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Sarah A. Conditt
Trinity University

David O. Ribble
Trinity University, dribble@trinity.edu

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Social Organization of *Neotoma micropus*, the Southern Plains Woodrat

SARAH A. CONDITT AND DAVID O. RIBBLE

Department of Biology, Trinity University, 715 Stadium Drive, San Antonio, Texas 78212

ABSTRACT.—This study described the social organization of *Neotoma micropus*, the southern plains woodrat, using radiotelemetry. We studied woodrats from September 1994 through April 1995 at the Urban Wilderness Reserve in S Bexar County, Texas. Sixteen individuals (three adult males, 11 adult females, and two subadult males) were radiocollared and located in the evening or early morning during January and February. Seventy-four percent of female radiolocations and 57% of male radiolocations were from their respective nests. No more than one adult individual was observed at any nest at the same time. Males had significantly larger ($\bar{x} = 1899 \text{ m}^2$) home ranges than females ($\bar{x} = 220 \text{ m}^2$). Male home ranges overlapped female home ranges more (35.9%) than female ranges overlapped other female home ranges (11.9%). Survival rates were similar for males and females. The results confirm previous studies indicating that these woodrats are asocial. The spacing of male and female home ranges indicated that these woodrats probably have a promiscuous mating system.

INTRODUCTION

Neotoma micropus is a medium-sized woodrat that inhabits the southern Great Plains of the S-central and southwestern United States (Texas, New Mexico and Oklahoma) and northeastern Mexico (Hall, 1981). It is usually described as solitary and asocial (Raun, 1966; Wiley, 1984; Braun, 1989), meaning that individuals show little social behavior beyond mating. Home range estimates from live-trapping studies have varied from 158 to 1335 m^2 for individuals of this species (Johnson, 1952; Raun, 1966). However, live-trapping data do not provide a sense of how often or how far an animal travels. Woodrats are normally trapped near their nests (Cranford, 1977) and any evaluations of home range use and social behavior based only on trapping data are suspect. Radiotelemetry can provide a more accurate picture of home range use and social organization (Madison, 1978, 1980). We wished to corroborate the observations from live-trapping studies that *N. micropus* is asocial using radiotelemetry. Specifically, we wanted to ascertain if adults spent any time with adult conspecifics at their nest.

We also desired to describe the home ranges and social organization of individuals, which provides good evidence for the particular mating system (Madison, 1980). The ensemble of behaviors and physical adaptations specific to mating, as well as some of the social consequences of these behaviors, describe a population's mating system (Vehrencamp and Bradbury, 1984). For mammalian mating systems there is an asymmetry in the interests of males and females because female gestation and lactation emancipate males from care of the young while imposing additional burdens on the female (Eisenberg, 1981; Ostfeld, 1985; Barlow, 1988). At one extreme, resources (especially food) may be of high quality and clumped in space or time. In this case, females are predicted to aggregate around the resource to maximize their reproductive success. This distribution sets the stage for monopolization by males; if the aggregation of females is defensible, there exists a high potential for polygyny (Emlen and Oring, 1977). In polygynous species, males typically defend territories during the breeding season that contain home ranges of one to several females (Heske and Ostfeld, 1990). Females may, or may not, show territorial behavior. A different type of mating system, promiscuity, results when males compete for and converge on re-

productive females. These adult females occupy exclusive home ranges during most of the breeding season and males have larger, extensively overlapping home ranges. Although subtle, the distinction between polygyny and promiscuity is important because the expected variance in male reproductive success is greater for polygynous mating systems (Clutton-Brock, 1988).

In this study we hoped to distinguish between polygyny and promiscuity based on the spatial relationships between males and females. If our study population is polygynous we expected female home ranges to be overlapped by only one territorial male. Males would have home ranges that do not overlap other male ranges. In a promiscuous mating system we would expect female home ranges to be nonoverlapping and their ranges would be overlapped by several males with larger home ranges. Males would have home ranges that overlap other male ranges.

