HOME-RANGE ATTRIBUTES AND SPATIAL STRUCTURE OF WOODCHUCK POPULATIONS

ROBERT K. SWIHART

Department of Plant Pathology and Ecology,
The Connecticut Agricultural Experiment Station,
P.O. Box 1106, New Haven, CT 06504
Present address: Department of Forestry and Natural Resources,
Purdue University, West Lafayette, IN 47907

Movements and patterns of burrow use by woodchucks (*Marmota monax*) in two Connecticut orchards were determined from 734 captures of 273 individuals and 1,213 radio locations of 46 individuals. All data were collected after the breeding season. Adults occupying home ranges used an average of eight burrow systems; males occupied home ranges 1.8 times larger than females. Burrow systems were located disproportionately often along woodland edges and brushy fence rows, and use of these areas was two–three times greater than expected based on their availability. Populations were loosely structured spatially. Territoriality may occur at occupied burrows. Although rare, simultaneous use of a burrow usually involved an adult male and a reproductive female. Overlap of home ranges of reproductive females and males was relatively large (36%). Although woodchucks are less social than other marmots, data from this and other recent studies lead me to suggest that a limited amount of social cohesion or tolerance may extend beyond the periods of breeding and weaning. I hypothesize that the prevailing social structure of woodchucks may partly reflect phenotypic responses to a diffuse distribution of resources engendered by the agricultural activities of humans.

Key words: *Marmota*, home-range, social structure, Connecticut

Woodchucks (*Marmota monax*) commonly inhabit agricultural areas characterized by a high proportion of habitats suitable for construction of burrows. Typically, burrow systems of woodchucks are not clustered spatially to the extent found with other North American marmots occupying more patchily distributed habitats (Barash, 1989). Woodchucks traditionally have been categorized as asocial, based primarily on direct observation (Barash, 1989; Bronson, 1964). However, the widespread dispersion of woodchuck burrows (de Vos and Gillespie, 1960; Henderson and Gilbert, 1978), coupled with the height of vegetation during summer, often restricts direct observation to a small fraction of the burrows at a site either in early spring or following mowing or harvest of crops. Consequently, studies of home-range attributes and spatial structure of woodchuck populations also must rely on livetrapping and telemetry to obtain location data.

Merriam (1966, 1971) used telemetry to document a clumped distribution of woodchuck burrows and frequent interburrow movements, and he suggested that burrow clusters and social groups may coincide. Ouellet and Ferron (1986) used telemetry to study home-range attributes of woodchucks, and they inferred that woodchucks were asocial and possibly exhibited defense of occupied burrows. However, the number of adults monitored was small in both studies (*n* = 1 in Merriam, 1966, 1971; *n* = 10 in Ouellet and Ferron, 1986). Herein, I re-
port on location data collected via telemetry and livetrapping of two woodchuck populations in central Connecticut, with emphasis on the home-range attributes and spatial structure of adults during the post-breeding season. Specifically, my objectives were to compare movements of adults that differed by reproductive maturity or sex, and also to examine patterns of burrow visitation and occupancy.

**Materials and Methods**

The study sites were 26 km apart and located in southcentral Connecticut on soils of glacial till origin. Soils primarily consisted of well-drained loams, silt loams, gravelly sandy loams, and fine-sandy loams from the Branford, Cheshire, Wethersfield, and Yalesville series. The landscape primarily consisted of undulating uplands characterized by slopes of 3–25%.

The study site in Southington, Connecticut, consisted of a 31.4-ha orchard, 16.7 ha of woods, and 4.3 ha of woodland edge. Woodland edge was defined as a 10-m strip of wooded habitat located along the perimeter of the woods and adjacent to the orchard. Ground-cover vegetation in the orchard predominantly was orchard grass (*Dactylis glomerata*), red clover (*Trifolium pratense*), white clover (*T. repens*), dandelion (*Taraxacum officinale*), common plantain (*Plantago major*), campion (*Lychnis alba*), common toadflax (*Linaria vulgaris*), poison ivy (*Rhus radicans*), and Virginia creeper (*Parthenocissus quinquefolia*). Woods were dominated by an overstory of oaks (*Quercus*) and maples (*Acer*), with eastern hemlock (*Tsuga canadensis*) prevalent on rock outcrops and steep slopes. Understory vegetation included seedlings of these woody species as well as black cherry (*Prunus serotina*), chokecherry (*P. virginiana*), brambles (*Rubus*), maple-leaf viburnum (*Viburnum acerifolium*), and spicebush (*Lindera benzoin*). Staghorn sumac (*Rhus typhina*) was abundant along woodland edges.

A second study site, located in Hamden, Connecticut, was composed of 9.4 ha of orchard and surrounding meadows, 2.4 ha of woods, and 2.7 ha of woodland edge and brushy fencelows. Ground-cover vegetation was similar in composition to the Southington orchard, but also included Kentucky bluegrass (*Poa pratensis*) and mugwort (*Artemisia vulgaris*). Woody vegetation was similar to that at the Southington site, except that overstory trees also included sassafras (*Sassafras albidum*) and red pine (*Pinus resinosa*).

