



**Fourth Colloquium
on Conservation of Mammals
in the Southeastern United States**

Edited by BRIAN R. CHAPMAN
and JOSHUA LAERM

Occasional Papers of the
North Carolina Museum of Natural Sciences and the
North Carolina Biological Survey
Number 12
Fall, 2000

ECOLOGY AND CONSERVATION OF A FRONTIER POPULATION OF THE ROUND-TAILED MUSKRAT (*NEOFIBER ALLENI*)

Bradley J. Bergstrom, Tim Farley, Harvey L. Hill, Jr., and Tip Hon

Department of Biology, Valdosta State University, Valdosta, GA 31698 (BJB)

Georgia Department of Natural Resources, Wildlife Resources Division,
Fitzgerald, GA 31750 (TF, HLH, TH)

Present address of TF: Florida Game and Fresh Water Fish Commission, Ocala, FL 34474

The round-tailed muskrat (*Neofiber alleni*) is endemic to the lower southeastern coastal plain of the United States, occurring locally in shallow freshwater wetland habitats, mainly in peninsular Florida. We report several new localities for the species in south-central Georgia. We studied the population ecology of these muskrats by quantification of habitat, live trapping, and radiotelemetry. We provided 10 years of censuses and data on individual home range and movement patterns for the population at Grand Bay, Georgia, and we challenged previous reports of round-tailed muskrats occupying only two houses and being strictly solitary. Ecological densities in this peripheral population were lower than densities reported from natural marshes in Florida, and crude densities appeared to fluctuate on a 2-year cycle. Floating mats of bog-like vegetation surrounded by open-water and emergent marsh dominated by sedges, such as *Carex* and *Eleocharis*, were the most commonly occupied habitats. We recommended controlled burning, hydroperiod management, and management of mats to increase habitat available to *N. alleni* in Georgia.

The round-tailed muskrat (*Neofiber alleni*), a semi-aquatic arvicoline rodent of freshwater marshes, is a member of a monotypic genus first described in 1884. *N. alleni* previously was known only from peninsular Florida, a possibly distinct population in the panhandle (Wassmer and Wolfe, 1983), and a few localities in south-eastern Georgia (Schantz and Jenkins, 1950). Pocosins and Carolina bays, which are shallow, peat-filled or muck-filled depressions common in parts of the south-eastern coastal plain (Sharitz and Gibbons, 1982), provide habitat for the round-tailed muskrat. Harper (1920) documented *Neofiber* in prairie habitats on the eastern side of Okefenokee Swamp. The only other published record of the species in Georgia (Schantz and Jenkins, 1950) is an account of skulls of *N. alleni* in pellets from barn owls (*Tyto alba*) near Woodbine, Camden Co. Unlike the muskrat, *Ondatra zibethicus*, *N. alleni* rarely is found in open water and is nocturnal, with crepuscular peaks (Birkenholtz, 1972). Round-tailed muskrats are non-territorial and build their houses in dense clusters or colonies.

Neofiber alleni is listed as a species of special concern in Florida (Lefebvre and Tilmant, 1992) and is a threatened species in Georgia, but has no status federally. The species is locally distributed in freshwater wetlands throughout Florida and, apparently, is subject to wide fluctuations in population density. Greatest reported densities are for sugarcane fields in southern Florida,

where the species may be considered a pest (Lefebvre, 1982; Steffen, 1978). On smaller natural marshes in central Florida, *N. alleni* may reach maximal densities of 250-300/ha, whereas on larger marshes (>1,000 ha), maximal densities are 50/ha (Birkenholtz, 1963). Round-tailed muskrats build small, tightly woven, dome-shaped houses from grasses, sedges, or cattails, which are attached to surfaces of floating mats of *Sphagnum*, plant roots and organic muck, or to bases of shrubs or small trees (Baker, 1889; Birkenholtz, 1972; Chapman, 1889; Harper, 1920, 1927; Tilmant, 1975). They also clip vegetation to build floating feeding platforms (Birkenholtz, 1963). However, when water levels drop, round-tailed muskrats abandon their houses and tunnel into the saturated peat substrate.

In autumn 1987, we discovered several colonies of *N. alleni* inhabiting three semi-isolated wetlands within the 5,200-ha Grand Bay wetland ecosystem (including Grand Bay Wildlife Management Area and adjoining lands) in northeastern Lowndes Co. and southeastern Lanier Co., Georgia. These three wetlands have had different management histories, and, therefore, varied in microhabitat composition. We attempted to describe the status and population ecology of populations at Grand Bay by live trapping, quantification of habitat, annual surveys by airboat and helicopter, and observation of radiotelemetered muskrats.

