

INTRASEXUAL TERRITORIALITY IN WOODCHUCKS (*MARMOTA MONAX*)

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Species demonstrating intraspecific variation in social systems can be powerful models for understanding evolution of those systems. As a group, marmots exhibit several types of spacing systems, usually involving some degree of territoriality. Researchers have described populations of 1 species, the woodchuck, *Marmota monax*, as territorial and as nonterritorial, and such variation has been linked to ecological conditions. I used direct observations of individually recognized animals to describe the spacing system of a high-density population of *Marmota monax* in southern Maine. This population exhibited intrasexual territoriality. Home range overlap generally was higher between males and females than between same-sex individuals, and woodchucks tended to approach more members of the same sex more quickly compared with members of the opposite sex. Time spent scent marking varied across the active season but did not vary by sex. Males had larger home ranges than females, and home range sizes varied over time, perhaps in response to resources. Amount of overlap also was greater in some years than others, and such changes may be related to kinship. Philopatry and timing of dispersal also vary in this species and have implications for the evolution of sociality.

Key words: intraspecific variation, *Marmota monax*, population density, territoriality, woodchucks

To understand evolution of social systems, researchers often have compared related species that vary in social organization, such as antelopes (Jarman 1974), voles (e.g., Cochran and Solomon 2000; Ostfeld 1990), and sciurids (Armitage 1981; Koprowski 1998; Michener 1983). We also gain information about social systems by exploring intraspecific variation, which controls for phylogeny (Johnson et al. 2002; Lott 1991). Intraspecific variation in social organization is now a widely recognized phenomenon (Foster and Endler 1999; Lott 1991). Different populations, different animals within the same population, and even the same individuals at different times may display plasticity in social systems such as mating systems (e.g., Dobson et al. 2000), group size (e.g., Lenihan and Van Vuren 1996), and territoriality (e.g., Brashares and Arcese 2002; Maher 2000).

One group of ground-dwelling sciurids, the marmots, *Marmota*, exhibits interspecific variation in social systems, including spatial organization (Blumstein and Armitage 1999). In highly social species (e.g., alpine marmots [*M. marmota*] and golden marmots [*M. caudata aurea*]), group members share home range, but groups do not overlap (i.e., they maintain territories—Arnold 1990; Blumstein and Arnold

1998; Perrin et al. 1993). In less social species (e.g., Olympic marmots [*M. olympus*] and some hoary marmots [*M. caligata*]), a male's range overlaps ranges of 1 or a few females; female ranges also overlap one another (Blumstein and Armitage 1999). Degree of overlap depends on several factors in yellow-bellied marmots (*M. flaviventris*), including age, reproductive status, population density, and kinship (Armitage 1975; Frase and Armitage 1984).

The least social marmot, the woodchuck, *M. monax*, displays variable social organization across populations. Males may defend areas against other males, especially during breeding season (Grizzell 1955), adults may attack juveniles on occasion (Anthony 1962), and animals do not share burrows (Anthony 1962; Grizzell 1955; Twichell 1939) or feed in close proximity (Anthony 1962). In other populations, woodchucks may share burrows (Bronson 1964; Ferron 1996; Meier 1992; Ouellet and Ferron 1986; Swihart 1992; Trump 1950) or feed near each other (Barash 1989; Bronson 1963; Grizzell 1955; Hamilton 1934; Smith 1972), and dominant individuals can move freely through a subordinate's home range (Bronson 1963, 1964).

Several underlying ecological conditions have been proposed to explain variation in woodchuck spacing systems (including intersexual overlap), such as access to food resources, cover, and availability of hibernacula (deVos and Gillespie 1960; Meier 1985, 1992). Population density also has been associated with woodchuck spatial organization (Ferron and Ouellet 1989): as density increases, home range size decreases, amount of overlap increases, and animals may be less territorial.

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My objectives were to describe spatial organization of woodchucks in southern Maine, and to identify ecological factors associated with the spacing system. I considered territories to be relatively exclusive areas that woodchucks actively defended. Based on data from the literature, I expected woodchucks to show less evidence of territoriality in this dense population, as indicated by higher amounts of home range overlap and longer latencies before approaching intruders, compared with less dense populations. By documenting spatial patterns in another population of a behaviorally flexible species, it is possible to further our understanding of marmot sociality and facilitate comparisons with previous and future work.

MATERIALS AND METHODS

Study area.—I studied woodchucks at Gilsland Farm Sanctuary, Falmouth, Maine (43°42'N, 70°14'W), a nature preserve that encompasses 26 ha and ranges 0–10 m in elevation. The study area consists of gently rolling hills covered with mixed hardwood–coniferous forest, salt marsh, and 3 meadows (6, 3.5, and 2.5 ha). The sanctuary is bordered by the Presumpscot River estuary to the west, U.S. Route 1 (3 lanes) to the east, salt marsh to the north, and housing developments to the north, south, and east.

Trapping and handling.—Field assistants and I used live traps (Tomahawk Live Trap, Tomahawk Live Trap Co., Tomahawk, Wisconsin; 81 × 25 × 30 cm) baited with peanut butter and fresh apple slices to capture woodchucks. I trapped only during daylight hours and monitored traps hourly. Upon capture, I transferred the animal to a cone-shaped cloth handling bag and weighed it with a spring scale to the nearest 0.25 kg. I determined age based on weight when possible (yearlings typically weigh <2.0 kg in spring), given that yearlings weigh less than adults early in the season (Kwiecinski 1998), and tooth color, given that yearlings have whiter teeth than adults (Davis 1964). I determined sex using anogenital distance as well as presence of scrotal testes or distended nipples, depending on time of year. I uniquely marked each animal on its dorsal side, applying Clairol Balsam Color hair dye (Clairol Inc., Stamford, Connecticut; black dye for brown and dark brown animals; palest blonde for melanistic animals); this mark allowed me to recognize animals from a distance and remained until animals molted in early summer. I also placed numbered metal ear tags (National Band and Tag Company, Newport, Kentucky; size 3) in each ear to provide a permanent identification mark. I then released each animal at the burrow where I caught it. I followed American Society of Mammalogists guidelines for animal care and use (Animal Care and Use Committee 1998), and these methods were approved by the Institutional Animal Care and Use Committee at the University of Southern Maine.

