Ethology

RESEARCH PAPERS

Social Organization in Woodchucks (*Marmota monax*) and its Relationship to Growing Season

Christine R. Maher

Department of Biological Sciences, University of Southern Maine, Portland, ME, USA

Correspondence
C. R. Maher, Department of Biological Sciences, 96 Falmouth Street, University of Southern Maine, Portland, ME 04104-9300, USA. E-mail: cmaher@usm.maine.edu

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Abstract

Among sciurids, delayed dispersal may result from slow rates of maturation associated with short growing seasons and large body mass. However, woodchucks (*Marmota monax*) experience a range of ecological conditions and display behavioral flexibility, often ignored in models of sociality. To investigate relationships between social organization and growing season, I collected data on interaction rates, timing of dispersal, and body mass of woodchucks in southern Maine, and I gathered comparative data from the literature. Interaction rates peaked in spring then declined, with agonistic interactions exceeding amicable interactions in adults and in yearling males. Adult males and females weighed comparable amounts early and late in the season, but female weights lagged behind those of males in early summer. Woodchucks did not attain adult mass until after their second hibernation period. Nearly 50% of juveniles postponed dispersal beyond their first summer, and nearly half of those individuals remained philopatric in the following year. Populations faced with longer growing seasons matured more slowly, but timing of dispersal did not correspond to growing season or maturation rate. Other ecological factors, including burrow density, or benefits associated with joint hibernation, may influence timing of dispersal and degree of sociality and deserve further study.

Introduction

Natal philopatry and delayed dispersal, linked with kin selection, have been commonly proposed to explain the evolution of sociality. Among mammals, females generally remain near their natal areas, whereas males disperse greater distances (Greenwood 1980; Murie & Harris 1984; Byrom & Krebs 1999). Ecological constraints, such as high population densities or limited resources, may increase dispersal costs by reducing the likelihood of successfully establishing a territory or reproducing. Because these costs may affect males and females differently, dispersal may become sex biased (Greenwood 1980). Constraints may favor philopatric individuals or reduce dispersal distances, creating populations of related individuals and setting the stage for further development of sociality (Greenwood 1980; Michener 1983; Koenig et al. 1992; Emlen et al. 1995; Ebensperger 2001; Cahan et al. 2002; Solomon 2003).

Rodents provide excellent opportunities to study evolutionary paths toward sociality because they occupy a continuum of social organization (Armitage 1981, 1999; Michener 1983; Koprowski 1996; Blumstein & Armitage 1998; Ebensperger 2001). At one end of that continuum lie species such as alpine marmots (*Marmota marmota*), black-tailed prairie dogs (*Cynomys ludovicianus*), prairie voles (*Microtus ochrogaster*), and colonial tuco-tucos (*Ctenomys sociabilis*), which live in family groups consisting of a dominant male and female plus offspring from more than 1 yr (King 1955; Barash 1989; Arnold 1990a,b; Solomon 2003; Lacey & Wieczorek 2004). Wood-

chucks (*Marmota monax*), Franklin's ground squirrels (*Spermophilus franklinii*), and Patagonian tuco-tucos (*Ctenomys haigi*) lie at the opposite end of the sociality continuum and are often characterized as solitary with both sexes dispersing as juveniles (Grizzell 1955; Snyder 1962; Michener 1983; Lacey et al. 1998).

Hibernators that do not store food must acquire sufficient fat reserves during the growing season to survive winter. Yet, short growing seasons and large body size mean that some rodents need more than 1 yr to mature, so they delay dispersal and remain in family groups until they reach sufficient size (Armitage 1999, 2000). Blumstein & Armitage (1999) used a maturity index (MI), a ratio of the emergence mass of younger animals to adults (Barash 1989), to indicate growth. They suggested that dispersal is possible when MI ≥ 0.5, and reproduction could occur when MI ≥ 0.65. Support for the hypothesis, however, is equivocal (Ebensperger 2001). For example, Gunnison's prairie dogs (*Cynomys gunnisoni*, Rayor 1985) and marmots, from which the hypothesis was derived (Blumstein & Armitage 1999), seem to fit the model well. However, juvenile Columbian ground squirrels (*Spermophilus columbianus*) reach 60% of adult mass and also postpone dispersal (Murie et al. 1980). Data from hystricognath (Ebensperger & Cofré 2001) and heteromyid (Jones 1993) rodents also do not support the hypothesis. Woodchucks may be another exception.

Woodchucks had the highest MI reported for marmots, which correlates with their early dispersal, early age at first reproduction, and solitary lifestyle (Blumstein & Armitage 1999). However, the model included only one source of data for woodchucks, a species that varies in social organization (Merriam 1971; Smith 1972; Ferron & Ouellet 1989; Meier 1992; Swihart 1992). Woodchucks occupy the largest geographic range of any marmot (Lee & Funderburg 1982) and thus experience a range of ecological conditions. Therefore, they may vary in the age at which they achieve adult mass, which in turn may influence behavioral interactions, dispersal and degree of sociality. Few studies have quantified interactions and dispersal or compared mass and social organization in more than one population of this species. Furthermore, most published studies have been conducted in a small subset of the species' range, primarily Pennsylvania. To expand our knowledge of woodchuck behavioral biology and to facilitate comparisons with other populations and species, I quantified agonistic and amicable interaction rates, which can provide insights into the extent of sociality in a population, throughout the active season for adults, yearlings and juveniles in southern coastal Maine. I also recorded body mass and timing of dispersal. Compared with most previously studied populations, this population occurs at higher latitude, and it experiences a growing season of intermediate length. Because woodchucks exhibit intraspecific variation, I also compared body mass, dispersal and growing season across populations to evaluate factors influencing social organization. I predicted that woodchucks would conform to Blumstein & Armitage's (1999) model, with animals reaching a higher proportion of adult mass and dispersing earlier when they experienced longer growing seasons.

Methods

Study Area and Population

I conducted this study at Gilsland Farm Sanctuary, a 26-ha wildlife preserve located in Falmouth, ME (43°42′N, 70°14′W). The site contains salt marsh, mixed coniferous-hardwood forest, and three meadows that measure 2.5, 3.5, and 6 ha. Woodchucks hibernated in wooded areas and moved into meadows after the spring thaw. Meadows were 15–60 m apart, separated by a gravel road or by salt marsh, which animals crossed occasionally. Therefore, I considered these meadows to be habitat for a single population of woodchucks. Elevation varies 0–10 m across the site, with gently rolling topography. The sanctuary is bordered on the west by the Presumpscot River estuary, on the east by US Route 1 (three lanes), and on the north, south and east by housing developments.

