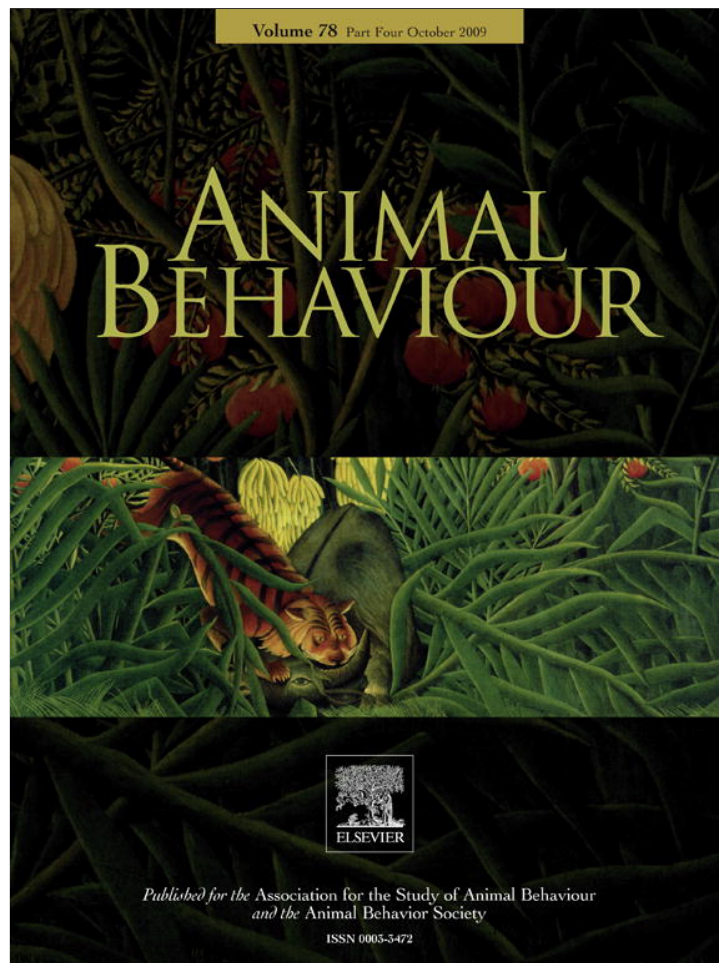


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Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Effects of relatedness on social interaction rates in a solitary marmot

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ARTICLE INFO

Article history:

Received 5 January 2009
 Initial acceptance 2 March 2009
 Final acceptance 22 June 2009
 Published online 13 August 2009
 MS. number: A09-00005R

Keywords:

interaction
 kinship
 marmot
Marmota monax
 sociality
 woodchuck

Kinship often influences social interactions, such that animals behave more amicably towards close kin than towards distant kin or unrelated individuals. However, competition also may affect interactions among kin and the degree of sociality in a population. I used microsatellite DNA markers and behavioural observations to examine effects of kinship on social interactions among woodchucks, *Marmota monax*, which generally are considered asocial or aggressive. Rates of agonistic interactions did not change with relatedness, but rates of amicable interactions increased with increasing relatedness. I observed more amicable interactions than expected between mother–offspring and littermate sibling dyads, but I observed fewer amicable interactions between nonlittermate siblings and more distant kin. Instances of physical aggression were less frequent than expected in mother–offspring, nonlittermate siblings and distant kin dyads, but more frequent than expected among littermate siblings. Interactions between mother–offspring dyads also changed with offspring age, with mothers behaving more amicably towards younger offspring and more agonistically towards older offspring, especially females. Among littermate siblings, rates of amicable interactions were highest between juveniles and yearlings, but then decreased between adult siblings. Social interactions reflected a balance between cooperation and competition. Although woodchucks in this population lived near kin and biased interactions based on kinship, many interactions were agonistic, and animals did not show greater degrees of sociality. Ecological factors, such as predation risk, resource distribution and climate, may favour solitary living in this population.

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Sociality may arise in several ways, such as via mutualism, reciprocal altruism and kin selection (Hamilton 1964; Trivers 1971). Among mammals, and particularly among rodents, attention has focused primarily on the importance of kinship in explaining the origins of sociality (Armitage 2007; Hare & Murie 2007; Lacey & Sherman 2007). Briefly, natal philopatry in females creates kin clusters, and in the classic view of kin selection, shared alleles among kin select for increased tolerance, higher rates of amicable interactions, and lower aggression (Hare & Murie 2007).

Studies across a range of taxa report that individuals treat kin differently and that kin generally interact more amicably with each other than do nonkin (reviewed in: Waser & Jones 1983; Hare & Murie 2007; Kappeler 2008). Kin rarely behave aggressively towards each other, and when it occurs, aggression is generally mild, involving threats rather than fights (Sherman 1980; Hanggi & Schusterman 1990; Ceacero et al. 2007). Family life, however, is not always harmonious (Mock 2004; Wahaj et al. 2004; Forbes 2005).

The degree to which kin cooperate or compete depends not only on the degree of relatedness but also on ecological factors that influence the costs and benefits of cooperative and competitive

interactions. Kin living in the same family group may compete for resources such as mates, food and burrows (Hoogland 1986; Hare & Murie 1996; Isbell 2004). Among sciurids, dominant pairs of alpine marmots, *Marmota marmota*, suppress reproduction in subordinates, including subordinate offspring that remain in the group (Arnold & Dittami 1997; Hacklander et al. 2003), and older yellow-bellied marmot, *M. flaviventris*, females may suppress reproduction in younger females, including members of the same matriline (Armitage 2003). Furthermore, levels of competition may change over time. Black-tailed prairie dogs, *Cynomys ludovicianus*, behave less amicably towards kin during the breeding season and during lactation than at other times of the year (Hoogland 1986). In hoary marmots, *M. caligata*, mother–offspring aggression increases with age (Barash 1989). Thus, competition may outweigh kin-related benefits, and the outcome is that kin may behave quite aggressively towards each other (Griffin & West 2002).

Effects of kinship on social behaviour are well documented in more social species such as primates (Kappeler 2008) and ground-dwelling sciurids (Hare & Murie 2007). Less social or solitary species have received less attention, partly because social interactions are less easily documented. None the less, these species can provide insights into the development of sociality and the relative influence of cooperation and competition on social behaviour (Hare & Murie 2007).