METHODS

We conducted this study at the Urban Wilderness Reserve, located at the intersection of Applewhite and Jett roads in south San Antonio, Bexar County, Texas (29°14'45", 98°33'10"). The habitat of the 10-ha study site was dominated by honey mesquite-brush (*Prosopis glandulosa*) and prickly pear cactus (*Opuntia* spp.) on the uplands, with riparian forest lowlands bordering the Medina River. *Neotoma micropus* inhabited only the honey mesquite uplands of the study site, which were approximately 4 ha. No woodrat nests were found in the riparian forest lowlands. The property was bordered to the S and W by cultivated fields, and to the N and E by paved roads. This area of Texas has a subtropical climate with hot, humid summers (\bar{x} high temp. = 29.3 C) and cool winters (\bar{x} low temp. = 10.4 C) with freezing temperatures occurring on average 20 days per year. The average annual rainfall is 70.0 cm (Tandy, 1987).

We trapped *Neotoma micropus* from late September 1994 through April 1995. Tomahawk and Sherman traps were placed in and parallel to woodrat runs within 3 m of nests. Traps baited with peanut butter and oats or rat chow were set in late afternoon and checked after sunrise the next morning. Generally, one or two traps were set at each of 10–15 active nests once a week. Active nests were identified by the presence of fresh scats on runways and freshly chewed cactus pads. Periodically, two Sherman traps would also be placed at nests suspected to house juveniles. Upon capture, woodrats were transferred to a nylon mesh bag and weighed to the nearest gram with a Pesola spring balance. Sex, breeding condition and age were noted. Animals were classified in age classes based on weight and breeding condition. Females that were pregnant, lactating or parous, and males that had enlarged testes were considered reproductive woodrats. All reproductive animals were classified as adults. Animals weighing less than 150 g were considered juvenile. Nonreproductive animals weighing more than 150 g were categorized as subadults. Woodrats were examined for external parasites, wounds and pelage condition, and ear-tagged with small aluminum numbered tags in both ears. Animals were released at the point of capture; the direction of retreat was noted.

Radiotelemetry was used to determine home ranges of adult and subadult *Neotoma micropus*. Upon capture, "mouse-style" single stage radiotransmitters (AVM Instruments, Inc.) were fitted to woodrats under Metofane anesthesia. The collar assembly was encapsulated with acrylic to hold the package together, waterproof it, prevent the antenna from pulling out, and prevent damage by the study animal. This whole transmitter package, mounted on plastic cable ties, was fastened snugly around the woodrat's neck. Radiotransmitters weighed 3.8 g on average (range 3.5–4.1 g) which was, on average, approximately 1.3% of the mass of the woodrat to which they were attached. Woodrats were fitted with radiotrans-

mitters in the field and were released upon recovery from anesthesia (approximately 30 min). After at least 24 h of acclimation, radiocollared woodrats were located with a Telonics TR-4 receiver and a 3-element Yagi antenna, or an AVM LA12-DSE receiver and 2-element antenna.

To accurately determine radiolocations of woodrats, we constructed a map of the study area that included the positions of all woodrat nests, specific landmarks (e.g., fence posts, large trees), and several semipermanent reference points marked with metal spikes. The locations of woodrat nests and other features were mapped using a Leitz digital total station (combination range finder and theodolite). The digital total station converted distance and angular coordinate data into Cartesian coordinates which were mapped using the Surface III (Kansas Geological Survey) computer program. The locations of some woodrat nests relative to surveyed points were determined with a tape measure and magnetic compass.

We tracked radiocollared woodrats 2 or 3 nights per week during January and February 1995. Woodrats were tracked for either 3–4 h beginning 1 h after sunset or 2–3 h before sunrise. We located radiocollared woodrats by walking pre-existing trails included on our map of the study area and scanning for the radio frequencies of local woodrats. The estimated location was noted on the map of the study area, along with the time and activity level (resting or active). Woodrats were considered resting if their signal was uniform and constant, or active if their radio signal was variable in intensity. We estimated the distance to radiotransmitters within a 20-m radius based on the strength of the signal. Our estimates of signal strength and distance were tested periodically with the location of radiotransmitters placed at known distances from the receivers. Focal samples were collected on selected individuals for periods of time ranging from 1–3 h. All sequential radiolocations were separated by a minimum of 15 min.

