NEOTOMA FLORIDANA FLORIDANA NATURAL HISTORY, POPULATIONS, AND MOVEMENTS IN NORTH-CENTRAL FLORIDA

Leslie HaySmith[1]

ABSTRACT

A behavioral ecology study on the eastern woodrat (*Neotoma floridana floridana*) was conducted between September 1988 and February 1990 on the Katharine Ordway Preserve-Swisher Memorial Sanctuary. The Preserve is located in north-central Florida, approximately 5 miles east of Melrose. The goal of the study was to investigate factors that may influence density and distribution of *Neotoma* on the Ordway Preserve.

Distribution of the eastern woodrat is closely associated with mesic hardwood hammocks on the Preserve. Five study sites were therefore selected in three habitat types: mesic hammock with open understory, mesic hammock with saw-palmetto understory, and bottomland hardwood swamp. Trapping along strip-transects at these sites demonstrated that the bottomland hardwood swamp consistently had the highest density of woodrats (4.3/ha at initiation of study). Densities fluctuated in all 5 study sites, and at Goose and Ashley lakes populations crashed.

Radio telemetry was used to evaluate woodrat movements, habitat utilization, and den use. Woodrats were nocturnal with peaks in nighttime activity between 2000-2200 and 0100-0330 hours. Mean home range size was larger in the mesic hammock with saw-palmetto understory (1.05 ha), which was least dense in horizontal woody growth. Home ranges were smaller in the mesic hammock with open understory (0.25 ha) and bottomland hardwood swamp (0.69 ha) which were more complex in horizontal and vertical vegetation structure. Home range size was positively correlated to number of dens used, which ranged from 1 to 3 dens in use at one time. Dens of woodrats were the center of all activity. Nest fidelity was high, but some individuals changed dens. Social tolerance was low; radiotelemetry and trapping observations rarely documented animals in close proximity to each other.

In summary, the bottomland hardwood swamp, which has the highest stem density and vegetation cover supports the highest density of woodrats. These habitat features may influence smaller home ranges. The density fluctuations in all study sites and subsequent population crashes in two mesic hammock habitats, suggest woodrats may be influenced by external factors such as predation and drought conditions. Forests with less horizontal and vertical structural complexity may be marginal to woodrats due to cover requirements and food resource distribution. Populations inhabiting these environments may therefore be more vulnerable when heightened stress levels occur, such as changes in climatic conditions.

---

[1] The author is the Coordinator of International Programs in the College of Forestry, Wildlife and Range Sciences, University of Idaho, Mosco ID 83843, U.S.A.

HAYSMITH, L. 1995. *Neotoma floridana floridana*: Natural history, populations, and movements in north-central Florida. Bull. Florida Mus. Nat. Hist. 38 Pt. II(8):211-243.

RESUMEN

Se realizó un estudio sobre la ecología conductual de la rata de bosque del este (*Neotoma floridana floridana*) entre septiembre de 1988 y febrero de 1990, en la Reserva Katharine Ordway-Swischer Memorial Sanctuary. La Reserva está localizada en el norte-centro de Florida, aproximadamente 5 millas al este de Melrose. El objetivo de este estudio fue investigar los factores que pueden influenciar la densidad y distribución de *Neotoma* en la Reserva Ordway.

La distribución de la rata de bosque del este en la Reserva está fuertemente asociada con los bosques de madera dura mésicos. Por lo tanto, se seleccionaron cinco sitios de estudio en tres tipos de habitat: bosque mésico con sotobosque abierto, bosque mésico con sotobosque de palma y pantano bajo de madera dura. El trampeo a lo largo de transectos en estos sitios, demostró que los pantanos bajos de madera dura tuvieron consistentemente la densidad más alta de ratas de bosque (4.3/ ha en la iniciación del estudio). La densidades poblacionales fluctuaron en los cinco sitios de estudio, colapsando éstas en los lagos Goose y Ashley.

Se usó radiotelemetría para evaluar los movimientos, el uso de habitat y de madrigueras de las ratas de bosque. Las ratas de bosque fueron nocturnas, con máxima actividad nocturna entre 2000-2200 y 0100-0330 horas. La media del tamaño del rango de hogar fue mayor en los bosques mésicos con sotobosque de palmas (1.05 ha), habitat que fue el menos denso en crecimiento leñoso horizontal. Los ámbitos de hogar fueron más pequeños en el bosque mésico con sotobosque abierto (0.25 ha) y en el pantano bajo de madera dura (0.69 ha), teniendo ambos una estructura vegetal más compleja horizontal y verticalmente. El tamaño del ámbito de hogar estuvo positivamente correlacionado con el número de madrigueras utilizado, variando éste de entre 1 a 3 madrigueras utilizadas cada vez. Las madrigueras de las ratas de bosque fueron el centro de toda actividad. La fidelidad a éstas fue alta, aunque algunos individuos cambiaron madrigueras. La tolerancia social fue baja; datos de telemetría y trampeo rara vez documentaron animales estrechamente cercanos unos de otros.

En resumen, el pantano bajo de madera dura, el cual tiene la mayor densidad de ramas y cobertura vegetacional, mantiene la mayor densidad de ratas de bosque. Estas características del habitat probablemente influencian ámbitos de hogar más pequeños. Las fluctuaciones poblacionales en todos los sitios de estudio, y el subsecuente colapso en dos habitats de bosque mésico, sugieren que las ratas de bosque pueden estar influenciadas por predación y condiciones de sequía en estos habitats. Los bosques con menor complejidad estructural horizontal y vertical pueden ser marginales para las ratas de bosque debido a sus requerimientos de cobertura y distribución de recursos alimenticios. Las poblaciones que habitan estos ambientes pueden, por lo tanto, ser más vulnerables a mayores niveles de estrés, tales como cambios en las condiciones climáticas.

INTRODUCTION

Few comprehensive studies on the ecology of the Eastern woodrat (*Neotoma floridana*) have occurred, despite its widespread geographical distribution in the eastern United States. Nine subspecies are currently recognized in this geographical range (Wiley 1980). *Neotoma f. floridana* is the southeasternmost subspecies located in Florida, Georgia, South Carolina, and North Carolina.

Woodrats have a long life expectancy and low reproductive rate compared to other small rodents (Hamilton and Whitaker 1981; Hamilton 1953). They are omnivorous, consuming a variety of invertebrates and plants (Hamilton and Whitaker 1981). Dens are a significant component in *Neotoma floridana* ecology. Movements are closely linked to their den, which is the base of all their operations (Fitch and Rainey 1956). Controversy exists on whether the woodrat is solitary or colonial. Some researchers indicate *Neotoma floridana* are colonial, communally occupying dens (Pearson 1952; Goertz 1970), and others list the species as strictly solitary and territorial (Poole 1940; Hamilton and Whitaker 1981).

While *Neotoma floridana* has a broad geographical range, it appears to have a patchy distribution throughout the range for unknown reasons (Schwartz and Odum 1957). Habitat requirements of this species are poorly understood; it is found in rocky cliffs, ravines, upland oak forests, hardwood bottomland forests, riparian woods, and lowland wet hammocks (Hamilton and Whitaker 1981). Their presence in widely different habitats throughout the eastern United States creates difficulty in understanding if optimal or suboptimal habitats can be distinguished and what specific habitat features are necessary to meet life history requirements.

In peninsular Florida, mammal distributions are very complex (Eisenberg 1989). *Neotoma floridana* distribution is likewise unclear, but it appears to occur throughout most of peninsular Florida. Layne (1974) indicated the range did not extend south of Lake Okeechobee, and Greer (1978) discovered woodrats in highly localized populations south to DeSoto County. Greer indicated south Florida *Neotoma* populations are disjunct for unknown reasons and speculated that coastal development may be influencing their distribution.

Populations of the eastern woodrat occur in a wide range of densities throughout its geographical distribution in the United States. Numerous researchers have attributed different densities to habitat conditions, food availability, predation pressure, and other ecological factors (Worth 1950; Pearson 1952; Goertz 1970). However, it is not clear what factors may be most important in influencing the highly variable densities.

While densities vary throughout its range, populations of the eastern woodrat appear to be stable in some areas, and vulnerable in others. Woodrats are endangered in Key Largo, Florida (subspecies, *N. f. smalli*; Humphrey 1988) and threatened in New Jersey, eastern Pennsylvania, and New York, where it has completely disappeared from much of its historical range (Sciascia 1990). While the woodrat is not threatened in most of the southeast, native habitats of mesic hardwood forests in Florida which appear to be the principal habitat are rapidly disappearing. Studies are needed to understand life history parameters, and those that influence their density and distribution.

Incongruent reports on the life history of *Neotoma floridana* prompted this investigation into population parameters, movement patterns, and habitat utilization on macro and micro levels. My goal was to investigate parameters that influence the density and distribution of *Neotoma f. floridana* in mesic forest habitats on the Ordway Preserve. I had four chief objectives in this study: (a) to assess woodrat population dynamics among and within mesic forests at the Ordway Preserve; (b) to identify whether this sub-species exhibits habitat preferences among and within mesic forest types; (c) to determine home range size, pattern, and nest use; and (d) to assess whether movement and nesting activity may be related to specific habitat features.

ACKNOWLEDGEMENTS

I would like to thank Margje Voeten, Leslie Straub, and Kathy Hallman for field assistance. John F. Eisenberg, Richard Franz, and Melvin E. Sunquist provided valuable advice on study design and analysis. I express gratitude to the Ordway Foundation for logistical and financial support for the duration of the project. I would also like to thank the reviewers for their time and effort in reviewing this manuscript.