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Marmots, a group of ground-dwelling sciurids, are noted for their sociality (Blumstein & Armitage 1999; Allainé 2000; Armitage 2007). Nearly all species live in family groups, and kin treat each other more amicably and less agonistically than do nonkin (Armitage 1996, 2007), whereas different families mainly interact aggressively (Johns & Armitage 1979; Perrin et al. 1993; Lenti Boero 2003). Woodchucks, *M. monax*, however, are considered solitary, asocial and aggressive (Bronson 1963, 1964; Blumstein & Armitage 1999; Armitage 2007), although they more accurately live in aggregations. Same-sexed individuals occupy exclusive areas, and males' and females' ranges overlap more extensively with each other (Ferron & Ouellet 1989; Swihart 1992; Maher 2004). Woodchucks typically are reported to disperse as juveniles (Barash 1974; Armitage 2007); yet, they may postpone dispersal until their second summer, as yearlings, or remain philopatric (Meier 1992; Swihart 1992; Maher 2006). Such delayed dispersal may create kin clusters, and in at least one population, woodchucks live closer to and share more space with more closely related individuals (Maher 2009). Thus, woodchucks associate with kin and may represent an early stage in the evolution of sociality, particularly since they are considered more basal members of the clade and may represent the ancestral condition of marmot sociality (Kruckenhauser et al. 1999; Steppan et al. 1999). According to models of social organization in ground-dwelling sciurids (Armitage 1981; Michener 1983), the next step would be the development of increased tolerance and amicable interactions. Alternatively, competition among kin may preclude further development of sociality.

My objective was to examine behavioural interactions in woodchucks and determine whether kinship correlated with rates of amicable and agonistic interactions. Since woodchucks are the least social marmots and have been described as aggressive (Armitage 1999), rates of agonistic interactions may not vary with kinship (i.e. kin treat each other aggressively). However, because this population shows evidence of kin structure and more closely related animals live closer to each other (Maher 2009), animals potentially interact with kin on the same or adjacent territories. Thus, like other marmots (Johns & Armitage 1979; Perrin et al. 1993; Lenti Boero 2003), woodchucks may display higher rates of amicable interactions towards kin.

METHODS

Study Area and Population

The study site was located at Gilsland Farm (43°42'N, 70°14'W), a 24 ha wildlife preserve located in Falmouth, Maine, U.S.A. The site consists of salt marsh, mixed hardwood–coniferous forest, and three meadows (6 ha, 3.5 ha and 2.5 ha) that are mowed late each summer or autumn. Elevation varies between 0 and 10 m with gently rolling hills. Woodchucks hibernate primarily in the forest or in hillsides at the edges of meadows, but they do not use meadows extensively until late spring when burrows are no longer flooded from snowmelt. They also occupy lawns and an apple orchard located near administrative buildings. Vegetation height in the meadows increases during the growing season, making behavioural observations more difficult. However, late in the summer, plants overgrow each other and compress the vegetation, improving visibility for observers. Areas around buildings are mowed regularly throughout the growing season, and animals are readily observed in those locations.

I could define three age classes of woodchucks. Juveniles represent young of the year, and females produce only one litter per year, giving birth in a burrow where we cannot observe parturition (Hamilton 1934). Litter size at this site averages 3.5 (range 1–7) offspring (C. R. Maher, unpublished data). Juveniles first emerge

when approximately 4–5 weeks old (Hamilton 1934; Ferron & Ouellet 1991), but I did not generally observe pups on their first day above ground. Thus, I could not reliably assign specific ages within a year. Yearlings represent animals born the previous year, and adults represent animals 2 or more years old. In some cases, I knew more exact ages of adults because I trapped them as juveniles, and they remained on the study site. However, since I did not know exact ages of all adults, I combined all adults into a single age category.

Woodchucks at this site emerge from hibernation in late February to mid-March, with adult males emerging first, followed by adult females, then yearlings (Maher 2006). Juveniles first emerge above ground in late May to early June when they are about 30 days old (Hamilton 1934; Grizzell 1955). Adults immerse in late summer, with juveniles immersing by mid-October (Maher 2006). Population density averaged 1.7 animals/ha and remained stable during the study period (C. R. Maher, unpublished data). Total population size, based on count data, was 30–35 adults and yearlings. The number of juveniles varied each year, but generally ranged from 30 to 45 animals. Sex ratios were nearly equal at 0.8:1 ($\chi^2_1 = 3.14$, $P = 0.076$).

Data Collection

For this study, I used data collected from March 2002 through October 2007. Field assistants and I captured woodchucks each season, beginning in early spring. We used Tomahawk live traps (Tomahawk Live Trap Co., Tomahawk, WI, U.S.A.; 81 × 25 × 30 cm) baited with peanut butter and fresh apples, and we monitored traps hourly, trapping only during daylight hours. Animals were transferred to a cloth handling bag, weighed and sexed using anogenital distance, the presence of descended testes (during spring) or distended nipples (late spring and summer). To collect DNA, I wore vinyl gloves and pulled 75–100 hairs from the animal's hindquarters, placing them in a self-sealing paper envelope and storing them in the laboratory until processing. Each animal received a unique dye mark, which I applied with hair dye (Clairol Balsam Color, Clairol Inc., Stamford, CT, U.S.A.) and a small artist's brush. Because animals shed the dye mark when they moulted each summer, I also attached numbered eartags (National Band and Tag Company, Newport, KY, U.S.A., Size 3) in each ear to identify them permanently. Animals then were released at the capture site.

To obtain data on social interactions, field assistants and I walked the property until we located a woodchuck of known identity. During the study period, 95% of adults and yearlings were tagged. If we disturbed the animal, we waited until it resumed its previous activity, then commenced a 15 min focal sample during which we continuously recorded activity (Martin & Bateson 2007). When an interaction occurred, we noted the identity of each interactant, when possible, and the type of interaction, which included nuzzles, greetings, displacements, chases, fights and play (Armitage 1962, 1973; Bronson 1964; Supplementary Material). Because juveniles often share their mother's home range for the first summer (Maher 2006, 2009), interactions involving juveniles generally occurred in the natal range. Woodchucks do not live in groups, and they maintain territories against same-sexed individuals (Maher 2004); thus, intrasexual interactions between older animals usually occurred between animals occupying different territories (C. R. Maher, unpublished data). Males and females overlap territories (Maher 2004), and intersexual interactions occurred within the individuals' area of overlap (C. R. Maher, unpublished data).