Population density of woodchucks averaged 1.7 animals/ha, with a population size, based on total counts, of 35–40 adults and yearlings. To capture animals, I used Tomahawk live traps (Tomahawk Live Trap Co., Tomahawk, WI; 81 × 25 × 30 cm) set during daylight hours only and monitored hourly. Field assistants and I transferred each captive animal to a cloth handling bag and weighed it to the nearest 0.25 kg (adults and yearlings) or 0.05 kg (juveniles) using a Pesola spring scale (Pesola AG, Baar, Switzerland). I determined sex by examining anogenital distance or by the presence of testes or distended nipples during the breeding season or lactation, respectively. I determined age class using weight, as yearlings are noticeably smaller than adults in spring, usually <2.0 kg (Kwiecinski 1998), or tooth color, as yearlings have whiter teeth than adults (Davis 1964). I also knew ages of

many animals first captured as juveniles that remained on the study site (animals of known age other than juveniles, 2000: 2.6% of trapped animals; 2001: 10.4%; 2002: 37.2%; 2003: 45%). I then applied a unique mark to each animal's hindquarters using a commercial hair dye (Clairol Balsam Color, Clairol Inc., Stamford, CT) and a small artist's brush. Finally, I attached numbered metal ear tags (National Band and Tag Company, Newport, KY; size 3) in each ear and released the animal at the same burrow where we caught it. Procedures were approved by the Institutional Animal Care and Use Committee at the University of Southern Maine.

Data Collection

From 1998 to 2003, field assistants and I collected data beginning as soon as animals emerged from hibernation in Mar. and Apr. and continuing until animals immerged in Sep. and Oct. We began monitoring the property in mid-Feb. to detect when animals first emerged from burrows, and we continued to survey the site into the fall until we no longer observed aboveground activity. On average, we observed woodchucks for 36 d in spring (Mar. to May), 47 d in summer (Jun. to Aug.), and 20 d in fall (Sep. to Oct.). During this period, we trapped 157 woodchucks, which included 95% of resident animals. Visibility was excellent until mid-Jun., when vegetation grew tall enough to hide animals in meadows. However, several sections of the study site were mowed throughout summer, enabling us to collect data then. Furthermore, all meadows were mowed for hay after late Jul., allowing us to again observe animals throughout the site until they immerged. We located animals by walking the property during daylight hours, and we used binoculars and spotting scopes, when necessary, to observe animals and to reduce interference with their behavior. Observation distances were 5–500 m. We logged nearly 7100 person-hours in the field, including 550 h of direct observations (focal h each yr: 1998: 44; 1999: 58; 2000: 91; 2001: 112; 2002: 131; 2003: 114).

During Mar. and Apr. when woodchucks emerged from hibernation, we monitored the study site 2–4 d each week, depending on weather. In early spring, we could readily detect when woodchucks emerged. They were visible above ground because of lack of vegetation, and fresh dirt removed from burrows was conspicuous on snow. Most animals were captured the same day that we first observed them above ground. However, for body mass to be used as emergence mass, we had to trap the animal within 1 wk of either seeing the animal or finding indirect evidence that it had emerged, e.g. fresh dirt at a burrow within a known animal's territory.

Upon locating an individual, we identified it using its dye mark or other unique markings. Once it resumed its previous activity or seemed undisturbed by our presence, we commenced focal sampling and continuous recording (Martin & Bateson 1993) of its activity, using a handheld tape recorder and stopwatch (1998 and 1999 field seasons) or a Psion Workabout handheld computer and Observer software (Noldus Information Technology, Leesburg, VA; 2000 field season and thereafter). Focal samples lasted a maximum of 15 min, but the animal had to remain in view at least 3 min or I discarded the data. If we observed an interaction during the focal sample, we recorded the identity of the interactant, whenever possible, as well as the initiator and recipient of the interaction. Interactions were converted into rates and were counted only for the focal animal, not the other participant. I sampled animals at intervals >24 h to ensure temporal independence of bouts.

I followed definitions of behavior patterns previously used for yellow-bellied marmots (*Marmota flaviventris*, Armitage et al. 1996). Amicable interactions included social play, nuzzle and greet, when animals approached each other and sniffed noses or made gentle contact in the head region. Agonistic interactions included threats, chases, avoidance, displacements, and fights.

Authors rarely reported length of growing season in their studies; however, they provided locations of study sites. Growing season may be defined by duration of snow cover or number of frost-free days. I chose number of frost-free days because snow cover may disappear after a brief warm period, then the ground may remain snow free while temperatures again drop below freezing and prohibit plant growth. Furthermore, I could obtain data on frost-free days from the USDA plant hardiness zone map (available: http://www.usna.usda.gov/Hardzone/ushzmap.html?) and the frost-free period map from the Atlas of Canada (available: http://atlas.gc.ca).

Statistical Analysis

To calculate maturity indices, I used mean weight of yearlings, 2-yr-olds, or 3-yr-olds at emergence/mean adult weight at emergence (Blumstein & Armitage 1999). For body mass data, I calculated a mean

value for each animal for each month and used that value in subsequent analyses. When the same animal was represented in different age classes (juvenile, yearling, adult), I calculated a value for each age class. Thus, some animals were present in more than one 1 yr but not in the same age class. To analyze interaction rates, I calculated mean values for each focal animal overall and for each month and for each age class. Again, animals could be present in more than one 1 yr but not in the same age class.

After testing that data fit a normal distribution, I used two-way analysis of variance to analyze interaction rates and weights across season and by age or sex. Because of small sample sizes, I also used nonparametric Kruskal–Wallis and Mann–Whitney *U*-tests to compare age or sex classes within the same month or one age class over time, and I compared types of interactions within age classes using Wilcoxon's signed-ranks tests. I analyzed data across populations using linear regression. When differences were not statistically significant, I report results from post hoc power analysis, including *d* scores for pairwise comparisons and r^2 for analysis of variance (Cohen 1988; Murphy & Myors 1998). I analyzed data in StatView 5.0 (SAS Institute Inc. 1998), used two-tailed tests, and considered differences statistically significant where $p \leq 0.05$.

Results

Dates of Active Season

Observers first saw adult males above ground, on average, on 3 Mar. (range = 27 Feb. to 12 Mar., n = 6 yr), whereas adult females first appeared on 25 Mar. (range = 20 – 31 Mar.). Yearling males first emerged nearly 1 mo after adult males, on 30 Mar. (range = 21 Mar. to 11 Apr.), and yearling females emerged, on average, on 2 Apr. (range = 21 Mar. to 13 Apr.). Juveniles emerged from natal burrows in late May (mean = 27 May, range = 22 May – 31 May).

Dates at which observers last observed animals were less reliable because of plant growth obscuring some areas of the study site and less intensive sampling efforts. Nonetheless, on average, we last saw adult males above ground on 22 Sep. (range = 15 Aug. to 23 Oct.) and adult females on 20 Sep. (range = 12 – 24 Sep.). We saw few yearlings late in the season, but the latest date at which we typically observed them was 19 Sep. (range = 3 – 30 Sep.). Juveniles were last seen approx. 3 wk later, on 13 Oct. (range = 7 – 17 Oct.).