Data collection and analysis.—I collected data for this study from February 1998 through October 2001. During this period, I captured 109 woodchucks on the study site, which represent nearly all (95%) yearling and adult animals inhabiting the area each year, plus juveniles born on site. Field assistants and I logged nearly 4,600 person-h in the field. Visibility for observing woodchucks was excellent from late February, when animals emerged from hibernation, through May. It then declined in many parts of the property as vegetation grew. However, several areas were mowed regularly, so I obtained data throughout summer. In late July or early August, meadows were cut for hay, and visibility was excellent until animals entered hibernation in September and October. Woodchucks were habituated to humans, permitting observations at distances of 1–100 m. However, field assistants and I frequently used binoculars and spotting scopes to

facilitate identification and observations and to reduce interference with animals' behavior.

I used a global positioning system to map active burrows within 0.1 m, then marked those burrows with numbered wooden stakes. When I saw an animal aboveground, I identified it and recorded its position with respect to the nearest numbered stake. To ensure statistical independence, I took position data ≥ 8 h apart, based on average body size (Swihart et al. 1985). I collected an average of 21 locations per animal. Home range data were analyzed using The Kernel (available on the Internet at http://www.nbb.cornell.edu/neurobio/jbsv_downloads/programs.html) and Wildtrak (Todd 1992), which calculated 95% adaptive kernel polygons and minimum convex polygons, respectively. I also used Wildtrak to calculate amount of home range overlap between pairs of individuals. I examined plots of percentage of range compared with number of fixes to ensure that I had sufficient numbers of points to estimate home range size accurately. To determine core area of a home range in Wildtrak, I examined a cumulative plot of percentage of home range area compared with percentage of minimum convex polygon size (Todd 1992). The minimum area at which this curve reached a plateau indicated the size of the core area. I calculated the amount of home range overlap between individuals that had potential to overlap; i.e., they were in the same area during the same time period. For example, I did not compare home ranges of a male seen only in the far northern part of the study site with a male seen only in the southern end of the site.

I recorded activity budgets during focal observations (Martin and Bateson 1993) of known individuals. I obtained 1.4% of observations ($n = 2,005$ total observations) during emergence and breeding periods (4 weeks in March), 44% during gestation and lactation (11 weeks from April to mid-June), and 54.7% during the postbreeding period (18 weeks from mid-June to mid-October). Samples lasted a maximum of 15 min and began when the animal resumed its original activity if I had disturbed it. Animals had to remain in view ≥ 3 min for the sample to be included in the analysis. Because samples did not always last the full 15 min, I converted times to percentage of length of observation period. I sampled individuals at intervals >24 h to ensure statistical independence. Although I collected data on many behavior patterns, I report only scent marking in this study because scent marking may serve a function in delineating territories in marmots (Barash 1989; Lenti Boero 1995).

I also recorded responses to intruders during focal samples and using ad libitum sampling (Martin and Bateson 1993). Animals defending territories against intruders are expected to approach intruders sooner (i.e., show shorter latencies) than animals that do not defend such areas (Maher 2000). When I observed 2 woodchucks in an area, I recorded their identities if possible, and I recorded latency from the moment when the resident woodchuck saw an intruder to the moment at which it first moved to encounter that intruder. If a resident never approached an intruder during a 15-min focal observation, I recorded a maximum latency of 15 min.

Degree of territoriality often is tied to ecological conditions, such as food abundance (Maher 2000; Maher and Lott 2000), because territories should be economically defensible (e.g., defense of scarce or superabundant resources may not be cost effective—Brown 1964). To sample food abundance, I randomly positioned a 1-m² quadrat constructed of polyvinyl chloride pipe within woodchuck home ranges and randomly chose one 0.25-m² quadrant in which I clipped all aboveground vegetation. I froze the plants in resealable plastic bags. Because woodchucks primarily consume forbs, especially later in the growing season (Arsenault and Romig 1985; Swihart 1990), I removed grasses and dead vegetation from samples and retained only green forbs. I weighed each sample on a top-loading balance to the nearest

0.1 g (fresh weight) then air dried each sample. To measure dry weight, I weighed each air-dried sample daily until its weight no longer fluctuated ± 0.1 g. I did not sample plants in 2000.

I combined data for yearlings and adults but did not include data for juveniles. For scent marking data, I calculated a mean percentage of time spent scent marking for each animal for each time period (month, year). Patterns varied across years, so data were analyzed for each year separately. However, some animals were present in >1 year. Because data were not normally distributed, I used nonparametric tests in StatView software (SAS Institute, Inc. 1998) to analyze data. Unless otherwise noted, I reported data as mean $\pm$ SE. Significance levels were set at $P \leq 0.05$ except when I performed multiple comparisons, some of which might be statistically significant by chance alone. In those cases, I used the sequential Bonferroni test (Rice 1989) to reduce the probability of type I errors and maintain $\alpha = 0.05$.

RESULTS

Home range size.—Minimum convex polygon analysis showed that males generally had larger core home ranges than females, although differences were statistically significant after Bonferroni correction only in 2001 (Mann–Whitney U -tests: 1998, $P > 0.99$; 1999, $P = 0.18$; 2000, $P = 0.072$; 2001, $U = 6$, $n = 9$ females, 6 males, $P = 0.013$; Fig. 1a). Home range sizes for males differed across years, but not for females (Kruskal–Wallis tests: males, $H = 8.32$, $df = 3$, $P = 0.040$; females, $H = 6.56$, $df = 3$, $P = 0.087$).

The kernel method yielded larger home range sizes than the minimum convex polygon method (Fig. 1b). The same overall patterns emerged in 3 of 4 years; however, males and females did not differ from each other ($P > 0.34$). Sizes of males' home ranges did not differ across years, but differences for females were nearly significant (females, $H = 7.558$, $df = 3$, $P = 0.056$; males, $P = 0.43$). Unfortunately, I could not collect sufficient numbers of locations to analyze home range size by season.