If the animal ran to a burrow or otherwise disappeared from view, we suspended the sample and recommenced sampling when it returned to view. If the animal did not reappear after at least 10 min,

we stopped the sample. Animals had to remain in view for at least 3 min for a sample to be included in the final data analysis. No animal was sampled more than once in 24 h to ensure statistical independence. We sampled animals during daylight hours between sunrise and dusk, and we recorded 870 focal hours of observations during the study period. We sampled animals throughout the active season (March: 39.3 h, April: 143.6 h, May: 140.5 h, June: 143.9 h, July: 110.2 h, August: 184.3 h, September: 90.3 h, October: 17.4 h), and we sampled throughout the day (0600–1200 hours: 360.2 h, 1200–2000 hours: 509.6 h). Interaction rates did not vary between morning and afternoon/evening periods (mean \pm SE: morning: 16.4 ± 1.1 interactions/h; afternoon/evening: 19.1 ± 1.9 interactions/h; $P = 0.16$). However, to control for changes in interaction rates across the active season, I used residuals of interaction rates regressed on month in the analyses.

All procedures were approved by the University of Southern Maine Institutional Animal Care and Use Committee (protocol number 1104-01).

Genetic Analysis

I used the Chelex-100 method (Walsh et al. 1991; Richlen & Barber 2005) to extract genomic DNA from 10 hairs per individual. Some animals were trapped repeatedly over time, in which case, I used the most recent sample. Extractions remained frozen at -20°C and were analysed within 3 months of processing. All extracts amplified successfully. I analysed relatedness for 201 animals.

To estimate relatedness, I used seven microsatellite loci: BIBL-1, BIBL-4, BIBL-18, BIBL-25, MS41, MS47 isolated from alpine marmosets (Goossens et al. 1998; Hanslik & Kruckenhauser 2000; Da Silva et al. 2003), and GS22 isolated from Columbian ground squirrels, *Spermophilus columbianus* (Stevens et al. 1997). Details on amplification protocols are presented in Maher (2009).

I examined the data for signs of allelic dropout (Broquet & Petit 2004) and calculated a dropout frequency of 0.0101 (Broquet & Petit 2004). Departures from Hardy–Weinberg equilibrium and tests for linkage disequilibrium were performed using the web version of GENEPOP (Raymond & Rousset 1995), and the probability of null alleles was estimated using CERVUS 3.0 (Kalinowski et al. 2007). To estimate relatedness between pairs of woodchucks, I used RELATEDNESS 5.0 (Queller & Goodnight 1989), which calculated a coefficient, R , that measures the degree to which two individuals share identical alleles (Queller & Goodnight 1989). Positive values of 0 to 1 indicate that a pair is more related than expected by chance, whereas negative values of -1 to 0 indicate a pair is less related than expected by chance. Relatedness values represent estimates and can be quite variable (Queller & Goodnight 1989; van Horn et al. 2008); yet, full siblings and mother–offspring pairs should have a mean value of 0.5 if the population is in Hardy–Weinberg equilibrium (Kays et al. 2000; Moyer et al. 2006). Furthermore, because I also observed animals in this population for many years, I could verify mother–offspring and grandmother–grandoffspring estimates using pedigrees (van Horn et al. 2008).

Statistical Analyses

Because animals did not always remain in view for the entire 15 min focal sample, I converted interactions to rates when appropriate. Several interactions were summed to create composite variables. Amicable interactions included nuzzles, greetings and play (Armitage 1962, 1973; Nowicki & Armitage 1979; Perrin et al. 1993; Koprowski 1996; Manno 2008; Blumstein et al. 2009; Supplementary Material), whereas agonistic interactions included threats, fights, chases, avoidance, bites and displacements

(Armitage 1962, 1973; Bronson 1964; Koprowski 1996; Supplementary Material). I distinguished between intensity of aggression by considering nonphysical aggression (threats, chases, avoidance and displacements) and physical aggression (bites and fights).

To determine whether interactions occurred randomly among different kin classes, I used equation (7) in Altmann & Altmann (1977) to calculate expected values (Armitage & Johns 1982; Rayor & Armitage 1991; Lenihan & Van Vuren 1996). For unlike pairs ($x \neq z$), the equation is:

$$E_{xz} = \frac{N \sum_j t_j m_{xj} m_{zj}}{\sum_{i,k} \sum_j t_j m_{ij} m_{kj} + \frac{1}{2} \sum_i \sum_j t_j m_{ij} (m_{ij} - 1)}$$

and for like pairs ($x = z$), the equation is:

$$E_{xz} = \frac{\frac{1}{2} N \sum_j t_j m_{xj} (m_{xj} - 1)}{\sum_{i,k} \sum_j t_j m_{ij} m_{kj} + \frac{1}{2} \sum_i \sum_j t_j m_{ij} (m_{ij} - 1)}$$

Thus, I calculated expected values using the total number of interactions (N), the number of hours of observation for individuals within the dyad (t) and the number of other relatives with which animals could potentially interact (m). I then calculated a χ^2 value summed across all dyads for each type of interaction. Kin classes for which I had sufficient samples included mother–offspring ($N = 28$ pairs), littermate siblings (i.e. born in the same year, $N = 45$ pairs), nonlittermate siblings (i.e. born in different years to the same mother, $N = 14$ pairs), and a combined group for aunts and uncles interacting with nieces and nephews ($N = 17$ pairs). I assigned animals to these kin classes using longitudinal behavioural observations to determine pedigrees. I could unequivocally assign juvenile offspring to mothers because of their close association when the young emerged and soon thereafter, but I could not definitively assign paternity based on observations of males courting females during the breeding season; thus, kin classes are based on maternity. To compare dyads, I considered values contributing more than 10% of the overall χ^2 value to indicate biological significance; that is, differences between observed and expected numbers were sufficiently large in those dyads (Armitage & Johns 1982; Rayor & Armitage 1991).