The area of a minimum convex polygon (Mohr, 1947) containing all radiolocations was calculated for each radiocollared *Neotoma micropus*. We chose this method because of its widespread use and insensitivity to dependence on successive observations (Swihart and Slade, 1987). The area within each polygon and the areas of overlap were calculated with the Calhome computer program (J. Kie, J. Baldwin and C. Evans, U.S. Forest Service, Pacific Southwest Research Station, Fresno, California). After collecting data for home ranges, we continued to monitor the locations of woodrats once per week by either radiotelemetry or trapping. At the conclusion of the study in late April 1995, radiocollared *Neotoma* were presumed dead if we could not trap them and no radio signal was detected. Assuming these "lost" woodrats were dead, we calculated survival rates using the software and methods of Heisey and Fuller (1985). Starting date for each animal was the date when we first tagged the woodrat with eartags. Ending date for a surviving woodrat was the day we removed the radiocollar. The ending date for a woodrat presumed dead was taken as the midpoint between the last day a signal was detected and the first day a signal was not found and the animal was not subsequently trapped.

We accepted statistical significance at $P \leq 0.05$. Means are presented ± 2 SE throughout, except where indicated. Proportions were arcsin-transformed before analyses.

RESULTS

During the 6 mo of this study, we set traps at 31 nests. Thirty-six individuals were trapped and tagged from 28 nests; 90% of nests were active at some time during the study. Tagged woodrats were captured 98 times in 346 trap nights (trap success rate of 28.3%). Ten of the tagged woodrats were captured only once. We trapped an area of 2.4 ha during September through December. Beginning in January, we expanded the trapping area 67% to include 3.6 ha and 12 additional active nests.

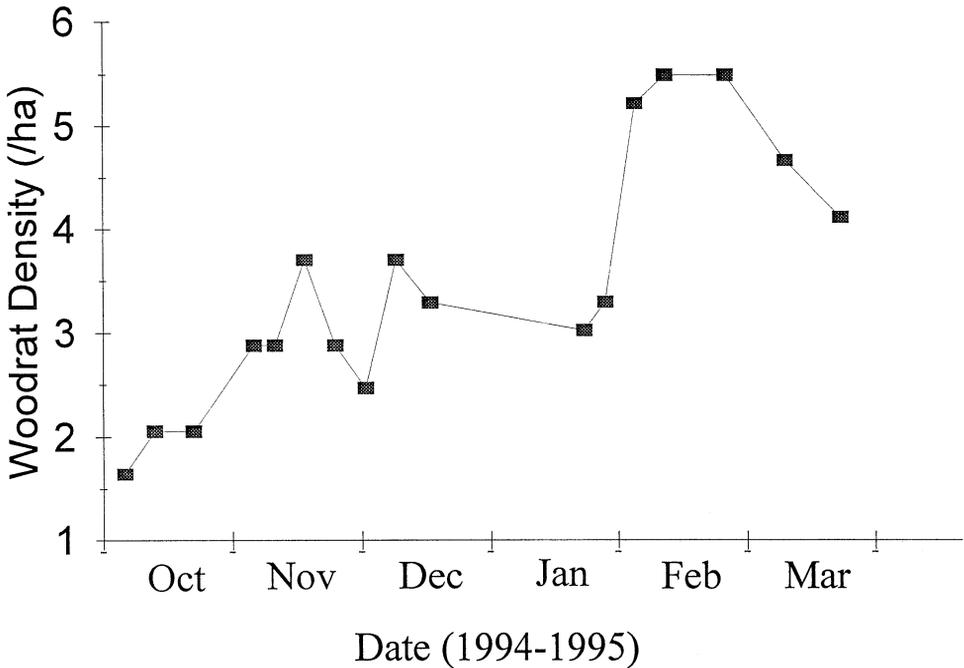


FIG. 1.—Population density (/ha) of woodrats during the study. The area trapped from September through December was 2.4 ha; the area trapped from January through March was 3.6 ha

More adult females than adult males were present in the population at all times. The average ratio of adult males to females was 1:1.6. Population density was calculated from the minimum number known alive divided by the area (4 ha) of honey mesquite woodland (Fig. 1). The lowest density was 2.0 woodrats per ha in the 1st wk of October. The population density peaked at 5.5 woodrats per ha in February. Female breeding activity was observed throughout the study. The proportion of females lactating or pregnant peaked at 50% in October. We found no evidence of lactating females through most of November. Lactating or pregnant females were found again sporadically between December and March, but did not exceed 45% of the adult females.