Amount of home range overlap.—The amount of intersexual overlap was significantly higher than the amount of intrasexual overlap in 2001, following Bonferroni corrections (Wilcoxon signed ranks test, $z = -3.21$, $n = 16$ woodchucks, $P = 0.0013$; Figs. 2 and 3). However, similar patterns were seen in all years (1998, $P = 0.92$; 1999, $P = 0.047$; 2000, $P = 0.064$; Fig. 2). Analyzed separately, females and males showed similar patterns, but only females had significantly higher amounts of intersexual overlap and only in 2001, probably due to small sample sizes (1998 females, $P = 0.89$; 1999, $P = 0.07$; 2000, $P = 0.37$; 2001, $z = -2.67$, $n = 9$, $P = 0.008$; 1998 males, $P = 0.89$; 1999, $P = 0.35$; 2000, $P = 0.04$; 2001, $P = 0.18$).

Females differed in amount of intrasexual overlap across years ($H = 7.52$, $df = 3$, $P = 0.048$), and differences in intersexual overlap approached statistical significance ($H = 7.11$, $df = 3$, $P = 0.068$; Table 1). Males, however, did not differ in amount of intersexual overlap across years ($P = 0.718$), although intrasexual overlap varied ($H = 8.11$, $df = 3$, $P = 0.044$; Table 1).

Males and females did not differ from each other in total (intrasexual and intersexual combined) amount of home range overlap (1998, $P = 0.25$; 1999, $P = 0.07$; 2000, $P = 0.23$; 2001, $P = 0.29$; Table 1) or in amount of intersexual overlap (1998, $P = 0.95$; 1999, $P = 0.03$; 2000, $P = 0.13$; 2001, $P =$

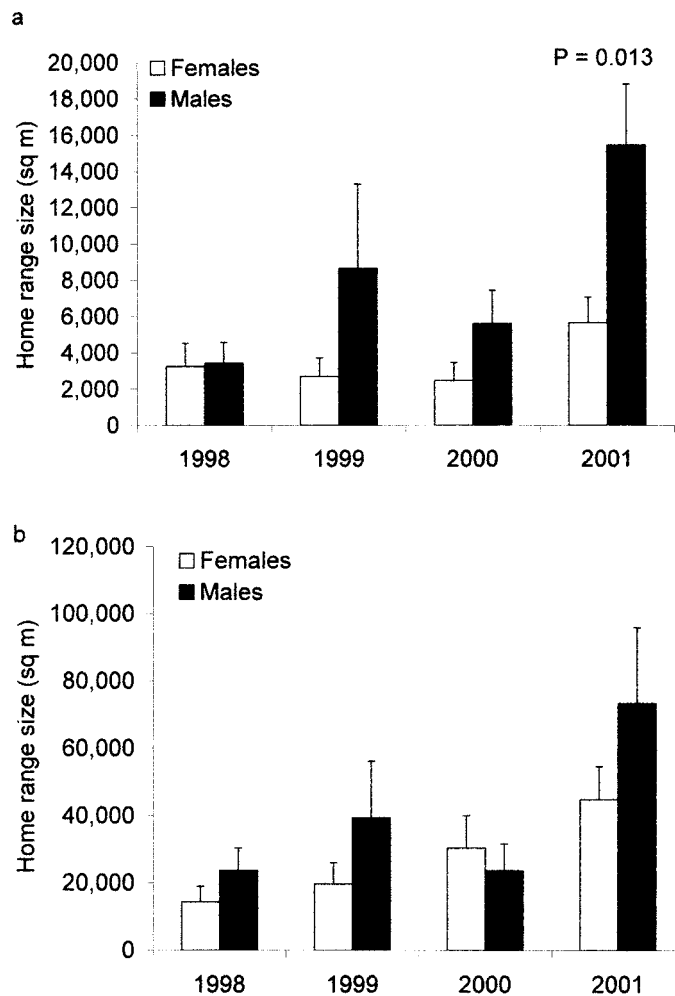


FIG. 1.—Mean ($\pm$ SE) home range size (square meters) for woodchuck males and females at Gilsland Farm Sanctuary, Maine, 1998–2001 using a) minimum convex polygon method, and b) 95% kernel method. Sample sizes for females were 8, 9, 10, and 9, respectively, and sample sizes for males were 9, 9, 6, and 8, respectively.

0.03; Table 1). Patterns were less clear for intrasexual overlap, although males showed nearly significantly higher amounts than females in 2001 after Bonferroni correction ($U = 11$, $n = 8$ males, 9 females, $P = 0.016$; Table 1).

Responses to intruders.—Sample sizes were small, but animals appeared to approach members of the same sex sooner than members of the opposite sex (Table 2). They also appeared to approach a higher percentage of members of the same sex than those of the opposite sex in most years (Table 2). When 1 woodchuck approached another, the next interaction was a chase, fight, or displacement (i.e., aggressive or submissive interactions).

Ad libitum observations revealed that males and females frequently (33 cases in 1998–2001) fed or rested <10 m from each other without any interaction, amicable or aggressive, even outside the breeding season. Yet, I rarely (2 cases in 1998–2001) witnessed same-sex tolerance except between mothers and juvenile daughters.

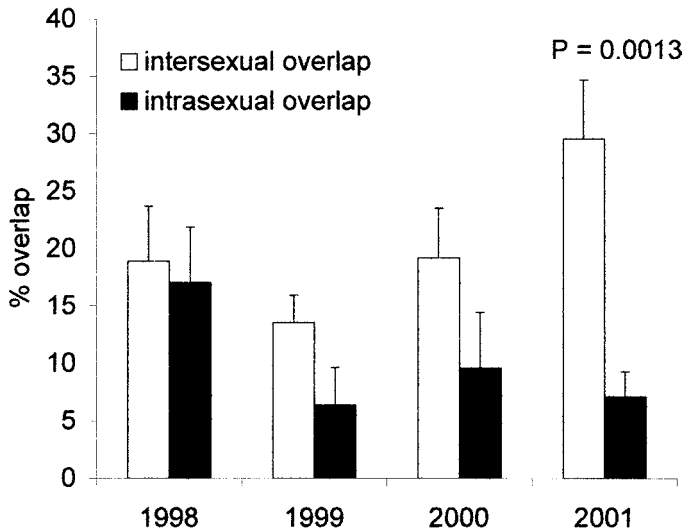


FIG. 2.—Mean ($\pm$ SE) percentage of intersexual and intrasexual overlap in home range among woodchucks, 1998–2001, in Maine.

