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INFLUENCE OF RELATEDNESS ON SNOWSHOE HARE SPACING BEHAVIOR

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Predation and food are dominant forces regulating snowshoe hare (*Lepus americanus*) population density, yet manipulations of these factors have not proven sufficient to explain all aspects of hare population dynamics. Social interactions among hares have often been dismissed as unimportant in population regulation, but the mechanisms and consequences of such interactions have not been well studied. In this study, we examined one aspect of social behavior in snowshoe hares that has been hypothesized to be important in the spacing behavior of other species of small mammals: interactions among related individuals. We sampled 68 hares on two 7.3-ha grids in the southwest Yukon Territory during a cyclic peak phase of population density and used livetrapping and radiotelemetry to quantify spacing behavior. Hares were genotyped at 7 microsatellite DNA loci, and relatedness (r) among individuals was estimated and correlated with spacing. Average relatedness was low on both grids (≤ 0) because very few close kin were present. Hares were not more or less likely to associate with kin than they were with nonkin. The results were similar when males, females, adults, and juveniles were considered together or separately and are thus consistent with a lack of sex-biased dispersal in snowshoe hares. Kin are not clustered in snowshoe hare populations, thus interactions among kin do not likely have a strong influence on hare spacing behavior. This study supports the idea that spacing behavior has little influence on hare population dynamics, at least during the peak phase of the cycle.

Key words: home range, kin structure, *Lepus americanus*, microsatellite DNA, radiotelemetry, relatedness, snowshoe hare, spacing behavior, Yukon

Studies of population regulation in snowshoe hares (*Lepus americanus*) have focused primarily on extrinsic rather than intrinsic factors (Keith 1990; Krebs 1996). Predation and food are the dominant forces influencing hare dynamics, but their direct effects are insufficient to explain all aspects of the 8- to 11-year density cycle (Hodges 2000; Hodges et al. 1999; Krebs et al. 1995). Recent models have focused on the interaction between predation and food and on the role of hare behavior in linking the two, for instance, through predator-sensitive foraging (Boonstra et al. 1998a; Hik 1995). Experimental manipulations of predation and food, however, have not always resulted in consistent or predicted changes in hare behavior (Hik 1994; Hodges 1998, 1999). The role of social interactions in these behavioral patterns remains unclear. Contrary to many other cyclic small mammals, interactions among hares seem unlikely to influence population dynamics due to a lack of obvious spacing behavior or direct social mortality (Boutin 1980; Krebs 1996). Nevertheless, the potential for significant behavioral interference has been demonstrated in hares (Boutin 1984; Ferron 1993; Graf 1985; Graf and Sinclair 1987; Quenette et al. 1997; Sinclair 1986), and the consequences of interference for individual

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fitness (e.g., reduced foraging efficiency, greater predation risk, increased stress, lower reproductive success) require further investigation.

Identifying mechanisms influencing social interactions is an important step in understanding their consequences. Such mechanisms remain poorly understood in snowshoe hares due to the difficulty of studying their behavior in the field (Graf 1985). In many species of small mammals, the degree of relatedness between individuals has been hypothesized to influence social interactions (Charnov and Finerty 1980; Lambin and Krebs 1991; Sherman 1981; Surridge et al. 1999). Individuals may react less aggressively toward kin than toward nonkin, thus the proportion of related individuals in a group could affect the frequency and severity of aggressive encounters experienced by a group member. This could directly or indirectly affect the survival, reproduction, or dispersal of individuals and therefore influence population dynamics (Lambin and Krebs 1993; Matthiopoulos et al. 1998). Relatedness may also be linked to dispersal through inbreeding avoidance and competition among kin (Ferriere et al. 2000).

Patterns of relatedness in natural populations of small mammals are not well known (Boonstra et al. 1998b; Krebs 1996), but recent studies using genetic markers have detected clusters of related individuals in some species (*Crocidura russula*—Balloux et al. 1998; *Clethrionomys rufocanus*—Ishibashi et al. 1997; *Oryctolagus cuniculus*—Surridge et al. 1999). No studies have investigated spatial population structure in snowshoe hares, and it is unknown whether or not relatives live near each other. The goal of this study was to examine the influence of kin interactions on snowshoe hare spacing behavior by determining the degree of relatedness among individuals in a wild population, and testing for an association between relatedness and spacing. If interactions among kin are less costly than those among nonkin (e.g., less aggressive encounters), we predict that hares should associate more closely with related individuals. Alternatively, if fitness costs associated with inbreeding or kin competition outweigh benefits of kin association, related individuals would be expected to avoid each other. If kin interactions do not play a role in hare social behavior, we expect related and unrelated individuals to associate randomly.