Some pairs of individuals interacted more than once. Therefore, I calculated a mean value for each pair and used that mean in the analyses. I also calculated a mean value for each individual if it interacted with multiple animals. I analysed patterns between interaction rates and relatedness using nonparametric correlations, and I compared interaction rates within kin classes using Wilcoxon signed-ranks tests. I used Mann–Whitney U tests to compare relatedness values and to compare rates between sexes, and I used Kruskal–Wallis tests to examine age effects. Analyses were performed in JMP 7 (SAS Institute, Inc., Cary, NC, U.S.A.) with $\alpha = 0.05$. All tests were two-tailed.

RESULTS

Genetic Analysis

Variation among the seven loci ranged from two to seven alleles per locus, with mean $H_E = 0.58$ (Table 1). No loci consistently deviated from Hardy–Weinberg equilibrium across all years after sequential Bonferroni corrections for multiple comparisons ($P > 0.002$). BIBL-25 deviated from expected values in some but not

Table 1

Characteristics of microsatellite loci, including number of alleles, allele sizes, and observed (O) and expected (E) heterozygosity, used to estimate relatedness in woodchucks, *Marmota monax*

Locus	Annealing temp (°C)	No. of alleles	Size range (base pairs)	Heterozygosity	
				H_O	H_E
BIBL-1	56	3	95–103	0.61	0.48
BIBL-4	56	5	176–184	0.35	0.54
BIBL-18	56.6	4	131–137	0.60	0.60
BIBL-25	56	6	135–149	0.24	0.48
MS41	50	5	177–197	0.74	0.70
MS47	49	7	168–190	0.84	0.80
GS22	57.5	2	163–167	0.56	0.50

in all years. Null alleles and inbreeding are possible explanations for such departures from equilibrium (Hartl & Clark 1997; Cutrera et al. 2005). However, when I compared genotypes of all known mother-offspring pairs (83 pairs from 30 litters), I detected no evidence of null alleles, and the frequency of null alleles at this locus also was low (-0.2077). Many animals in the population were related (e.g. uncle-niece) such that inbreeding was possible. However, inbreeding should result in departures at multiple loci (Cutrera et al. 2005), and most loci did not deviate from Hardy-Weinberg equilibrium. Two other studies reported that BIBL-25 deviated from Hardy-Weinberg equilibrium. Kyle et al. (2007) also found inconsistent results across hoary marmot groups and retained the locus in their analyses. However, Da Silva et al. (2006) noted sex differences in mean heterozygosities and excluded the locus. In this woodchuck population, mean heterozygosities were similar for males (0.22) and females (0.27). For these reasons and to maintain power, I included all seven loci in the analyses.

On average, relatedness for mother-offspring pairs was 0.39 ± 0.024 ($N = 66$ pairs), significantly lower than the predicted value of 0.5 if the population was in Hardy-Weinberg equilibrium (Wilcoxon signed-ranks test: $T = -615.5$, $P < 0.0001$) and significantly higher than for randomly selected pairs in the population (0.045 ± 0.05 ; Wilcoxon signed-ranks test: $T = -120$, $P = 0.016$). Relatedness may be underestimated in this population, perhaps because of higher than expected numbers of close relatives (Kays et al. 2000), but such values can still be useful when comparing individuals within the same population (de Ruiter & Geffen 1998). Lower relatedness values may also result because RELATEDNESS uses allele frequencies to estimate relatedness, leading to lower values when individuals share very common alleles (Wimmer & Kappeler 2002). Furthermore, patterns based on kinship represent conservative results.

Interaction Rates and Relatedness

Interaction rates did not vary across years (Kruskal-Wallis tests: $P > 0.45$), so all years were combined. I generated a mean value for each animal or for each pair of individuals if animals were present in multiple years, and then used that mean in subsequent analyses.

Males and females did not differ in total interaction rates (Mann-Whitney U test: $\chi^2_1 = 0.565$, $P = 0.45$), nor did they differ in rates of amicable and agonistic interactions (amicable: $\chi^2_1 = 0.184$, $P = 0.67$; agonistic: $\chi^2_1 = 1.21$, $P = 0.27$). Therefore, in some cases, I included both sexes in further tests, whereas in other cases, I analysed sexes separately.

Total interaction rates did not vary with relatedness (Spearman rank correlation: $r_s = 0.154$, $N = 65$ woodchucks, $P = 0.73$). Similarly, agonistic rates were not related to degree of relatedness ($r_s = -0.096$, $N = 65$ woodchucks, $P = 0.445$; Fig. 1a). Rates of amicable interactions, however, varied with kinship such that

woodchucks interacted more amicably with more closely related individuals ($r_s = 0.376$, $N = 65$ woodchucks, $P = 0.002$; Fig. 1b).

Analysing the sexes separately, the same patterns held. Females behaved more amicably towards more closely related individuals ($r_s = 0.40$, $N = 29$ females, $P = 0.032$), and so did males ($r_s = 0.356$, $N = 36$ males, $P = 0.033$).

Duration of time spent interacting also was related to kinship. Animals spent a smaller percentage of time interacting with more closely related individuals ($r_s = -0.365$, $N = 61$ woodchucks, $P = 0.0099$; Fig. 2). When I examined sexes separately, females interacted for shorter amounts of time with closer kin ($r_s = -0.579$, $N = 28$ females, $P = 0.003$), but the relationship for males was not significant ($r_s = -0.295$, $N = 32$ males, $P = 0.153$).