Scent marking.—When woodchucks scent mark, they sniff an area, such as tree trunks, branches, wooden stakes, and the ground; they may chew tree trunks, branches, and stakes; and they rub their muzzles against a surface (Ouellet and Ferron 1988). The amount of time that woodchucks spent scent marking varied significantly after Bonferroni corrections during the active season in 1998 and 2001 (1998, $H = 16.89$, $d.f. = 5$, $P = 0.005$; 1999, $P = 0.29$; 2000, $P = 0.033$; 2001, $H = 22.13$, $d.f. = 7$, $P = 0.002$). Scent marking occurred most often in spring (March and April), then declined over the remainder of the year (Fig. 4). Males and females did not differ in percentage of time spent scent marking ($P > 0.05$; Fig. 4).

Ecological conditions.—Food abundance did not vary significantly across years (dry weights per 0.25 m^2 in 1998, $21.0 \pm 2.3 \text{ g}$, $n = 30$ plots; 1999, $25.0 \pm 5.1 \text{ g}$, $n = 15$ plots; 2001, $40.1 \pm 8.4 \text{ g}$, $n = 14$ plots; $H = 2.72$, $d.f. = 2$, $P = 0.26$). In addition, precipitation totals recorded in nearby Portland, Maine, from March to September were similar in most years (1998, 77.2 cm ; 1999, 57.6 cm ; 2000, 57.2 cm ; 2001, 59.2 cm ; Climate Information Library, National Weather Service, <http://www.erh.noaa.gov/er/gyx>; $H = 3.0$, $d.f. = 3$, $P = 0.39$).

Using total counts, I estimated that woodchuck population density from 1998 to 2001 was 1.8, 2.1, 1.4, and 1.6 woodchucks/ha, respectively, excluding juveniles. Mean home range size did not vary significantly with population density (males, $r^2 = 0.003$, $P = 0.95$; females, $r^2 = 0.038$, $P = 0.81$). Similarly, neither mean intrasexual nor mean intersexual overlap varied significantly with population density (intrasexual overlap, $r^2 = 0.002$, $P = 0.92$; intersexual overlap, $r^2 = 0.13$, $P = 0.39$).

DISCUSSION

Contrary to my initial prediction, woodchucks displayed intrasexual territoriality in this population. Males maintained exclusive areas separate from other males, as did females separate from other females, whereas male and female ranges

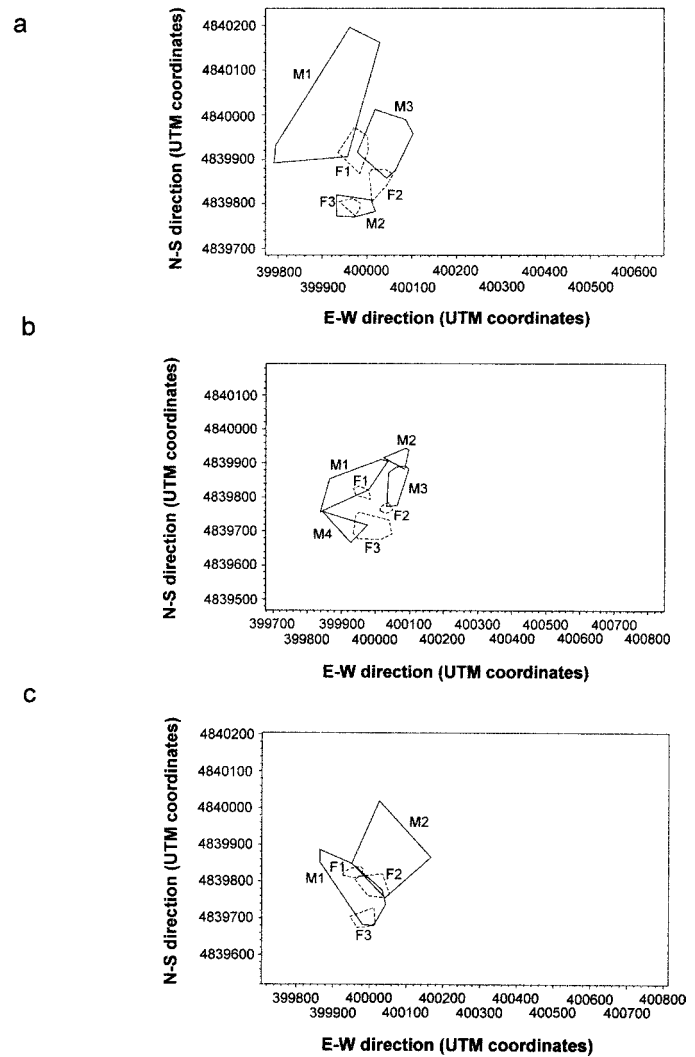


FIG. 3.—Representative core home range maps illustrating size and overlap among male and female woodchucks for a) 1999, b) 2000, and c) 2001, in Maine. Solid lines represent males' home ranges, and dotted lines indicate females' ranges. M = male; F = female. Axes indicate universal transverse mercator (UTM) coordinates.

overlapped. Animals also tended to show shorter latencies for approaching an animal of the same sex compared with the opposite sex and approached a higher percentage of same-sex intruders, consistent with intrasexual territoriality. I often saw males and females feeding within 10 m of each other, but I rarely saw adults of the same sex doing so. Males and females also showed similar patterns of territoriality. Although males occupied larger home ranges than females, sexes did not differ in amounts of intrasexual or intersexual overlap or in percentage of time spent scent marking. Scent marking behavior peaked in spring then declined for the rest of the active season, coinciding not only with breeding season but also with emergence from hibernation and territory establishment.

Previous studies of woodchuck spatial organization detail a high degree of variability in behavior and home range overlap (Bronson 1963, 1964; Ferron and Ouellet 1989; Meier 1985, 1992; Smith 1972; Swihart 1992). Such variation in spatial

TABLE 1.—Percentage of total, intrasexual, and intersexual overlap for woodchuck males and females in Maine, 1998–2001.