Interaction Rates

Differences in total interaction rate across age classes, calculated for the entire season, approached statistical significance (Kruskal–Wallis test: $H = 5.02$, df = 2, $p = 0.08$; Fig. 1), with adults engaging in more interactions than juveniles (Mann–Whitney *U*-test: $U = 1253$, n = 48 adults, 67 juveniles, $p = 0.034$). Rate of amicable interactions did not vary with age class ($p = 0.69$, power = 0.25, $r^2 = 0.016$); however, agonistic rate varied significantly ($H = 13.93$, df = 2, $p = 0.001$), with adult rate again exceeding that of juveniles ($U = 1005$, $p < 0.001$). Differences between adults and yearlings

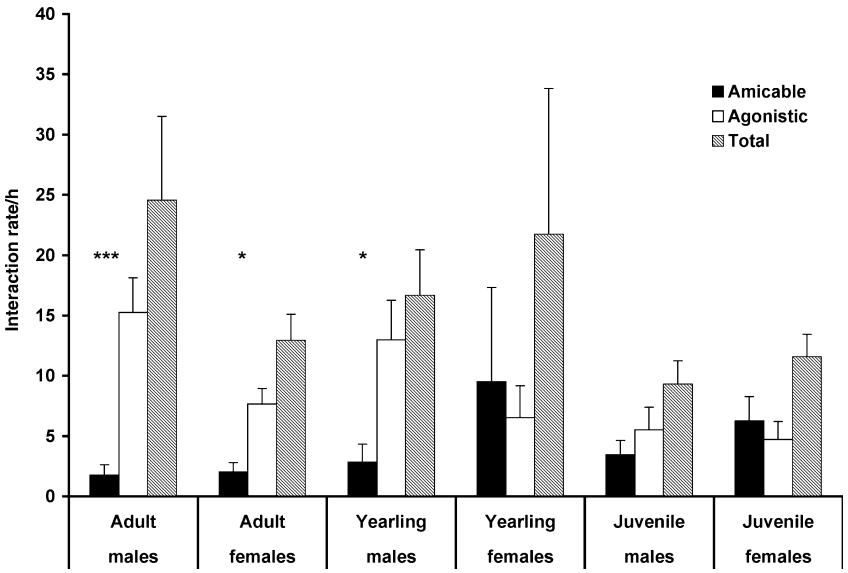

Fig. 1: Rates of amicable, agonistic and all interactions ($\bar{x}$ + SE) for three age classes of woodchuck males and females over the entire active season in Maine, 1998–2003. Sample sizes: 26 adult males, 22 adult females, 28 yearling males, 13 yearling females, 33 juvenile males, 26 juvenile females. *p < 0.05, *** p < 0.001

in total rate and agonistic rate approached statistical significance (total: $U = 796$, n = 48 adults, 41 yearlings, p = 0.10; agonistic: $U = 787.5$, p = 0.08). Males and females did not differ in any interaction rates in any age class (p > 0.13, power <0.42, $d < 0.67$).

Adult males and females as well as yearling males engaged in higher rates of agonistic interactions than amicable interactions (Wilcoxon signed ranks test: adult males: $z = -3.62$, n = 26 animals, p = 0.0003; adult females: $z = -2.36$, n = 22, p = 0.019; yearling males: $z = -1.94$, n = 28 animals, p = 0.053; Fig. 1). Yearling females and juveniles of either sex did not differ significantly in these interaction rates (yearling females: p = 0.34, $d = 0.44$; juvenile males: p = 0.25, $d = 0.16$; juvenile females: p = 0.81, $d = 0.32$).

Rates of all interactions changed over time for all age classes (month: $F = 6.94$, df = 4, p < 0.0001; age: $F = 9.06$, df = 2, p = 0.0001; month × age: $F = 2.98$, df = 8, p = 0.003; Table 1). Adults and yearlings interacted at highest rates in Mar., and then rates declined through the season. Similar to older animals, juveniles' rates of interaction were highest at first emergence in May, and then declined. Only juvenile males and females differed in total rates, primarily because of high rates for juvenile females interacting with other woodchucks in May (sex: $F = 9.45$, df = 1, p = 0.003; month × sex: $F = 2.76$, df = 5, p = 0.021).

Rates of amicable interactions also changed over time and by age class (month: $F = 13.76$, df = 4, p < 0.0001; age: $F = 26.70$, df = 2, p < 0.0001; month × age: $F = 8.13$, df = 8, p < 0.0001; Table 1). Again, interaction rates for adults and yearlings were highest in spring and early summer then fell to zero late in summer. Juveniles had high rates of amicable interactions in May, also followed by a decline for the rest of the year ($F = 7.59$, df = 5, p < 0.0001). Adults and yearlings did not differ by sex (adults: p = 0.31, power = 0.17, $d = 0.17$; yearlings: p = 0.47, power = 0.11, $d = 0.23$; Table 1). However, juvenile females interacted at higher rates than males, but only in May (month: $F = 5.52$, df = 5, p = 0.0001; sex: $F = 11.46$, df = 1, p = 0.0009; month × sex: $F = 3.67$, df = 5, p = 0.007).

Agonistic interaction rates varied over time for adults and yearlings (month: $F = 7.05$, df = 6, p < 0.0001; age: p = 0.138, power = 0.31; month × age: $F = 2.02$, df = 6, p = 0.063; Table 1). Older animals interacted most frequently in Mar., followed by

Table 1: Monthly rates (number/h) of all interactions, amicable interactions, and agonistic interactions ($\bar{x} \pm SE$) based on focal sampling for three age classes of woodchuck males and females in Falmouth, ME during their active season, 1998–2003