MATERIALS AND METHODS

Trapping and telemetry.—This study was carried out on two 7.3-ha grids (‘‘Flint’’ and ‘‘Chitty’’) separated by approximately 20 km near Kluane Lake, Yukon Territory, Canada (61°N, 138°W), during a peak phase of the snowshoe hare cycle. The local forest is dominated by white spruce (*Picea glauca*) with an understory of gray willow (*Salix glauca*), bog birch (*Betula glandulosa*), and soapberry (*Sheperdia canadensis*), as described by Douglas (1974). Tomahawk live traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin) were set 30 m apart in a 10 by 10 pattern, and trapping sessions were conducted weekly from early June to mid-August 1999. Captured hares were eartagged (Monel #3 tags, National Band and Tag Co., Newport, Kentucky), weighed, sexed, and aged (adult or juvenile based on weight and foot color, with juveniles defined as young of the year). A small amount of ear tissue was collected from each hare using a 3-mm biopsy punch (Mader Instrument Corp., Stamford, Connecticut). Tissue samples were placed in 95% ethanol at the time of collection and frozen within 1–2 h. The majority of adult hares captured more than twice on a grid (and thus more likely to be resident) were fitted with 40-g radiocollars (Lotek, Newmarket, Ontario, Canada). Radiotelemetry locations were collected daily by tracking hares to within about 5–10 m (without disturbing them), using handheld receivers and antennas (TR2, Telonics, Mesa, Arizona—Hodges 1998). Locations were recorded at different times of the day to obtain observations when hares were both active and resting. Each location was recorded using the trap grid stakes as reference points. Locations for hares found away from the grids were estimated by measuring the direction and distance to the nearest reference point. Universal Transverse Mercator (UTM) coordinates for grid stakes and off-grid reference points were collected using a handheld global positioning system (GPS) unit (GPS II plus, Garmin International Inc., Olathe, Kansas).

Microsatellite analysis and relatedness.—Deoxyribonucleic acid was extracted from tissue samples, and 7 microsatellite loci originally developed in the European rabbit were amplified and scored (*Sat2*, *Sat3*, *Sat12*, *Sat13* and *Sat16*—Mougel et al. 1997; *Sol03*—Rico et al. 1994; *Sol33*—Surridge et al. 1997). Amplification conditions were similar to those originally described by these authors and are detailed by Burton et al. (2002). Loci were tested for deviations from Hardy–Weinberg equilibrium and genotypic linkage equilibrium in the computer program GENEPOP version 3.1 (Raymond and Rousset 1995), with significance levels adjusted using the sequential Bonferroni correction for multiple comparisons (Rice 1989).

We estimated genetic relatedness among all individuals captured on the grids using the computer program KINSHIP version 1.2 (Goodnight and Queller 1999). The coefficient of pairwise relatedness (r) was calculated by comparing the proportion of shared alleles between 2 individuals with the allele frequencies in the whole population (Queller and Goodnight 1989). Resulting r values can range from -1 to 1, with negative values indicating that individuals share fewer alleles than average. Theoretical r values in a randomly mating population are 0.5 for full siblings and 0.25 for half-siblings, but in reality there is considerable variation around these values (Blouin et al. 1996; Queller and Goodnight 1989). We calculated mean pairwise relatedness for all hares on a grid and separately for the radiocollared subset and for each sex and age class.

Pseudoreplication in the multiple pairwise comparisons precluded customary statistical tests of the means; therefore, we determined significance using randomization tests performed in the software program RT version 2.1 (Manly 1997b). The observed mean, or difference between 2 means, was compared with a randomized distribution generated by reordering the data 5,000 times (Manly 1997a). For comparisons of 2 means, observed values were randomly reassigned into the 2 sample groups being compared, and the proportion of randomized differences greater than or equal to the observed difference was calculated (with significance at the 5% level). For tests of a single mean, the signs of the observed values were randomized and the new values summed. In this case, significance was based on the proportion of randomized sums either greater than or less than the observed sum (depending on the direction of the test). As an alternative method of assessing the general level of relatedness among adults on each grid, we compared the distribution of r values for the sampled hares with a distribution generated from the random simulation of 1,000 unrelated pairs (i.e., having mean $r \approx 0$), using the allele frequencies for the population (Blouin et al. 1996; Surridge et al. 1999). The significance of pairwise relatedness estimates was also further evaluated by using program KINSHIP to test the likelihood that pairs of individuals were either full siblings or half siblings against the null hypothesis that they were not related. The program calculates a ratio of likelihoods for the primary (i.e., full or half siblings) and null (i.e., unrelated) hypotheses and determines significance based on the ratio needed to exclude 95% of 1,000 null-related simulated pairs (Goodnight and Queller 1999).