STUDY AREA

The Katharine Ordway Preserve/Swisher Memorial Sanctuary was established as a reserve in 1979. Because of its brief history of protection, mixed historical use has resulted in a composite landscape of contiguous expanses of native xeric and mesic forests, wetlands, and prairies, as well as fragmented forest patches, bounded by old fields and former pastures. The habitat fragmentation, particularly evident near black water lakes, is a result of agricultural, pastoral, and silvicultural activities from the last century.

The complexity of topography and soil conditions, the position of the Ordway Preserve on the Central Florida ridge, and past human perturbations lead to a unique assemblage of vascular plant flora (Franz and Hall 1990). Major communities represented are: high pine forests, sand live oak hammocks, mesic hardwood hammocks, swamp forests, freshwater marshes, sandhill lake fringes, permanent lakes and ponds, and culturally derived sites (Franz and Hall 1990).

METHODS

This study was conducted over a 16-month study period from September 1988 to January 1990. I selected five study sites in three habitat types: the bottomland hardwood swamp (Mill Creek Swamp), mesic hammock with saw-palmetto understory (Ross and Goose lakes), and mesic hardwood hammock with open understory (Ashley and Suggs lakes) (Fig. 1). The bottomland swamp is a large continuous tract of forest with numerous tree species and dense ericaceous shrubs. The mesic hammock with saw-palmetto understory (Goose and Ross lakes) and

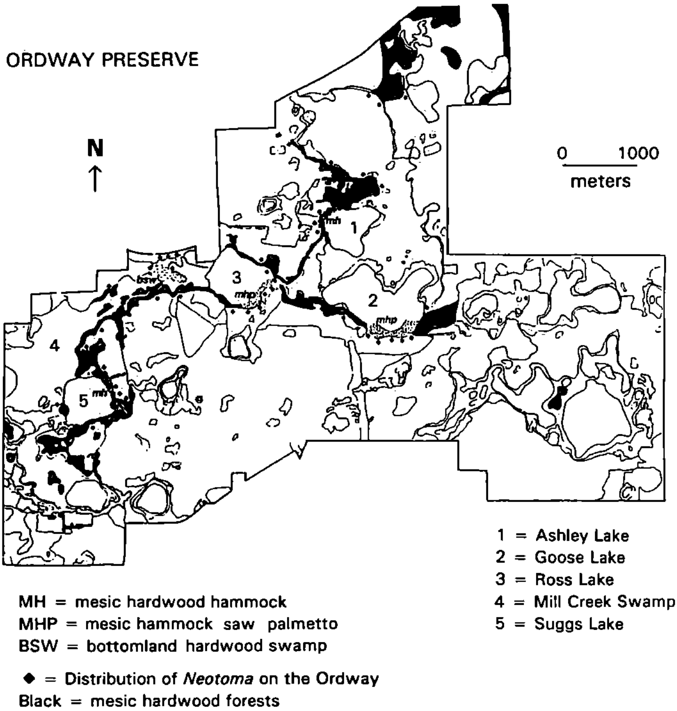

Figure 1. Mesic forests, study areas, and distribution of *Neotoma f. floridana* on the Ordway Preserve.

mesic hardwood forests with open understory (Suggs and Ashley lakes) are narrow belts of mesic forest on the perimeter of the black water lakes which are 50-200 m in width and are bounded by the lake, a road, and old fields, resulting in fragmented habitats.

Throughout the last decade other mammalian surveys (over 10,000 trap nights) have been conducted in various habitats on the Preserve. The results of these surveys indicated that woodrats were primarily distributed in mesic forests. I selected my five study sites based on previous records of woodrats at these sites.

Vegetation measurements were collected using the point-center-quarter method (Hays et al. 1981; Ludwig and Reynolds 1988). Because of the linear nature of the habitats, two randomly located transects were established at 90° angles in each study site, which were parallel and perpendicular to the lakes. A vegetation station, which was divided into four quarters, was established every 50 m.

Woodrats were captured in squirrel size Tomahawk traps (61 x 17 x 17 cm) baited with a mixture of peanut butter and oatmeal. Standard biological measurements were taken which included: weight, head and body length, tail length, and right hind foot length. Data were also collected on gender, age class (adult or juvenile), and reproductive condition. Ectoparasites were evaluated and collected. Animals were initially marked with ear tags (#1L, National Band and Tag Company, Newport, KY), but were later marked with ear notches using a standard numbering system, due to problems with infections.

Traps were placed at 15-20 m intervals along 400 m strip transects near vegetation, logs, and in brushpiles. Transects were established parallel to lake edges due to the linear nature of the study sites. The two parallel strip transects were set on random compass bearings, intersecting microhabitats and ecotonal areas. Trapping effort was systematically varied throughout the 16-month study period, corresponding to twice per month in each study site. Trapping schedule was 4-5 days per session. In addition to trapping on transects, den sites were trapped.

Ecological densities, defined as the number of individuals per unit habitat, were calculated as the minimum number of animals known alive (MNKA) per hectare (capture of the total population could never be assumed). Density was calculated as the number of individuals captured per unit area. Total area was calculated using aerial photos.

I also evaluated 42 woodrat dens for 21 structural and vegetative characteristics in all three habitat types. At each den measurements were taken on: location of den, substrate species, height, DBH (diameter basal height), cover, distance to water, and debris at den.

Selected individuals were equipped with 10 gram radio collars. Transmitters and collars consisted of a small mercury oxide hearing aid battery, an electrical board, and a rubberized collar, which was covered with epoxy and electrical tape. The total weight of the transmitter and collar was less than 5% of the total body weight.

A total of 27 animals (16 males and 11 females) were radiotracked. Individual animals were tracked for periods varying from two weeks to six months. Telemetry data were collected from 1800 to 0600 EST. To obtain data on activity periods, a reading was taken on each animal every two hours. Animals were radiotracked by triangulation and the "homing in" technique (Harris et al. 1990). The latter method was primarily used in daylight hours when animals were in their dens. Data recorded using triangulation were: date, individual animal and frequency; time, station number, and location; azimuth; and animal activity. The estimated degree of error with triangulation was 7.25 m, forming a relatively small error radius around the estimated location of the animal.

Home range data were analyzed using the minimum convex polygon (MCP) and modified concave polygon methods (COC). The MCP is the 'total area of activity' following Burt (1943). The COC is the core area, or "central area of consistent or intense use" (Kaufmann 1962) whereby 50% of the maximum distance between points is utilized (Michener 1979). The concept of center of activity in home range analysis (Harris, et al. 1990) is simplified with woodrats, because woodrat dens are the center of all their activity, as documented in this and other studies. Home ranges were analyzed by individual animal, gender, daily and monthly time periods, and habitat type.

The minimum convex polygon is the traditional method used in radiotelemetry studies. It is constructed by connecting the outermost animal locations, and calculating the area within this polygon. The modified concave polygon is similar to the minimum convex polygon, but uses a prespecified maximum distance between perimeter points in the analysis, eliminating outlying points (Harvey and Barbour 1965). Observations that are farthest from the arithmetic center are thus removed and several use areas are produced, therefore the modified concave polygon (COC) method yields the smallest ranges.

Fluorescent pigments were used to evaluate three-dimensional movements and habitat utilization. Two methods were implemented: full-body dusting and attachment of fluorescent capsules. Full-body dusting was done by placing an animal in a bag with fluorescent powder, lightly shaking the bag with the woodrat, and immediately releasing the animal. The capsule method involved fabricating a small capsule from paraffin wax, and dental acrylic (Goodyear 1989), injecting powder, and gluing the capsule to the animals pelage. Powder trails were followed with a battery operated UV light, using stakes and flags to mark the trails (Leman and Freeman 1985; Goodyear 1989).

Micro-habitats in heterogenous mesic forests were mapped in the field to obtain information on understory strata not discernible on aerial photographs. These maps were later transformed to habitat maps drawn to the output scale of the Telem88 home range program (Coleman and Jones 1988) for plotting animal home ranges, with delineations set at proper compass bearings.

Utilization of habitat by woodrats was assessed by plotting all animal home range locations and overlaying these points onto the habitat maps, using X and Y coordinates. The radiotelemetry locations were thereby assigned to a habitat, and points were tallied for each of these categories (Sunquist 1989).

RESULTS

Habitat

Ground, herbaceous, and canopy cover, in addition to litter depth was evaluated between the three habitat types. Parametric tests (ANOVA) and non-parametric tests (Kruskal-Wallis) were used to determine if differences existed between habitat types for vegetative parameters. Mean values for the three types of cover and litter depth were similar, and an ANOVA demonstrated no significant differences for cover and litter between habitats (p=0.05).

Species composition of plants between the three habitat types were similar in canopy, midstory, shrub, and herbaceous strata. Tree species diversity was high in all three habitats, with each habitat including between 9 and 11 species. Dominant tree species in the canopy, midstory and ground cover strata were water oak (*Quercus nigra*), live oak (*Quercus virginiana*, laurel oak (*Quercus laurifolia*, sweet gum (*Liquidambar styraciflua*), swamp bay (*Persea palustris*), sweet bay (*Magnolia virginiana*), and pignut hickory (*Carya glabra*) (Tables 1, 2 and 3).

The shrub layer differed the most in species composition among the three habitat types. Dominant shrubs were saw-palmetto (*Serenoa repens*), fetterbush (*Lyonia lucida*), and wax myrtle (*Myrica cerifera*). The most prevalent difference occurred in the bottomland swamp (Mill Creek Swamp) with the predominance of ericaceous shrubs (Table 4).