Interactions within Kin Classes

Within kin classes, observed numbers of interactions differed significantly from expected values for amicable (chi-square test: $\chi^2_3 = 138.94$, $P < 0.001$) and agonistic interactions ($\chi^2_3 = 19.38$, $P < 0.001$) as well as for physical ($\chi^2_3 = 21.83$, $P < 0.001$) and nonphysical aggression ($\chi^2_3 = 20.71$, $P < 0.001$; Table 2). Amicable interactions occurred more often than expected between mothers and offspring and between littermate siblings; however, those interactions occurred less than expected for nonlittermate siblings and among aunts/uncles and nieces/nephews. Observed and expected numbers of agonistic interactions did not differ for mother-offspring dyads or nonlittermate siblings. However, littermate siblings interacted more agonistically than expected, and aunt/uncle-niece/nephew dyads interacted less agonistically than

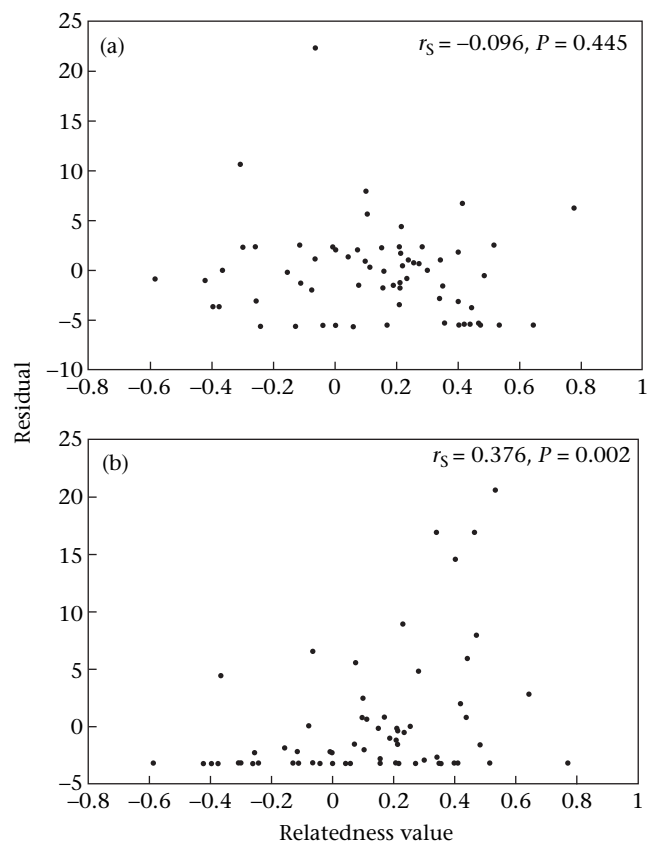


Figure 1. Relationship between residuals of (a) agonistic and (b) amicable interaction rates regressed on month and relatedness values (R) for pairs of woodchuck males and females ($N = 65$ woodchucks).

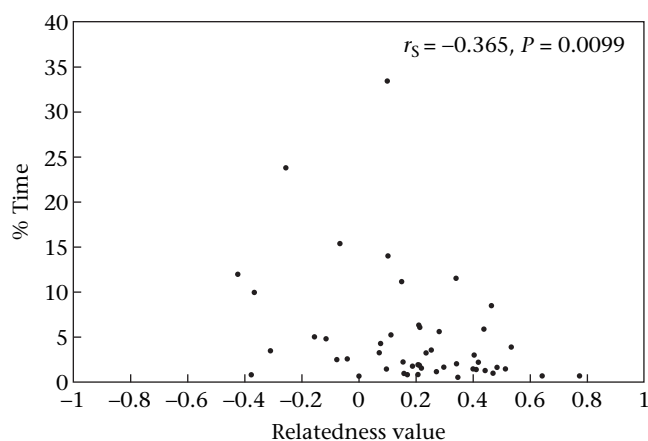


Figure 2. Relationship between mean percentage of time spent interacting and relatedness values (R) for woodchucks ($N = 49$ woodchucks).

expected. Physical aggression was observed less than expected among mothers and offspring, nonlittermate siblings and aunts/uncles–nieces/nephews, but more than expected among littermate siblings. Nonphysical aggression, however, occurred more than expected among mothers and offspring and less than expected in aunt/uncle–niece/nephew dyads (Table 2).

I then compared amicable and agonistic interaction rates within classes of kin, using matched-pairs tests. Mother–offspring dyads and littermate siblings did not differ in rates of amicable versus agonistic interactions (Wilcoxon signed-ranks test: mother–offspring: $T = 16.0$, $N = 36$ woodchucks, $P = 0.81$; littermate siblings: $T = -33.0$, $N = 36$, $P = 0.61$; Table 3). However, mothers and offspring tended to engage in significantly higher rates of nonphysical aggression than physical aggression ($T = -110.0$, $N = 36$, $P = 0.082$; Table 3). Nonlittermate siblings engaged in higher rates of agonistic than amicable interactions ($T = 36$, $N = 13$, $P = 0.002$; Table 3), but the comparison for unrelated animals did not reach statistical significance ($T = 66$, $N = 23$, $P = 0.057$; Table 3). Both classes did not differ in rates of nonphysical aggression versus physical aggression (nonlittermate siblings: $T = -4.0$, $N = 13$, $P = 0.79$; unrelated: $T = 19.0$, $N = 23$, $P = 0.60$; Table 3).

I also compared amicable and agonistic rates between kin classes. Although trends ran in the predicted direction, with higher rates of amicable behaviour among more closely related kin (Table 3), sample sizes were small, and differences were not statistically significant after sequential Bonferroni corrections ($P > 0.003$).

Age Effects

Offspring included juveniles, yearlings and adults that delayed dispersal and were recruited into the population, so I examined mother–offspring interactions based on offspring age and sex. Total interaction rates did not differ (Kruskal–Wallis test: $\chi^2_2 = 1.75$,