	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.
Total interactions								
AD males	12.6 ± 9.21	3.8 ± 2.0	0.9 ± 0.38	0.41 ± 0.24	0	0.96 ± 0.71	0	–
AD females	3.7 ± 2.1	2.7 ± 1.8	0.48 ± 0.24	1.5 ± 0.67	0.07 ± 0.06	0.22 ± 0.12	0.34 ± 0.23	–
YL males	10.0 ± 4.3	2.7 ± 1.2	0.64 ± 0.39	0.10 ± 0.10	0.53 ± 0.53	0.25 ± 0.17	1.3 ± 1.1	–
YL females	–	3.0 ± 2.1	1.4 ± 1.1	0.87 ± 0.63	0.39 ± 0.39	0.22 ± 0.22	0	–
JU males	–	–	1.0 ± 1.0	0.80 ± 0.48	0.99 ± 0.73	0.49 ± 0.32	0.19 ± 0.15	0
JU females	–	–	10.4 ± 10.4	1.6 ± 0.53	2.0 ± 1.0	0.11 ± 0.07	0.45 ± 0.24	0
Amicable interactions								
AD males	0	0.11 ± 0.05	0.22 ± 0.16	0	0	0	0	–
AD females	0	0.70 ± 0.54	0.04 ± 0.03	0.46 ± 0.28	0.04 ± 0.04	0.02 ± 0.02	0	–
YL males	0	0.76 ± 0.49	0.08 ± 0.08	0	0	0	0	–
YL females	–	1.5 ± 1.3	0.29 ± 0.22	0.25 ± 0.25	0	0	0	–
JU males	–	–	1.0 ± 1.0	0.97 ± 0.48	0.12 ± 0.12	0	0	0
JU females	–	–	10.4 ± 10.4	1.4 ± 0.54	0.82 ± 0.66	0	0.12 ± 0.09	0
Agonistic interactions								
AD males	3.7 ± 3.7	3.7 ± 2.0	0.57 ± 0.30	0.41 ± 0.24	0	0.96 ± 0.71	0	–
AD females	3.7 ± 2.1	2.0 ± 1.2	0.35 ± 0.19	0.13 ± 0.07	0.03 ± 0.02	0.18 ± 0.09	0.34 ± 0.23	–
YL males	10.0 ± 4.3	1.7 ± 0.95	0.56 ± 0.33	0.10 ± 0.10	0.53 ± 0.53	0.25 ± 0.17	1.3 ± 1.1	–
YL females	–	0.75 ± 0.53	1.1 ± 1.1	0.46 ± 0.46	0.39 ± 0.39	0.22 ± 0.22	0	–
JU males	–	–	0	0	0.76 ± 0.52	0.49 ± 0.32	0.19 ± 0.15	0
JU females	–	–	0	0.14 ± 0.14	1.1 ± 0.79	0.11 ± 0.07	0.23 ± 0.15	0

AD, adult; YL, yearling; JU, juvenile.

Sample sizes (number of animals) for each month, adult males: 10, 21, 24, 14, 11, 17, 7, 0; adult females: 10, 21, 24, 14, 11, 17, 7, 0; yearling males: 5, 16, 16, 11, 9, 12, 7, 0; yearling females: 0, 8, 9, 8, 5, 6, 3, 0; juvenile males: 0, 0, 2, 12, 10, 27, 22, 13; juvenile females: 0, 0, 3, 16, 15, 16, 15, 4.

a decline for the remainder of the season. Males and females did not differ for any age class (adults: p = 0.58, power = 0.08, d = 0.27; yearlings: p = 0.58, power = 0.08, d = 0.15; juveniles: p = 0.91, power = 0.05, d = 2.85).

Weights

Despite variation in emergence dates from year to year, adult weights did not differ significantly across years (p = 0.11, power = 0.62, r^2 = 0.085). For males and females combined, weight varied significantly across months and age classes (month: F = 72.64, df = 3, p < 0.0001; age: F = 386.86, df = 2, p < 0.0001; month × age: F = 7.63, df = 6, p < 0.0001; Fig. 2). Juveniles rapidly gained weight over summer but always weighed less than both adults and yearlings (May: H = 19.79, df = 2, p < 0.0001; Jun.: H = 40.38, df = 2, p < 0.0001; Jul.: H =11.52, df = 2, p = 0.003; Aug.: H = 49.38, df = 2, p < 0.0001). Furthermore, yearlings weighed less than adults for the first three months of the active season (Mar.: U = 5, n = 27 adults, four yearlings, p = 0.004; Apr.: U = 93.0, n = 33 adults, 21 yearlings, p < 0.0001; May: U' = 55.0, n = 11 adults, five yearlings, p = 0.002). In Jun. and Jul., yearlings and adults no longer differed in mass (p > 0.22, d = 0.78, 0.61, respectively), although yearlings weighed less than adults in Aug. (U = 24.0, n = 20 adults, eight yearlings, p = 0.004).

Neither yearlings nor juveniles differed in weight between sexes (yearlings: p = 0.45, power = 0.11, d = 0.45; juveniles: p = 0.12, power = 0.32, d = 0.71; Fig. 2). Adult males and females differed across months (month: F = 45.95, df =5, p < 0.0001; sex: F = 23.69, df = 1, p < 0.0001; month × sex: F = 4.70, df =5, p = 0.0007); however, sex differences did not appear until summer (Fig. 2). Males weighed more than females in Jun. (U = 5.0, n = six males, 10 females, p =0.007), with differences approaching significance in Jul. with small sample sizes (U' = 6.0, n = two males, three females, p = 0.08). By Aug., however, adult males and females no longer differed in mass (p = 0.17, d = 0.96).

Woodchucks did not achieve adult weight upon emergence from their first or even second hibernation periods. Maturity indices indicated that animals nearly attained adult weights by emergence in their third season (juveniles: 0.74, n = 25; yearlings: 0.94, n = 10; 2-yr-olds: 0.97, n = 4). Note that juvenile and yearling MI refers to the mass of yearlings and 2-yr-olds, respectively, upon emergence from hibernation and follows terminology of Barash (1989) and Blumstein & Armitage (1999). It measures body growth for these age classes while reducing effects of fattening prior to hibernation (Blumstein & Armitage 1999). After their first hibernation, males and females reached 73% and 77% of adult mass, respectively. After two seasons, males attained 91% of adult male mass, whereas females had reached adult female mass. After their third hibernation, males attained adult mass, and females weighed 96% of adult mass.

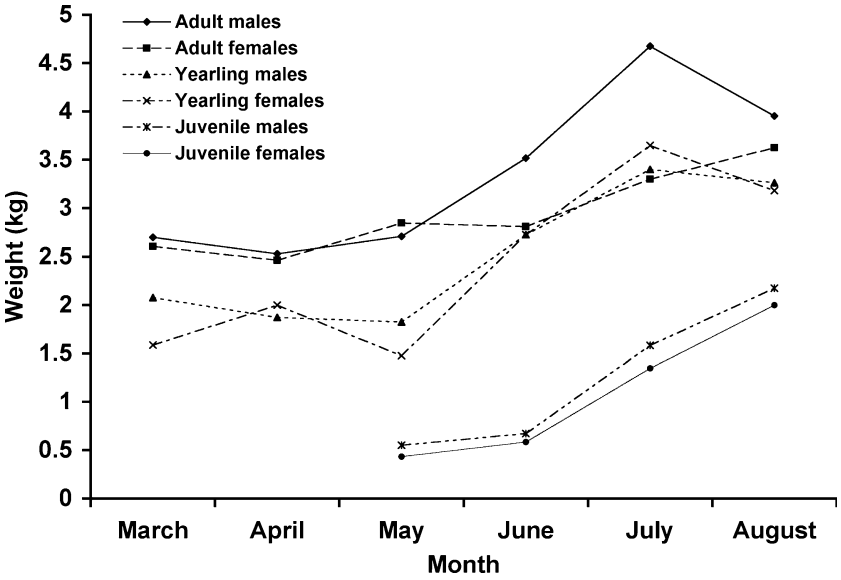

Fig. 2: Mean weights for different age and sex classes of woodchucks in Maine over the active season, 1998–2003. Sample sizes for adult males: 17, 16, 3, 6, 2, 9; adult females: 10, 17, 8, 10, 3, 11; yearling males: 3, 15, 3, 2, 2, 4; yearling females: 2, 6, 2, 1, 1, 4; juvenile males: 4, 23, 3, 28; juvenile females: 4, 25, 5, 13

