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Woodrat Population Dynamics Following Modification of Resource Availability

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ABSTRACT.—We examined the influence of four experimental brush treatments on relative population density, reproduction and body condition of eastern woodrat (*Neotoma floridana*) populations on Cross Timbers rangeland in Oklahoma. Experimental brush treatments were tebuthiuron and triclopyr herbicides, applied with and without annual prescribed burning. Untreated reference sites also were evaluated. A total of 333 eastern woodrats were collected from March 1986 through December 1988. Relative population density varied among seasons and experimental treatments. Maximum summer peaks in density were observed each year on triclopyr treatments. Density was similar between populations on tebuthiuron treatments and reference sites. Reproductive activity of females varied among seasons but not among experimental treatments; peaks occurred in spring and autumn 1986 and summer 1987. Percentage of reproductively active males, as evidenced by spermatogenesis, was less than expected in winter. Mean body weights and condition scores were highest in autumn and spring but were not influenced by experimental treatments. Mean stomach content weight did not differ among seasons or experimental brush treatments.

INTRODUCTION

Livestock producers desire to clear brush-infested rangelands for grazing, which has led to widespread application of herbicides and fire as brush management tools. These range management techniques usually initiate retrogression of the plant community and thus alter vegetation composition and structure (Scifres, 1980). Composition and structural changes of vegetation can alter the suitability of the habitat for some small mammal species (Kaufman and Fleharty, 1974; M'Closkey and Lajoie, 1975; Austin and Urness, 1976; Ormiston, 1984; Scheibe, 1985). Demographic responses of small mammal communities to habitat modification following herbicide use [*e.g.*, 2,4-D (Keith *et al.*, 1959); 2,4,5-T (Kirkland, 1978); atrazine (Borrecco *et al.*, 1979), and glyphosate (Santillo *et al.*, 1989)], prescribed burning (Lawrence, 1966; Kaufman *et al.*, 1988) and wildfires (Cook, 1959; Buech *et al.*, 1977) have occurred in a variety of ecosystems. Herbicide applications are often followed by prescribed fire to suppress posttreatment resprouting of woody species, but few studies (Senzota, 1985) have examined effects of combinations of herbicide and prescribed fire on small mammal populations.

Two herbicides, tebuthiuron (N-[5-(1,1-dimethyl-ethyl)-1,3,4-thiadiazol-2 yl]-N,N'-di-

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methylurea) and triclopyr ([[(3,5,6-trichloro-2-pyridinyl) oxy] acetic acid), are used for managing hardwood overstory in the Cross Timbers of Oklahoma. We monitored population dynamics and reproductive condition of eastern woodrats (*Neotoma floridana*) following alterations in habitat composition and structure after applications of tebuthiuron and triclopyr. Our interest was to assess the importance of vegetation composition and habitat structure in regulating the population by evaluating demographics, reproduction and physical condition.

STUDY AREA AND METHODS

Study area.—Our study was conducted on the Cross Timbers Experimental Range (CTER), located approximately 11 km SW of Stillwater, Oklahoma. The CTER encompasses 648 ha of typical Cross Timbers rangeland composed of upland forest with interspersed grassland-cedar savannas. The CTER has a long land-use history of cultivation, abandonment and livestock grazing that has resulted in a general decline in range condition (Ewing *et al.*, 1984). Upland forest habitats are dominated by post oak (*Quercus stellata*) and black-jack oak (*Q. marilandica*) in the overstory and eastern redcedar (*Juniperus virginiana*), rough-leaf dogwood (*Cornus drummondii*), redbud (*Cercis canadensis*), American elm (*Ulmus americana*) and coralberry (*Symphoricarpos orbiculatus*) in the understory. Understory herbaceous dominants include little bluestem (*Schizachyrium scoparium*), indiagrass (*Sorghastrum nutans*), rosette panicgrass (*Panicum oligosanthos*) and western ragweed (*Ambrosia psilostachya*).

Experimental design.—The CTER was divided into 20, 32.4-ha pastures, which represented four replications of both reference sites and four experimental brush treatments in a randomized block design. Pastures were assigned to respective blocks according to their similarity in total woody canopy cover and soil type. The four experimental treatments included: (1) tebuthiuron (Dow Elanco, 9002 Purdue Road, Indianapolis, Ind. 46285) applied aerially at 2.2 kg per ha in March 1983; (2) tebuthiuron (as with treatment #1) with annual prescribed burning beginning April 1985; (3) triclopyr (Dow Elanco) applied aerially at 2.2 kg per ha in June 1983, and (4) triclopyr (as with treatment #3) with annual prescribed burning beginning in April 1985. Reference sites were not treated with herbicide or prescribed burns. All experimental treatments and reference sites were fenced and moderately grazed by yearling cattle from April to September of each year.

