	0.08a
FO5	201.09	77.00	13.21	197.60	56.30	9.65	0.83t
AG 1 (ha)	0.18	0.51	0.09	1.11	2.30	0.39	0.05a*
AG 2	2.97	5.68	0.97	6.51	10.40	1.78	0.25a
AG 3	22.77	27.04	4.64	30.85	28.30	4.85	0.25b
AG 4	3.15	6.13	1.05	7.63	12.56	2.15	0.25a
AG 5	25.92	32.32	5.54	38.47	39.76	6.82	0.20b
BU 1 (#)	0.21	1.20	0.21	4.74	12.49	2.14	0.0002a**
BU 2	3.18	10.53	1.81	14.59	44.52	7.64	0.03a*
BU 3	24.35	34.97	6.00	42.71	74.14	12.71	0.32c
BU 4	3.38	10.98	1.88	19.32	56.50	9.69	0.02a*
BU 5	27.74	43.45	7.45	62.03	127.84	21.93	0.17c
CL 1 (ha)	0.10	0.41	0.07	0.62	1.45	0.25	0.01a**
CL 2	0.49	1.16	0.20	3.45	5.68	0.97	0.02a*
CL 3	8.02	12.49	2.14	9.79	15.05	2.58	0.41a
CL 4	0.59	1.20	0.21	4.07	6.83	1.17	0.02a*
CL 5	8.61	13.25	2.27	13.85	19.76	3.39	0.15a
LR 1 (m)	94.27	168.67	28.93	372.11	507.72	87.07	0.002a**
LR 2	532.18	646.70	110.91	926.43	1122.41	192.49	0.10b
LR 3	3562.40	1899.80	325.81	3351.13	2532.58	434.33	0.67t
LR 4	626.45	757.97	129.99	1298.53	1584.81	271.79	0.04b*
LR 5	4188.88	2381.36	408.40	4649.66	3914.07	671.26	0.90b

Appendix E - continued

Variable	Mean-Active Sites	Stdev	Standard Error	Mean-Null Sites	Stdev	Standard Error	P-value
PI 1 (ha)	0.83	2.93	0.50	2.64	4.70	0.81	0.09a
PI 2	3.04	7.94	1.36	5.31	9.52	1.63	0.15a
PI 3	13.63	24.74	4.24	20.19	37.54	6.44	0.31a
PI 4	3.87	10.63	1.82	7.94	13.63	2.34	0.12a
PI 5	17.50	34.15	5.86	28.13	49.19	8.44	0.12a
PR 1 (m)	8.96	52.24	8.96	35.15	145.27	24.91	0.54a
PR 2	62.18	205.11	35.18	121.08	309.99	53.16	0.42a
PR 3	409.04	740.85	127.06	516.03	876.07	150.24	0.68a
PR 4	71.14	236.22	40.51	156.23	417.20	71.55	0.41a
PR 5	891.94	2702.24	463.43	672.26	1120.13	192.10	0.64a
RD 1 (ha)	0.10	0.57	0.10	0.22	0.47	0.08	0.009a**
RD 2	0.25	0.76	0.13	0.85	1.50	0.26	0.03a*
RD 3	2.53	3.65	0.63	5.82	5.78	0.99	0.004c**
RD 4	0.35	1.26	0.22	1.07	1.93	0.33	0.008a**
RD 5	2.87	3.93	0.67	6.89	6.35	1.09	0.002c**
SR 1 (m)	11.01	64.19	11.01	71.64	166.47	28.55	0.05a*
SR 2	63.19	194.63	33.38	195.65	320.97	55.05	0.05a*
SR 3	537.72	846.51	145.17	888.95	1084.92	186.06	0.11a
SR 4	77.84	236.49	40.56	291.23	462.64	79.34	0.03a*
SR 5	611.91	964.48	165.41	1156.23	1381.23	236.88	0.06a
UD 1 (ha)	0.04	0.23	0.04	1.15	3.47	0.59	0.15a
UD 2	0.60	1.99	0.34	3.61	9.95	1.71	0.40a
UD 3	6.77	16.22	2.78	10.26	25.39	4.35	0.52a
UD 4	0.63	2.18	0.37	4.75	13.38	2.29	0.40a
UD 5	7.34	17.86	3.06	15.01	38.49	6.60	0.34a

Appendix E - continued

Variable	Mean-Active Sites	Stdev	Standard Error	Mean-Null Sites	Stdev	Standard Error	P-value
TM6 (ha)	61.70	89.08	15.28	56.44	116.89	20.05	0.51a
TM7	163.41	199.73	34.25	116.45	179.38	30.76	0.49a
TM8	964.05	748.23	128.32	619.52	613.01	105.13	0.13a
SW6 (ha)	137.46	140.22	24.05	92.33	84.93	14.57	0.29
SW7	261.23	218.60	37.49	263.40	207.74	35.63	0.85
SW8	795.95	522.34	89.58	1099.83	654.05	112.17	0.07
SL6 (ha)	15.03	13.83	2.37	10.83	11.22	1.92	0.09
SL7	34.70	23.06	3.95	28.66	21.82	3.74	0.12
SL8	140.73	56.67	9.72	124.16	49.58	8.50	0.20
MF3 (ha)	8.30	20.39	3.50	5.02	12.00	2.06	0.87a
MF5	17.53	33.11	5.68	15.69	30.32	5.20	0.75a
MF10	90.50	141.01	24.18	142.40	127.66	21.89	0.05*
ST3 (m)	7634.73	4260.07	730.60	7244.34	4192.54	719.01	0.70
ST5	19183.68	8823.29	1513.18	19925.44	10012.09	1717.06	0.75
ST10	69726.18	27870.43	4779374	81652.51	32617.23	5593.81	0.14

a = significance value from Mann-Whitney U test, comparing active colony sites and null sites
* $P<0.05$, ** $P<0.01$