We radiocollared 14 adults (three males and 11 females) and two subadults (both males; Fig. 2). On average, 33.5 locations (range 7–51) were collected from each female and 36.6 locations (range 26–43) from each male. There was no significant correlation between number of radiolocations and home range area (Spearman's $r_s = -0.07$, $P > 0.8$). The area of the cultivated field was subtracted from the home range calculation for male 2605 since we never observed him crossing this field. Adult male home ranges ($\bar{x} = 1899.3 \pm 884.0$ m²; median = 1696 m²) were significantly larger than female home ranges ($\bar{x} = 220.9 \pm 98.1$ m²; median = 188 m²; Mann-Whitney U-test $P = 0.01$). Subadult male ranges ($\bar{x} = 385.8 \pm 704.5$ m²) were not significantly different from females ($P = 0.84$).

Overlap of female home ranges by males was greater ($35.9 \pm 15.0\%$) than overlap by other females ($11.9 \pm 10.9\%$; paired t-test on arcsin-transformed percentages, $t = 3.11$, d.f. = 10, $P < 0.02$). The percent of male home ranges overlapped by females ($14.6 \pm 16.2\%$)

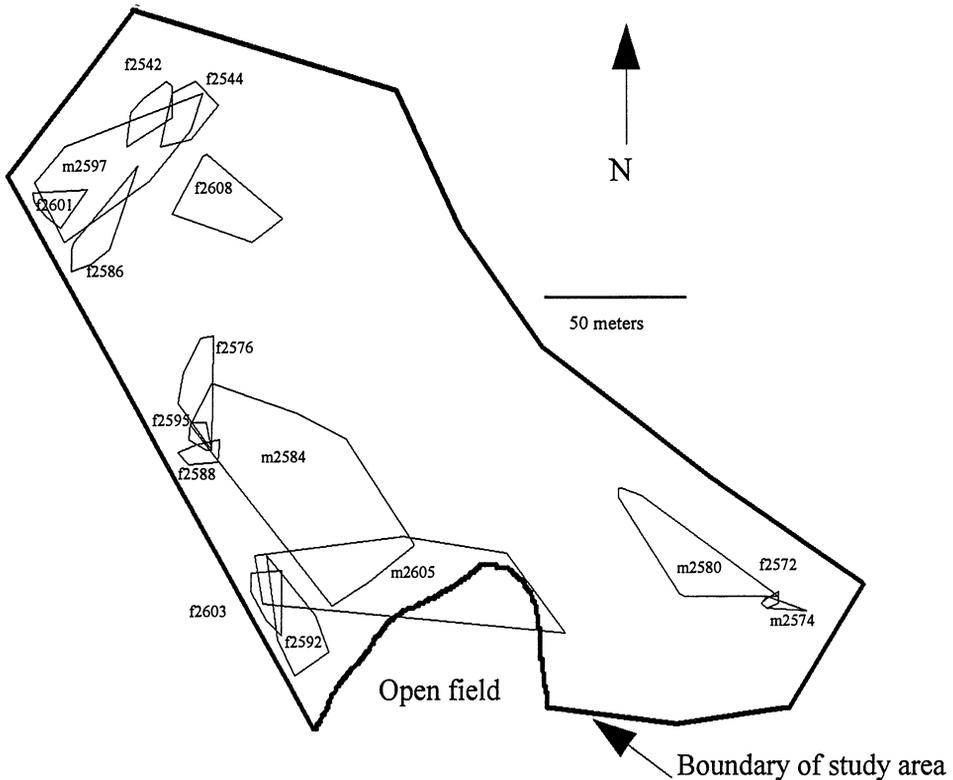


FIG. 2.—Minimum convex polygons of *Neotoma micropus* radiotelemetry locations for 14 adult and two subadult animals during January and February of 1995. Woodrats are identified by sex (m = male, f = female) and tag identification number. The heavy line marks the boundaries of the honey mesquite uplands of the study area

was similar to that overlapped by other males ($16.0 \pm 17.2\%$). Mature male home ranges overlapped an average of three female home ranges.

The majority of both male and female radiolocations were made at their respective nests (male: $56.5 \pm 25.0\%$; female: $74.3 \pm 10.7\%$). Individuals did use multiple nests during this study. Four females occupied two different nests. Two radiocollared males had a single nest to which they returned during the day. The male with the largest home range used three different nests as shelter sites during the study. The two subadult males only visited a single female nest. These radiocollared woodrats had nest sites close (12 and 30 m) to a large female nest. The subadult male closest to the female spent most of his time in the female nest (78.8% of radiolocations). The other subadult visited the female nest only twice.