	Total		Intrasexual		Intersexual	
	<i>n</i>	$\bar{X} \pm SE$	<i>n</i>	$\bar{X} \pm SE$	<i>n</i>	$\bar{X} \pm SE$
1998						
Males	8	10.4 $\pm$ 3.3	7	14.1 $\pm$ 8.2	6	16.6 $\pm$ 7.3
Females	8	16.8 $\pm$ 3.7	8	19.6 $\pm$ 5.9	8	20.6 $\pm$ 6.7
1999						
Males	8	8.1 $\pm$ 3.1	8	6.7 $\pm$ 4.4	7	8.1 $\pm$ 2.2
Females	9	14.2 $\pm$ 2.3	9	6.1 $\pm$ 5.0	9	17.8 $\pm$ 3.3
2000						
Males	6	11.7 $\pm$ 5.9	5	0.58 $\pm$ 0.4	6	15.4 $\pm$ 9.0
Females	10	19.0 $\pm$ 3.9	9	14.6 $\pm$ 7.1	10	21.4 $\pm$ 4.6
2001						
Males	8	14.3 $\pm$ 4.2	8	12.1 $\pm$ 4.0*	7	15.5 $\pm$ 5.7
Females	9	22.2 $\pm$ 3.4	9	2.6 $\pm$ 0.9*	9	40.4 $\pm$ 5.8

* $P = 0.016$.

organization may reflect underlying differences in ecological conditions (Armitage and Blumstein 2002; Maher and Lott 2000). Populations occupy latitudes of 39–48°N, with active seasons for adults ranging from 5 to 7 months (Ferron 1996; Meier 1992). However, spacing systems are not clearly linked to latitude or length of growing season.

Meier (1985, 1992) proposed that availability of hibernacula influenced spacing systems but supporting data were not presented. Hibernacula probably were not limiting in my study population, but quality or quantity of that resource may have changed over time.

Based on data from 4 populations located in Quebec, Ontario, Pennsylvania, and Ohio, Ferron and Ouellet (1989) proposed that population density influences woodchuck social organization. Woodchucks display territoriality at lower (0.12 woodchucks/ha) and intermediate (0.5 woodchucks/ha) densities, and they do not maintain territories at higher (0.9 and 17.1 woodchucks/ha) densities. However, density in my study averaged 1.7 woodchucks/ha, and animals displayed intrasexual territoriality. Likewise, in Connecticut marmots with a density of 1.9 woodchucks/ha, females maintained intrasexual territories (Swihart 1992). Some population differences may be explained by a different interpretation of original articles. Bronson (1963, 1964) described home ranges as overlapping 4–77% in a high-density (0.9 woodchucks/ha) population;

however, he did not analyze males and females separately, and animals may have maintained intrasexual territories. Smith (1972:38) reported a much higher density ($\bar{X} = 17.1$ woodchucks/ha), but he did not explicitly state whether woodchucks were territorial or not. Instead, he suggested woodchucks lived in “rudimentary family groupings.”

Within the population I studied, spatial organization changed somewhat over time; home range sizes fluctuated, and woodchucks exhibited greater amounts of overlap in some years than in others. In 1999, 1 male occupied a home range nearly 5 times larger than ranges of other males, which increased mean size. Home range sizes also increased in 2001, although total precipitation and food abundance did not differ from previous years. Nonetheless, precipitation totals were 193% and 164% of average in March and June, respectively, whereas totals were just 30% of average in April and May and 62% of average in July. These lower totals, especially in spring, may have influenced forage quantity (Sneva and Hyder 1962) on finer scales than measured, forcing animals to feed over larger areas. In many rodent populations, food and home range or territory size are closely linked, such that food supplementation decreases range sizes (Ims 1987; Ostfeld 1986), and species with larger home ranges also have lower plant biomass available (Armitage and Blumstein 2002). In addition, other characteristics of food resources that I did not measure may have changed (e.g., quality or distribution), leading to changes in range size.

In this population, home range overlap varied over time, and intrasexual overlap showed more fluctuation than intersexual overlap. One qualitative study described increased amounts of spatial overlap with increased amounts of food and cover (deVos and Gillespie 1960), but changes in overlap were not associated clearly with changes in either food abundance or population density in my study. Rather, such changes may be linked to kinship.

Marmots display a range of social systems, but most species live in some form of kin group (Armitage 1981, 1999; Blumstein and Armitage 1999). Woodchucks are considered the exception to that rule (Allainé 2000; Armitage 1999; Barash 1989; Blumstein and Armitage 1999; Michener 1983); however, I suggest they are more similar to their congeners, particularly yellow-bellied marmots, than previously suggested. Among yellow-bellied marmots, amount of home range overlap depends partly on population density as well as kinship, with closely related females exhibiting greater amounts of overlap (Armitage 1975; Frase and Armitage 1984). Woodchuck

TABLE 2.—Median latency to approach woodchucks of the opposite sex or the same sex and mean ($\pm SE$) percentage of intruders of the same or opposite sex that woodchucks approached, 1998–2001, in Maine. Sample size (*n*) = number of animals.

Variable	1998	1999	2000	2001
Latency to approach (s)				
Opposite sex	240 (3)	900 (11)	900 (4)	525 (12)
Same sex	900 (1)	0 (5)	450 (4)	10 (8)
Percentage approached				
Opposite sex	87.5 $\pm$ 12.5 (4)	31.8 $\pm$ 13.9 (11)	0.0 (4)	48.6 $\pm$ 13.8 (12)
Same sex	0.0 (1)	80.0 $\pm$ 20.0 (5)	50.0 $\pm$ 28.9 (4)	62.5 $\pm$ 18.3 (8)