STUDY AREA

The three wetland habitats where colonies of *N. alleni* were found within the Grand Bay ecosystem displayed characteristics of Carolina bays (Sharitz and Gibbons, 1982), which are elliptical, peat-filled or muck-filled shallow depressions manifesting a variety of wetland vegetative types. During 1987-1988, habitats could be classified as open marsh with floating-mat vegetation (Grand Bay), shrub bog (Oldfield Bay), and chain-fern (*Woodwardia virginica*) marsh with saturated peat soil, but little open water (Rat Bay). Due to fire exclusion, shrub-bog and chain-fern habitats were succeeding toward dense-understory, quasi-terrestrial habitats in 1987. Rat Bay, a 340-ha portion of a Carolina bay that was isolated by construction of water-control dikes, was dominated by chain fern, with a thick mat of *Sphagnum* and widely scattered shrubs and small trees. The water table was at, or below, the surface in most areas. Grand Bay was a 550-ha Carolina bay with habitats ranging from open water to emergent marsh to shrub bog to pond cypress (*Taxodium ascendens*) and black gum (*Nyssa biflora*) swamp. Evidence of round-tailed muskrats was found mostly on floating mats at edges of small patches of shrub bog and near open water.

Water levels on Grand Bay, which were maintained by permanent water-control structures, were much higher than on Rat Bay; consequently, vegetative growth was higher and denser on Rat Bay, where there was little or no open water. A thick layer of sphagnum had accumulated over most of the site. A successful burn in late autumn 1987, and completion of water-control structures, allowed managers to raise and maintain water levels and, thereby, return Rat Bay to a more open, emergent, marsh habitat by 1989. Oldfield Bay (2,400 ha) was still succeeding and most of it, apparently, was abandoned by *N. alleni* during the first 6 years of the study.

MATERIALS AND METHODS

Preliminary surveys of nesting and feeding structures, and of habitat structure and plant composition, were conducted on Grand Bay and Rat Bay from late winter through summer 1988. Surveys by helicopter of suitable wetland habitats in Brooks, Thomas, Lowndes, Lanier, Berrien, Cook, and Clinch counties, Georgia, were conducted in March 1991 to try to discover additional colonies of *N. alleni*.

Characterization of habitat.—Centered on occupied areas of marsh habitat within both Grand Bay and Rat Bay,

a rectangular survey grid 180 by 680 m (12.24 ha) with 350 stations spaced 20 m apart was established in each wetland. Using a stratified-random procedure, we chose 48 stations at each of the two sites for a modified point-quarter survey (Müeller-Dombois and Ellenberg, 1974) of all plants. At each station, four 1-m² Daubenmire plots were located by a random procedure near each station, and four 10-m surface-cover transects radiated from the station marker at random compass directions, but at right angles to each other. Number of stems of each species of plant was recorded, as was depth of standing water and average height of vegetation. For cover transects, a tape scored on 0.1-m intervals was used to estimate percentage coverage of the following: 1, open water; 2, open floating mat or mud flat; 3, vegetated floating mat; 4, peat soil; 5, emergent vegetation; 6, tree or shrub. Species name of any tree or shrub whose branches overlaid the tape or whose trunk came within 0.1 m of the tape was recorded. All habitat data were collected in June and July 1988.

Live trapping.—Preliminary attempts to live-trap round-tailed muskrats on the three Grand Bay habitats were made in winter 1987-1988, and again in summer 1988. We used single-entry, Tomahawk 201, wire-cage live-traps, Fitch live-traps, and Gregerson snares (size 0) placed around exposed plunge holes. Beginning in later winter 1991, and continuing through summer, we again attempted to live-trap rats, but this time only in Grand Bay using Haguruma live-traps (Honolulu Sales, Ltd., Honolulu, HI). Traps were baited with halved golden delicious apples, and natural vegetation (grasses, sedges) was placed over the floor of the wire-mesh trap surrounding the treadle.

Radiotelemetry.—In 1991, live-captured *N. alleni* from Grand Bay were implanted within 24 h with 7-g radiotransmitters (Telemetry Systems, Inc., Mequon, WI) sealed in epoxy resin and equipped with magnetic switches. Frequencies of radiotransmitters were 164-168 KHz. Animals were sedated with an intramuscular injection of ketamine hydrochloride at 0.05 cc/100 g of body weight, which generally took effect in 5 min and lasted for 20 min. Radiotransmitters were soaked for 24 h prior to surgery in a povidone-iodine solution, and were implanted intraperitoneally between the rectus abdominus and external oblique muscles through a 30-mm incision. A 0.1-cc injection of penicillin was given following surgery. Each animal was released at its point of capture after a 24-h recovery and observation period.

A Telonics TR-2 receiver and 3-element Yagi antenna

were used to locate muskrats after release, using an air-boat as observation points. Each animal was located at least twice each day; around dawn and dusk, and some animals were tracked continuously throughout the night. All houses of round-tailed muskrats and occupied mats were mapped in reference to the Grand Bay grid, and each telemetry fix was recorded in terms of distance and compass direction from the nearest house. Each muskrat was followed daily until its signal disappeared, it was found dead, or a loose radiotransmitter was found. As an estimate of area of home range, Minimum Convex Polygon (MCP; Bergstrom, 1988) was calculated for all telemetered animals for which eight or more different locations were recorded.