$N = 29$ juveniles, 11 yearlings, 6 adults, $P = 0.42$). However, agonistic and amicable rates differed with offspring age (agonistic: $\chi^2_2 = 13.91$, $P = 0.001$; amicable: $\chi^2_2 = 27.39$, $P < 0.0001$; Fig. 3a). Mothers interacted amicably at higher rates with juveniles than with older offspring (Mann–Whitney U tests: adult–juvenile: $\chi^2_1 = 12.27$, $P = 0.0005$; yearling–juvenile: $\chi^2_1 = 20.56$, $P < 0.0001$; Fig. 3a) and more amicably with juvenile daughters than with juvenile sons (females: 11.97 ± 4.31 interactions/h; males: 6.32 ± 2.45 /h; $\chi^2_1 = 4.02$, $N = 10$ females, 16 males, $P = 0.045$). Rates of agonistic interactions were higher between mothers and their yearling or adult offspring compared to younger offspring (adult–juvenile: $\chi^2_1 = 4.52$, $P = 0.033$; yearling–juvenile: $\chi^2_1 = 12.46$, $P = 0.0004$; Fig. 3a). Furthermore, mothers interacted agonistically at higher rates with adult female offspring than with adult male offspring (females: 10.97 ± 2.68 /h, males: 4.37 ± 2.21 /h; $\chi^2_1 = 3.86$, $N = 3$ females, 3 males, $P = 0.05$), whereas rates did not differ between younger males and females ($P > 0.41$). Rates of physical aggression did not vary with offspring age ($\chi^2_2 = 2.05$, $P = 0.359$; Fig. 3a) or with sex ($P > 0.18$), but rates of nonphysical aggression were higher between mothers and their yearling or adult offspring than between mothers and their juvenile offspring (Kruskal–Wallis tests: $\chi^2_2 = 8.87$, $P = 0.012$; Mann–Whitney U tests: adult–juvenile: $\chi^2_1 = 4.14$, $P = 0.042$; yearling–juvenile: $\chi^2_1 = 6.77$, $P = 0.009$; Fig. 3a). Mothers interacted at higher rates with yearling females than with yearling males (females: 7.64 ± 2.52 /h, males: 3.2 ± 0.8 /h; $\chi^2_1 = 4.11$, $N = 6$ females, 5 males, $P = 0.043$).

Similarly, I examined interactions between littermate siblings of different ages. Rates of total interactions did not vary with age of littermates ($\chi^2_2 = 5.43$, $P = 0.066$). Rates of agonistic, physically aggressive and nonphysically aggressive interactions did not vary by age of littermates (agonistic: $\chi^2_2 = 4.71$, $N = 26$ juveniles, 15 yearlings, 5 adults, $P = 0.095$; physical aggression: $\chi^2_2 = 3.64$, $P = 0.16$; nonphysical aggression: $\chi^2_2 = 3.82$, $P = 0.15$; Fig. 3b). However, rates of amicable interactions differed by age ($\chi^2_2 = 13.66$, $P = 0.0011$), with adults interacting at lower rates than yearlings or juveniles (adult–juvenile: $\chi^2_1 = 12.24$, $P = 0.0005$; adult–yearling: $\chi^2_1 = 9.65$; $P = 0.0011$; Fig. 3b).

DISCUSSION

In this population, interactions among woodchucks illustrated the effects of kinship. Although kinship did not influence overall rates of interactions or agonistic interactions, closely related individuals were more amicable than distantly related individuals, as expected under kin selection (Hamilton 1964).

Amicable interactions increased significantly with relatedness among both females and males. In this population, both males and females may delay dispersal beyond their first summer (Maher 2006). Social interactions may serve as the proximate mechanism for dispersal, as it does for other species (Ferrerias et al. 2004; Nunes 2007; Long et al. 2008). In yellow-bellied marmots, females that are more integrated into the group and interact with more individuals

Table 2 Observed (O) and expected (E) numbers of social interactions for different kin classes of woodchucks

Dyad	Amicable		Agonistic		Physical aggression		Nonphysical aggression	
	O	E	O	E	O	E	O	E
Mother–offspring	89*	45	49	40	8*	14	41*	27
Littermate siblings	114*	78	88*	71	42*	24	46	46
Nonlittermate siblings	0*	29	25	26	3*	9	22	17
Aunt/uncle–niece/nephew	1*	52	22*	47	10*	16	12*	31
	$P < 0.001$		$P < 0.001$		$P < 0.001$		$P < 0.001$	

* Chi-square for the cell contributed more than 10% to the overall chi-square value and can be considered biologically significant (Rayor & Armitage 1991).

Table 3
Matched-pairs comparisons of mean (\pm SE) interaction rates (number/h) within and between different kin classes of woodchucks

Kin class	N	Amicable	Agonistic	Physical aggression	Nonphysical aggression
Mother–offspring	36	7.7 \pm 2.6 <i>P</i> =0.81	3.2 \pm 0.75	0.69 \pm 0.31	2.5 \pm 0.59 <i>P</i> =0.08
Littermate sibs	36	6.5 \pm 2.1 <i>P</i> =0.61	6.2 \pm 1.7	4.3 \pm 1.7	1.9 \pm 0.51 <i>P</i> =0.22
Nonlittermate sibs	13	0 <i>P</i>=0.002	5.9 \pm 1.1	0.55 \pm 0.41	5.4 \pm 0.97 <i>P</i> =0.79
Unrelated	23	0.23 \pm 0.18 <i>P</i> =0.057	5.7 \pm 1.3	1.1 \pm 0.52	4.6 \pm 1.2 <i>P</i> =0.60
Mother–offspring vs Littermate sibs	17	8.2 \pm 5.1 9.9 \pm 4.1 <i>P</i> =0.55	4.7 \pm 1.1 4.8 \pm 2.0 <i>P</i> =0.39	1.3 \pm 0.61 2.9 \pm 1.9 <i>P</i> =0.30	3.4 \pm 0.80 2.0 \pm 0.77 <i>P</i> =0.90
Littermate sibs vs Nonlittermate sibs	7	11.9 \pm 8.8 0 <i>P</i> =0.062	9.5 \pm 7.5 5.6 \pm 1.4 <i>P</i> =0.56	8.1 \pm 7.6 0.74 \pm 0.74 <i>P</i> =0.19	1.4 \pm 0.95 4.8 \pm 1.2 <i>P</i> =0.84
Littermate sibs vs Unrelated	8	9.6 \pm 7.8 0.5 \pm 0.5 <i>P</i> =0.20	12.2 \pm 6.2 5.3 \pm 2.2 <i>P</i> =0.46	9.0 \pm 6.5 0.66 \pm 0.66 <i>P</i> =0.46	3.2 \pm 1.3 4.7 \pm 1.8 <i>P</i> =0.74
Mother–offspring vs Unrelated	7	6.1 \pm 3.0 0 <i>P</i> =0.03	5.8 \pm 2.4 5.9 \pm 2.0 <i>P</i> =0.95	1.6 \pm 1.1 1.3 \pm 0.87 <i>P</i> =0.69	4.4 \pm 1.7 4.5 \pm 1.7 <i>P</i> =0.74

Values for each pair of kin classes were compared using Wilcoxon signed-ranks tests.