Animal collection.—Eastern woodrat populations were censused in March, June, September and December in 1986 and 1987 and in June and December in 1988. During each of the 10 sampling periods, we censused two of the four replications of the reference sites and each of the experimental brush treatments using removal trapping on randomly placed 1.10-ha grids. Each grid consisted of eight transect lines (four stations 30 m apart) with 15-m spacing between transect lines placed in upland forest habitat. Trapping grids were relocated in each new sampling period so that no area within an experimental pasture was trapped more than once. After every two successive sampling periods, we censused the alternate two replications of each experimental treatment and reference sites. One Victor rat trap was placed within a 1-m radius of each of the 32 stations on each grid. A peanut butter and rolled oat mixture was used as bait. Each grid was trapped for 3 consecutive nights with daily removal of all captures. Relative density was expressed as number of animals caught per 100 trap-nights with corrections for sprung traps (Nelson and Clark, 1973). Woodrat nests on each grid also were enumerated.

Collected animals were returned to the laboratory and total, body, tail and hindfoot lengths (± 1 mm) and body weight (± 0.1 g) were determined. Animals ≥ 200.0 g were classified as adults, and those ≤ 199.9 g were considered juveniles (Goertz, 1970). Reproductive status of each male was assessed using epididymal sperm smears, mass of testes and

mass of seminal vesicle gland. Presence of spermatozoa in the epididymis was ascertained by cutting the caudal pole, extruding its contents, and smearing across a glass slide. Slides were examined microscopically, and relative abundance of sperm was assessed by assigning a numerical rank of 0 (none), 1 (trace), 2 (moderate) and 3 (abundant). Females were classified as pregnant only when embryos were visible during necropsy. Embryos were enumerated if present, and presence or absence of uterine scars recorded except during spring 1986. Females were recorded as lactating if mammary tissue was conspicuous with hair-free areas surrounding nipples. Females were considered reproductively active when pregnant or lactating. Condition of males and females was assessed by examining weights (± 0.1 mg) of liver, spleen, paired adrenal glands and oven-dry stomach contents. Stomach contents were removed and dried to constant weight at 55 C. A general condition index was calculated for each animal as body weight expressed as a percentage of body length.

Statistical analyses.—Because there were only two replicated grids/treatment sampled in any season, grids for each treatment were pooled by season prior to analysis. Differences in age and sex ratios and male and female reproductive parameters among experimental treatments and seasons were analyzed using chi-square statistics (Koopmans, 1981). Differences in relative population density among experimental treatments and seasons were tested by analysis of variance (SAS, 1985) using arcsine transformed data (Sokal and Rohlf, 1981). Main and interactive effects of experimental treatment and season on condition and morphometric characters were examined by analysis of variance for the rank transformed data (Conover and Iman, 1981). Specific contrasts were used in all analysis of variance procedures to compare differences between major experimental treatment components. Statistical significance was $P \leq 0.05$.

RESULTS

Population characteristics.—Mean relative population densities of eastern woodrats (based on total $n = 333$) differed significantly among seasons ($P < 0.001$) and experimental brush treatments ($P < 0.005$) (Fig. 1). Relative population density and seasonal fluctuations in density were similar in reference and burned and unburned tebuthiuron-treated pastures ($P > 0.100$). However, the amplitude of seasonal fluctuations in density was considerably more pronounced in burned and unburned triclopyr-treated than other pastures ($P < 0.005$). These fluctuations were characterized by prominent summer peaks, where relative population density ranged from 14.0 to 18.7 animals/100 trap-nights, followed by a large decline in autumn (0.5–3.3). Relative densities in all herbicide-treated pastures as a group were significantly greater than reference sites ($P < 0.004$). Densities of eastern woodrats also were greater on pastures treated with triclopyr than tebuthiuron ($P < 0.001$). However, prescribed burning had no effect on relative population density on either tebuthiuron- or triclopyr-treated pastures ($P > 0.100$).