By the conclusion of this study in late April, seven (two males, five females) of the 16 radiocollared *Neotoma micropus* were lost and presumably dead. The 30-day survival rates were approximately the same for males (0.83, 95% C.I. 0.64–1.00) and females (0.86, 95% C.I. 0.75–0.98). The pooled 30-day survival rate for both males and females was 0.85 (95% C.I. 0.75–0.96) and the pooled yearly survival rate was 0.14 (95% C.I. 0.03–0.60).

DISCUSSION

This is the first study to examine the social organization of *Neotoma micropus* using radiotelemetry. The majority of our radiolocations for both male and female woodrats were made while individuals were at their nests and we never observed more than one adult woodrat at a nest at the same time. These observations support previous claims that this species is relatively asocial (Johnson, 1952; Raun, 1966). We did observe two subadult males that occupied a nest with a mature female. It is possible that these younger males were offspring of the adult female. Our results also indicated that male home ranges were significantly larger than female home ranges and female home ranges were significantly overlapped by male home ranges. These observations on spacing and the female tendency to have more exclusive home ranges than males (Fig. 2) led us to conclude that in this population, *N. micropus* tend to have a promiscuous mating system. However, it is likely that the mating system of this species can range from polygyny (as seen by male 2597; Fig. 2) to promiscuity (males 2605 and 2584; Fig. 2). The distribution and dispersion of females probably dictates the options available to males in these woodrat populations (Ostfeld, 1985).

The home range sizes in this study are larger than those in most previous studies of *Neotoma micropus*. Raun (1966) determined home ranges of *N. micropus* from trapping data in southwestern Texas and concluded that female home ranges were similar to the area of cactus patches used. The difference between male (232 m²) and female (158 m²) home ranges was not significantly different. Johnson (1952) reported that males had smaller home ranges than females (971 m² and 1335 m², respectively). The average adult male home range size calculated in this study (1899 m²) is much larger than that calculated by either Johnson (1952) or Raun (1966). Much of this difference may be attributed to different operational definitions of home range used in each study. Raun (1966) calculated home ranges using minimum convex polygons, but he excluded points that were far from the center of activity and were assumed to represent "occasional sallies outside the area, perhaps exploratory in nature." Raun described the center of activity as the nest and associated cactus patch. This method yields acceptable results with females because they do not seem to travel far from their nests, but is inaccurate for male home ranges because their movement is associated not only with feeding in cactus patches, but with breeding activities. We avoided these operational problems by defining home range as all the area traversed by the individual in its normal activities of food gathering, mating and caring for young (Burt, 1943). In this study, points that Raun (1966) considered abnormal, occasional sallies were shown to occur frequently with the use of radiotelemetry.

The population density determined during this study (1.6 to 5.8 woodrats per ha) was lower than that found in other studies. The larger home range sizes observed in this study may be due to the lower population density. High den densities have been recorded in mesquite-cactus habitat (74.1 dens/ha) and prickly pear-short grass habitat (30.6 dens/ha) (Box, 1959). In one study (Raun, 1966), woodrat density increased from 14.8 to 31.1/ha in 8 mo, remained stable at 24.7/ha for 10 mo, decreased to 9.1/ha 6 mo later and 0/ha 6 mo later. The difference in the density between this study and others may be due to census methods or habitat differences. Even if every single woodrat nest we observed was occupied, the density would not exceed 9/ha. Raun (1966) found a significant positive correlation between the density of cactus and the population density of woodrats, although he concluded that cactus is not absolutely necessary to support woodrats. This observation was supported at our study site. No *Neotoma micropus* were found in the 6 ha of cactus-free

riparian woodland. The lower population density in this study may be due to lower cactus density and the lack of appropriate shelter sites.

Neotoma micropus is a member of the *floridana* species group that also contains *N. floridana* and *N. albigula* (Birney, 1973). The social organization of *N. micropus* is comparable to at least one of the other species in this group. *Neotoma floridana* is usually described as solitary and asocial (Kinsey, 1976, 1977). The den is the base of operations and home ranges are small (Fitch and Rainey, 1956). Tate (1970) found that the mean home range for adult *N. floridana* was 662 m². Adult males had larger home ranges than adult females (Goertz, 1970; Tate, 1970). Less is known about *N. albigula*, although population studies have indicated that females survive longer than males (Boggs, 1974; Brown and Zeng, 1989), suggesting that the mating system is polygynous. There appears to be variation in social and mating systems both within and among these closely related woodrats. These species deserve further study in order to understand the effects of ecology and phylogeny on their social and mating systems.

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