Boldface indicates significant differences after sequential Bonferroni corrections. Sample sizes differ because each animal did not interact with animals from every possible kin class.

are less likely to disperse (Blumstein et al. 2009). When juvenile woodchucks disappeared from the natal range, I usually could not determine whether they died or dispersed; therefore, I could not compare interaction rates between dispersers and philopatric animals. None the less, future work could explore the proximate basis for dispersal in woodchucks.

Because some yearlings become resident within or adjacent to their natal range (Maher 2006), mothers continue to interact with older offspring; however, those interactions change over time. Mothers behaved most amicably towards juvenile offspring, as expected because competition between mothers and young should be lowest and juveniles benefit most from parental investment (Trivers 1974). As herbivores that feed primarily on forbs (Hamilton 1934; Swihart 1990), resources presumably were abundant, minimizing competition for food. Juveniles are more vulnerable to predators (Grizzell 1955) and thus may benefit by remaining within the familiar natal range (Jacquot & Solomon 1997). As yearlings, interactions with their mothers became more agonistic. Few yearling females (12%) reproduce in this population; however, adult females typically rear one litter each year, shifting parental investment towards younger offspring (C. Maher, unpublished data). Females usually start to reproduce at 2 years (C. Maher, unpublished data), and the potential competition between mothers and adult offspring for resources such as mates, food or burrows may increase accordingly. Such increased competition is suggested by the change in interactions as offspring mature. Mothers engaged in higher rates of amicable interactions with juvenile daughters than with juvenile sons; however, rates of nonphysical aggression and agonistic interactions were higher between mothers and their yearling and adult female offspring, respectively, compared to male offspring.

Interactions between other kin classes also reflected different levels of competition as well as different degrees of relatedness. Based on microsatellite DNA data, littermate siblings were more closely related than were nonlittermate siblings (littermates:

$R = 0.284 \pm 0.052$, $N = 41$ dyads; nonlittermates: $R = 0.0185 \pm 0.116$, $N = 15$ dyads; Mann–Whitney U test: $\chi^2 = 4.65$, $P = 0.031$). I observed greater numbers of amicable interactions than expected among littermate siblings, whereas I never observed nonlittermate siblings behave amicably. Furthermore, nonlittermate sibling dyads engaged in significantly higher rates of agonistic interactions. The latter observation may be partly due to age differences, since by definition, one member of a nonlittermate sibling dyad was older than the other. Indeed, among littermates, amicable interaction rates varied with age; adult littermates never interacted amicably. Thus, competition for resources may be greater among these individuals, particularly if one animal is capable of reproduction.

Nonlittermate siblings displayed the same pattern of interactions as unrelated dyads (i.e. agonistic rates exceeded amicable rates). The kin class consisting of aunts and uncles interacting with nieces and nephews also resembled nonlittermate siblings in that numbers of amicable and physically aggressive interactions were fewer than expected. Overall, animals in that kin class interacted less than expected across all types of interactions. Although I combined aunts, uncles, nieces and nephews into one category to increase sample sizes, most interactions occurred between males and females, which overlapped home ranges and thus may have tolerated each other's presence to a greater degree than they would tolerate same-sexed individuals. In other sciurids, animals often do not distinguish distant kin from nonkin in their patterns of interactions (Sherman 1980, 1981; Armitage 1987; Koprowski 1996). Kin

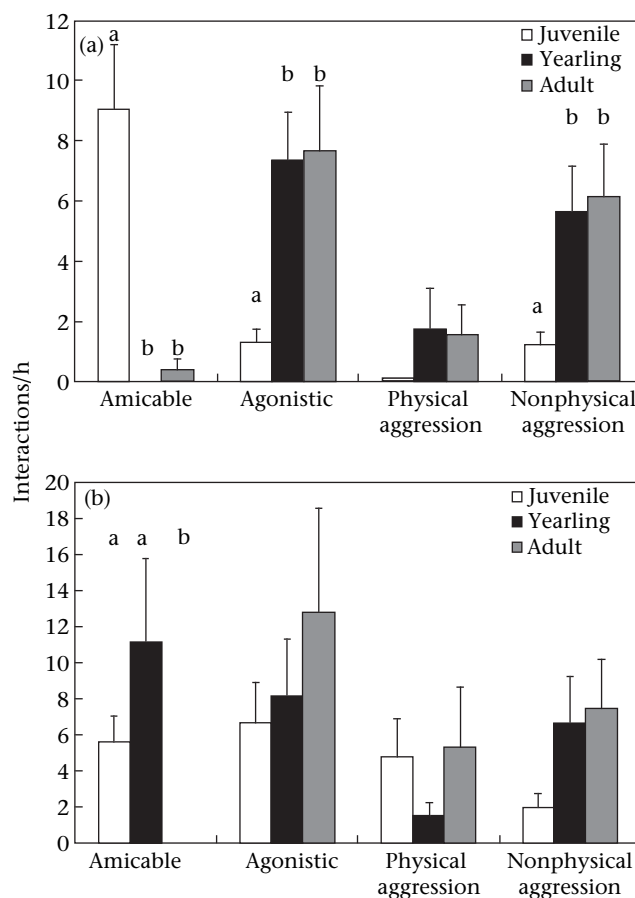


Figure 3. Mean \pm SE interaction rates for different types of interactions between (a) mothers and their juvenile, yearling or adult offspring ($N = 29$ juveniles, 11 yearlings and 6 adults) and (b) littermate siblings of different ages ($N = 26$ juveniles, 15 yearlings and 5 adults). Within each type of interaction, different letters indicate statistically significant differences ($P < 0.05$).

selection may not favour increased amicability among more distant kin, and animals may not have developed the ability to recognize distant kin as related (Sherman 1980, 1981; Silk 2002). We know virtually nothing about kin recognition in woodchucks; thus, we cannot determine whether animals recognize distant kin but do not bias interactions between them and unrelated individuals, or if they just cannot make fine-grained distinctions in relatedness.