Farming practices at both sites were typical of orchard operations in southern New England. Ground cover was mowed periodically, and residual brush and trees from replanting operations were bulldozed into piles along woodland edges of the orchards. Before initiation of the study, farmers at the two sites attempted to control woodchucks by hunting and by using gas cartridges (Dolbeer et al., 1991). Upon commencement of the study, no control measures were used at Hamden, whereas limited hunting was done at the Southington site during the 2nd year of research.

A census of both study sites was conducted during spring 1987 to locate burrow systems. Each burrow system was assigned a number, marked with flagging, and its location plotted on an enlarged (1:1,200) aerial photograph. Burrow systems were considered distinct if main entrances were separated by >10 m (Henderson and Gilbert, 1978). New burrow systems were added to the original list during 1987 and 1988 at Southington and during 1989 at Hamden.

Woodchucks were captured using 80 by 25 by 30-cm wire-mesh Tomahawk live traps. Traps were baited with apples and placed <1.5 m from burrow entrances. Newly captured woodchucks were immobilized with an intramuscular injection of ketamine hydrochloride and xylazine hydrochloride at dosages of 0.15 and 0.10 ml/kg, respectively. All individuals were fitted with numbered ear tags. I also recorded the burrow number at which a capture occurred, as well as the body mass, sex, reproductive maturity, and age class of each individual. Reproductive maturity was assessed only before mid-July and was determined for males by the presence of scrotal testes. For females, reproductive maturity was confirmed using evidence of pregnancy or lactation, as indicated by palpation and by condition of the nipples (Snyder and Christian, 1960). Juveniles were easily distinguished from yearlings and adults on the basis of body mass, pelage, and tooth characteristics (Snyder et al., 1961). However, newly captured yearlings usually could not be reliably distinguished from adults, because trapping was not conducted before mid-April (Snyder et al., 1961). Consequently, adults and yearlings were pooled in most analyses. Recaptured individuals were weighed and released.
without immobilization, unless the elapsed time between consecutive captures was >2–3 weeks.

Trapping was conducted at the Southington site from the latter one-half of April to mid-October in 1987 and 1988 and at the Hamden site from mid-April to mid-September 1989. This period encompasses 2–4 weeks before emergence of juveniles from natal burrows until about the time that individuals begin to enter hibernation (de Vos and Gillespie, 1960; Hamilton, 1934; Snyder et al., 1961). Natal burrows were identified from mid-May to mid-June by captures of juveniles and reproductively mature females, typically within a 1-week period. Trapping intensity varied, with little trapping done during August 1987, July 1988, or August 1989. During other months, traps generally were checked for 4–5 consecutive days each week. In addition, too few traps were available in 1987 and 1988 to enable all burrow systems (n = 308) to be sampled simultaneously. Consequently, traps were rotated among burrow systems so that each active burrow system was sampled every 3–5 weeks. Sufficient traps were available in 1989 to enable nearly all active burrow systems at the Hamden site to be sampled simultaneously.

Radiocollars were fitted to 46 woodchucks during the study. Collars were placed loosely on immobilized individuals, and during nonhibernation periods collared individuals were tracked at irregular intervals for 10–241 days (median duration of radiotracking = 95 days) using remote triangulation as well as direct approaches to occupied burrows. The median time between successive relocations was 2 days. I recaptured individuals at ca. 4-week intervals and adjusted the size of the collars. Because of the rapid growth of juveniles (Snyder et al., 1961), only six young were fitted with radiocollars, and then only in September and October.

I used a chi-square goodness-of-fit test to determine whether burrows were distributed among habitats in proportion to abundance of each habitat. I also tested the null hypothesis that natal burrows did not differ from all burrows in terms of their occurrence in various habitats.

Selection of resources can occur in a spatial hierarchy (Johnson, 1980; Porter and Church, 1987; Wiens et al., 1986). Consequently, I examined habitat use at two spatial scales. Within each home range, I calculated the percentage of observations that occurred in each habitat type and compared these values with the percentage of each habitat type occurring in the home range by plotting the difference (Thomas and Taylor, 1990). I then repeated the calculation using the percentage of each habitat type found over the entire study area. Statistical tests were not conducted because successive observations were autocorrelated for most woodchucks.

I adopted the functional definition of Munger (1984) of home range, that is, the occurrence of site fidelity. To determine whether an individual exhibited a significant level of site fidelity, I compared observed measures of home-range size and use with a distribution of each measure that was generated under the rules of random movement described in Danielson and Swihart (1987). Four measures were calculated: minimum convex polygon, which estimates home-range size based on information contained in a peripheral set of convex-location observations (Jennrich and Turner, 1969); mean-squared distance from the arithmetic center of activity, which measures the bivariate variance of a set of location observations (Calhoun and Casby, 1958); home-range length, the maximum distance between observations (Abramsky and Tracy, 1980); linearity ratio, the ratio of the distance between the first and last positions of an individual and the total distance moved (Bell and Kramer, 1979). For each woodchuck, I generated 500 home ranges using a Monte Carlo simulation of randomized distance vectors from the observations collected for an individual (Danielson and Swihart, 1987). The four measures then were calculated for each of the 500 random home ranges. A home range (site fidelity) was judged to exist if each of the observed measures of home range (minimum-convex polygon, mean-squared distance from the center of activity, and home-range length) was <90% of the randomly generated measures. Similarly, stationary home ranges were identified as those home ranges for which the observed value of the linearity ratio was <90% of the randomly generated values (Danielson and Swihart, 1987).