Timing of Natal Dispersal and Age at First Reproduction

I trapped a total of 87 juveniles between 1998 and 2003. Nearly half of those animals disappeared from the population, fates unknown, and <5% were known to disperse in their first summer, i.e. they moved >1 home range diameter (mean = 193 m, calculated using Wildtrak [Todd 1992], see Maher 2004) from their natal range (Table 2). However, 49% of trapped pups remained within or immediately adjacent to their natal home ranges through their first summer, i.e. they did not disperse. In their second summer, at least 21% of those animals subsequently dispersed as yearlings, whereas 42% were recruited into the population within or adjacent to their natal home ranges. Furthermore, both males and females delayed dispersal, although males were more likely than females to disperse in their second summer, and females were more likely to be recruited into the population (χ^2 = 3.89, df = 1, p = 0.049; Table 2). In two cases, females settled in adjacent ranges that became vacant when the resident female died, but I know of no situations where mothers died and daughters inherited the natal territory.

Three of 19 yearling females (15.8%) reproduced during the study, whereas 16 of 17 adult females (94%) were known to produce litters. The other adult female may have lost her litter to red fox (*Vulpes vulpes*) predation before we observed offspring. Determining age at first reproduction was more difficult for males as they do not provide parental care, and we did not witness copulations above ground. Nonetheless, we observed three of 11 yearling males (27.3%) courting females during the breeding season. I did not examine yearling males for descended testes during spring trapping until 2002. Since then, all (n = 4) yearling males examined had descended testes.

Table 2: Fates of trapped juvenile woodchucks at Gilsland Farm Sanctuary, Maine, 1998–2003

	Males	Females	Combined
Number trapped	49	38	87
% fate unknown	40.8	52.6	46.0
% dispersed first summer	2.0	5.3	2.3
% philopatric through first summer	57.1	39.4	49.4
% dispersed second summer			
of all trapped	16.3	2.6	10.3
of philopatric animals	28.6	6.7	20.9
% recruited			
of all trapped	18.4	23.7	20.7
of philopatric animals	32.1	60.0	41.9

Other Populations

Few authors reported data needed to calculate maturity indices for other woodchuck populations. Nevertheless, I compiled data from the literature for four populations: Maine (this study), Ohio (Meier 1985, 1992), Pennsylvania (Snyder et al. 1961), and Maryland (Grizzell 1955). Woodchucks experiencing the longest and shortest growing seasons weighed less at emergence compared with animals experiencing growing seasons of intermediate length (Table 3). MI was strongly related to growing season: populations experiencing longer seasons had lower MI (r^2 = 0.997, p = 0.002; Table 3). Thus, woodchucks were smaller at emergence from their first hibernation in populations with longer growing seasons.

Table 3: Data reported in the literature for woodchuck populations. Length of growing season was calculated as the number of days between last and first frosts

Population location	Length of growing season (d)	Population density (per ha)	Yearling mass at emergence (kg)	Adult mass at emergence (kg)	Juvenile MI	Postpone dispersal beyond first summer? (% philopatric)	Reference
Ste-Luce, QC	120	0.1			–	No	Ferron 1996
Guelph, ON	140	9.1			–	Yes (unknown)	Smith 1972
Puslinch, ON	140	0.53			–	No	deVos & Gillespie 1960
Falmouth, ME	160	1.7	1.91	2.56	0.74	Yes (49%)	This study
Southington, CT	165	1.05			–	Yes (53%)	Swihart 1992
Athens, OH	180	0.5	2.2	3.3	0.67	Yes (75%)	Meier 1985, 1992
Pyatt, IL	180	1.1			–	No	Anthony 1962
Chambersburg, PA	190	0.9	2.39	3.78	0.63	No	Snyder et al. 1961; Snyder 1976
Laurel, MD	230	1.9	1.39	2.64	0.53	No	Grizzell 1955

MI = maturity index (emergence mass after first hibernation/emergence mass of adults).

Juveniles did not always disperse in their first summer, but delayed dispersal showed no clear relationship to length of growing season (Table 3). Animals experiencing similar numbers of frost free days may or may not postpone dispersal (e.g. Ohio and Illinois, Ontario). Indeed, woodchucks in two populations with higher MI, Maine and Ohio, delayed dispersal, whereas populations with lower MI, Pennsylvania and Maryland, did not (Table 3).

Discussion

Adult woodchuck males emerged from hibernation first, followed by adult females then yearlings, and adults and yearlings immerged before juveniles. Other sciurids exhibit similar patterns (Snyder & Christian 1960; Michener 1983), although in yellow-bellied marmots, adults and yearlings sometimes emerge simultaneously from the same burrow system (Blumstein et al. 2004).

Regardless of age class, interaction rates peaked at the start of the active season then declined over time. Among adults and yearling males, agonistic interaction rates exceeded amicable rates. Amicable and agonistic rates were most similar in juveniles, which remain in family groups with their mother and siblings for at least part of the summer. Social play did not occur frequently in this population. I primarily observed play behavior when juveniles initially emerged from burrows, at approx. 4 wk old, then they quickly devoted more time to foraging (C. Maher, unpubl. data). Seasonal patterns in interaction rates are representative of other woodchuck and marmot populations (Bronson 1963, 1964; Barash 1973, 1974, 1976; Hébert & Prescott 1983; Taulman 1990; Meier 1992; Sala et al. 1992; Perrin et al. 1993). In spring, interaction rates are highest as animals establish territories and breed (Bronson 1964). Once boundaries are determined and the breeding season ends, interaction rates decline. As vegetation grows, visibility declines, which may inhibit social interactions (Bronson 1964); however, even in areas mowed regularly, interactions declined. Instead, competition for resources may decrease as food becomes more abundant (Johns & Armitage 1979).