RESULTS

Populations of *N. alleni* at Grand Bay represent a range extension of ≥ 72 km north and 80 km west of previously reported localities in northern Florida and southeastern Georgia, respectively (Fig. 1). The closest distance of these colonies to any published locality for *Neofiber* is 58 km NNE Madison, Madison Co., Florida (Hall, 1981). In 1991, surveys conducted by helicopter of all likely habitats in seven counties in south-central Georgia resulted in discovery of one additional colony of 13 houses in Brooks Co., 2 km N Florida state line (13 km SSE Quitman). Several other small colonies were observed just across the state line in Madison and Hamilton counties, Florida. Colonies that previously were reported from southern Thomas Co. (W. Baker, pers. comm.) and southwestern Lowndes Co. (T. Hon, pers. comm.) were not found. In 1996, a large colony with 146 active houses, not seen in 1991, was discovered in Bowen Mill Pond, 5 km W Quitman, Brooks Co.

Houses and other structures.—In 1987-1988, in Grand Bay and Oldfield Bay, *N. alleni* built conspicuous houses woven from *Carex* or other sedges and anchored to either a floating mat or the base of a shrub. Although numerous inactive houses remained in Rat Bay, by autumn 1987, the water table was below the surface, and muskrats tunneled directly into the sphagnum mat, rather than build houses. Houses typically were constructed of the sedge *Carex striata* (= *walteriana*), which usually grew near houses or tunnels. Blades of slender spikerush (*Eleocharis*) also were sometimes used. Houses were ca. 25-38 cm tall, 30 cm wide at the base, and dome-shaped. Inside, there was a medial nesting or feeding platform and two lateral plunge holes beginning just above water

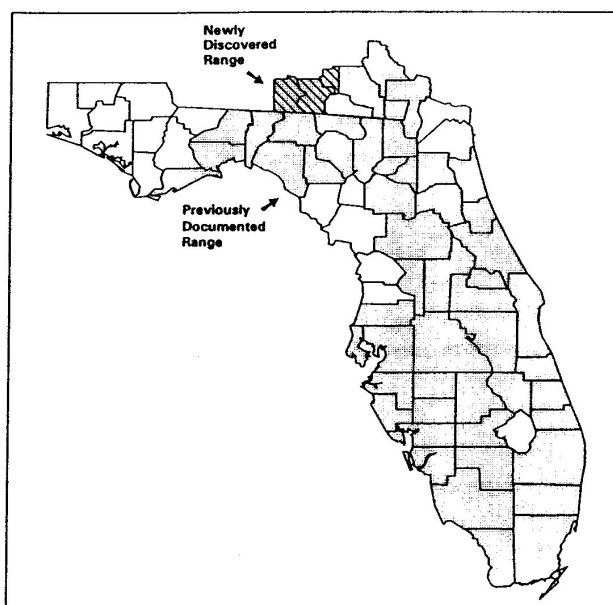


Fig. 1.—Map of Florida and southern Georgia showing distribution by county of *Neofiber alleni*, as previously reported and as newly discovered (adapted from Wassmer and Wolfe, 1983)

level and ca. 5-7 cm in diameter. In two or three active houses that were examined on Grand Bay in 1991, one of the plunge holes went straight down into the water below the mat, while the other curved and extended horizontally through the mat. Several plunge holes usually were found on larger mats that contained active houses; these may have connected with horizontal tunnels through the mat or led to the water below. Feeding platforms were areas ca. 20 cm wide that were cleared of growing vegetation, exposing the peat or muck, and usually were located close to the edge of the mat. Plant fragments in evidence around feeding platforms included roots of *Lachnanthes* and *Xyris*, stems of *Eleocharis* and *Carex*, and seedheads of *Lachnanthes* and *Carex*.

Most construction of new houses was observed during March and April. Old houses were repaired with fresh blades of green sedge (*Carex* and *Eleocharis*) that were conspicuously woven among the brown blades of the existing house. Before emergent vegetation started its rapid growth and wetlands greened up was the best time to census houses aerially. Many abandoned houses were seen on occupied mats; many of these had been taken over by swarms of fire ants (*Solenopsis*), and were not