Herb composition within the habitats was more diverse than other strata. Several species of ferns were present in all three habitats. Other species of herbs and grasses occurred in highest abundance in the mesic hardwood hammock with open understory (Table 5). Several species of vines, including *Smilax* and muscadine grape, occurred in nearly all sites (Table 6).

Relative densities of plant species in all three habitat types in the three strata were similar. Relative density of trees, saplings, and seedlings were concentrated in four species with a range between 12% and 31% (Tables 1, 2, and 3). Differences in relative densities for shrubs were most pronounced in the mesic hammock with saw-palmetto understory (Ross and Goose lakes) and bottomland hardwood swamp habitats with palmetto (44.4%) and fetterbush (54.2%) (Table 4). Concentrations of relative densities for herbs and vines occurred in four species, ranging between 13% and 38% (Tables 5 and 6).

The most significant difference between habitat types was vertical and horizontal structure, rather than species composition or relative density. Structural complexity of vegetation in horizontal and vertical planes measured by height, stem density, and crown diameter varied considerably among habitat types.

The mean values of vegetation height in the three habitat types are presented in Table 7. An ANOVA of vegetation height demonstrated significant differences in all strata for saplings and shrubs by habitat where saplings were tallest in the bottomland swamp and shortest in mesic hardwoods; shrubs were tallest in mesic hammock with saw-palmetto understory. Trees, seedlings, and herbs showed no significant difference in height by habitat type (p=0.05).

Diameter basal height (DBH) was measured as an index of plant dominance. An ANOVA demonstrated significant differences for DBH of trees, saplings, and shrubs between habitats (p=0.05). Mean DBH for trees was highest in the mesic hardwood forests; shrub DBH was highest in mesic hammock-saw-palmetto; and the highest DBH for saplings occurred in the bottomland swamp (Table 8).

Table 1. Relative density (%) of trees in three habitat types on the Ordway Preserve

Habitat Species	Sites[1]				
	MH		MHP		BSW
	SUG	ASH	ROS	GOS	MCS
Live oak (*Quercus virginiana*)		20.00	14.29	18.18	12.77
Sweet gum (*Liquidambar styraciflua*)	30.95		12.50		10.64
Pignut hickory (*Carya glabra*)	19.05				
Water oak (*Quercus nigra*)	16.67	6.66	21.43	38.63	21.28
Black gum (*Nyssa sylvatica*)	7.14		1.79	13.63	
Longleaf pine (*Pinus palustris*)	2.38		2.27	21.28	
Swamp bay (*Persea palustris*)	2.38	20.00	26.79		8.51
Dahoon holly (*Ilex cassine*)	2.38		3.57	2.13	
Loblolly bay (*Gordonia lasianthus*)	2.38	6.66		2.13	
Sweet bay (*Magnolia virginiana*)		6.66	1.79	17.02	
Red maple (*Acer rubrum*)		26.60			
Laurel oak (*Quercus laurifolia*)		20.00	7.14	4.26	
Bull bay (*Magnolia grandiflora*)			7.14		
Coastal plain willow (*Salix caroliniana*)			1.79		
Wild olive (*Osmanthus americana*)			1.79		
Loblolly pine (*Pinus taeda*)			2.27		
Turkey oak (*Quercus laevis*)			2.27		

[1] MHP=mesic hammock-saw-palmetto understory; MH=mesic hammock-open understory BSW=bottomland hardwood swamp; SUG=Suggs Lake; ASH=Ashley Lake; ROS=Ross Lake; GOS=Goose Lake; MCS=Mill Creek Swamp.

Table 2. Relative density (%) of saplings in three habitat types on the Ordway Preserve

Habitat Species	Sites[1]				
	MH		MHP		BSW
	SUG	ASH	ROS	GOS	MCS
Sweet gum (*Liquidambar styraciflua*)	30.95	12.50	16.36		13.33
Pignut hickory (*Carya glabra*)	19.05		1.82	7.32	
Water oak (*Quercus nigra*)	16.67	43.75	30.91	46.34	11.11
Laurel oak (*Quercus laurifolia*)	14.29	18.75	12.73	2.44	6.67
Live oak (*Quercus virginiana*)			9.09	17.07	17.78
Black gum (*Nyssa sylvatica*)	7.14			9.75	2.22
Swamp bay (*Persea palustris*)	2.38	6.25	7.27	2.43	22.22
Longleaf pine (*Pinus palustris*)	2.38				4.44
Sweet bay (*Magnolia virginiana*)	2.38		1.82	7.31	15.56
Dahoon holly (*Ilex cassine*)	2.38		3.64	4.87	6.67
Carolina holly (*Ilex ambigua*)			1.82		
Loblolly bay (*Gordonia lasianthus*)	2.38		1.82	2.44	
Red maple (*Acer rubrum*)		12.50		9.75	
Red bay (*Persea barbonia*)		16.25	1.82		
Wild olive (*Osmanthus americana*)		3.64	4.88		
Bull bay (*Magnolia grandiflora*)			3.64		
Coastal plain willow (*Salix carliniana*)		1.82			
Walking stick (*Aralia spinosa*)			1.82		

[1] MHP=mesic hammock-saw-palmetto understory; MH=mesic hammock-open understory BSW=bottomland hardwood swamp; SUG=Suggs Lake; ASH= Ashley Lake; ROS=Ross Lake; GOS=Goose Lake; MCS=Mill Creek Swamp.

Table 3. Relative density (%) of seedlings in three habitat types on the Ordway Preserve.

	Sites[1]				
	MH		MHP		BSW
Habitat Species	SUG	ASH	ROS	GOS	MCS
Laurel oak (*Quercus laurifolia*)	38.46	6.25	2.50	23.21	4.88
Water oak (*Quercus nigra*)	30.77	56.25	62.50	32.14	9.76
Live oak (*Quercus virginiana*)			17.50	14.29	21.95
Sweet gum (*Liquidambar styraciflua*)	12.82			3.57	
Black gum (*Nyssa sylvatica*)	7.69		5.00		
Swamp bay (*Persea palsutris*)	5.13	18.75	5.00	25.00	36.59
Red bay (*Persea borbonia*)		2.56	12.50	2.50	1.79
Pignut hickory (*Carya glabra*)	2.56				
Longleaf pine (*Pinus palustris*)		6.25	2.50		
Red maple (*Acer rubrum*)			2.50		
Loblolly bay (*Gordonia lasianthus*)			2.50		
Sweet bay (*Magnolia virginiana*)					21.95
Dahoon holly (*Ilex cassine*)					4.88

[1] MHP=mesic hammock-saw-palmetto understory; MH=mesic hammock-open understory BSW=bottomland hardwood swamp; SUG=Suggs Lake; ASH= Ashley Lake; ROS=Ross Lake; GOS=Goose Lake; MCS=Mill Creek Swamp.

Table 4. Relative density (%) of shrubs in three habitat types on the Ordway Preserve.

Habitat Species	Sites[1]				
	MH		MHP		BSW
	SUG	ASH	GOS	ROS	MCS
Saw-palmetto (*Serenoa repens*)			64.28	44.44	31.25
Wax myrtle (*Myrica cerifera*)	21.43	57.14	4.76	16.67	
Fetterbush (*Lyonia lucida*)	16.67	42.85	2.38	24.07	54.17
Beauty berry (*Callicarpa americana*)		23.81			
Buttonbush (*Cephalanthus occidentalis*)	9.52			5.56	2.08
Virginia willow (*Itea virginica*)	9.52	2.38			
Common persimmon (*Dyospyros virginiana*)	9.52				
Highbush blueberry (*Vaccinium corybosum*)	7.14			1.85	2.08
Southern dewberry (*Rubus trivialis*)		2.38			
Partridge berry (*Mitchella repens*)		2.38			
Gallberry (*Ilex glabra*)			2.38	1.85	
Rosemary (*Ceratiola ericoides*)			4.76		
Staggerbush (*Lyonia ferruginea*)		2.38		6.25	
Tree sparkleberry (*Vaccinium arboreum*)				5.56	
Deer berry (*Vaccinium stamineum*)				4.17	

[1] MHP=mesic hammock-saw-palmetto understory; MH=mesic hammock-open understory BSW=bottomland hardwood swamp; SUG=Suggs Lake; ASH= Ashley Lake; ROS=Ross Lake; GOS=Goose Lake; MCS=Mill Creek Swamp.

Table 5. Relative density (%) of herbs in three habitat types on the Ordway Preserve.

	Sites[1]				
	MH		MHP		BSW
Habitat Species	SUG	ASH	ROS	GOS	MCS
Fringed panicum (*Panicum ciliatum*)	32.56	30.00	66.66	12.90	
Virginia chain fern (*Woodwardia virginica*)	6.98	60.00	11.29	23.40	
Lizard tail (*Saururus cernuus*)	2.32	10.00	5.55	3.22	
Dymorphic chainfern (*Woodwardia aerolata*)	6.98				10.64
Saw grass (*Cladium jamaicense*)		11.11			
Maidencane (*Panicum hemitomon*)	11.63		5.55	8.06	
Cinnamon fern (*Osmunda cinnamomea*)			5.55	1.61	10.64
Sedge spp.			5.55	50.00	
Elephant's foot (*Elephantopus elatus*)	13.95				
Green arum (*Peltandra* spp.)	6.98			6.38	
Virginia creeper (*Parthenocissus quinquefolia*)	6.97				
Bracken fern (*Pteridium aquilinum*)				8.06	29.79
Resurrection fern (*Polypodium polypodioides*)				1.61	
Primrose-willow (*Ludwigia* spp.)				1.61	
Royal fern (*Osmunda regalis*)				19.15	

[1] MHP=mesic hammock-saw-palmetto understory; MH=mesic hammock-open understory BSW=bottomland hardwood swamp; SUG=Suggs Lake; ASH= Ashley Lake; ROS=Ross Lake; GOS=Goose Lake; MCS=Mill Creek Swamp.