The ratio of amicable to agonistic interactions, a relative index of sociality, supports the idea of woodchucks as more aggressive and less social than other marmots. In alpine marmots, ratios of amicable to agonistic interactions vary from 2.8 to 25 within groups but decrease to 0.1 between groups (Perrin et al. 1993; Lenti Boero 2003). Yellow-bellied marmots also exhibit more amicable than agonistic interactions within groups (3.0) but much lower levels (0.2) outside their immediate burrow systems (Johns & Armitage 1979). Some authors included sniff and greet as amicable interactions, whereas others reported them as recognitive; however, the pattern remains the same if recognitive behavior patterns are not included. Woodchucks, although more aggressive than other marmots, vary across populations. A study in Pennsylvania reported no amicable interactions (Bronson 1963), whereas a population in Ohio engaged in 16× more amicable than agonistic interactions (Meier 1992). The Maine population falls between these values (0.4) and resembles other marmots when they interact with animals outside family groups. In many sciurids, amicable behavior patterns occur between family members at the same burrow system, and interactions between groups tend to be agonistic (Johns & Armitage 1979; Perrin et al. 1993; Lenti Boero 2003; Hare & Murie, in press). However, amicable interactions also occur outside family groups (Hare 1994; Hare & Murie 1996), and agonistic behavior can increase with increasing competition despite close relatedness (Hoogland 1986). As older woodchucks tend not to live in groups, it is not surprising that most interactions among adults and yearlings are agonistic.

Neither juveniles nor yearlings exhibited differences in mass between sexes, and adult males and females were comparable at emergence. Adult mass declined slightly but not significantly between Mar. and Apr., a pattern observed in other populations and attributed to lack of feeding because of breeding activity and lack of forage at this time of year (Snyder et al. 1961; Michener 1984; Holekamp & Nunes 1989); however, this pattern also could be explained by later emergence of lighter animals (Grizzell 1955; Boag & Murie 1981). Yearlings exhibited a similar pattern to adults, with a slight but non-significant decrease in mass between Apr. and May and again in Aug. Since forage was available then, the drop was probably because of later emergence and later immergence of lighter animals and small sample sizes. By Jun., adult males began to gain mass and weighed more than females, as seen in other woodchuck populations (Hamilton 1934; Snyder et al. 1961; Zervanos & Salsbury 2003). Nearly all females over 2 yr old bred in this population, and energetic demands of reproduction could explain the delay in weight gain until later in summer (Armitage et al. 1976). Adult males declined in mass by Aug., a pattern seen in other species when heavier animals enter hibernation first (Grizzell 1955; Armitage et al. 1976). In some areas, differences in adult weight

persisted until hibernation (Snyder et al. 1961), whereas in others, males and females were comparable at immergence (Zervanos & Salsbury 2003).

Yearlings reached 74% of adult mass upon emergence from their first hibernation, then caught up to adult female mass during summer. In some populations, yearlings are distinguishable from adults in spring (deVos & Gillespie 1960; Davis et al. 1964); however, in other areas, they are difficult to differentiate (Swihart 1992). Only 16% of yearling females trapped or observed during this period reproduced, so most females were not constrained by reproduction and could gain weight at the same time as males.

Body mass may be linked to dispersal and sociality in sciurids (Barash 1973, 1989; Nunes et al. 1998; Blumstein & Armitage 1999). Species experiencing longer growing seasons can attain adequate size to both disperse and survive hibernation and thus are not social, whereas species that grow more slowly delay dispersal and remain in natal groups (Armitage 1981, 1999, 2000). Woodchucks fit this pattern to some degree. They experience some of the longest growing seasons among hibernating, ground dwelling sciurids, and they are among the least social. However, their broad geographic range ensures that they experience a range of conditions, including settings comparable to more social marmots. For example, a Québec population of woodchucks hibernated for a similar number of days as a population of alpine marmots (Ferron 1996), perhaps because sandy soil insulated animals better than rocky conditions in the Alps (J. Ferron, pers. comm.).

Although woodchucks attain adult body mass sooner than other marmots (Blumstein & Armitage 1999), populations varied in maturation rates and relationships between MI and dispersal. Woodchucks that experienced longer growing seasons reached a lower proportion of adult mass after their first hibernation. Perhaps because they experienced shorter winters, they could afford to grow more slowly than animals at higher latitudes, i.e. they did not need more mass to survive a longer hibernation period (Armitage 1999). Yet, absolute weights were higher at intermediate latitudes. Habitat quality may differ among study sites, leading to differences in body mass, but researchers did not report such information. Studies are needed at additional locations, particularly more northern and southern ends of the range, to better understand the relationship between growing season and rate of maturation.

Contrary to expectations, in populations with relatively high MI, juveniles often postponed dispersal beyond their first season. However, the studies that provided the data differed in objectives and methods. Older studies (Grizzell 1955; Snyder et al. 1961; Snyder 1976) primarily relied on recaptures using live traps to determine when animals left natal ranges and settled elsewhere. These authors did not document kin relationships or observe the same individuals over time. Meier (1985, 1992) observed known individuals over time, measured home ranges, and reported that some juveniles remained within the natal home range through their first hibernation. No authors explicitly defined dispersal, nor did they distinguish between disappearances because of predation vs. dispersal. In many parts of their range, vegetation obscures woodchucks during summer, making observations of dispersal difficult. Radiotelemetry would help to distinguish between disappearances because of predation or dispersal. Nonetheless, delayed dispersal and philopatry are easier to document than dispersal as animals remain in or near their natal area.

Another explanation for delayed dispersal and philopatry includes the delayed dispersal threshold model, which incorporates costs and benefits of dispersal vs. philopatry and recognizes that ecological conditions influence such decisions (Koenig et al. 1992; Solomon 2003). High population density may favor animals that postpone dispersal or remain philopatric (Jones et al. 1988; Cochran & Solomon 2000); yet woodchucks from a range of population densities postponed dispersal. Burrow, specifically hibernaculum, density could be another constraint (Meier 1992; Ebensperger 2001), but no one has yet quantified this variable or examined its impact on dispersal in woodchucks. One potentially important benefit of philopatry for marmots accrues during winter, i.e. joint hibernation (Arnold 1990b; Allainé et al. 2000). Some marmots hibernate in family groups (Blumstein & Armitage 1999), and social thermoregulation may improve juvenile survival (Allainé et al. 2000). Although woodchucks in Québec hibernated for about the same time as alpine marmots, woodchucks lost more weight, perhaps because they were less efficient hibernators (Armitage et al. 2000) or because they hibernated alone, whereas alpine marmots hibernate in groups (Ferron 1996). Woodchucks reportedly do not hibernate in groups because juveniles disperse in their first summer. However, at least two females in Québec hibernated in the same burrow system (Ferron 1996). I have anecdotal evidence that juveniles from five

litters in three winters hibernated with their mothers and (or) siblings; however, they may not have shared the same chamber within the burrow system. Future studies will examine this phenomenon in more detail.

Data from this and other woodchuck populations are neither completely dismissive nor supportive of Blumstein & Armitage's (1999) model. Their position at the asocial end of the sociality continuum is supported by higher levels of agonistic vs. amicable interactions. However, length of growing season and maturity indices were not related to timing of dispersal as predicted. Woodchucks appear to be facultatively philopatric, and facultatively philopatric species may be affected more strongly by ecological conditions, whereas obligately philopatric species may be more influenced by life history (Solomon 2003). Given woodchucks' wide geographic range, ecological conditions could favor flexibility and influence decisions about timing of dispersal, which in turn, shapes social organization. Philopatry is not confined to social species (e.g. *Meriones tamariscinus*, Tchabovsky & Bazykin 2004), and studies of solitary species, particularly behaviorally flexible species, should provide further insights into philopatry's role in the evolution of sociality.