Because different home-range models make different assumptions regarding use of space by an animal, each portrays a home range in a different manner (Anderson, 1982; Dixon and Chapman, 1980; Swihart and Slade, 1985a; Worton, 1987). Also, because no two individuals use their home range in the same way, the suitability of different estimators may vary among individuals. I estimated home-range size using six different estimators. The estimators were chosen primarily
based on their popularity and the degree to which they presented differing conceptual portrayals of home-range size. They included: the minimum-convex polygon method; the grid-cell method, which sums the areas of quadrats in which an individual was observed (Siniff and Tester, 1965); the 95% confidence ellipse for a bivariate normal probability distribution (Koeppl et al., 1975); the 95% contour based on the harmonic-mean center of activity (Dixon and Chapman, 1980); the 50% contour from the harmonic-mean model, which provides an estimate of the size of core areas; the mean-squared distance from the arithmetic center of activity.

After the six estimates were calculated for each woodchuck, I used principal components to construct orthogonal, linear combinations of the estimates. The component corresponding to the major axis of variation (principal component I) incorporates spatial information from each estimator into a single, standardized measure of home-range size; I used this measure for comparison of home ranges of males and females. Estimates of home range were calculated for all radiocollared woodchucks with \( \geq 10 \) location observations obtained via telemetry or livetrapping. To account for the influence of sample size, home ranges of males and females were compared using an analysis of covariance, in which the number of location observations was the covariate. For individuals exhibiting dependence between successive observations (see below), independent subsets of observations were selected for estimation of home-range size (Swihart and Slade, 1985b).

I tested for dependence between successive location observations using the procedure described by Swihart and Slade (1985b, 1986) for the \( t^2/r^2 \) statistic developed by Schoener (1981). Significant levels of autocorrelation between observations may result either from a limited amount of time elapsing between observations or from spatial patterning of movements (Swihart and Slade, 1987). Woodchucks are capable of extensive movements over relatively short time intervals (Hamilton, 1934; Merriam, 1971). Moreover, the median time interval between successive observations in my study was several times greater than the time interval necessary to obtain statistically independent observations for Spermophilus columbianus and Cynomys ludovicianus (Swihart et al., 1988), two ground-dwelling sciurids that occupy home ranges roughly comparable in size to those of woodchucks. Hence, any significant autocorrelation in my study probably was caused by spatial patterning of movements.

A simple form of spatial patterning of movements that would result in autocorrelated observations is prolonged concentration of activity at a particular site. Thus, I calculated the mean duration of tenure at a burrow for each woodchuck occupying a home range. Only successive observations separated by \( \leq 4 \) days were used in calculations. The distributions of tenure times of males and females were compared using a Kolmogorov-Smirnov two-sample test (Conover, 1980).

I also tested for patterns of interburrow movements. Both the frequency of interburrow movements as well as the frequency of revisitation to the burrow system just vacated were determined. A chi-square test was used to compare observed frequencies with expected values computed under the null hypothesis that all burrows within a home range were equally likely to be occupied at any particular observation period. The association between spatial separation of burrows and the frequency of movements between burrows was examined by computing a cumulative distribution of distances of interburrow movements for males and females at both sites. Each of these distributions was then compared to the cumulative distribution of nearest-neighbor distances for all burrow systems at a site using a Kolmogorov-Smirnov two-sample test.

Overlap of polygonal home ranges was calculated for all nearest-neighbor pairs of radiocollared woodchucks whose centers of activity were separated by \(< 150 \) m. For reproductively mature individuals, the percent of overlap between males, between females, and between males and females was compared using a Kruskal-Wallis test with multiple comparisons (Conover, 1980).

Patterns of use of a burrow system among individuals were examined after combining telemetry and trapping data. I recorded the frequency with which a pair of adult woodchucks was observed at the same burrow on the same day, 1–5 days apart, and 6–10 days apart. Pairs of woodchucks were categorized by sex and reproductive status, and a chi-square goodness-of-fit test was used to compare the observed frequencies with frequencies predicted from the overall proportions of each group in the adult segment of the population. Expected frequencies were calculat-
Table 1.—Percentage occurrence of woodchuck burrows in three habitats in Connecticut, 1987–1989. Expected percentages (Exp) are based upon the overall availability of habitat (for all burrows) or of burrows in each habitat (for natal burrows). P-values represent results from chi-square goodness-of-fit tests conducted on frequencies of occurrence.

<table>
<thead>
<tr>
<th>Site</th>
<th>Percentage occurrence in habitat</th>
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<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Orchard</td>
<td>Edge</td>
<td>Woods</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>n</td>
<td>Obs</td>
<td>Exp</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All burrows</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Southington</td>
<td>308</td>
<td>49.7</td>
<td>59.9</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hamden</td>
<td>61</td>
<td>36.1</td>
<td>64.8</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Natal burrows (sites pooled)</td>
<td>25</td>
<td>40</td>
<td>47</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

From a hypergeometric-sampling distribution. A separate test was conducted for each time interval.