Table 6. Relative density (%) of vines in three habitat types on the Ordway Preserve.

Habitat	Sites[1]				
	MH		MHP		BSW
Species	SUG	ASH	ROS	GOS	MCS
Bamboo vine (*Smilax laurifolia*)	4.88	33.33	5.00	3.08	63.16
Wild bamboo (*Smilax auriculata*)	41.46	20.00	2.50	1.54	10.53
Wild sarsaparilla (*Smilax glauca*)	4.88	40.00	45.00	53.85	13.16
Smilax pumilo (*Sarsaparilla* vine)			5.00	1.54	
Highbush blackberry (*Rubus argutus*)		6.66	2.50		
Wild muscadine grape (*Vitis rotundifolia*)	43.90		35.00	32.31	13.16
Crossvine (*Bignonia capreolata*)	2.44		2.50		
Ground nut (*Apios americana*)			2.50	7.70	
Yellow jessamin (*Gelsemium sempervirens*)	2.44				

[1] MHP=mesic hammock-saw-palmetto understory; MH=mesic hammock-open understory BSW=bottomland hardwood swamp; SUG=Suggs Lake; ASH=Ashley Lake; ROS=Ross Lake; GOS=Goose Lake; MCS=Mill Creek Swamp.

Stem density, also referred to as point-to-plant distance, was the most important measurement for estimating horizontal complexity. An ANOVA indicated significant differences in stem density by habitat for seedlings, shrubs, saplings, herbs, and vines, excluding only trees (p=0.05). Stem density was highest for saplings and seedlings in the mesic hardwood hammock with open understory (Suggs and Ashley lakes), and highest for shrubs in the bottomland swamp. A Kruskal-Wallis test demonstrated significant differences between habitat types (Zar 1984) for sapling, seedling, and shrub species but not for trees or herbs; herbs were the only factor excluded from the ANOVA results. After determining that significant differences were found among these strata, I conducted a multiple comparisons non-parametric test to indicate in which habitat point-to-plant distances were significant. This demonstrated that sapling and

Table 7. Mean vegetation[1] heights (in mm) categorized by habitat type.

Plant		N	Mean	SE
Trees				
	MHP	109	10.65	0.48
	MH	57	11.87	0.67
	BSW	47	11.16	0.73
Saplings				
	MHP	108	3.10	0.29
	MH	59	2.75	0.26
	BSW	44	4.50	0.30
Seedlings				
	MHP	107	0.28	0.04
	MH	60	0.36	0.05
	BSW	41	0.31	0.06
Shrubs				
	MHP	105	1.76	0.11
	MH	55	1.13	0.16
	BSW	47	1.59	0.17
Herbs				
	MHP	79	1.01	0.48
	MH	50	0.31	0.61
	BSW	47	0.43	0.63

[1] MHP=mesic hammock-saw-palmetto understory; MH=mesic hammock-open understory; BSW=bottomland hardwood swamp

seedling stem density was highest in mesic hardwood habitats, but shrub stem density was highest in the bottomland swamp.

Data on crown diameter also were analyzed using an ANOVA, and the Kruskal-Wallis and non-parametric multiple comparisons tests (p=0.05). The ANOVA indicated significant differences for saplings and shrubs by habitats, with the largest crown diameter for saplings, shrubs, and herbs, in the bottomland swamp. Comparison of the parametric and non-parametric analyses demonstrate that sapling and shrub crown diameter is largest in the bottomland swamp. This comparison also demonstrates that herb crown diameter is largest in the mesic hammock-saw-palmetto, and the bottomland swamp.

Vegetation cover was assumed to be high in the mesic hammock with saw-palmetto understory, due to the dominance of saw-palmetto. However, stem density of saw-palmetto is low, and when viewed from an aerial position, shrub cover is consequently patchy. These factors were difficult to quantify using chosen vegetation sampling methods. It appears that by combining the evaluation for stem density with vegetation cover a more representative depiction of vegetation cover and consequent habitat quality for small mammals, such as woodrats, can be obtained.

Table 8. Mean values (in cm) of diameter basal height (DBH) of vegetation[1] categorized by habitat.

Variable		N	Mean	SE
Tree				
	MHP	110	23.9	1.6
	MH	57	25.8	2.2
	BSW	46	17.2	2.4
Sapling				
	MHP	107	2.9	0.19
	MH	59	2.6	0.25
	BSW	45	4.0	0.29
Shrub				
	MHP	105	5.6	0.62
	MH	56	2.4	0.85
	BSW	42	4.9	0.98
Herb				
	MHP	80	1.2	0.22
	MH	52	0.6	0.28
	BSW	46	0.5	0.30
Vine				
	MHP	105	0.7	0.11
	MH	58	0.6	0.15
	BSW	36	0.9	0.19

[1] MHP=mesic hammock-saw-palmetto understory; MH=mesic hammock-open understory; BSW=bottomland hardwood swamp.

Population Variables

Trap success varied per study site, but the mean for all study sites was 0.07, with 2755 total trap nights. Of the 218 captures, 78% (*n*=164) were recaptures (Table 9). Total animals captured at all study sites consisted of 32 males and 22 females, which resulted in a sex ratio of 1.6:1, favoring males. Weights of adult woodrats fluctuated considerably throughout the study period; a phenomenon also observed by Fitch and Rainey (1956). A *t*-test demonstrated that although male woodrats weighed significantly more than females, their body measurements were not larger (p=0.05). (The mean values for weight and body measurements are presented in Table 10.)

Reproduction occurred throughout the year. A Chi-square test demonstrated that no significant differences existed in reproductive activity for males or females between months or seasons (p=0.05). However, peaks occurred in April and November for males, and July and November for females (Fig. 2).

Table 9. Capture number and success rate per study site.

	Study sites[1]				
	ROS	GOS	SUG	ASH	MCS
Total	75	46	39	6	52
NR[2]	11	10	14	2	17
Trap success rate	.08	.05	.07	.02	.11

[1] ROS=Ross Lake; GOS=Goose Lake; SUG=Suggs Lake; ASH=Ashley Lake; MCS=Mill Creek Swamp.
[2] NR=Excluding recaptures.

Table 10. Mean weights and body measurements of male and female woodrats.

	Weight	HB Length	Tail length	RH foot
Males	245.6	20.5	15.0	3.6
SE	4.3	0.4	0.6	0.03
N	107.0	43.0	45.0	44.0
Females	211.3	19.8	16.0	3.6
SE	3.9	0.4	0.4	0.03
N	65.0	27.0	28.0	25.0

During the 16-month study, a total of 54 animals were captured from all study sites, but densities of woodrats varied dramatically at all study sites. The population in the bottomland hardwood swamp and Ross Lake declined but rose again (4.3 to 2.4, to 2.9 and 3.9 to 1.1, to 2.4 individuals/ha, respectively; Fig. 3); populations declined at Suggs Lake (2.3 to 2.0, to 1.3 individuals/ha; Fig. 3) and two populations at Goose and Ashley lakes completely disappeared (2.4 to 0.67, to 0; and 2.9, to 0.82, to 0 individuals/ha, respectively; Fig. 3). Suggs and Ashley lakes are mesic hammock with open understory habitat, and Ross and Goose lakes are mesic hammock with saw-palmetto understory habitat.

Of the 54 animals captured in the study, 11% (n=6) survived after 12 months. Animals were resident in the study an average of seven months. Mortality accounted for 70% of the total animals lost (n=38); other disappearances were for unknown causes. Twelve animals were lost to predation; 50% were taken by owls (*Strix varia* and *Bubo virginianus*), 25% by snakes (*Crotalus adamanteus* and *Elaphe obsoleta*), one by an opossum (*Didelphis virginiana*), and two incidences of

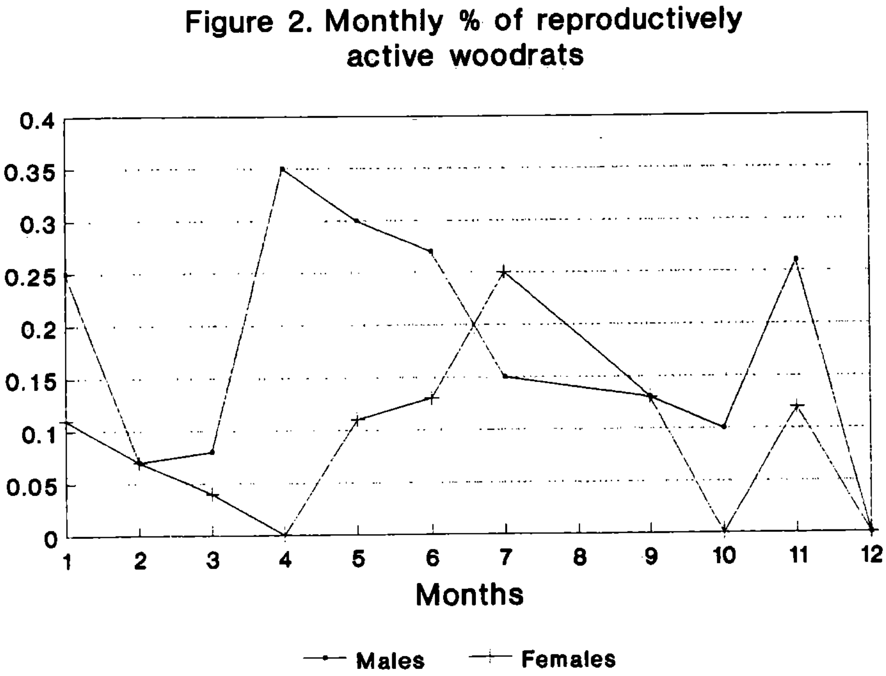

Figure 2. Monthly percentages of reproductively active woodrats.