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Literature Cited

Allainé, D., Brondex, F., Graziani, L., Coulon, J. & Till-Bottraud, I. 2000: Male-biased sex ratio in litters of alpine marmots supports the helper repayment hypothesis. Behav. Ecol. **11**, 507—514.

Anthony, M. 1962: Activity and behavior of the woodchuck in southern Illinois. Occas. Pap. C. C. Adams Cent. Ecol. Stud. **6**, 1—25.

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. J. Mammal. **80**, 1—10.

Armitage, K. B. 2000: The evolution, ecology and systematics of marmots. Oecologia Montana **9**, 1—18.

Armitage, K. B., Downhower, J. F. & Svendsen, G. E. 1976: Seasonal changes in weights of marmots. Am. Midl. Nat. **96**, 36—51.

Armitage, K. B., Salsbury, C. M., Barthelmess, E. L., Gray, R. C. & Kovach, A. 1996: Population time budget for the yellow-bellied marmot. Ethol. Ecol. Evolut. **8**, 67—95.

Armitage, K. B., Woods, B. C. & Salsbury, C. M. 2000: Energetics of hibernation in woodchucks (*Marmota monax*). In: Life in the Cold: 11th International Hibernation Symposium (Heldmaier, G. & Klingenspor, M., eds). Springer, New York, pp. 73—80.

Arnold, W. 1990a: The evolution of marmot sociality: I. Why disperse late? Behav. Ecol. Sociobiol. **27**, 229—237.

Arnold, W. 1990b: The evolution of marmot sociality: II. Costs and benefits of joint hibernation. Behav. Ecol. Sociobiol. **27**, 239—246.

Barash, D. P. 1973: The social biology of the Olympic marmot. Anim. Behav. Monogr. **6**, 171—245.

Barash, D. P. 1974: The social behaviour of the hoary marmot (*Marmota caligata*). Anim. Behav. **22**, 256—261.

Barash, D. P. 1976: Social behaviour and individual differences in free-living alpine marmots (*Marmota marmota*). Anim. Behav. **24**, 27—35.

Barash, D. P. 1989: Marmots: Social Behavior and Ecology. Stanford Univ. Press, Stanford, CA.

Blumstein, D. T. & Armitage, K. B. 1998: Life history consequences of social complexity: a comparative study of ground-dwelling sciurids. Behav. Ecol. **9**, 8—19.

Blumstein, D. T. & Armitage, K. B. 1999: Cooperative breeding in marmots. Oikos **84**, 369—382.

Blumstein, D. T., Im, S., Nicodemus, A. & Zugmeyer, C. 2004: Yellow-bellied marmots (*Marmota flaviventris*) hibernate socially. J. Mammal. **85**, 25—29.

Boag, D. A. & Murie, J. O. 1981: Weight in relation to sex, age, and season in Columbian ground squirrels (Sciuridae: Rodentia). Can. J. Zool. **59**, 999—1004.

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. Anim. Behav. **12**, 470—478.

Byrom, A. E. & Krebs, C. J. 1999: Natal dispersal of juvenile arctic ground squirrels in the boreal forest. Can. J. Zool. **77**, 1048—1059.

Cahan, S. H., Blumstein, D. T., Sundstrom, L., Liebig, J. & Griffin, A. 2002: Social trajectories and the evolution of social behavior. Oikos **96**, 206—216.

Cochran, G. R. & Solomon, N. G. 2000: Effects of food supplementation on the social organization of prairie voles (*Microtus ochrogaster*). J. Mammal. **81**, 746—757.

Cohen, J. 1988: Statistical Power Analysis for the Behavioral Sciences, 2nd edn. Lawrence Erlbaum Associates, Hillsdale, NJ.

Davis, D. E. 1964: Evaluation of characters for determining age of woodchucks. J. Wildl. Manage. **28**, 9—15.

Davis, D. E., Christian, J. J. & Bronson, F. 1964: Effect of exploitation on birth, mortality, and movement rates in a woodchuck population. J. Wildl. Manage. **28**, 1—9.

Ebensperger, L. A. 2001: A review of the evolutionary causes of rodent group-living. Acta Theriol. **46**, 115—144.

Ebensperger, L. A. & Cofré, H. 2001: On the evolution of group-living in the New World cursorial hystricognath rodents. Behav. Ecol. **12**, 227—236.

Emlen, S. T., Wrege, P. H. & Demong, N. J. 1995: Making decisions in the family: an evolutionary perspective. Am. Sci. **83**, 148—157.

Ferron, J. 1996: How do woodchucks (*Marmota monax*) cope with harsh winter conditions? J. Mammal. **77**, 412—416.

Ferron, J. & Ouellet, J.-P. 1989: Temporal and intersexual variations in the use of space with regard to social organization in the woodchuck (*Marmota monax*). Can. J. Zool. **67**, 1642—1649.

Greenwood, P. J. 1980: Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. **28**, 1140—1162.

Grizzell, R. A. 1955: A study of the southern woodchuck, *Marmota monax monax*. Am. Midl. Nat. **53**, 257—293.

Hamilton, W. J., Jr 1934: The life history of the rufescent woodchuck, *Marmota monax rufescens* Howell. Ann. Carnegie Mus. **23**, 85—167.

Hare, J. F. 1994: Group member discrimination by Columbian ground squirrels via familiarity with substrate-borne chemical cues. Anim. Behav. **47**, 803—813.

Hare, J. F. & Murie, J. O. 1996: Ground squirrel sociality and the quest for the ''holy grail'': does kinship influence behavioral discrimination by juvenile Columbian ground squirrels? Behav. Ecol. **7**, 76—81.

Hare, J. F. & Murie, J. O. in press: Ecology, kinship and ground squirrel sociality: insights from comparative analyses. In: Rodent Societies (Wolff, J. O. & Sherman, P. W., eds). Univ. of Chicago Press, Chicago.

Hébert, P. & Prescott, J. 1983: Étude du marquage olfactif chez la marmotte commune (*Marmota monax*) en captivité. Can. J. Zool. **61**, 1720—1725.

Holekamp, K. E. & Nunes, S. 1989: Seasonal variation in body weight, fat, and behavior of California ground squirrels (*Spermophilus beecheyi*). Can. J. Zool. **67**, 1425—1433.

Hoogland, J. L. 1986: Nepotism in prairie dogs (*Cynomys ludovicianus*) varies with competition but not with kinship. Anim. Behav. **34**, 263—270.

Johns, D. W. & Armitage, K. B. 1979: Behavioral ecology of alpine yellow-bellied marmots. Behav. Ecol. Sociobiol. **5**, 133—157.