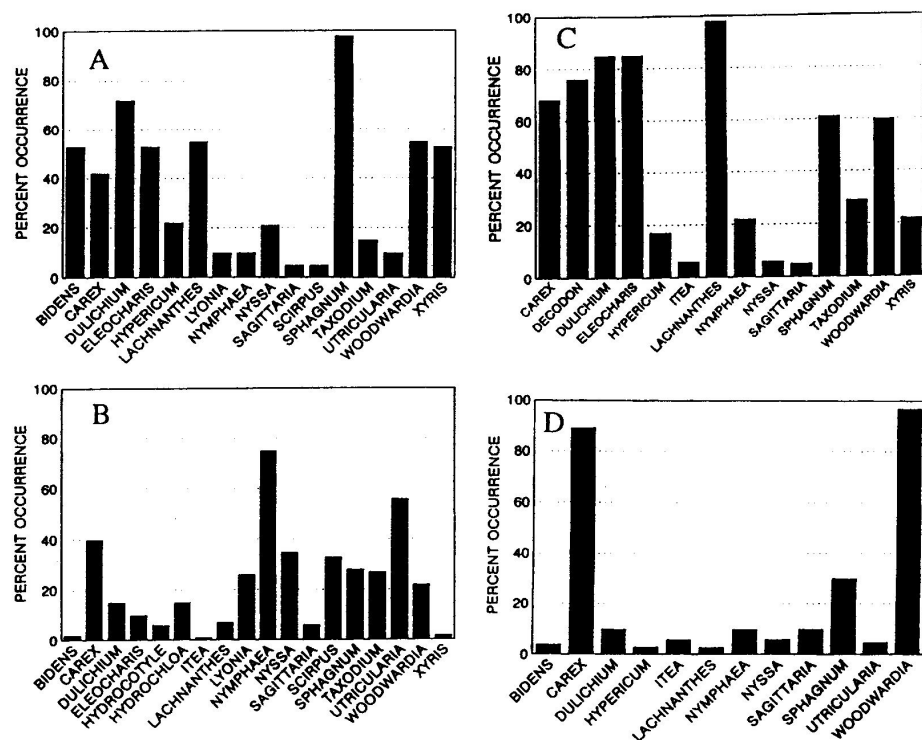


Fig. 2.—Percentage occurrence of herbaceous and woody plants of various species on 192 1-m² Daubenmire plots randomly placed in four plant-community types in Grand Bay, Georgia, in decreasing order of suitability as habitat for *Neofiber alleni*: a) floating-mat bog/marsh; b) mixed emergent marsh; c) sledge marsh; d) chain-fern marsh.

counted during surveys conducted by airboat and helicopter in spring.

Characterization of habitat.—In summer 1988, Rat Bay had a thick and continuous mat and little or no standing water (mean height of water, 0.19 cm; minimum, 0; maximum, 5.0). There were two dominant plant-community types in Rat Bay; sedge emergent marsh (27% coverage) and chain-fern emergent marsh (73% coverage). In the sedge emergent community, the wetland grass *Lachnanthes caroliniana* (redroot) was the most dominant species, and four taxa of sedges (Cyperaceae); *Carex striata*, *Eleocharis*, *Dulichium arundinaceum*, and *Cyperus erythrorhizos*, along with the semi-woody perennial *Decodon verticillatus*, were codominant (Fig. 2c). *Sphagnum* and *Woodwardia virginica* (chain-fern) also were encountered frequently. Chain-fern habitat had much lower species equitability and was dominated by *W. virginica* and *L. caroliniana* (Fig. 2d). Sedge marsh at the time of low water levels was a more mesic habitat, having

a substantial layer of sphagnum and greater density of shrub and tree roots. Plunge holes and freshly excavated organic matter were noted mainly in sedge areas. We presume that *N. alleni* selected sedge areas preferentially because of both moisture conditions and greater abundance of natural foods. Mean height of vegetation at Rat Bay under these low water levels was higher and less variable (mean, 93.6 cm; minimum, 67.7; maximum, 142.9) than Grand Bay (mean, 54.9 cm; minimum, 0; maximum, 110).

The Grand Bay site was more diverse due to much higher water levels (mean, 62.35 cm; minimum, 47.5; maximum, 85.1) and included four distinct habitat types. Mixed emergent marsh (25% coverage) was dominated by fragrant water lily (*Nymphaea odorata*) and bladderwort (*Utricularia*; Fig. 2b); other

species were limited to floating mats or tree and shrub islands. *Nymphaea* would have been more dominant had it not been for prior treatment of the open-water areas of Grand Bay with the herbicide Sonar (Dow Elanco Co., Harbor Beach, MI), which selectively killed water lilies. Sedge emergent marsh (32% coverage) included areas of more extensive vegetation, which probably represented old floating mats that had coalesced and had been colonized for a longer time, displaying a greater abundance and diversity of plants. In this habitat, *Carex* and *Scirpus* were more abundant than in more open habitat, as were small black gum and pond cypress trees. Because this habitat contained portions of deep, open water, *Carex* had relatively low percentage occurrence (Fig. 2c).

Floating-mat communities (20% coverage) usually were covered by herbaceous and shrubby growth. *Carex*, *Lachnanthes caroliniana*, *Xyris*, and *Lyonia ludida* were common (Fig. 2a), but these areas also exhibited 50-80% open water. True floating-mat community had the greatest

diversity of plant species of the four habitat types and was the habitat where houses, plunge holes, and feeding platforms of *N. alleni* most often were found. Although vast expanses of chain-fern marsh (Fig. 2d) were found on the edge of Grand Bay, it covered 25% of sampling grids and apparently was used little, or not at all, by *N. alleni*.

The area of Grand Bay where houses and other evidence of *Neofiber* were found 1988-1994 was an ecotone between mixed emergent marsh and dense chain-fern marsh and was where floating mats and sedge emergent marsh (with scattered small trees and shrubs) were found. This ecotonal area constituted suitable habitat for *N. alleni* in Grand Bay and covered an area of 34 ha, on average, throughout the study.