I also examined the composition of adults occurring at natal burrows before 1 July, the date at which litters seemed to disband as judged by trapping data. Because of the difficulty in separating adults from yearlings, and because nearly all yearling males had scrotal testes, I chose to separate males on the basis of body mass for this analysis. I arbitrarily grouped males according to whether their maximum mass before 1 July was <3 kg. This cutoff probably separates most yearling and adult males; 12 of 14 yearlings of known age were <3 kg, whereas seven of nine adults (≥2 years) were ≥3 kg. A chi-square goodness-of-fit test was used to compare the observed frequency of these classes of males, as well as reproductively mature and immature females, to expected frequencies derived from the overall proportions of these groups in the adult segment of the population. To ensure adequate sample sizes, data from the two study sites were combined for all analyses of spatial structure. I used Bonferroni protected α levels (Morrison, 1976) when assessing the significance of multiple tests performed on data from each woodchuck.

Results

Trapping at the Southington site during 1987 and 1988 yielded 602 captures of 228 woodchucks. Trapping at the Hamden site in 1989 yielded 132 captures of 45 woodchucks. My trapping design did not permit estimation of population size by typical mark-recapture procedures (Caughley, 1977). However, enumeration of all adults captured both before and after 30 June provided a crude measure of population density in the period before the dispersal of the majority of juveniles. Using this method, the predispersal density at Southington averaged 0.87 adults/ha, whereas at Hamden it was 1.23 adults/ha. Inclusion of juveniles increased the density estimates to 1.59 woodchucks/ha at Southington and 2.19 woodchucks/ha at Hamden.

Radiocollars were placed on 31 woodchucks at Southington and 15 woodchucks at Hamden. Seven individuals shed their collars or moved from the study areas shortly after being released. The 39 remaining woodchucks consisted of 20 adult females, 13 adult males, and 6 juvenile males, for which an average of 30 observations were recorded per individual (range, 10–69).

The distribution of burrows among habitats was similar for both sites, with fewer burrows occurring in orchard and woods habitats than expected based on the extent of these habitats, whereas a disproportionately large number of burrows occurred in edge habitat (Table 1). In addition, significantly more natal burrows occurred in edge habitat than predicted from the overall frequency of burrows occurring there (Table 1).

Orchard was the principal habitat in home ranges of radiocollared adults, comprising 75.1% of an average home range, with 15.5%
in woods and 9.4% in edge. Woodchucks also were located a greater percentage of the time in orchards (64.9%) than in either woods (9.9%) or edge (25.2%) habitat. However, only edge habitat was used consistently more than expected based on its availability in each home range (Fig. 1a). The same pattern also emerged when use of habitats was compared with availability over an entire study area (Fig. 1b).

Four of 13 (31%) adult males and two of 20 (10%) adult females exhibited movements that did not differ from the random-movement model, as determined using minimum-convex polygon, mean-squared distance from the center of activity, and home-range length. Five of six (83%) juvenile males also failed to maintain significant levels of site fidelity. Home-range shifts, as determined using the linearity ratio, were exhibited by five (38%) adult males and four (20%) adult females, as well as by all six of the juvenile males.

For adults exhibiting significant levels of site fidelity, males occupied larger home ranges than females, regardless of the estimator used (Table 2). Moreover, significant sex-specific correlations occurred between nearly all of the estimators (Table 3). Combining the measures for both sexes, the first principal component represented 78.8% of the total variation and provided a general measure of home-range size (Table 3). A comparison of scores (generalized home-range sizes) of males and females indicated that males on average occupied significantly larger areas ($F = 5.78, d.f. = 1.24, P = 0.02$).

![Graph](image)

Fig. 1.—Differences in the percentage of use and availability of orchard, edge, and wooded habitats by adult woodchucks during the post-breeding season, 1987–1989. Results are presented for use and availability of individuals within a home range (a) and within a study site (b).

The number of locational observations did not explain a significant proportion of the variation ($F = 1.83, d.f. = 1.24, P = 0.19$). The mean number of burrow systems used by adult males (9.1) and females (6.8) did not differ ($P = 0.77$).

Seventy-four percent of adults occupying

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**Table 2.** Estimates of home-range size (ha) for radiocollared adult male ($n = 9$) and female ($n = 18$) woodchucks in Connecticut, 1987–1989, based on independent observations for each individual.