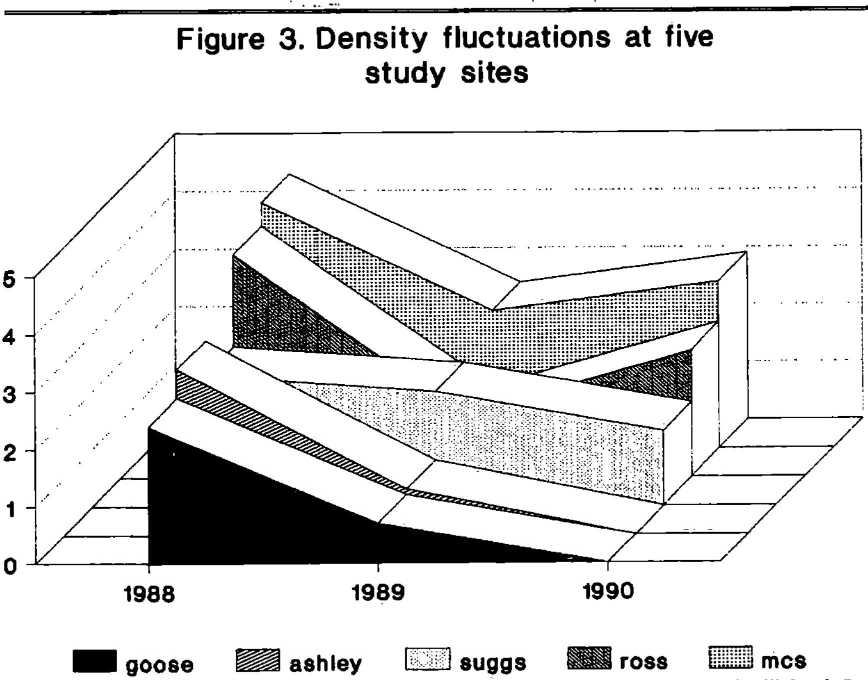

Figure 3. Density fluctuations of woodrats at Goose, Ashley, Suggs, and Ross lakes and Mill Creek Swamp.

raccoon (*Procyon lotor*) predation. Owl and snake predation occurred at Ross and Goose lakes (mesic hammock with saw-palmetto understory) and at Suggs Lake (mesic hammock with open understory), with no predation observed in the bottomland hardwood swamp.

Home Range and Activity

A total of 27 animals (16 males and 11 females) were radiotracked in all months of the year. The time period that each animal was tracked ranged from less than 1 month to 6 months. Home ranges of woodrats did not overlap in most of the study areas. Of the total home ranges plotted (n=23), only three overlapped, and all were male/female associations.

Home range sizes of woodrats varied from small to very large in all three habitat types (Fig. 4) and belonged to both males and females. Home ranges larger than 1.0 ha (n=7) were recorded for 57% males and 43% females. Mean home range size for females was 0.72 ha (n=14) and 0.68 ha for males (n=10). However, a t-test showed no significant differences in home range size between the sexes (p=0.05).

The minimum convex polygon (MCP) method produced larger home range sizes than the modified concave polygon (COC) method (Table 11). However, an ANOVA indicated no significant differences existed for home range between gender and habitat types, for either the MCP (Table 12) or COC methods (p=0.05). In order to compare parametric and non-parametric results of home range analysis, a Kruskal-Wallis, non-parametric test was used to analyze home range by habitat type using the MCP and COC methods. The test indicated no significant differences existed (p=0.05) for either of these analyses by habitat (Table 12).

The mean home range size for animals in the bottomland swamp (BSW) (n=5) using the minimum convex polygon method (MCP) was 0.60 ha; in the mesic hardwood with saw-palmetto understory (MHP) it was 1.09 ha (n=12; and in the mesic hammock with open understory (MH) it was 0.27 ha (n=7) (Table 13).

Home range size was also analyzed in relationship to the number of dens used. Mean home range size for woodrats using one den site was 0.43 ha (n=14). The mean home range size for animals subsequently using different dens was 0.27 ha (n=4), and mean home range size for woodrats concurrently using two dens was 1.22 ha (n=10) (Table 14). Of the total animals monitored with known den sites (n=27), 60% used one den, while 19% concurrently used two dens, 26% used two dens subsequently, and 7% used three dens (category overlap). Of the seven woodrats subsequently using two or three dens, five were females in reproductive condition, and two were males moving to recently abandoned dens. One male had an unusually large range of 2.34 ha which had been expanded from 0.05 ha to

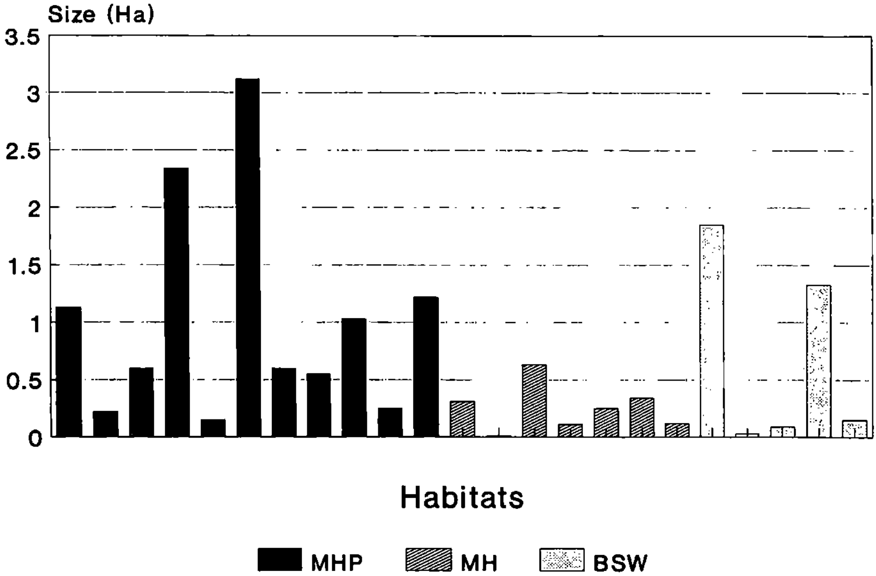

Figure 4. Comparison of home range size in three habitats.

Table 11. Comparison of home range analyses: means and standard errors (n=24). MCP = minimum convex polygon; MCONP = modified concave polygon.

	Mean (ha)	SE
MCP	0.68	0.18
MCONP (COC)	0.30	0.07

include two other male ranges after the animals disappeared, concurrently using all three woodrat dens. Popular or "preferred den sites" existed in most of the study sites, and animals moved to these sites if they were vacant.

Nightly radiotracking observations were evaluated to estimate distance travelled per night. All individual nightly home ranges were relatively small, ranging from 0.01 to 0.18 ha (Table 15). Analyses of nighttime movements was

Table 12. Kruskal-Wallis test for home range size per habitat using minimum convex polygon (MCP) and modified concave polygon (COC) methods. MHP = mesic hammock-palmetto understory; MH = mesic hammock-open understory; BSW = bottomland hardwood swamp.

Variables	Test statistic	Df	Prob
MCP:			
BSW MH MHP	3.94	2	0.14
COC:			
BSW MH MHP	2.37	2	0.31

conducted by dividing the evening session into five time blocks: 1800 to 2000 h, 2001 to 2200 h, 2201 to 0100 h, 0101 to 0330 h, and 0331 to 0600 h (EST). Animals were active during all periods of the evening, and variability between time periods was high. Woodrats were least active from 1800 to 2000 h, and from 2200 to 0100 h. The highest activity occurred between 2000-2200, 0100 to 0330, and 0331 to 0600 h (Fig. 5).

Trapping results and radiotelemetry observations show that woodrats are socially intolerant of each other. For example, of 200 radiotelemetry observations and 450 trap nights at woodrat dens, only 1% (*n*=7) of the trapping records and 2% (*n*=4) of the telemetry observations documented two animals at one den. Social intolerance was also indicated through several scarred and injured animals; 26 adults and juveniles had large wounds or scars.

Dens

In the five study sites, 42 woodrat dens were located and evaluated. The large den structures made from sticks that are found in other geographical locations of *Neotoma floridana*, such as northern populations and in the Florida Keys, were not present at the Ordway Preserve. Only small stick piles were found outside of their dens. Of the total, 90.5% of the dens were subterranean. Dens were associated with 10 different plant species (Table 16). They were found in live trees, decaying logs, tree stumps, and roots of fallen trees, but the highest percentage occurred in fetterbush (*Lyonia lucida*) tussocks. Dens had more than one entrance, ranging from 2 to 12 openings. Nests contained sticks, bones, seeds and nuts, research flagging, and insect remains, but acorns were the most abundant item.

Table 13. Analysis of variance of home range (minimum convex polygon) for sex (A) and habitat (B) (p=0.05). MHP = mesic hammock-palmetto understory; MH = mesic hammock-open understory; BSW = bottomland hardwood swamp.