Jones, W. T. 1993: Social systems of heteromyids. In: Biology of Heteromyidae (Genoways, H. H. & Brown, J. H., eds). Am. Soc. Mammal., Spec. Pub. **10**, 575—595.

Jones, W., Waser, P., Elliott, N., Link, N. & Bush, B. 1988: Philopatry, dispersal, and habitat saturation in the banner-tailed kangaroo rat, *Dipodomys spectabilis*. Ecology **67**, 1466—1473.

King, J. A. 1955: Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota. Contrib. Lab. Vert. Biol., Univ. Michigan **67**, 1—126.

Koenig, W. D., Pitelka, F. A., Carmen, W. J., Mumme, R. L. & Stanback, M. T. 1992: The evolution of delayed dispersal in cooperative breeders. Q. Rev. Biol. **67**, 111—150.

Koprowski, J. L. 1996: Natal philopatry, communal nesting, and kinship in fox squirrels and gray squirrels. J. Mammal. **77**, 1006—1016.

Kwiecinski, G. G. 1998: *Marmota monax*. Mammalian Species **591**, 1—8.

Lacey, E. A. & Wieczorek, J. R. 2004: Kinship in colonial tuco-tucos: evidence from group composition and population structure. Behav. Ecol. **15**, 988—996.

Lacey, E. A., Braude, S. H. & Wieczorek, J. R. 1998: Solitary burrow use by adult Patagonian tuco-tucos (*Ctenomys haigi*). J. Mammal. **79**, 986—991.

Lee, D. S. & Funderburg, J. B. 1982: Marmots. In: Wild Mammals of North America: Biology, Management and Economics (Chapman, J. A. & Feldhamer, G. A., eds). Johns Hopkins Univ. Press, Baltimore, pp. 176—191.

Lenti Boero, D. 2003: Social interactions in a colony of alpine marmots (*Marmota marmota* L.). In: Adaptive Strategies and Diversity in Marmots (Ramousse, R., Allainé, D. & Le Berre, M., eds). International Network on Marmots, Lyon, pp. 47—50.

Maher, C. R. 2004: Intrasexual territoriality in woodchucks (*Marmota monax*). J. Mammal. **85**, 1087—1094.

Martin, P. & Bateson, P. 1993: Measuring Behaviour: an Introductory Guide, 2nd edn. Cambridge Univ. Press, Cambridge, UK.

Meier, P. T. 1985: Behavioral ecology, social organization and mating system of woodchucks (*Marmota monax*) in southeast Ohio. PhD Thesis, Ohio Univ., Athens.

Meier, P. T. 1992: Social organization of woodchucks (*Marmota monax*). Behav. Ecol. Sociobiol. **31**, 393—400.

Merriam, H. G. 1971: Woodchuck burrow distribution and related movement patterns. J. Mammal. **52**, 732—746.

Michener, G. R. 1983: Kin identification, matriarchies and the evolution of sociality in ground-dwelling sciurids. In: Advances in the Study of Mammalian Behavior (Eisenberg, J. F. & Kleiman, D. R., eds). Spec. Pub., Am. Soc. Mammal. **7**, 528—572.

Michener, G. R. 1984: Sexual differences in body weight patterns of Richardson's ground squirrels during the breeding season. J. Mammal. **65**, 59—66.

Murie, J. O. & Harris, M. A. 1984: The history of individuals in a population of Columbian ground squirrels: source, settlement, and site attachment. In: The Biology of Ground-Dwelling Squirrels: Annual Cycles, Behavioral Ecology and Sociality, (Murie, J. O. & Michener, G. R., eds). Univ. of Nebraska Press, Lincoln, pp. 353—373.

Murie, J. O., Boag, D. A. & Kivett, V. K. 1980: Litter size in Columbian ground squirrels (*Spermophilus columbianus*). J. Mammal. **61**, 237—244.

Murphy, K. R. & Myors, B. 1998: Statistical Power Analysis: a Simple and General Model for Traditional and Modern Hypothesis Tests. Lawrence Erlbaum Associates, London.

Nunes, S., Ha, C.-D. T., Garrett, P. J., Mueke, E.-M., Smale, L. & Holekamp, K. E. 1998: Body fat and time of year interact to mediate dispersal behaviour in ground squirrels. Anim. Behav. **55**, 605—614.

Perrin, C., Coulon, J. & Le Berre, M. 1993: Social behavior of alpine marmots (*Marmota marmota*): seasonal, group, and individual variability. Can. J. Zool. **71**, 1945—1953.

Rayor, L. S. 1985: Effects of habitat quality on growth, age of first reproduction, and dispersal in Gunnison's prairie dogs (*Cynomys gunnisoni*). Can. J. Zool. **63**, 2835—2840.

Sala, L., Sola, C., Spampanato, A. & Tongiorgi, P. 1992: The marmot population of the Tuscan–Emilian Apennine Ridge. In: Proceedings of the First International Symposium on Alpine Marmot and Genus *Marmota*. (Bassano, B., Durio, P., Gallo Orsi, U. & Macchi, E., eds). International Marmot Network, Lyon, France. Electronic edition.

SAS Institute Inc. 1998: StatView. SAS Institute Inc., Cary, NC.

Smith, M. C. 1972: Seasonal variations in home ranges of woodchucks. MS Thesis, Univ. of Guelph, Guelph, Ontario.

Snyder, R. L. 1962: Reproductive performance of a population of woodchucks after a change in sex ratio. Ecology **43**, 506—515.

Snyder, R. L. 1976: The Biology of Population Growth. St Martin's Press, NY.

Snyder, R. L. & Christian, J. J. 1960: Reproductive cycle and litter size of the woodchuck. Ecology **41**, 647—655.

Snyder, R. L., Davis, D. E. & Christian, J. J. 1961: Seasonal changes in the weights of woodchucks. J. Mammal. **42**, 297—312.

Solomon, N. G. 2003: A reexamination of factors influencing philopatry in rodents. J. Mammal. **84**, 1182—1197.

Swihart, R. K. 1992: Home range attributes and spatial structure of woodchuck populations. J. Mammal. **73**, 604—618.

Taulman, J. F. 1990: Late summer activity patterns in hoary marmots. Northwest. Nat. **71**, 21—26.

Tchabovsky, A. & Bazykin, G. 2004: Females delay dispersal and breeding in a solitary gerbil, *Meriones tamariscinus*. J. Mammal. **85**, 105—112.

Todd, I. A. 1992: Wildtrak: Non-Parametric Home Range Analysis for Macintosh Computers. Univ. of Oxford, Oxford, UK.

deVos, A. & Gillespie, D. I. 1960: A study of woodchucks on an Ontario farm. Can. Field-Nat. **74**, 130—145.

Zervanos, S. M. & Salsbury, C. M. 2003: Seasonal body temperature fluctuations and energetic strategies in free-ranging eastern woodchucks (*Marmota monax*). J. Mammal. **84**, 299—310.