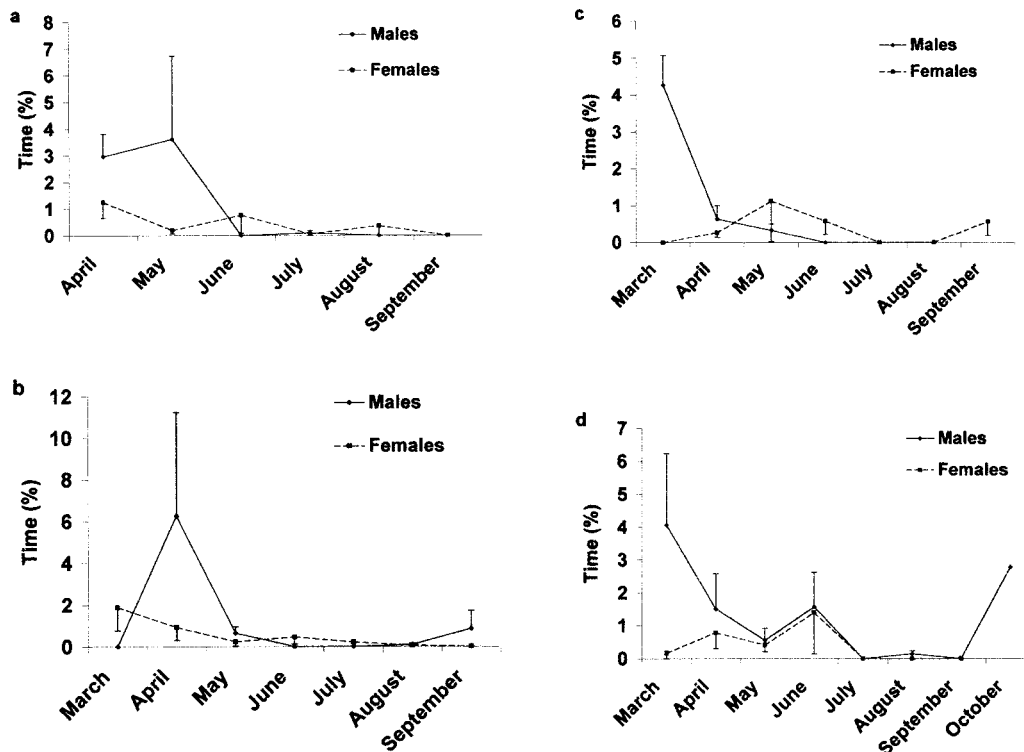


FIG. 4.—Mean ($\pm$ SE) percentage time that woodchuck males and females spent scent marking in Maine in a) 1998, b) 1999, c) 2000, and d) 2001.

females do not share much space with other females, but that overlap varies, perhaps due to kinship patterns, and currently I am analyzing microsatellite DNA to determine genetic relationships. In yellow-bellied marmots, males' ranges overlap extensively with females' ranges but not with ranges of other males, although males and females do not interact extensively (Blumstein and Armitage 1999). Similarly, woodchuck males' and females' home ranges overlap, and males and females do not interact either amicably or agonistically; rather, they tolerate each other's presence.

In many mammals, females share more space with relatives than with nonrelatives (Sera and Gaines 1994; van Staaden et al. 1994; Vestal and McCarley 1984), and they are more philopatric and disperse shorter distances than males (Byrom and Krebs 1999; Greenwood 1980; Holekamp 1984; Murie and Harris 1984; van Staaden et al. 1994, 1996). Such patterns set the stage for formation of kin groups (Armitage 1981; Emlen 1994, 1997; Greenwood 1980; Holekamp 1984; Koenig et al. 1992; Michener 1983; Smale et al. 1997). Degree of philopatry or dispersal varies depending on several factors, including population density and number of vacant territories within the habitat (Cochran and Solomon 2000). Although density and dispersal are not closely related in all species (e.g., arctic ground squirrels, *Spermophilus parryi plesius*—Byrom and Krebs 1999; San Joaquin kit foxes, *Vulpes macrotis mutica*—Koopman et al. 2000), many species exhibit reduced dispersal or increased philopatry at higher densities, with offspring retained within the family or population (e.g., prairie voles, *Microtus ochrogaster*—Cochran and Solomon 2000; European rabbits,

Oryctolagus cuniculus—Richardson et al. 2002; Alabama beach mice, *Peromyscus polionotus ammobates*—Swilling and Wooten 2002).

Woodchucks show variation in degree of philopatry and timing of dispersal. Juveniles may disperse soon after emergence (deVos and Gillespie 1960; Ouellet and Ferron 1986). However, it has been suggested that some juveniles remained in or near natal home ranges until at least their 2nd summer, with some animals moving away from the natal area once young of the year emerged (Meier 1985, 1992; Smith 1972; Swihart 1992). Furthermore, yearlings sometimes established home ranges overlapping or adjacent to their parents' home ranges (Meier 1992). Red squirrel (*Tamiasciurus hudsonicus*) mothers may bequeath portions of their territory to offspring by dispersing and allowing offspring to remain in the natal range (Berteaux and Boutin 2000, Boutin et al. 2000). In my study population in some years, up to 50% of juveniles, both males and females, delayed dispersal until their second summer (C. Maher, in litt.). For example, I witnessed dispersal of 6 daughters of 1 particular female over a period of 3 years. In 2001, 2 daughters settled as yearlings in home ranges adjacent to their mother's home range. In 2002, 2 additional yearling daughters also settled in adjacent areas. Most recently, 2 daughters remained within their natal home range. Some males also were philopatric; e.g., 1 grandson of this female settled within his natal range and adjacent to his grandmother's home range.

Subtle changes in habitat quality or limited vacant territories may raise costs of dispersal such that woodchucks delay dispersal or settle near natal home ranges. Mothers also may

tolerate presence of their offspring, leading to increased amounts of home range overlap (Waser and Jones 1983), especially with daughters. Future studies will examine questions of philopatry, dispersal, and spacing patterns to better identify the variation in social organization and origins of sociality.