Variable	Df	Sum-squares	Mean Square	F-ratio	Prob.
A (Sex)	1	0.59	0.59	0.76	0.39
B (Habitat)	2	2.95	1.48	1.90	0.18
AB	2	0.89	0.45	0.58	0.57
Error	18	14.01	0.78		
Total	23	18.14			

Variable	Number	Mean (ha)	SE
A: Sex			
Male	13	0.48	0.25
Female	11	0.82	0.27
B: Habitat			
BSW	5	0.60	0.39
MHP	12	1.09	0.25
MH	7	0.27	0.33
AB: Sex, Habitat			
Male\BSW	2	0.12	0.62
Male\MHP	8	0.96	0.31
Male\MH	3	0.35	0.51
Female\BSW	3	1.07	0.51
Female\MHP	4	1.22	0.44
Female\MH	4	0.18	0.44

Of the dens located, 69% were in an ecotone, between the mesic forest type and adjacent habitats such as lake fringe habitats. The mean distance to water for the dens close to lakes was 28 m. Average substrate height was 8.5 m. Average canopy and midstory cover at den sites was 62% and 68%, respectively. An ANOVA demonstrated that no significant differences occurred for canopy cover among the three habitat types, but significant differences occurred for midstory cover by habitat (p=0.05). The bottomland swamp had the highest mean value for midstory cover.

Table 14. Home range sizes categorized by number of dens used by woodrats. 1 = one den used; 2 = two subsequent dens used; 3 = two dens used simultaneously.

		Home range size (ha)		
Individual	Sex	1 den	2 dens	3 dens
Nahum	M			1.03
Malachi	M			0.63
Hummis	M			0.15
Abel	M			2.34
Byr	M			0.05
Ruth	F		0.60	
Hanna	F			3.12
Lois	F		0.34	
Chloe	F		0.03	
Maira	F		0.11	
Bathshee	F	0.01		
Liz	F	0.25		
AC	M	0.12		
Abe	M	1.13		
Ice	M	0.33		
Anias	M	0.25		
Ganz	M	0.98		
Mupke	M	0.03		
Aline	F	0.60		
Elisha	M	0.55		
Mean =		0.43	0.27	1.22

Habitat Utilization

A Chi-square goodness of fit test indicated significant differences existed for woodrat use of different habitats (p=0.05). A Bon-ferroni analysis showed that woodrats used saw-palmetto habitat more than would be expected and used fringe habitats less than would be expected (Table 17). Use of different micro-habitat types was otherwise similar to the proportion of the micro-habitats available (Byers and Steinhorst 1984). Micro-distribution observations via trapping are anecdotal, but trap success was consistently higher in ecotonal areas than in homogenous micro- or macrohabitats.

Table 15. Home range size of five woodrats based on a single night of radiotracking. MHP = mesic hammock-saw-palmetto understory; MH = mesic hammock-open understory; BSW = bottomland hardwood swamp.

				Size (ha)	
Individual	Sex	Habitat	#Obs	MCP	COC
Nahm	M	MHP	6	0.04	0.03
Abel	M	MHP	5	0.18	0.18
Lois	F	MH	7	0.03	0.01
Byr	M	MH	7	0.02	0.02
Malachi	M	MH	7	0.04	0.03

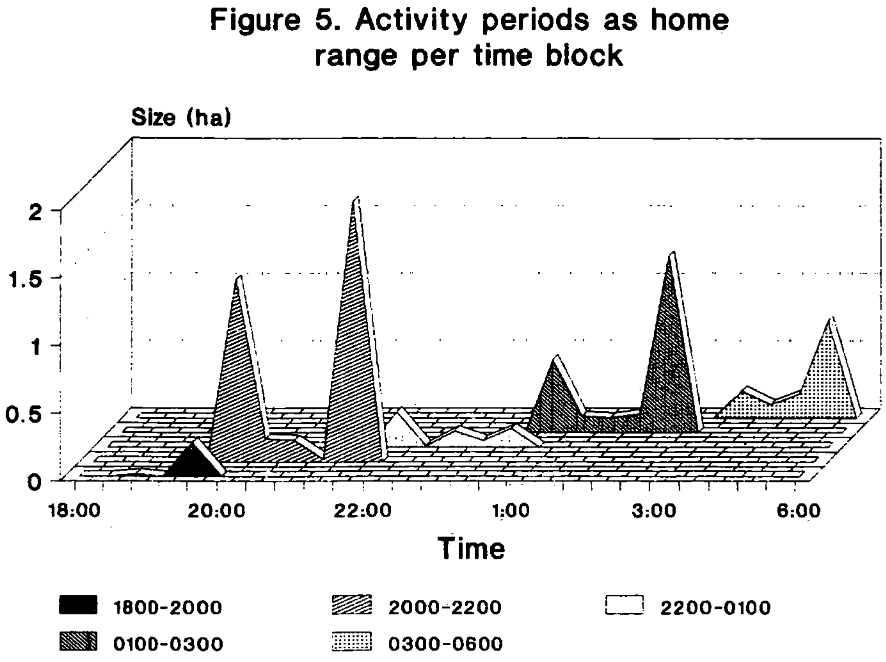

Figure 5. Activity periods of woodrats displayed as home range size per time block.

Table 16. Percentages of woodrat den plant substrate types.

Plant species	N	Percentage
Fetterbush (*Lyonia lucida*)	11	29.7
Oak log (*Quercus* spp.)	9	24.3
Saw-palmetto (*Serenoa repens*)	8	21.6
Swamp bay (*Persea palustris*)	2	5.4
Water oak (*Quercus nigra*)	2	5.4
Live oak (*Quercus virginiana*)	1	2.7
Black gum (*Nyssa sylvatica*)	1	2.7
Wax myrtle (*Myrica cerifera*)	1	2.7
Sweet gum (*Liquidambar styraciflua*)	1	2.7
Loblolly pine (*Pinus taeda*)	1	2.7

Table 17. Habitat utilization using the Bon-ferroni confidence interval approach (p=0.05).

Habitat[1]	Proportion Available	Proportion Utilized	Bon-ferroni C.I.	Selection
Ross and Goose lakes:				
A	0.36	0.54	0.44 < P < 0.64	+
C	0.29	0.26	0.18 < P < 0.34	
E	0.23	0.11	0.05 < P < 0.17	-
B	0.06	0.03	-0.003 < P < 0.06	
G	0.05	0.05	0.008 < P < 0.09	
Mill Creek Swamp:				
S	0.87	0.81	0.66 < P < 0.97	
C	0.12	0.11	- 0.01 < P < 0.23	
A	0.01	0.08	- 0.03 < P < 0.19	

[1] A = saw-palmetto; C = hardwood MH vegetation > 50cm in height; E = fringe (black gum and fetterbush/wax myrtle); S = bayhead swamp; B = hardwood MH vegetation < 50 cm in height; P = proportion of utilization; G = grasses.

Microhabitat Use

The fluorescent pigment body-dusting and capsule techniques were not highly successful. Fluorescent trails from body dusted animals were difficult to follow beyond a 4-m radius of the den. Trails that could be located were found in leaf litter, fetterbush, and on logs. Two animals whose dens were located in structurally complex vegetation provided the most important data. Pigment trails were located on a multitude of branches and stems at various heights. At one male den, 4720 cm of fluorescent trails were measured; 84.6% were arboreal and 15.4% were terrestrial. At one female den, I measured 5837 cm of trails; 75.1% were arboreal and 24.9% were terrestrial.

DISCUSSION

Habitat

Woodrats occupy an array of habitats across their range. It is clear that northern populations of the eastern woodrat prefer rocky terrain. However, in the southeastern coastal plain, where these habitats are not abundant, *Neotoma floridana* are found in various woodlands. It is not clear if specific habitats are preferred among forest types. Barbour and Humphrey (1982) found the highest density in mature hardwood forests in Key Largo, Florida. Chamberlain (1928) recorded *Neotoma floridana* in wooded swampy areas in South Carolina. Pearson (1952) documented high densities of woodrats along mesic forest ecotones, but trapped them in swamps and high and low mesic hammocks in Gulf hammocks of Florida. This study confirms these researchers' reports, documenting woodrats in hardwood forests and swamps. However, in this study woodrats were strongly associated with three mesic forest habitats on the Ordway Preserve: hardwood hammock with saw-palmetto understory, hardwood hammock with open understory, and bottomland hardwood swamp.

I documented similar plant species composition and relative densities of vegetation in the three mesic habitats occupied by woodrats. A notable feature of species composition is the species richness in all strata and in all habitats. However, significant differences were observed in vegetation structure on horizontal and vertical planes. The shrub stratum, followed by sapling and seedling strata, are probably the most significant to woodrat foraging and movement activities. Stem density was highest for shrubs in the bottomland swamp and for saplings and seedlings in the mesic hardwood habitat. The dense shrub stratum in the bottomland hardwood swamp results in an impenetrable wall of ericaceous shrubs. This attribute of structural complexity in the bottomland swamp habitat is probably the most significant vegetative component in all of the study sites. The bottomland swamp is also where densities remained the highest. This structural complexity can offer a woodrat protection from predators and higher food resource availability, particularly on a 3-dimensional scale.

Population Variables

Natural history characteristics documented in this study agree with observations by other researchers that woodrats are nocturnal (Fitch and Rainey 1956). Nocturnal behavior may be influenced by predation coupled with the longer daylight periods in the southern U.S., which would increase susceptibility to diurnal predators. Diurnal activity was infrequently recorded in previous studies, but diurnal observations by Schwartz and Schwartz (1959) and Rainey (1956) may be associated with shorter daylight periods, a dissimilar suite of predators, or different weather conditions.

The sex ratio observed in this study was skewed towards males (1.6:1). Hersh (1981) documented a sex ratio of 1.2:1 on Key Largo woodrats. The skewed sex ratio towards males, may represent a population bias for males, or may be an artifact of female trap shyness.