Sex and age ratios showed no significant differences among burned and unburned herbicide treatments and references ($P > 0.100$). Overall male-to-female and adult-to-juvenile ratios were 1.08:1 and 0.85:1, respectively. In addition, there was no significant difference in sex ratios among seasons ($P > 0.100$). However, percentage of juveniles in eastern woodrat populations exhibited significant seasonal variation ($\chi^2 = 43.0$, $df = 3$, $P < 0.001$). Percentage of juveniles was higher in summer and lower in winter as compared to other seasons (Fig. 2).

Reproductive activity.—Adult female eastern woodrats were reproductively active throughout the study except in winter 1988 (Fig. 3). Distinct seasonal peaks of reproductive activity were evident ($\chi^2 = 22.7$, $df = 3$, $P < 0.001$); all adult females captured in spring and autumn 1986 and summer 1987 were reproductively active. Percent of adult females that

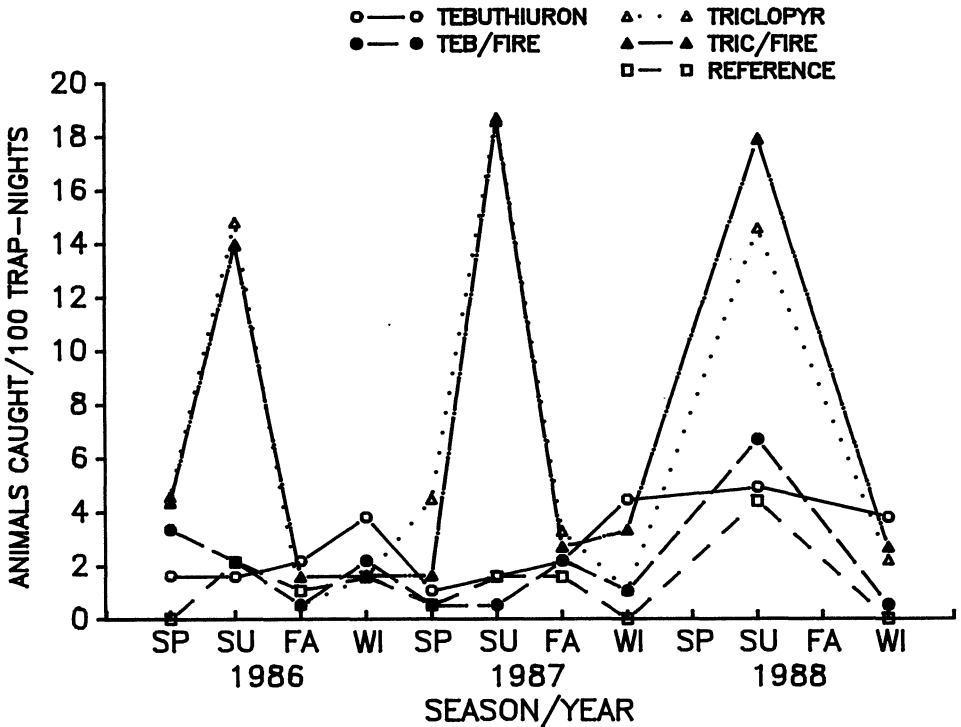


FIG. 1.—Total catch/unit effort of eastern woodrats on four experimental brush treatments and reference sites at the Cross Timbers Experimental Range from spring 1986 to winter 1988

were reproductively active showed no significant relationship to experimental brush treatments ($P > 0.100$). A total of nine pregnant eastern woodrats were captured: eight from triclopyr-treated pastures and one from a tebuthiuron treatment. Litter size ranged from 1 to 4 with a mean of 2.89 ± 0.26 (SE) fetuses/pregnant female. Pregnant eastern woodrats were captured at least once in all seasons except winter and all years except 1988 (Fig. 3). Percentage of adult females with uterine scars was greater than expected in summer (76.0%) compared to autumn (44.4%) and winter (36.4%) ($\chi^2 = 7.9$ df = 2, $P < 0.025$) but did not differ among pastures ($P > 0.100$).

Timing of the reproductive cycle of males, as indicated by the relative degree of spermatogenesis (Fig. 4), did not resemble that of adult females. Percentage of adult males that had relative sperm abundance scores ≥ 2 was less in winter than other seasons (all years pooled; $\chi^2 = 8.4$, df = 3, $P < 0.050$). Reproductive activity of adult males appeared to be influenced by brush treatment because the percentage of adult males with sperm abundance scores ≥ 2 tended to be higher on burned and unburned herbicide treatments than reference sites ($\chi^2 = 3.1$, df = 1, $P < 0.100$; Fig. 4).