<table>
<thead>
<tr>
<th>Measure</th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\bar{X}$</td>
<td>$SE$</td>
</tr>
<tr>
<td>Minimum-convex polygon</td>
<td>4.01</td>
<td>0.88</td>
</tr>
<tr>
<td>Grid cell</td>
<td>1.32</td>
<td>0.26</td>
</tr>
<tr>
<td>Mean-squared distance from</td>
<td></td>
<td></td>
</tr>
<tr>
<td>center of activity</td>
<td>0.97</td>
<td>0.14</td>
</tr>
<tr>
<td>Bivariate-normal ellipse (95%)</td>
<td>10.55</td>
<td>1.57</td>
</tr>
<tr>
<td>Harmonic-mean contour (95%)</td>
<td>5.31</td>
<td>1.08</td>
</tr>
<tr>
<td>Harmonic-mean contour (50%)</td>
<td>0.85</td>
<td>0.25</td>
</tr>
</tbody>
</table>
Table 3.—Matrix of correlations between selected measures of home-range size for woodchucks in Connecticut, 1987–1989. Correlations above the diagonal are for males, whereas those below the diagonal are for females. Elements of the dominant eigenvector of the correlation matrix for both sexes combined are listed on the diagonal in italics and were used to calculate a multivariate estimate of home-range size for each individual. All correlations were significant at the 0.05 level unless otherwise noted.

<table>
<thead>
<tr>
<th></th>
<th>Minimum-convex polygon</th>
<th>Grid cell</th>
<th>Mean-squared distance</th>
<th>Bivariate normal (95%)</th>
<th>Harmonic mean (95%)</th>
<th>Harmonic mean (50%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Minimum-convex polygon</td>
<td>0.45</td>
<td>0.82</td>
<td>0.76</td>
<td>0.58&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.94</td>
<td>0.94</td>
</tr>
<tr>
<td>Grid cell</td>
<td>0.70</td>
<td>0.37</td>
<td>0.41&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.22&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.68</td>
<td>0.90</td>
</tr>
<tr>
<td>Mean-squared distance</td>
<td>0.89</td>
<td>0.53</td>
<td>0.42</td>
<td>0.94</td>
<td>0.75</td>
<td>0.60&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Bivariate normal (95%)</td>
<td>0.82</td>
<td>0.47</td>
<td>0.97</td>
<td>0.38</td>
<td>0.52&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.45&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Harmonic mean (95%)</td>
<td>0.94</td>
<td>0.68</td>
<td>0.84</td>
<td>0.76</td>
<td>0.43</td>
<td>0.80</td>
</tr>
<tr>
<td>Harmonic mean (50%)</td>
<td>0.60</td>
<td>0.66</td>
<td>0.68</td>
<td>0.72</td>
<td>0.54</td>
<td>0.40</td>
</tr>
</tbody>
</table>

<sup>a</sup> 0.05 < P < 0.10.<br>
<sup>b</sup> P > 0.10.

Home ranges (n = 27) exhibited significant levels of autocorrelation between successive observations, with equal proportions for males and females (χ² = 0.08, d.f. = 1, P > 0.50). Within a home range, mean tenure time (±SE) at a burrow was 4.5 ± 0.8 days for males and 5.8 ± 0.6 days for females. No difference occurred in the distribution of tenure times between the sexes (Kolmogorov-Smirnov T = 0.11, d.f. = 1, P > 0.20).

I recorded 110 interburrow movements for males with home ranges, significantly (χ² = 11.2, d.f. = 1, P < 0.05) fewer than the 151 expected if burrows were equally likely to be visited from one observation to the next. Differences between observed and expected frequencies of interburrow movements were even more pronounced for females (χ² = 79.5, d.f. = 1, P < 0.001), with the 219 observed movements representing only 55.2% of the total expected. For males, the frequency of revisitation to burrows that they had just vacated did not differ from the frequency expected from random movement among burrows (χ² = 0.03, d.f. = 1, P > 0.95). Females, though, revisited burrows disproportionately often (χ² = 10.64, d.f. = 1, P < 0.005).

Distances of interburrow movements were significantly (P < 0.05) greater than distances between nearest-neighbor burrows for males and females at both sites (Fig. 2). Males tended to exhibit greater distances for interburrow movements than females (Fig. 2), although this difference was not statistically significant (0.05 < P < 0.10 at both sites).

Mean overlap between home ranges of adult males was 31.2%, whereas overlap between males and reproductively active females was 35.5%, and overlap between reproductively active females was 13.5%. Mean overlap differed significantly among these three groups (Kruskal-Wallis T = 6.01, d.f. = 2, P = 0.05). Pairwise comparisons indicated that overlap between males and reproductively active females was greater than overlap between females (P < 0.05); neither of the other comparisons were significant.

Of the 258 burrow systems at which adult woodchucks were recorded, 93 (36.0%) were used by two or more adults during a given year (maximum was six). A pair of adults was recorded at a burrow on the same day on 17 occasions, 1–5 days apart on 42 occasions, and 6–10 days apart on 24 occasions. The proportion of paired records at 0 or 1–5 days apart for individuals of various sex and reproductively categories differed significantly from the overall proportion of these categories in the populations (0 days, χ² = 15.28, d.f. = 4, P < 0.005; 1–
5 days, $\chi^2 = 10.78$, $d.f. = 4$, $P < 0.05$). Reproductively mature males and females were captured at the same burrow disproportionately often 0 ($P < 0.005$) and 1–5 ($P < 0.025$) days apart (Fig. 3). Because the sample size at 0 days was smaller than the minimum of 20–25 observations suggested by Fienberg (1980) for use of the $\chi^2$ test, the significance level should be viewed as approximate. No difference between observed and expected proportions was noted for records occurring at a burrow and separated by 6–10 days ($\chi^2 = 4.47$, $d.f. = 4$, $P > 0.25$), although this interval exhibited the same trend as those at 0 and 1–5 days (Fig. 3).