Reproduction of *Neotoma f. floridana* occurred throughout the year in this study, which also was observed by Pearson (1952) in a study in Gulf Hammock, Florida. Pearson discovered reproductive peaks in the spring and fall, and peaks in this study occurred in April and November. Year-round reproduction in the southeastern U.S. is most likely influenced by climatic conditions, with warmer temperatures facilitating reproductive activities possibly due to higher availability of food resources.

The social behavior of *Neotoma* is controversial, both social tolerance and intolerance have been reported in the literature. In this study woodrats were determined to be socially intolerant. They used solitary den sites, and rarely were observed in close proximity to each other. Social intolerance may be influenced by several factors including competition for food resources, shelter, and intrinsic population regulation. Kinsey (1976) reported seasonal differences in agonistic interactions between males and females of *Neotoma* that may have been associated with reproduction and rearing of young. However, no differences were observed in this study in seasonality and signs of social intolerance, which may have been actual or an artifact of sampling.

Numerous intrinsic and extrinsic factors may influence the observed population fluctuations or declines of *Neotoma f. floridana* on the Ordway Preserve. These may include social factors, resource scarcity, decreased reproduction, habitat differences, predation, or climatic factors. The population declines may be more profound due to the lower reproductive potential of *Neotoma*, compared to other small mammals. For example, high densities caused population declines in *Rattus* species (Davis 1953; Calhoun 1962), due to increased aggressive interactions, and decreased reproduction.

The bottomland hardwood swamp consistently supported the highest densities of woodrats and may represent optimal habitat. The bottomland swamp is a large continuous tract of forest, and vegetation was the most structurally complex on horizontal and vertical planes. Plant species composition in the three habitats was very similar, but the mesic hammock with saw-palmetto understory and hardwood hammock with open understory were structurally less diverse. These habitats also are fragmented. Because of this fragmentation, woodrat densities may be restricted. The bottomland swamp may also serve as a 'source' to other connected but marginal habitats.

Declines in density may also have been due to predation. The most significant amount of predation was attributed to barred owls (*Strix varia*) and great horned owls (*Bubo virginiana*). Snake predation was the second most commonly observed incidence of predation, attributed to the eastern diamondback rattlesnake (*Crotalus adamanteus*) and the yellow rat snake (*Elaphe obsoleta*).

Of the incidences of predation, all known predation occurred to animals in the mesic hardwood hammock with open understory, and the mesic hardwood hammock with saw-palmetto understory. No predation was observed in the bottomland hardwood Mill Creek Swamp, which is dominated by extremely dense fetterbush that is impenetrable to large, avian predators, but presents no difficulty to reptilian predators. Timmerman (1989) and Franz (pers.comm.) suggested that reptile populations may be relatively abundant in the bottomland hardwood swamp. Wright (1989) considered owls to be one of the top predators to opossum (*Didelphis virginiana*) in the mesic hardwood and xeric oak forests. If true for *Neotoma*, then near absence of owl predation in Mill Creek Swamp as observed in this study, could offer a partial explanation for the consistent higher densities found there. Conversely, the joint impact of snakes and owls in mesic forests, where both predators occur, may be partially responsible for the observed sharp fluctuations and declines in density.

This study occurred in the middle of a severe drought in north-central Florida and may have been another factor influencing densities. During this period, Dodd (1992) documented a dramatic decline in densities of upland amphibians and reptiles on the Ordway Preserve, which was positively correlated to the reduction in rainfall. Additionally, Jones (1990) documented dramatic declines in Florida mice (*Podomys floridanus*) in the sandhill community which was positively correlated to declining rainfall levels. Woodrat densities at Goose and Ashley lakes crashed, and water levels in these two lakes dropped sharply. These two study sites also are isolated from other mesic forest types which could potentially limit woodrat dispersal.

Negative effects from climatic changes such as drought on small mammal populations can result from numerous factors including a decrease in food supplies, lack of water, and other impacts on vegetation. Dependence by woodrats on drinking water for metabolic requirements is probably minimal; researchers have shown that *Neotoma* obtain their drinking water requirements primarily from vegetation (Linsdale and Tevis 1951; Dial 1988). Reduction in rainfall therefore, would likely impact woodrat populations primarily through vegetational changes. *Neotoma f. floridana* are largely herbivorous in their feeding requirements. They consume a wide variety of plants (Voeten 1990), but dependence on specific plant products, such as oak mast, has been suggested by Murphy (1952) and Neal (1967) among other researchers. If long-term drought conditions reduce plant production such as fruiting and flowering, reduction in one or several major food resources could also influence woodrat densities.

Resource scarcity can likewise affect reproduction which may be a critical factor for *Neotoma* because of its lower reproductive rate. Fitch and Rainey (1956) recorded declines in woodrat densities over a several year period. Neal (1967) documented sharp declines in a two year period. These researchers attributed the population declines to poor acorn crops and harsh winter conditions. Finally, secondary and compounded effects from declines in rainfall could affect plant resources and thus influence prey movement patterns as well as predator behavior (i.e. concentrations of predators in mesic habitats), which could influence densities of woodrat populations that live in these restricted mesic hammocks.

Home Range and Activity

Activity patterns of *Neotoma* observed in this study are similar to the activity periods observed by Wiley (1971), with high activity peaks between 2000 and 2200 h. Peaks of activity may be related to environmental variables, such as changes in temperature, precipitation, or light. Activity may also be influenced by foraging and gathering activities, related to the compulsive habit of woodrats to collect and store large quantities of food and other items in their dens (Worth 1950).

Numerous factors may influence the home range size and movement patterns of woodrats such as: density fluctuations of woodrats in all study sites, year round reproductive activity, the presence or absence of horizontal and vertical vegetation complexity, and use of multiple dens. These factors most likely influence the high variability of home range sizes observed in this study.

The importance of food resources to woodrat activities is apparent; while *Neotoma floridana* do not depend on single plant taxa, they are undoubtedly highly tuned to micro- and macro-distribution of food resources, plant phenologies, and environmental variables. Food resources likely influence woodrat movement patterns and home range size, but are extremely difficult to quantify. Fitch and Rainey (1956) documented changes in home ranges over time, attributing it to changes in food resources. Therefore, the variability in home range size over time documented in this study undoubtedly is linked to the diverse plant species composition in the forests and consequent production of diverse plant products.

Male and female home range sizes were similar in this study, although females were slightly larger than males. This contrasts to other studies where male home range sizes were larger than those of females (Fitch and Rainey 1956; Neal 1967). These results may be influenced by sample size and the high within-sample variability of the radiotelemetry observations. Contrary to many other mammalian radiotelemetry studies, male and female home ranges did not overlap in most of the study sites. The three ranges that did overlap (n=23) were male-female, and may have been associated with reproductive periods.

In the analyses of woodrat home ranges according to habitat type, size was on average smaller in the mesic hardwood and bottomland swamp habitats. In these areas densities were lowest, although all sites had wide-ranging individuals. However, this relationship between home range and habitat type was statistically significant in this study.

The influence of density on home range size documented by many researchers can result in a negative correlation between density and home range. Hence, when densities are low, home ranges frequently increase. That relationship was documented in this study, where individuals increased home ranges after the disappearance of other woodrats who had adjacent home ranges.

Another factor possibly influencing home range size is the complex horizontal and vertical vegetation structure in the bottomland hardwood swamp and mesic hammock with open understory habitats (e.g. high stem density coupled with large crown diameter). This complex vegetation structure may influence animal home range size due to higher 3-dimensional space use in this study. In other words, arboreal habitat use increased when woodrat dens were located in structurally complex vegetation. In contrast, where vegetation structure is less complex on vertical and horizontal planes, home ranges may be larger due to less three dimensional space use: animals may be travelling out rather than up in their movements (Mel Sunquist, pers.comm.). This could contribute to a smaller linear home range size in less complex habitats.

The bottomland swamp is also a large contiguous area. The other habitats, mesic hammock with saw-palmetto understory (MHP) at Ross and Goose lakes and mesic hardwood forest (MH) at Suggs and Ashley lakes, are narrow strips of mesic forest ranging from 50 m to 200 meters in width. Based on captured immigrants and disappearance of radio-collared animals, I suspect woodrats may make large scale movements. The Mill Creek Swamp populations remained the highest throughout the study, and the Ross and Suggs lakes populations declined but rebounded. These two areas are distally connected to Mill Creek Swamp, facilitating potential animal movements. The Ashley and Goose lakes sites are farther away and are disjunct from Mill Creek Swamp, potentially causing difficulties for woodrat dispersal into these areas, and populations disappeared in these two areas.

Dens

Large stick piles that are typical of *Neotoma floridana* den structures in other geographical areas were rare in this study. Most dens were subterranean, which agrees with findings by Pearson (1952) in Florida. Among other factors, these could be related to plant substrate types available in the habitat or soil types. Dens were also associated with several plant species. High variability in plant species at dens may be indicative of the importance of numerous plant resources, or plant structure for making dens, rather than specific species composition in den site selection.

Cover and complex vegetation structure at several of the dens were also high. Radiotelemetry in this study documented highly variable home ranges, but 54% were less than 0.5 ha. Rainey (1956) suggested woodrat home ranges were frequently in close proximity to the den. This vegetation complexity at dens would be advantageous to small ranging animals for protection and food resource availability. The most significant characteristic of den site location was that 69% of all dens were located on an ecotone. Access to diverse resources may therefore be an important influencing factor in den site selection.