Mean-ranked testes ($P < 0.003$) and seminal vesicle gland ($P < 0.001$) mass (all years pooled) of adult male eastern woodrats varied significantly among seasons (Fig. 4). Mean testes mass was heaviest from spring to autumn and lightest in winter, but seminal vesicle gland mass was heaviest in spring and lightest in winter. No differences ($P > 0.100$) in testes or seminal vesicle gland weights were observed among burned and unburned herbicide treatments and reference sites.

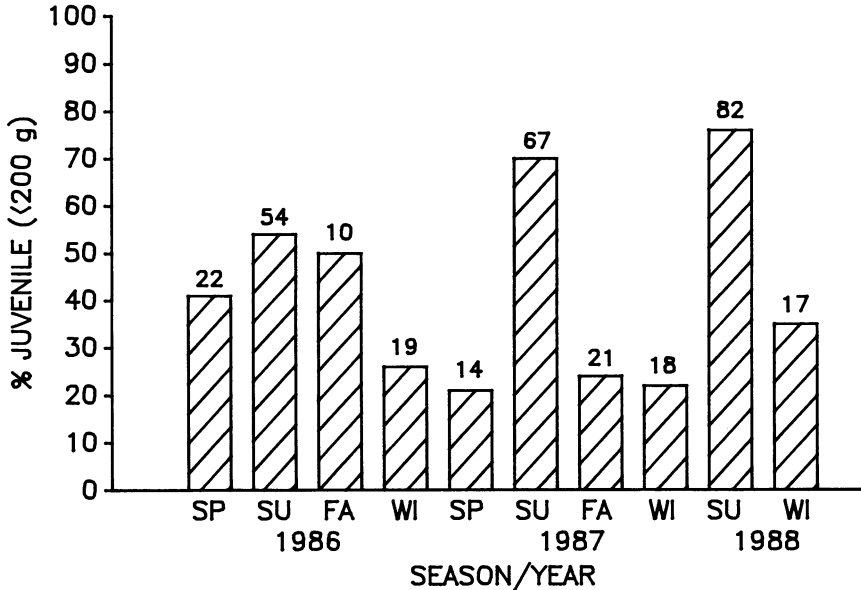


FIG. 2.—Differences in percent juvenile in populations of eastern woodrats among seasons at the Cross Timbers Experimental Range from spring 1986 to winter 1988. Values above bars represent sample size (n)

Condition.—Body mass and relative condition scores did not vary between sexes; therefore, males and females were pooled for statistical analyses. Differences in mean adult body mass (all years pooled) approached significance among seasons; body mass in autumn (294.7 ± 12.3 SE) and spring (295.2 ± 12.1 SE) was greater than winter (267.4 ± 10.1 SE) ($P < 0.053$). Relative condition scores of adults also were significantly different among pooled seasons ($P < 0.020$); they were highest in autumn (141.2 ± 5.7 SE) and spring (138.3 ± 4.5 SE) and lowest in winter (125.0 ± 3.6 SE). Mean body mass and condition scores were not significantly influenced by experimental treatment ($P > 0.100$). Dried stomach content weights did not differ among seasons or experimental treatments ($P > 0.100$).

DISCUSSION

Vegetative composition and structure of the habitat was altered by the experimental treatments. Empirically, sites treated with tebuthiuron were characterized by substantial forb and grass production and copious numbers of snags and fallen timber (Schulz *et al.*, 1992). Triclopyr-treated sites exhibited substantial forb and browse production, often so dense that movement through these areas was virtually impossible. Reference sites had a closed canopy of medium-sized oaks with trace amounts of forb or grass growth.