Before 1 July, records were obtained at natal burrows for 60 juveniles, 22 reproductively mature females, 3 reproductively immature females, 8 males $\geq 3.0$ kg, and 13 males <3.0 kg. Excluding the juvenile class, records at natal burrows did not represent a random sample of the populations ($\chi^2 = 11.45$, $d.f. = 3$, $P < 0.01$). Reproductively mature and immature females at natal bur-

rows were significantly ($P < 0.05$) more and less common than expected, respectively; males of neither mass class differed from their relative frequencies in the adult populations ($P > 0.25$). Of 20 natal burrows, a single reproductively mature female was recorded at 18. A maximum of five juveniles was captured at each of three natal burrows; at two of these burrows I observed two mature females.

Six of the 33 radiocollared adults (four males, two females) failed to exhibit significant levels of site fidelity, that is, their movements were nomadic. A comparison of movements of nomads and home-range occupants categorized by sex was not possible because of the small number of nomads observed. However, nomads travelled farther ($P < 0.01$) on average during interburrow movements ($\bar{X} = 199$ m) than did home-range occupants ($\bar{X} = 83$ m). The same trend held for distances between consecutive observations (nomad $\bar{X} = 91$ m, home-range occupant $\bar{X} = 60$ m), although the difference was not significant ($P = 0.11$).

Most records of juveniles before late July were within one home-range diameter of their natal site (Fig. 4), in which the home-
Fig. 4.—Distances at which male \((n = 32)\) and female \((n = 30)\) woodchucks were observed from natal burrows during their first and second seasons above ground. Lower and upper dashed horizontal lines indicate distances equivalent to one radius and one diameter, respectively, of a circular home range equal to the mean home-range size (minimum-convex polygon) observed for adult females.

range diameter was obtained using the mean of minimum convex-polygon values of adult females. Two notable exceptions were a male and a female recorded 768 and 685 m, respectively, from their natal sites before mid-July. Distances from natal sites appeared to increase for juvenile males as the season progressed (Fig. 4). Too few observations of juvenile females were recorded during late summer and autumn to permit an assessment of temporal patterns of female dispersal. However, records of yearlings indicated a tendency for at least some females to remain close to their natal home range well into their second growing season; this tendency was less pronounced for males (Fig. 4).

**DISCUSSION**

Burrows occurred in highest densities in edge habitat at both study sites, and use of edge habitat by woodchucks was consistently greater than predicted from its availability at both a local (home range) and expanded (study site) spatial scale. In agricultural settings, burrows located adjacent to fields provide easy access to foraging areas and serve as refuges that are subjected less to human disturbance (Henderson and Gilbert, 1978). Consistent with this interpretation, Grizzell (1955) and Hamilton (1934) noted that burrows in woods, hedges, or brushy habitat were selected as hibernacula, and Meier (1985) observed that burrows in these habitats also were used preferentially as natal sites. I found that natal burrows occurred disproportionately often in edge habitat, although no tendency for selection of woodland burrows as natal sites was noted.

Although edge habitat was selected by woodchucks, the majority of activity during the post-reproductive season occurred in orchards. Woodchucks are generalist herbivores (Hamilton, 1934; Swihart, 1990), and consumption of food increases after cessation of breeding (Fall, 1971). Moreover, woodchucks often move during spring and summer from woodland sites to herbaceous areas more suitable for feeding (Meier, 1985; Wright, 1985). Hence, considerable use of areas containing palatable species of ground cover (e.g., orchards and meadows) is inevitable.

Few estimates of home-range size have been reported for male and female woodchucks. Mean minimum-area estimates of home-range size of radiocollared adult males (7.8 ha, \(n = 6\)) and females (2.8 ha, \(n = 4\)) differed significantly during summer and autumn in Quebec (Ouellet and Ferron, 1986). Trump (1950) used an unspecified
method of measurement to estimate mean male and female home-range sizes of 4.12 ha \((n = 4)\) and 0.73 ha \((n = 3)\), respectively, for individuals captured four or more times in Iowa. My results in Connecticut similarly indicate that, after the breeding season, adult males occupy significantly larger home ranges than adult females.

Clearly, absolute measures of home-range size are dependent upon the method used to obtain location data (Jones and Sherman, 1983) and the method of areal estimation (Table 2). Because woodchucks concentrate much of their aboveground activity near burrow systems, an estimator such as the grid-cell method may provide the best overall measure of the actual area visited. Although the convex polygon and bivariate normal probably overestimate the actual area visited, they contain useful information regarding the separation and dispersion of locations. In spite of the conceptual and technical differences among the estimators I used, the generally high levels of correlation (Table 3) are encouraging. Moreover, a general measure of home-range size was adequately expressed as a linear combination of these estimators (Table 3). Quantification in a multivariate context such as this permits comparison of home-range size for values grouped according to age, sex, mass, or other categorical variables, without the uncertainty of interpretation attendant to comparisons made with a single univariate measure of home-range size.