Several woodrats changed den sites, which may be attributed to preferred structural features at specific dens (i.e. stem density and cover), geographical location, or avoidance of parasites. Woodrat dens may be a limiting factor in the community. Many times woodrats relocated into a den after the previous occupant disappeared, and some dens were subsequently used by several different tenants, indicating there may be "preferred den sites." Dial (1988) reported "preferred den sites" also, indicating that dens may be in limited supply. Other studies have documented that mammals will evacuate dens when parasite loads become too high. Bot fly larvae infestation in woodrats was relatively high, and bot flies are known to lay their eggs at rodent dens. Therefore, this could account for some of the den infidelity observed. However, "preferred dens" may simply be more “functional” as houses than others. The use of one or more dens also influences home range size, particularly if dens are not in close proximity.

Habitat Utilization

Utilization of micro-habitats by woodrats was proportional to the habitats available. As expected, they utilized all of the micro-habitat types available except bare ground. A preference was exhibited towards saw-palmetto in the mesic hammock-saw-palmetto habitat, and swamp for the animals inhabiting the edge of Mill Creek Swamp, which may be related to vegetation cover requirements.

Woodrats were distributed in clusters in continuous habitats, forming what I entitled "woodrat neighborhoods," although they used solitary den sites. The reported "colonial" nature of woodrats in previous studies in Florida (Pearson 1952; Chamberlain 1928) may be factual, but also may be an interpretation of large scale "coloniality," or a cluster distribution, observed in this study. It is not clear whether these cluster distributions are associated with micro-habitats, although they do not appear to be associated with macro-habitat types because woodrats were not trapped throughout continuous habitats.

While I had minimal success using fluorescent pigment powders to document three dimensional space use, the data in this study suggest the arboreal nature of *Neotoma f. floridana*. The fluorescent pigment technique has been highly successful in some studies (Mullican 1988) to document home range and arboreal activity (Goodyear 1989). However, if vegetation density is high, and if the animal grooms compulsively, release of pigment powder can be significantly reduced.

LITERATURE CITED

Barbour, D.B., and S.R. Humphrey. 1982. Status and habitat of the Key Largo woodrat and cotton mouse (*Neotoma floridana smalli* and *Peromyscus gossypinus allapaticola*). J. Mamm. 63:144-148.

Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. J. Mamm. 24:346-352.

Byers, C.R., and B.K. Steinhorst. 1984. Clarification of a technique for analysis of utilization-availability data. J. Wildl. Mgmt. 48: 1050-1053.

Calhoun, J.B. 1962. The ecology and sociology of the Norway rat. Washington, D.C., U.S. Dept. Health Educ. Welfare, Public Health Serv. 288 pp.

Chamberlain, E.B. 1928. The Florida wood rat in South Carolina. J. Mamm. 9:152-153.

Coleman, J.S., and A.B. Jones, III. 1988. User's guide to TELEM88: Computer analysis system for radiotelemetry data. Dept. Fish. Wildl., Virginia Polytechnic Inst. and State Univ., Blacksburg, VA. 49 pp.

Davis, D.E. 1953. The characteristics of rat populations. Quart. Rev. Biol. 28:373-401.

Dial, K.P. 1988. Three sympatric species of Neotoma: dietary specialization and coexistence. Oecologia 76:531-537.

Dodd, C.K. 1992. Biological diversity of a temporary pond herpetofauna in North Florida sandhills. Biodiv. Conserv. 1:125-142.

Eisenberg, J.F. 1989. Mammalian species of the Ordway Preserve. Univ. Florida, Florida Mus. Nat. Hist., Ordway Preserve Rept.1, Gainesville. 73 pp.

Fitch, H.S., and D.G. Rainey. 1956. Ecological observations on the woodrat *Neotoma floridana*. Univ. Kansas Publ.Mus. Nat. Hist. 8:499-533.

Franz, R., and D.W. Hall. 1990. Vegetative communities and annotated plant lists for the Katharine Ordway Preserve-Swisher Memorial Sanctuary, Putnam County,Florida. Univ. Florida, Florida Mus. Nat. Hist., Ordway Preserve Rept.3, Gainesville. 89 pp.

Goertz, J.W. 1970. An ecological study of *Neotoma floridana* in Oklahoma. J. Mamm. 51:94-104

Goodyear, N.C. 1989. Studying fine scale habitat use in small mammals. J. Wildl. Mgmt. 53:941-946.

Greer, R.E. 1978. Eastern woodrats in south-central Florida. Florida Sci. 41:191-192.

Hamilton, W.J.,Jr., and J.O. Whitaker. 1981. Mammals of the Eastern United States. Cornell Univ. Press, Ithaca, New York. pp. 207-211.

Hamilton, W.J.,Jr. 1953. Reproduction and young of the Florida woodrat, *Neotoma f.floridana*. J. Mamm. 34: 180-189.

Harris, S., W.J. Cresswell, P.G. Forde, W.J. Trewhella, T.Wollard, and S. Wray. 1990. Home range analysis using radiotracking data: a review of problems and techniques particularly as applied to the study of mammals. Mamm. Rev. 20:97-123.

Harvey, M.J., and R.W. Barbour. 1965. Home range of *Microtus ochrogaster* as determined by a modified minimum area method. J. Mamm. 46:398-402.

Hays, R.L., C. Summers, and W. Seitz. 1981. Estimating wildlife habitat variables. Washington, D.C. U.S. Dept .Int., Fish Wildl. Serv. FSW/OBS-81/47. 111 pp.

Hersh, S. 1981. Ecology of the Key Largo woodrat (*Neotoma floridana smalli*). J. Mamm. 62: 199-201.

Humphrey, S.R. 1988. Density estimates of the endangered Key Largo woodrat and cotton mouse (*Neotoma floridana smalli* and *Peromyscus gossypinus allapaticola*) using the nested grid approach. J. Mamm. 69:524-531.

Jones, C.A. 1990. Microhabitat use by *Podomys floridanus* in the high pine lands of Putnam County, Florida. Ph.D. Dissertation, Univ. Florida, Gainesville.

Kaufmann, J. H. 1962. Ecology and social behavior of the coati, *Nasua narica* on Barro Colorado Island, Panama. Univ. California Publ. Zool. 60:95-222.

Kinsey, K.P. 1976. Social behavior in confined populations of the Allegheny woodrat, *Neotoma floridana magister*. Anim. Behav. 24:181-187.

Layne, J.N. 1974. The land mammals of South Florida. Pp.386-413 *in* P.J. Gleason, ed. Environments of South Florida: Present and past. Mem. Miami Geol. Soc. 2:1-452.

Leman, C.A., and P.W. Freeman. 1985. Tracking mammals with fluorescent pigments: A new technique. J. Mamm.66:134-136.

Linsdale, J.M., and L.P. Tevis, Jr. 1951. The Dusky Footed Woodrat. Univ. California Press, Berkeley. 664 pp.

Ludwig, J.A., and J.F. Reynolds. 1988. Statistical Ecology. John Wiley and Sons, New York. 337 pp.

Michener, G.R. 1979. Spatial relationships and social organization of adult Richardson's ground squirrels. Canadian J. Zool. 57:125-139.

Mullican, T.R. 1988. Radiotelemetry and fluorescent pigments: A comparison of techniques. J. Wildl. Mgmt. 52:627-631.

Murphy, M.F. 1952. Ecology and helminths of the Osage woodrat, *Neotoma floridana osagensis*, including descriptionof *Longistriata neotoma* n. sp. (Trichostrongylidae). Amer. Midl. Nat. 48:204-218.

Neal, W.A. 1967. A study of the ecology of the woodrat in the hardwood forests of the lower Mississippi River Basin. M.S. Thesis, Louisiana State Univ., Baton Rouge. 116 pp.

Pearson, P.G. 1952. Observations concerning the life history and ecology of the wood rat *Neotoma floridana floridana* (Ord). J. Mamm. 33:459-463.

Poole, E.L. 1940. A life history sketch of the Allegheny woodrat. J. Mamm. 21:249-270.

Rainey, D.G. 1956. The Eastern woodrat, life history and ecology. Univ. Kansas Mus. Nat. Hist. 8:499-533.

Schwartz, A., and E.P. Odum. 1957. The woodrats of the eastern United States. J. Mamm. 38:197-206.

Schwartz, C.W., and E.R. Schwartz, 1959. The Wild Mammals of Missouri. Univ. Missouri Press, Columbia. 341 pp.

Sciascia, J. 1990. Eastern woodrats decline in tri-state area. Nongame News. New Jersey Dept. Envir. Prot., Hampton. 2 pp.

Sunquist, M.E. 1989. Comparison of spatial and temporal activity of red foxes and gray foxes in north-central Florida. Florida Field Nat. 17:11-18.

Timmerman, W. 1989. Home range, habitat use, and behavior of the Eastern diamondback rattlesnake. M.S. Thesis. Univ. Florida, Gainesville.

Voeten, M.M. 1990. Aspects of the feeding ecology of the Eastern woodrat. M.S. Thesis, Univ. Utrecht, The Netherlands. 41 pp.

Wiley, R.W. 1971. Activity periods and movements of the Eastern woodrat. Southwestern Nat. 16:43-54.

Wiley, R. W. 1980. Mammalian species. *Neotoma floridana*. No. 139, pp. 1-7

Worth, C.B. 1950. Observations on the behavior and breeding of captive rice rats and woodrats. J. Mamm. 31:421-426.

Wright, D. 1989. Mortality and dispersal of juvenile opossums (*Didelphis virginiana*). M.S. Thesis, Univ. Florida, Gainesville.

Zar, J.H. 1984. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, New Jersey. 718 pp.