Surveys of houses.—In spring and summer 1988, 67 houses were located by airboat in Grand Bay; 32% of these were located in three areas of high concentration or colonies. Of the area of available habitat sampled in Grand Bay (34 ha), <25% was used by *N. alleni* in 1988. In 1989 and 1990, number of houses in the area increased gradually (Fig. 3). In 1990, houses were surveyed both by airboat and helicopter, and we found 20% more houses during the helicopter survey than during the airboat survey. In subsequent years, only surveys by helicopter were done. Numbers of houses increased from 1991 to 1992, declined in 1993, and recovered in 1994. The increase in 1992 may have been due to long-term effects of treatment in 1988 of fragrant water lily with aquatic herbicide, which produced a massive kill. After a few years, this substantial amount of partially decayed biomass floated to the surface, producing new mats. Many of the new houses in 1992 were built on new mats in an area of Grand Bay that previously had been mixed emergent marsh dominated by fragrant water lily.

Decline in number of houses in 1993 may have been an anomaly due to a severe winter storm just prior to the census. Perhaps, many houses were obliterated by wave action or hidden from aerial view by debris. In fact, several houses used by muskrats with radiotransmitters in 1991 apparently were still in use in February 1994. However, following establishment and colonization of new mats by 1992, fluctuation in the census of houses suggested a 2-year cycle. Oldfield Bay was surveyed only during the last 4 years of the study and also showed a possible 2-year cycle, with trends reciprocal with those of Grand Bay (Fig. 3).

Using an index of 2.2 houses/round-tailed muskrat (Birkenholtz, 1963) and our counts of active houses, the

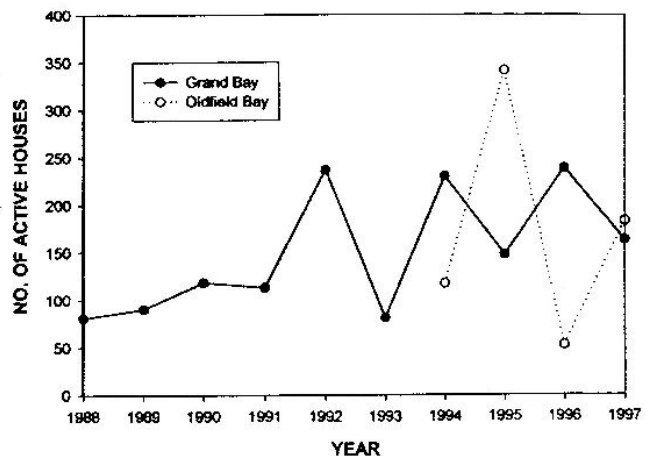


Fig. 3.—Number of active houses of *Neofiber alleni* counted from a helicopter in early spring on Grand Bay (solid) and Oldfield Bay (dashed), Georgia. Surveys in 1988 and 1989 were conducted by airboat and their results adjusted upward by 20%; all subsequent surveys were conducted by helicopter.

population in Grand Bay ranged from 36 to 108 animals. Given that there was 34 ha of suitable habitat in the inhabited portion of Grand Bay, we estimated that population density ranged from ca. 1 to ca. 3 muskrats/ha. During the 3 years in which Oldfield Bay was surveyed, population estimates ranged from 23 to 155 round-tailed muskrats.

Live trapping.—Our attempts at live trapping in 1987 and 1988 proved labor-intensive and ineffectual, yielding only one capture in >800 trap nights using Tomahawk and Fitch traps and snares. Other species that were captured frequently in or near dwellings and tunnels of *N. alleni* included *Oryzomys palustris*, *Sigmodon hispidus*, and *Peromyscus gossypinus*. The latter two species were encountered most frequently in Oldfield Bay where houses had little evidence of recent work and where floating mats had coalesced into continuous expanses of dense, wet-savannah habitat, dominated by grasses and small trees and shrubs.

In 1991, we began using Haguruma live traps, and although trap success was still low, it was greater than in previous attempts. Activity of round-tailed muskrats on Grand Bay was relatively high in late winter through early summer and declined in late summer. A total of 15 captures of eight individuals was made March-August 1991 (2,790 trapnights with Haguruma traps). Six were adult males and two were adult females. Five of the six

Table 1.—Radiotelemetry data for eight *Neofiber alleni* from Grand Bay, Georgia, 1991.

Muskrat	Sex and reproductive condition ^a	Mass (g)	Number of traps and telemetry locations	Number of days observed	Number of mats occupied	Number of houses occupied	Size of home range (m ²)	Maximum dimension of home range (m)	Fate
LD	M+	276	67	55	5	10	58 (activity areas) 130 (plus movement corridor)	72	lost signal
ME	M+	249	10	7	1	2	20	7.5	predation by alligator
CU	M+	265	8	7	1	4	13	7.5	predation by owl
JA	F+	242	6	5	2	3			predation by alligator
JR	M	239	5	2	2	2			lost signal
CP	M+	211	7	1	1	1			lost signal
PP	M+	304	3	1	1	1			died in trap
NO	F	201	2	2	1	2			found dead

^a A + indicates a male with scrotal testes or a female with one or more of the following: pregnant; perforate vagina; swollen nipples, open pubic symphysis.

males had scrotal testes, and one female had a perforate vagina and possibly was pregnant (Table 1).