I observed frequent and often extensive movements of woodchucks within home ranges. Nonetheless, statistical dependence between successive observations was pronounced for 75% of adults. The autocorrelation I observed apparently was caused by the relatively lengthy (5-day) tenure of individuals at a particular burrow. Because the median interval between successive observations was 2 days, two to three successive observations were likely to be recorded in the vicinity of a burrow system before a significant movement occurred to another burrow system in the home range. Short-term fidelity to a particular burrow resulted in observed frequencies of interburrow movements that were 72.8% (males) and 55.2% (females) of the frequencies expected if no such fidelity was exhibited. Short-term fidelity to a site did not preclude use of numerous \((\bar{X} = 7.5)\) burrow systems, though. Use of multiple burrows by woodchucks appears widespread; a mean of 7.4 burrows was used in Ohio (Meier, 1985), 5.9 burrows in New York (Merriam, 1963), and 5.1 burrows in Quebec (Ouellet and Ferron, 1986).

Perhaps it is more pertinent to determine why, particularly during the post-breeding season, woodchucks move among several different burrow systems rather than maintain exclusive use of one or two closely spaced burrows. Contact with and subsequent avoidance of conspecifics appear to be likely explanations for this pattern. Bronson (1964) noted that subordinate woodchucks avoided contact with dominant individuals in aboveground encounters. The frequency of interburrow movements by woodchucks tends to increase during midday (Merriam, 1966). Merriam (1966) hypothesized that foraging during morning resulted in encounters of individuals and subsequent avoidance movements to other burrows by subordinate individuals. Encounters of occupants and invaders underground probably are frequent and also could result in interburrow movements (Merriam, 1963). Such encounters often would result in sequential use of burrow systems by different individuals. I observed sequential use at 36% of burrow systems at which woodchucks were recorded, and Bronson (1964) also noted time sharing of burrows in Pennsylvania.

Woodchucks typically follow paths radiating out from burrows and connecting burrow systems (Merriam, 1963). Under conditions of low density of woodchucks and high burrow density (a low ratio of woodchucks to burrows), then, movements prompted by avoidance of a dominant individual should be to an adjacent burrow. But in my study, numbers of woodchucks
were moderate to high (Davis et al., 1964; de Vos and Gillespie, 1960; Meier, 1985; Woodward, 1990). Consequently, a woodchuck repulsed from a burrow could quite likely have travelled to an adjacent burrow that was occupied. I observed distances for interburrow movements that were greater than distances for nearest-neighbor burrows both for a study site (Fig. 2) and within a home range, consistent with an interpretation of availability of empty burrows as a determinant of the extent of movement, at least for subordinate individuals.

Woodchucks have been characterized as asocial, reacting agonistically to neighbors and transients (Barash, 1989; Bronson, 1964). Ouellet and Ferron (1986) also suggested that defense of occupied burrows was likely. In my study, the low frequency of burrow sharing, the low degree of overlap between neighboring reproductive females, the relative scarcity with which reproductively immature females were captured at natal burrows, and the general tendency for juveniles to disperse from natal home ranges all indicate a low degree of sociality, at least relative to other marmots (Barash, 1989).

Reproductively mature females in particular appear intolerant of each other. Barash (1989) and Wright (1985) presented evidence that dominance relationships were established among neighboring females. Thus, low levels of home-range overlap between neighboring females (Barash, 1989; Meier, 1985; present study) could reflect avoidance by subordinate individuals (Barash, 1989).

Although less abundant, evidence from several studies leads me to suggest that woodchucks may be more tolerant of conspecifics than previously believed. After noting that groups of woodchucks in New York were associated with fairly discrete, spatially clumped groups of burrows, Merriam (1971) concluded that a vestigial form of coloniality could occur in woodchucks. Bailey (1965) showed that visual contact between captive woodchucks resulted in more rapid growth during spring, and Merriam (1971:745) pointed out that “Behaviorally based spatial contagion and cooperative group interactions are likely forms of vestigial coloniality.”

Barash (1989) concluded that a consistent social structure in woodchucks appeared limited to an association of an adult male and female for a few days during the breeding season, as well as mother-young associations that terminate at weaning, at which time dispersal occurs (Barash, 1974; de Vos and Gillespie, 1960). After parturition, aggressiveness and the minimum distance eliciting interactions between woodchucks both decline (Bronson, 1963, 1964). Thus, any sharing of burrows and overlap of home ranges I observed could merely have reflected an increased tolerance of conspecifics during the post-breeding season. However, high levels of home-range overlap and sharing of burrows were strongly skewed toward adult male-female pairs (Fig. 3), suggesting that at least some contact was maintained after cessation of breeding. In addition, associations between adult male and female woodchucks in Ohio apparently were retained throughout the year and often from year to year (Meier, 1985). In Quebec, simultaneous occupancy of a burrow during the post-breeding season was recorded five times, and four of these involved an adult male with an adult female (Ouellet and Ferron, 1986). Armitage (1986) hypothesized that heterosexual contact during the post-breeding season may be a male tactic designed to enhance the likelihood of mating with familiar females the following year.