Appendix F

Correlation tables

Swamp variables

	SW1	SW2	SW3	SW4	SW5
SW1	1	.9005**	.7553**	.9573**	.8713**
SW2	.9005**	1	.8660**	.9793**	.9508**
SW3	.7553**	.8660**	1	.8112**	.9744**
SW4	.9573**	.9793**	.8112**	1	.9204**
SW5	.8713**	.9508**	.9744**	.9204**	1

Shoreline variables

	SL1	SL2	SL4
SL1	1	.8877**	.9395**
SL2	.8877**	1	.9917**
SL4	.9395**	.9917**	1

Number of Buildings variables

	BU1	BU2	BU4
BU1	1	.9259**	.9542**
BU2	.9259**	1	.9965**
BU4	.9542**	.9965**	1

Cleared Land variables

	CL1	CL2	CL4
CL1	1	.7219**	.8150**
CL2	.7219**	1	.9893**
CL4	.8150**	.9893**	1

Appendix F - continued

Light Roads variables

	LR1	LR4
LR1	1	.9069**
LR4	.9069**	1

Rural Development variables

	RD1	RD2	RD3	RD4	RD5
RD1	1	.7776**	0.0809	.8868**	.3350**
RD2	.7776**	1	0.208	.9802**	.4776**
RD3	0.0809	0.208	1	0.1784	.9569**
RD4	.8868**	.9802**	0.1784	1	.4566**
RD5	.3350**	.4776**	.9569**	.4566**	1

Secondary Roads variables

	SR1	SR2	SR4
SR1	1	.6983**	.8264**
SR2	.6983**	1	.9340**
SR4	.8264**	.9340**	1

** = $p < .01$

Appendix F - continued

Correlation table testing variables used for discriminant analysis

	SR4	LR1	BU1	RD5	AG1	CL1	SW1	SL1	FO1
SR4	1	-0.00052	0.117282	0.119696	0.252213	0.207552	-0.18304	-0.18675	-0.11332
LR1	-0.00052	1	0.763959	0.302441	0.008436	0.096139	-0.26726	-0.12162	-0.41898
BU1	0.117282	0.763959	1	0.321244	-0.07105	0.056309	-0.11922	-0.12849	-0.43971
RD5	0.119696	0.302441	0.321244	1	0.165863	0.077368	-0.13264	-0.27412	-0.08932
AG1	0.252213	0.008436	-0.07105	0.165863	1	-0.02625	-0.1904	-0.16572	-0.19176
CL1	0.207552	0.096139	0.056309	0.077368	-0.02625	1	-0.04929	0.045752	-0.22305
SW1	-0.18304	-0.26726	-0.11922	-0.13264	-0.1904	-0.04929	1	0.100117	0.302014
SL1	-0.18675	-0.12162	-0.12849	-0.27412	-0.16572	0.045752	0.100117	1	-0.50212
FO1	-0.11332	-0.41898	-0.43971	-0.08932	-0.19176	-0.22305	0.302014	-0.50212	1

Appendix G

Chi-square analysis for Table 2: Presence or absence of habitat or disturbance factors within 250m, 500m, and 1000m

	Active vs. Null within 250m		Active vs. Null within 500m		Active vs. Null within 1000	
Factor	Chi-square value	P-value	Chi-square value	P-value	Chi-square value	P-value
Marsh	2.71	0.10	0.71	0.40	0.57	0.45
Swamp	15.27	0.0001**	8.47	0.004**	8.97	0.003**
Shoreline	5.58	0.02*	6.07	0.01**	1.96	0.16
Pines (PI)	2.72	0.10	1.64	0.20	2.24	0.13
Primary Roads (PR)	0.35	0.50[a]	0.57	0.35[a]	0.28	0.59
Secondary Roads (SR)	3.98	0.05[a]*	3.84	0.05*	2.12	0.15
Light Roads (LR)	7.27	0.007**	0.33	0.57	1.01	0.31
Buildings (BU)	14.46	0.0001**	2.88	0.09	0.16	0.69
Rural Development (RD)	7.50	0.006**	6.44	0.01**	3.64	0.06
Urban Development (UD)	1.94	0.18[a]	0.47	0.49	1.08	0.30
Agriculture (AG)	2.94	0.09	0.24	0.63	0.10	0.76
Cleared Land (CL)	7.70	0.01**	3.89	0.05*	1.83	0.18

a = Fisher's exact test used on these variables; * = $P \leq 0.05$, ** = $P \leq 0.01$

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