The general patterns seen here are well known in mammals (Armitage 1987; Koprowski 1996; Hare & Murie 2007; Kappeler 2008; Perry et al. 2008), and interactions can vary over time or with age of kin. Lemurs (*Lemur* spp.) normally treat close kin more favourably than distant kin or unrelated conspecifics; yet, relatives may engage in targeted aggression as group size increases or when females produce new offspring (Vick & Pereira 1989). Aggression between mothers and offspring increases with age in hoary marmots (Barash 1989). Black-tailed prairie dogs behave least amicably towards kin during the breeding season, when competition for mates intensifies, and during early lactation, when females may commit infanticide (Hoogland 1986). Even at peak times of competition, however, kin still treat kin more amicably than nonkin (Hoogland 1986). Similarly, Belding's ground squirrels, *Spermophilus beldingi*, behave more cooperatively than competitively, even when mothers interact with adult daughters (Sherman 1981). In woodchucks, however, even among close kin, agonistic interactions prevailed among older animals, suggesting that benefits of cooperation do not outweigh costs of competition as females enter the breeding cohort.

Woodchucks live near kin, show differences in social behaviour based on kinship, and also give alarm calls (Barash 1989). What prevents them from expressing a more advanced degree of sociality such as cooperative defence of territories? Woodchucks in different populations show different social organization in terms of the extent of territoriality, timing of dispersal and degree of natal philopatry (Smith 1972; Ferron & Ouellet 1989; Meier 1992; Swihart 1992; Maher 2004, 2006), so they may be capable of shifting towards the more social end of the continuum.

Several factors may influence sociality in ground-dwelling sciurids, including predation, the distribution of resources such as food or burrows, and harsh environments (Ebensperger 2001; Armitage 2007; Hare & Murie 2007). Groups gain many antipredator benefits (Ebensperger 2001; Ebensperger & Wallem 2002; Ebensperger & Blumstein 2006). However, because this population is situated on a wildlife sanctuary in a suburban setting, predation pressure may not favour increased group size. Domestic dogs, *Canis lupus familiaris*, were prohibited, although they trespass and kill woodchucks occasionally. Red foxes, *Vulpes vulpes*, sometimes established territories within the study site, but they were not permanent residents.

Resource distribution also can affect sociality. Generally, because of distribution and abundance, food resources are not considered limiting or defensible for most ground-dwelling sciurids (Hare & Murie 2007). Nevertheless, in Ontario, woodchuck females experiencing more abundant food and cover overlap home ranges to a greater extent than females living in less ideal areas (DeVos & Gillespie 1960), but patterns of social interactions and kinship are unknown. Typically, woodchucks have access to abundant forage, so living in a group may not secure them additional resources.

Many sciurids defend nest burrows cooperatively (Hoogland 1986; Armitage 1987), but woodchucks do not. They maintain territories, defending them against same-sexed individuals, although the resource being defended is not clear (Maher 2004). Burrows may not be limiting resources at this site, which is characterized by sandy soil that is relatively easy to excavate, as evidenced by the speed (<2 h) with which woodchucks can dig new tunnels to avoid traps.

Sociality may be favoured in marmots for reasons related to life in harsh environments and to social thermoregulation (Arnold 1990; Armitage 2007). Short growing seasons and harsh environments may favour sociality because animals take longer to grow and reach reproductive maturity (Armitage 1999; Armitage & Blumstein 2002). Thus, marmots postpone dispersal or remain within the natal range, and parents continue to invest in offspring (Armitage 1999; Armitage & Blumstein 2002). However, woodchucks facing a range of growing seasons do not show clear patterns in the timing of dispersal, so environmental harshness alone does not explain the patterns we see (Maher 2006). At this latitude, climate plus the availability of suitable hibernacula (Arnold 1990) may make joint hibernation unnecessary in that it would not increase overwinter survival. Woodchucks vary latitudinally in hibernation patterns, with more northern populations hibernating longer than more southern populations (S. M. Zervanos, C. R. Maher, J. A. Waldvogel & G. L. Florant, unpublished data). Yet, woodchucks in northern locales do not lose more mass and thus may not expend more energy compared to those located further south (S. M. Zervanos, C. R. Maher, J. A. Waldvogel & G. L. Florant, unpublished data). Future studies should investigate woodchucks living in more northern populations to determine their social organization, including the presence of social thermoregulation. Indeed, the sole report of joint hibernation came from Québec, the northernmost population studied (Ferron 1996).

Woodchucks may not show greater degrees of sociality because they do not achieve greater benefits in terms of reproductive output. Even among social species, individuals may experience fitness costs associated with group living (Lacey 2004; Dugdale et al. 2007; Silk 2007; Ebensperger & Hayes 2008). Woodchucks may be less social because the costs of such cooperation could be too great. Both reproductive suppression and infanticide occur widely in ground-dwelling sciurids, generally, and marmots, specifically (Hacklander & Arnold 1999; King & Allainé 2002; Armitage 2007). Infanticide has not been reported in woodchucks, but reproductive suppression may occur (C.R. Maher, unpublished data).

To conclude, mothers and their dependent young behaved amicably, as did younger littermates, but such amicability declined with increasing age. These patterns suggest limited indirect fitness benefits that do not outweigh costs associated with competition among breeding adults. The balance between cooperation and competition may differ across populations, and we should expect to see different social systems as a result. Such behavioural flexibility also can provide a means to understand underlying mechanisms leading to differences in social organization within this species.

Acknowledgments

I thank the staff of the Maine Audubon Society for permission to conduct this study on their property and for their assistance over the years. K. Armitage, L. Ebensperger, J. Hare, N. Solomon and two anonymous referees provided helpful comments on a previous version of the manuscript. I offer special thanks to J. Rhymer for hosting me in her lab and to her and J. Muhlin for their assistance with microsatellite DNA analyses. Many undergraduate students assisted in the field, and I especially thank T. Daigle, S. Long, Y. Seko and J. Wright. Funding was provided by the National Science Foundation, University of Southern Maine Faculty Senate Research Grants, a University of Southern Maine Summer Research Award, and the Maine Economic Improvement Fund.

Supplementary Material

Supplementary material for this article is available in the online version at doi: [10.1016/j.anbehav.2009.06.027](https://doi.org/10.1016/j.anbehav.2009.06.027).

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