Meier (1985) noted that 35% \((n = 17)\) of juvenile females did not disperse from their natal home range, whereas only 9% \((n = 11)\) of juvenile males did not disperse. Wright (1985) reported that in southern Illinois, males typically dispersed farther than females as juveniles, and he also observed three instances in which juvenile females remained in their natal home range. My data on dispersal are too few to draw definitive conclusions, but they do indicate a tendency for some young, particularly females, to re-
main as yearlings within their natal home range, at least during the period preceding emergence of juveniles (Fig. 4). Although adult females appear capable of suppressing reproduction by yearling females (Davis et al., 1964), limited data indicate that yearling females surrounded primarily by kin are more likely to reproduce than yearling females in other circumstances (Barash, 1989).

Among North American Marmota for which data are available, interspecific differences in the degree of sociality can be summarized as: M. olympus = M. caligata > M. flaviventris > M. monax (Barash, 1989). In his appraisal of interspecific variation in social behavior among marmots, Barash (1989) interpreted differences as resulting primarily from adaptations modulated by the different environments in which each species evolved. Woodchucks differ from other North American Marmota by generally occurring at lower latitudes with longer growing seasons and by occupying more continuous and extensive areas of suitable habitat (Barash, 1989). Although latitudinal differences likely contributed to the evolution of differing social systems among marmots, the evolutionary role of habitat patchiness is less clear. Before the settlement of eastern North America by Europeans, most areas were heavily forested (Delcourt and Delcourt, 1987). The eastern forest probably was interspersed with occasional meadows and early successional habitat created by natural disturbances or by prescribed burning by native Americans (Delcourt and Delcourt, 1987; Lorimer, 1989; McCabe and McCabe, 1984), particularly along coasts and rivers (Stephens, 1976). Consequently, woodchucks historically may have occurred at low densities overall (Hoffmeister, 1989) and as distinct groups in localized areas of resource abundance, separated by relatively large expanses of inhospitable habitat. These conditions closely match those of the more social alpine marmots occupying habitats that have been subjected to fewer human disturbances (Barash, 1989). If this scenario is correct, then the localization of resources in the past should have favored increased tolerance among females, territoriality among males, and perhaps the formation of simple matriline (Armitage, 1986; Downhower and Armitage, 1971). Recent changes in resource distributions caused by humans may influence the social structure of woodchuck populations in a proximate manner. Thus, the prevailing social structure may have resulted from phenotypic responses of individuals to changes in resource distribution (Lott, 1984).

Indeed, resource distribution can serve as a proximate factor influencing social structure. Mating systems and social organization in M. caligata, M. flaviventris, and M. olympus apparently can be affected by the patchiness and size of meadows used as feeding sites, and by the juxtaposition of meadows and suitable burrow sites (Armitage and Johns, 1982; Barash, 1989; Holmes, 1984; Johns and Armitage, 1979). For female woodchucks, de Vos and Gillespie (1960) noted that the likelihood of burrow sharing and the extent of home-range overlap should increase in habitats with abundant food and cover. Alternatively, Meier (1985) proposed that the ratio of defendable hibernacula and undefendable food resources was an important determinant of social structure of woodchucks; an increasing ratio would lead to increasing interactions and costs of defense and hence increasing tolerance among females.

Reproductive success in montane marmots is inversely related to harem size, and resident females of M. caligata repulse immigrant females (Barash, 1989), indicating that tolerance among females may reflect a strategy of minimizing individual costs in a resource-limited environment. Although similar conditions of localized resources may have prevailed historically over much of the range of the woodchuck, modern agro-ecosystems, by providing relatively large expanses of suitable habitat, afford conditions within which costs of tolerance are reduced
for females, whereas the benefit of behaving agonistically toward neighboring females and young is enhanced. Latitudinal differences in climatic regimes and primary productivity have contributed to the variation in social behavior among species of marmots by, for example, influencing age at first reproduction (Armitage, 1981). However, the role of phenotypically flexible responses to resource distribution deserves further study at the intraspecific level.

Conclusions

My results indicate that woodchucks, relative to other marmots, are characterized by a rather fluid spatial structure in which males range more widely than females, transients comprise a significant proportion of the population, reproductive females are widely dispersed, and juvenile dispersal often occurs. However, from my findings I also suggest that adult male-female associations persist after reproduction and that some juveniles, particularly females, do not disperse from their natal home ranges. Combined with data from other sources, it appears that woodchucks may exhibit a rudimentary social structure that extends beyond the breeding season, unlike the territorial (Hamilton, 1934), asocial (Bronson, 1964) characterization traditionally invoked.

Evolutionarily derived differences in social structure between woodchucks and other North American marmots are evident, and these differences may have arisen because of the different climatic regimes and resource distributions to which the species were exposed. However, interspecific differences in the distribution of limiting resources probably were less apparent before the onset of clearing, settlement, and agricultural practices by people in large portions of the range of M. monax. Consequently, the prevailing social structure of woodchucks may reflect in part a phenotypic response to the relatively recent alteration of resource distribution.

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