Radiotelemetry.—Each animal captured in 1991 was implanted with a radiotransmitter, and with one exception, each was released within 48 h of capture. The first muskrat released (NO in Table 1) probably died of trauma related to the operation and was found only 5 m from the house near which she had been trapped. Only three muskrats were tracked ≥ 1 week and were located enough times to enable us to arrive at reasonable estimates of home range (Table 1).

Compared to muskrats ME and CU, the much greater size of home range and number of houses occupied by muskrat LD (Table 1; Fig. 4a) was not a function of time under observation, as LD covered nearly the length of his home range twice within a 24-h period on

several occasions and occupied three houses within one 2.5-h period. No other muskrat was seen or trapped within the vicinity of these five mats, although the possibility of a mate or even another male with overlapping home range is not precluded, especially because LD was not known to use four of the active houses on the five mats.

Muskrats ME and CU were relatively sedentary and were found on two occasions in the same house (Fig. 4b), which contradicts Birkenholtz's (1963, 1972) assumption that *N. alleni* is strictly solitary. Both muskrats also used another house, but not at the same time.

Radiotelemetry also provided some insights into predation pressure on the population. Three round-tailed muskrats released with radiotransmitters appeared to have been predated (Table 1), two by alligators (*Alligator mississippiensis*) and one by a raptor, probably a barred owl

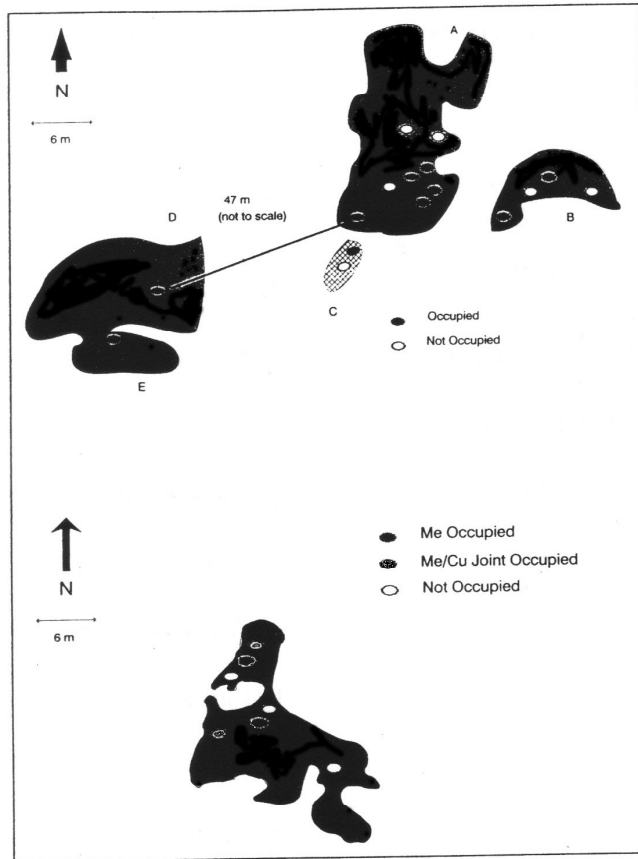


Fig. 4.—A, top half: Diagram of five mats (A-E) used by round-tailed muskrat LD over 55 days of observation, including all 14 houses appearing on mats and indication of the 10 houses that radiotelemetry revealed he was occupying. B, bottom half: Diagram of round-tailed muskrats CU and ME over 7 days of observation, including all seven houses appearing on mats and indication of the four houses that radiotelemetry revealed one or both were occupying.

(*Strix varia*). CU's radiotransmitter was found in shallow water at the base of a whitewashed snag where an owl had been spotted previously. In 1988 at Grand Bay, we observed a red-shouldered hawk (*Buteo lineatus*) flying away, clutching a round-tailed muskrat in its talons. The three apparent cases of predation occurred within 1 week of release of muskrats with radiotransmitters. Radio-signals of two other muskrats, which may have been predated, were lost within 1 and 2 days, respectively, of release (Table 1).

We found, as have other studies, that, even in suitable habitat, houses of *N. alleni* were tightly clumped into colonies, perhaps because of limited availability of mats in the appropriate successional stage (Birkenholz, 1963; Lefebvre, 1982; Steffen, 1978). Houses and mats were occupied for ≤ 3 years in our study, compared to 5 months reported by Birkenholz (1963). Our study, the first to present movement and home-range data from radio-telemetry, suggests that the estimate of 2.2 houses/ animal (Birkenholz, 1963) may be low, given that one of our animals occupied 10 houses. Our radiotelemetry data indicate remarkably small home ranges for *N. alleni* compared to mammals of similar body size (Table 1; Swihart et al., 1988), and sharing of houses by two males suggests *N. alleni* may not be entirely solitary. Predation of *N. alleni* by alligators had not been documented prior to our study (Birkenholz, 1963; Porter, 1953).