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LITERATURE CITED

- ALLAINÉ, D. 2000. Sociality, mating system and reproductive skew in marmots: evidence and hypotheses. *Behavioural Processes* 51: 21–34.
- ANIMAL CARE AND USE COMMITTEE. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy* 79:1416–1431.
- ANTHONY, M. 1962. Activity and behavior of the woodchuck in southern Illinois. *Occasional papers of the C.C. Adams Center for Ecological Studies* 6:1–25.
- ARMITAGE, K. B. 1975. Social behavior and population dynamics of marmots. *Oikos* 26:341–354.
- ARMITAGE, K. B. 1981. Sociality as a life-history tactic of ground squirrels. *Oecologia* 48:36–49.
- ARMITAGE, K. B. 1999. Evolution of sociality in marmots. *Journal of Mammalogy* 80:1–10.
- ARMITAGE, K. B., AND D. T. BLUMSTEIN. 2002. Body-mass diversity in marmots. Pp. 22–32 in *Holarctic marmots as a factor of biodiversity—Proceedings of the 3rd International Conference on Marmots* (K. B. Armitage and V. Yu. Rumiantsev, eds.). Commission on Marmot Investigations, Theriology Society of the Russian Academy of Sciences, Moscow, Russia.
- ARNOLD, W. 1990. The evolution of marmot sociality: II. Costs and benefits of joint hibernation. *Behavioral Ecology and Sociobiology* 27:239–246.
- ARSENAULT, J. R., AND R. F. ROMIG. 1985. Plants eaten by woodchucks in three northeast Pennsylvania counties. *Proceedings of the Pennsylvania Academy of Sciences* 59:131–134.
- BARASH, D. P. 1989. *Marmots: social behavior and ecology*. Stanford University Press, Stanford, California.
- BERTEAUX, D., AND S. BOUTIN. 2000. Breeding dispersal in female North American red squirrels. *Ecology* 81:1311–1326.
- BLUMSTEIN, D. T., AND K. B. ARMITAGE. 1999. Cooperative breeding in marmots. *Oikos* 84:369–382.
- BLUMSTEIN, D. T., AND W. ARNOLD. 1998. Ecology and social behavior of golden marmots (*Marmota caudata aurea*). *Journal of Mammalogy* 79:873–886.
- BOUTIN, S., K. W. LARSEN, AND D. BERTEAUX. 2000. Anticipatory parental care: acquiring resources for offspring prior to conception. *Proceedings of the Royal Society of London, B. Biological Sciences* 267:2081–2085.
- BRASHARES, J. S., AND P. ARCESE. 2002. Role of forage, habitat and predation in the behavioural plasticity of a small African antelope. *Journal of Animal Ecology* 71:626–638.
- BRONSON, F. H. 1963. Some correlates of interaction rate in natural populations of woodchucks. *Ecology* 44:637–643.
- BRONSON, F. H. 1964. Agonistic behaviour in woodchucks. *Animal Behaviour* 12:470–478.
- BROWN, J. L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bulletin* 76:160–169.
- BYROM, A. E., AND C. J. KREBS. 1999. Natal dispersal of juvenile arctic ground squirrels in the boreal forest. *Canadian Journal of Zoology* 77:1048–1059.
- COCHRAN, G. R., AND N. G. SOLOMON. 2000. Effects of food supplementation on the social organization of prairie voles (*Microtus ochrogaster*). *Journal of Mammalogy* 81:746–757.
- DAVIS, D. E. 1964. Evaluation of characters for determining age of woodchucks. *Journal of Wildlife Management* 28:9–15.
- DEVOS, A., AND D. I. GILLESPIE. 1960. A study of woodchucks on an Ontario farm. *Canadian Field-Naturalist* 74:130–145.
- DOBSON, F. S., A. T. SMITH, AND W. X. GAO. 2000. The mating system and gene dynamics of plateau pikas. *Behavioural Processes* 51: 101–110.
- EMLÉN, S. T. 1994. Benefits, constraints and the evolution of the family. *Trends in Ecology and Evolution* 9:282–285.
- EMLÉN, S. T. 1997. Predicting family dynamics in social vertebrates. Pp. 228–253 in *Behavioural ecology: an evolutionary approach* (J. R. Krebs and N. B. Davies, eds.). 4th ed. Blackwell Science, Oxford, United Kingdom.
- FERRON, J. 1996. How do woodchucks (*Marmota monax*) cope with harsh winter conditions? *Journal of Mammalogy* 77:412–416.
- FERRON, J., AND J.-P. OUELLET. 1989. Temporal and intersexual variations in the use of space with regard to social organization in the woodchuck (*Marmota monax*). *Canadian Journal of Zoology* 67:1642–1649.
- FOSTER, S. A., AND J. A. ENDLER, EDS. 1999. *Geographic variation in behavior: perspectives on evolutionary mechanisms*. Oxford University Press, New York.
- FRASE, B. A., AND K. B. ARMITAGE. 1984. Foraging patterns of yellow-bellied marmots: role of kinship and individual variability. *Behavioral Ecology and Sociobiology* 16:1–10.
- GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140–1162.
- GRIZZELL, R. A., JR. 1955. A study of the southern woodchuck, *Marmota monax monax*. *American Midland Naturalist* 53:257–293.
- HAMILTON, W. J., JR. 1934. The life history of the rufescent woodchuck, *Marmota monax rufescens* Howell. *Annals of Carnegie Museum* 23:85–167.
- HOLEKAMP, K. E. 1984. Dispersal in ground-dwelling sciurids. Pp. 297–320 in *The biology of ground-dwelling squirrels: annual cycles, behavioral ecology and sociality* (J. O. Murie and G. R. Michener, eds.). University of Nebraska Press, Lincoln.
- IMS, R. A. 1987. Responses in spatial organization and behaviour to manipulations of the food resource in the vole *Clethrionomys rufocanus*. *Journal of Animal Ecology* 56:585–596.
- JARMAN, P. V. 1974. The social organisation of antelope in relation to their ecology. *Behaviour* 48:215–266.