Both herbicides killed most of the dominant overstory oak species although woody understorey species such as buckbrush (*Symphocarpus orbiculatus*), American elm (*Ulmus americana*) and chittamwood (*Bumelia lanuginosa*) were controlled less by triclopyr than tebuthiuron (Stritzke *et al.*, 1991). As a result, grass production posttreatment was less on triclopyr sites (780 kg/ha, average 1986–1987) than on tebuthiuron sites (1795 kg/ha) (Engle *et al.*, 1991). However, standing crop of forbs was essentially equal on both herbicide

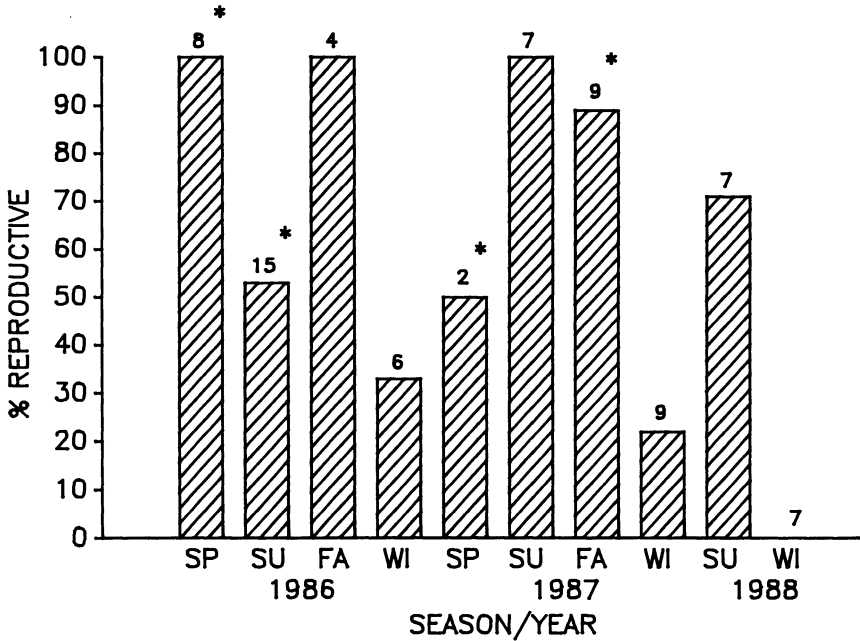


FIG. 3.—Seasonal trends in percent reproductively active (pregnant or lactating) adult female eastern woodrats at the Cross Timbers Experimental Range from spring 1986 to winter 1988. Values above bars represent sample size (n) and asterisks (*) above bars represent seasons in which pregnant females were caught

treatments, which collectively produced more grasses and forbs than reference sites (Engle *et al.*, 1991). Canopy cover of understory woody species (<1 m height) in 1988 was 91% greater on triclopyr treatments compared to tebuthiuron-treated pastures, but very similar (50.5% vs. 47.0%) to reference sites (Stritzke *et al.*, 1991). Nonuniform burns in brushy upland sites were common and had little impact on woody plant overstory because of inadequate accumulation of fine fuel and presence of cool season grasses (Engle *et al.*, 1991).

Although forage resources are important, habitat structure and availability of nest-building materials and security cover may be the primary factors limiting woodrat survival (Cranford, 1977; Rainey, 1956). Birney (1973) believed that vegetative cover was the most important habitat requisite for woodrats, and others have noted a preference for structurally diverse habitats for nest sites and predator avoidance (Rainey, 1956; Goertz, 1970; Cranford, 1977). Herbicide-killed trees produced an abundant supply of nest-building material on both triclopyr- and tebuthiuron-treated pastures. However, mean nest densities on trap grids in 1986 differed among triclopyr (8.2 ± 1.3 nests/ha), tebuthiuron (5.7 ± 1.2) and reference (0.43 ± 0.15) sites. Our inability to locate all nest sites on triclopyr treatments because of dense vegetation likely resulted in an underestimation of actual nest density.

The most obvious response to habitat modification by woodrats was the large increase in numbers during each summer on triclopyr-treated pastures (Fig. 1). These pastures had more forage and nest-building material than reference sites and more security cover than tebuthiuron treatments. However, it is difficult to explain why woodrat density on tebuthiuron treatments was never significantly greater than on reference sites. Food and nest material were certainly more abundant on tebuthiuron sites, although security cover was