Population densities, as assessed by counts of houses at Grand Bay, were as much as one or two orders of magnitude lower than those from central Florida (Birkenholz, 1963), and long-term population dynamics suggest a 2-year cycle (Fig. 3), which may be a response to the cyclical succession of formation and die-back of the floating-mat habitat.

Although population densities are low, distribution of *N. alleni* appears fairly continuous within suitable habitat from north-central Florida into south-central Georgia. Although not documented previously in the latter area, populations probably have existed here since pre-settlement times. Subspecific affinities of these populations are not known, but the new localities in Lowndes and Brooks counties are closer to the previously described range of *N. a. apalachicola* in northern Florida than to the range of *N. a. exoristus*, known from the eastern Okefenokee Swamp in Georgia (Hall, 1981; Schwartz, 1953). There is an apparent 80-km gap in distribution between populations at Grand Bay and Okefenokee Swamp, although suitable habitat is present in this area.

Perceived distributional gaps at this northern limit of distribution may result from a combination of the fragmented, isolated distribution of palustrine wetlands and the generally low population densities causing localized extinction. Birkenholtz (1963) documented dispersal of *N. alleni* across roads and other upland habitats and via ditches from populations south of Gainesville, Florida. The degree of isolation of habitat also may have been lesser and availability of dispersal corridors greater farther

south. With ecological densities of 1-3 muskrats/ha, a litter size of 2.2 (low for an arvicoline—Birkenholtz, 1963), and high rates of predation we witnessed in the population in Grand Bay, the species may not sustain a viable population so far from its center of abundance where suitable habitat is so isolated. This seems a more plausible explanation for the northern distributional limit than the direct effects of cooler climate (Birkenholtz, 1972).

Populations of *N. alleni* in Georgia may be the most peripheral sinks for species dispersal and, therefore, may be recolonized only following periods of exceptionally high densities in more central populations. However, natural dispersal is an unlikely event given continuing fragmentation and destruction of wetland habitats in the Southeast (Mitsch and Gosselink, 1993). This may explain why two colonies observed previously in southwestern Georgia were not found in our recent aerial surveys. A viable population may survive in the 30,000 ha of wet prairies and islands of Okefenokee Swamp. Harper (1927) estimated the population at 10,000, but Porter (1953) and recent visits (T. Hon) found few signs of active houses.

Another potential problem for viability of populations is interruption of the natural hydroperiod and suppression of natural fires. During droughts, summer burns historically consumed much of the shrubby and hardwood growth that encroached on the marsh and burned accumulated peat to considerable depths, restoring a deeper-water system conducive to the cyclical succession of the round-tailed muskrat's floating-mat habitat. Winter droughts also occasionally exposed roots of aquatic macrophytes to a killing frost, causing die-backs of such plants as *Nymphaea*, *Pontederia*, and *Sagittaria*, and yielding organic matter for production of mats in the future. Loss of habitat through hydrarch succession may be a problem throughout the range of the round-tailed muskrat and may explain why Porter (1953) found *N. alleni* to be either extirpated or rare in many areas of Florida that previously had supported dense populations.

Densities also may react negatively to introduced fire ants (Harper, 1927; Johnson, 1961; Porter, 1953; Steffen, 1978). We found many abandoned muskrat houses taken over by colonies of fire ants, and other colonies of muskrats often were close to fire-ant mounds. Infestations of fire ants may negatively affect survival of nestlings. As succession proceeds toward a dense, shrub bog community, fire ants may become more abundant and may serve as an additional link between anthropogenic fire exclusion or water management and decline in populations of *N. alleni*.

A rapid, cyclical succession of the mat community can occur, based on our observations at Grand Bay. After an open-water area with floating macrophytes or low emergents experiences a die-off due to winter drought, drawdown, or treatment with herbicides, the partially decayed mass of vegetation floats up to the surface as a mat of peat or muck. The new mat becomes colonized by *Lachnanthes* and *Carex*, followed by a second wave of plant colonists, including *Dulichium*, *Eleocharis*, *Hypericum*, *Xyris*, *Bidens*, and *Decodon*. This densely vegetated mat yields dominance to *Woodwardia*, and eventually to woody shrubs such as *Lyonia* and *Itea*, and trees such as *Nyssa* and *Taxodium*. At this stage, mats usually attain coalescence and anchor to woody plants rooted in the substrate, and vertical filling of the wetland begins. Preferred food plants of *N. alleni* are crowded out and escape routes severely limited. A natural agent of retrogression in this system is the greater sandhill crane (*Grus canadensis tabida*), which winters on Grand Bay wetlands. We saw cranes dig up and eat fleshy roots of plants such as *Lachnanthes* and in the process quickly denude mats. Cranes may carry seeds of earlier seral species on their feet or feathers or in their feces, further prolonging earlier successional states more amenable to *N. alleni*.