- JOHNSON, D. D. P., W. JETZ, AND D. W. MACDONALD. 2002. Environmental correlates of badger social spacing across Europe. *Journal of Biogeography* 29:411–425.
- KOENIG, W. D., F. A. PITELKA, W. J. CARMEN, R. L. MUMME, AND M. T. STANBACK. 1992. The evolution of delayed dispersal in cooperative breeders. *Quarterly Review of Biology* 67:111–150.
- KOOPMAN, M. E., B. L. CYPHER, AND J. H. SCRIVNER. 2000. Dispersal patterns of San Joaquin kit foxes (*Vulpes macrotis mutica*). *Journal of Mammalogy* 81:213–222.
- KOPROWSKI, J. L. 1998. Conflict between the sexes: a review of social and mating systems of the tree squirrels. Ecology and evolutionary biology of tree squirrels (M. A. Steele, J. F. Merritt, and D. A. Zegers, eds.). Special Publications, Virginia Museum of Natural History 6:33–41.
- KWIECINSKI, G. G. 1998. *Marmota monax*. *Mammalian Species* 591: 1–8.
- LENIHAN, C., AND D. VAN VUREN. 1996. Costs and benefits of sociality in yellow-bellied marmots (*Marmota flaviventris*): do noncolonial females have lower fitness? *Ethology Ecology and Evolution* 8: 177–189.
- LENTI BOERO, D. 1995. Scent-deposition behaviour in alpine marmots (*Marmota marmota* L.): its role in territorial defence and social communication. *Ethology* 100:26–38.
- LOTT, D. F. 1991. Intraspecific variation in the social systems of wild vertebrates. Cambridge University Press, Cambridge, England.
- MAHER, C. R. 2000. Quantitative variation in ecological and hormonal variables correlates with spatial organization of pronghorn (*Antilocapra americana*) males. *Behavioral Ecology and Sociobiology* 47:327–338.
- MAHER, C. R., AND D. F. LOTT. 2000. A review of ecological determinants of territoriality within vertebrate species. *American Midland Naturalist* 143:1–29.
- MARTIN, P., AND P. BATESON. 1993. Measuring behaviour: an introductory guide. 2nd ed. Cambridge University Press, Cambridge, United Kingdom.
- MEIER, P. T. 1985. Behavioral ecology, social organization and mating system of woodchucks (*Marmota monax*) in southeast Ohio. Ph.D. dissertation, Ohio University, Athens.
- MEIER, P. T. 1992. Social organization of woodchucks (*Marmota monax*). *Behavioral Ecology and Sociobiology* 31:393–400.
- MICHENER, G. R. 1983. Kin identification, matriarchies and the evolution of sociality in ground-dwelling sciurids. In *Advances in the study of mammalian behavior* (J. F. Eisenberg and D. R. Kleiman, eds.). Special Publications, American Society of Mammalogists 7:528–572.
- MURIE, J. O., AND M. A. HARRIS. 1984. The history of individuals in a population of Columbian ground squirrels: source, settlement, and site attachment. Pp. 353–373 in *The biology of ground-dwelling squirrels: annual cycles, behavioral ecology and sociality* (J. O. Murie and G. R. Michener, eds.). University of Nebraska Press, Lincoln.
- OSTFELD, R. S. 1986. Territoriality and mating system of California voles. *Journal of Animal Ecology* 55:691–706.
- OSTFELD, R. S. 1990. The ecology of territoriality in small mammals. *Trends in Ecology and Evolution* 5:411–415.
- OUELLET, J.-P., AND J. FERRON. 1986. L'utilisation de l'espace par la marmotte commune (*Marmota monax*). *Le Naturaliste Canadien* 113:263–273.
- OUELLET, J.-P., AND J. FERRON. 1988. Scent-marking behavior by woodchucks (*Marmota monax*). *Journal of Mammalogy* 69:365–368.
- PERRIN, C., D. ALLAINÉ, AND M. LE BERRE. 1993. Socio-spatial organization and activity distribution of the alpine marmot *Marmota marmota*: preliminary results. *Ethology* 93:21–30.
- RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 41:223–225.
- RICHARDSON, B. J., R. A. HAYES, S. H. WHEELER, AND M. R. YARDIN. 2002. Social structures, genetic structures and dispersal strategies in Australian rabbit (*Oryctolagus cuniculus*) populations. *Behavioral Ecology and Sociobiology* 51:113–121.
- SAS INSTITUTE INC. 1998. StatView. Cary, North Carolina.
- SERA, W. E., AND M. S. GAINES. 1994. The effect of relatedness on spacing behavior and fitness of female prairie voles. *Ecology* 75: 1560–1566.
- SMALE, L., S. NUNES, AND K. E. HOLEKAMP. 1997. Sexually dimorphic dispersal in mammals: patterns, causes and consequences. *Advances in the Study of Behavior* 26:181–250.
- SMITH, M. C. 1972. Seasonal variations in home ranges of woodchucks. M.S. thesis, University of Guelph, Guelph, Ontario, Canada.
- SNEVA, F. A., AND D. N. HYDER. 1962. Estimating herbage production on semiarid ranges in the Intermountain Region. *Journal of Range Management* 15:88–93.
- SWIHART, R. K. 1990. Common components of orchard ground cover selected as food by captive woodchucks. *Journal of Wildlife Management* 54:412–417.
- SWIHART, R. K. 1992. Home range attributes and spatial structure of woodchuck populations. *Journal of Mammalogy* 73:604–618.
- SWIHART, R. K., N. A. SLADE, AND B. J. BERGSTROM. 1985. Relating body size to the rate of home range use in mammals. *Ecology* 69: 393–399.
- SWILLING, W. R., JR., AND M. C. WOOTEN. 2002. Subadult dispersal in a monogamous species: the Alabama beach mouse (*Peromyscus polionotus ammobates*). *Journal of Mammalogy* 83:252–259.
- TODD, I. A. 1992. Wildtrak: non-parametric home range analysis for Macintosh computers. University of Oxford, Oxford, United Kingdom.
- TRUMP, R. F. 1950. Home range of the southern woodchuck. *Iowa Academy of Science* 57:537–540.
- TWICHELL, A. R. 1939. Notes on the southern woodchuck in Missouri. *Journal of Mammalogy* 20:71–74.
- VAN STAADEN, M. J., R. K. CHESSER, AND G. R. MICHENER. 1994. Genetic correlations and matrilineal structure in a population of *Spermophilus richardsonii*. *Journal of Mammalogy* 75:573–582.
- VAN STAADEN, M. J., G. R. MICHENER, AND R. K. CHESSER. 1996. Spatial analysis of microgeographic genetic structure in Richardson's ground squirrels. *Canadian Journal of Zoology* 74:1187–1195.
- VESTAL, B. M., AND H. MCCARLEY. 1984. Spatial and social relations of kin in thirteen-lined and other ground squirrels. Pp. 404–423 in *The biology of ground-dwelling squirrels: annual cycles, behavioral ecology and sociality* (J. O. Murie and G. R. Michener, eds.). University of Nebraska Press, Lincoln.
- WASER, P. M., AND W. T. JONES. 1983. Natal philopatry among solitary mammals. *Quarterly Review of Biology* 58:355–390.

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