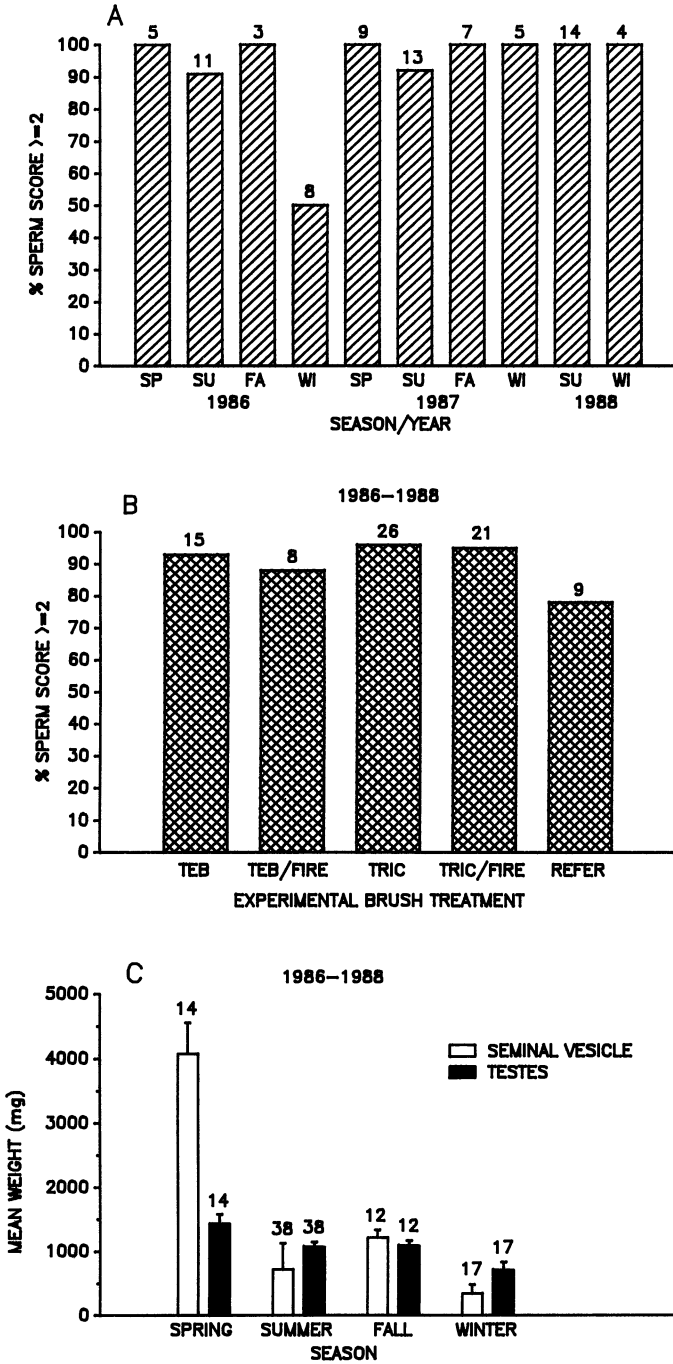


FIG. 4.—Relative sperm abundance scores among seasons (A) and treatments (years pooled) (B) and differences in mean weights (\pm SE) of testes and seminal vesicle glands among seasons (years pooled). (C) Values above bars represent sample size (n)

probably less than optimal. Although catch per unit effort was not different, absolute numbers of captures during the study were higher on burned (36) and unburned (48) tebuthiuron treatments compared to reference sites (23).

Woodrats appeared to select triclopyr-treated pastures for their greater structural complexity, thereby maximizing benefits of increased food resources, nesting materials and security cover. We expected differences in density to be accompanied by greater recruitment on triclopyr treatments compared to other sites. However, no differences were observed in percent juveniles or percent reproductively active females among triclopyr, tebuthiuron or reference sites. The only evidence of differential recruitment came from the nine pregnant females, eight of which came from triclopyr-treated pastures.

Prescribed burning had no influence on eastern woodrat populations; burning apparently did not alter any habitat features important to eastern woodrats. Senzota (1985) monitored eastern woodrat populations on burned tebuthiuron-treated Cross Timbers in Texas. Burning reduced brush in Senzota's study area and the population densities of eastern woodrats.

Although more woodrats inhabited triclopyr-treated sites than tebuthiuron-treated and reference sites and their site affinity was likely due to the optimal combination of habitat features, our results failed to adequately explain the large summer increase (ca. 100%) in adult animals. Possibly adults and subadults were dispersing from other treatments to triclopyr sites during the interim between spring and summer sampling. Goertz (1970) documented movement of a subadult male (160 g) of 244 m. Although dispersing juveniles will establish home ranges in close proximity to maternal ranges, occupation is usually temporary and serves as a refuge during an exploratory period before moving to an unoccupied but suitable area (Cranford, 1977). Triclopyr sites may have provided more vacant sites for woodrat colonization 5- to 6-yr posttreatment than tebuthiuron and reference sites.

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