The majority of marsh habitat at Grand Bay, itself, and in the 5,200-ha Grand Bay wetlands complex is not currently in suitable condition for long-term viability of populations of *N. alleni*. Much of it has succeeded rapidly in recent years due to low water levels and fire exclusion. One side benefit to the herbicide treatment of water lilies was proliferation of new mats, which quickly were colonized and led to a relatively dramatic increase in population from one year following a 4-year low. We hope to incorporate management of mats as a new tool in providing additional habitat. Mats could be moved into new positions, anchored, and seeded, or planted with sedges, redroot, or species of grasses (e.g., *Panicum hemitomum*) providing fleshy roots or leaves suitable for construction of houses (Birkenholtz, 1963; Porter, 1953). A recent successful introduction of the non-migratory Florida sandhill crane (*G. c. pratensis*) to the Grand Bay wetlands should further enhance survival and reproduction of *N. alleni* by promoting early mat-successional phases and emergent marsh. High densities of *N. alleni* sometimes reported for populations in Florida may never be attained, but through prescribed burning, water-level management, management of mats, and restoration of sandhill cranes, habitat available to the round-tailed muskrat may be increased and the

prospects for its long-term survival in Georgia enhanced.

ACKNOWLEDGMENTS

We thank D. Watson and M. Day for assistance with fieldwork, R. Carter and W. Faircloth for help with identification of plants, J. Davis for performing surgeries, and W. Abler for computer graphics. Georgia Department of Natural Resources Nongame and Endangered Species Program provided funding for fieldwork. The Nature Conservancy, Georgia Field Office, helped purchase field supplies. B. Klein, B. Vaughn, and D. Wade of Georgia Department of Natural Resources piloted helicopters for aerial surveys.

LITERATURE CITED

- Baker, F. C. 1889. Remarks upon the round-tailed muskrat, *Neofiber alleni* True. Proceedings of the Academy of Natural Sciences of Philadelphia, 41:271-273.
- Bergstrom, B. J. 1988. Home ranges of three species of chipmunks (*Tamias*) as assessed by radiotelemetry and grid trapping. Journal of Mammalogy, 69:190-193.
- Birkenholtz, D. E. 1963. A study of the life history and ecology of the round-tailed muskrat (*Neofiber alleni* True) in north central Florida. Ecological Monographs, 33:225-280.
- . 1972. *Neofiber alleni*. Mammalian Species, 15:1-4.
- Chapman, F. M. 1889. On the habits of the round-tailed muskrat (*Neofiber alleni* True). Bulletin of the American Museum of Natural History, 2:119-122.
- Hall, E. R. 1981. The mammals of North America. Second ed. John Wiley & Sons, New York, 2:601-1181 + 90.
- Harper, F. 1920. The Florida water-rat (*Neofiber alleni*) in the Okefinokee Swamp, Georgia. Journal of Mammalogy, 1:65-66.
- . 1927. Mammals of the Okefinokee Swamp region of Georgia. Proceedings of the Boston Society of Natural History, 38:191-396.
- Johnson, A. S. 1961. Antagonistic relationships between ants and wildlife with special reference to imported fire ants and bobwhite quail. Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners, 15:88-104.
- Lefebvre, L. W. 1982. Population dynamics of the round-tailed muskrat (*Neofiber alleni*) in Florida sugarcane. Ph.D. dissertation, University of Florida, Gainesville, 204 pp.
- Lefebvre, L. W., and J. T. Tilmant. 1992. Round-tailed muskrat. Pp. 276-286, in Rare and endangered biota of Florida: mammals (S. R. Humphrey, ed.). University Presses of Florida, Gainesville, 1:1-292.
- Mitsch, W. J., and J. G. Gosselink. 1993. Wetlands. Second ed. Van Nostrand and Reinhold, Co., New York, 722 pp.
- Müeller-Dombois, D., and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, New York, 547 pp.
- Porter, R. P. 1953. A contribution to the life history of the water rat, *Neofiber alleni*. M.S. thesis, University of Miami, Coral Gables, Florida, 84 pp.
- Schantz, V. S., and J. H. Jenkins. 1950. Extension of the range of the round-tailed muskrat, *Neofiber alleni*. Journal of Mammalogy, 31:460-461.
- Schwartz, A. 1953. A systematic study of the water rat (*Neofiber alleni*). Occasional Papers of the University of Michigan Museum of Zoology, 547:1-27.
- Sharitz, R. R., and J. W. Gibbons. 1982. The ecology of southeastern shrub bogs (pocosins) and Carolina bays: a community profile. United States Fish and Wildlife Service, Division of Biological Services, Washington, D.C., FWS/OBS-82/04:1-93.
- Steffen, D. E. 1978. The occurrence and damage by the Florida water rat in Florida sugar-cane production areas. M.S. thesis, Virginia Polytechnic Institute, Blacksburg, 104 pp.
- Tilmant, J. T. 1975. Habitat utilization by round-tailed muskrats (*Neofiber alleni*) in Everglades National Park. M.S. thesis, Humboldt State University, Arcata, California, 91 pp.
- Wassmer, D. A., and J. L. Wolfe. 1983. New Florida localities for the round-tailed muskrat. Northeast Gulf Science, 6:197-199.