Activity centers and home range.—All hare locations were converted to UTM coordinates based on their distance and direction from the reference UTM locations. An ‘‘activity center’’ was determined for each sampled hare by calculating the arithmetic mean of its locations (using both trapping and telemetry locations). For animals with more than 5 locations, we calculated the mean using only the 80% core locations. The distance between activity centers for each pair of hares was calculated and grouped by sex and age categories, and group means were tested by randomization in program RT.

We compared distance between activity centers for each pair of hares with their degree of relatedness using a nonparametric Mantel test (Mantel 1967). For this test, relatedness values were transformed into dissimilarity measures by subtracting from 1. Significance was determined by comparing the observed Mantel Z statistic with the distribution of Z statistics obtained in 1,000 random permutations of the distance and relatedness matrices. Males, females, adults, and juveniles were tested separately.

Activity centers provide only a coarse estimate of hare home ranges and may not give a reliable representation of spacing behavior (Boutin 1979; Hodges 1998). We performed a more detailed analysis of spacing for the radiocollared hares, using the computer program RANGES V (Kenward and Hodder 1996). The 95% fixed kernel estimates of home range (a nonparametric, probability-based estimation method described by Worton 1989) were determined, and the degree to which each hare's home range was overlapped by that of every other hare was calculated to provide a measure of space sharing. Because the degree of overlap between 2 hares depended on the size of each individual's home range, each hare had a unique overlap value, and a matrix of pairwise overlap could not be made. Consequently, we used 2 alternative methods of testing for an association between overlap and relatedness (Knight et al. 1999). In the 1st method, separate regressions of overlap versus *r* were made for each individual hare and the slopes compared across all hares. In the 2nd method, *r* values and corresponding degrees of overlap were ranked for each hare, the means across all hares were calculated for every level in the ranking, and the regression of mean *r* on mean overlap was tested. Nonparametric Wilcoxon tests were used to compare slopes and test for differences between males and females (Sokal and Rohlf 1995). Significance levels were adjusted using the sequential Bonferroni correction when assessing multiple tests.

The amount of home-range overlap may not reveal the full extent of interaction among snowshoe hares. Boutin (1980) suggested that female hares use their home ranges in such a manner as to avoid neighboring females. It is thus possible that 2 animals could seldom encounter each other despite sharing a large proportion of their ranges. For this reason, we further examined the spacing behavior of overlapping hares by testing for ''dynamic interaction'' (Macdonald et al. 1980) using RANGES V. An index of cohesion (Jacob's index—Jacobs 1974; Kenward and Hodder 1996; Kenward et al. 1993) was calculated by determining the tendency of pairs of individuals to be close together at the same time. We arbitrarily defined ''same time'' as radio locations obtained within 60 min. The index is a measure of the difference between observed and possible distances separating 2 individuals and can range from -1 to 1, with negative values indicating avoidance, positive values indicating attraction, and a value of 0 suggesting no interaction. Possible distances were calculated assuming that one of the hares being compared could be at any of its observed locations when the other hare is at each of its locations. The interaction values were plotted against pairwise *r* values and the significance of the relationship tested in program RT using 5,000 randomized regressions (where y values were reordered). Values are reported as mean ± *SD.*

RESULTS

Sample sizes and genetic variation.—On the Flint grid, 56 hares were caught. Forty were adults (16 males, 24 females), and 16 were juveniles (6 males, 10 females). An average of 3.4 trapping locations was obtained for each hare (range, 1–10; many juveniles were caught only once). Twenty-two of the adults (7 males, 15 females) were radiocollared, and an average of 18.7 radiolocations per hare was obtained for 21 of them (range, 12–24). One female died after only 5 locations had been determined and was excluded from the telemetry analyses.

The Chitty grid had a lower density of hares. Eight adults (5 males, 3 females) and 4 female juveniles were trapped, and an average of 2.7 trapping locations was obtained per hare (range, 1–9). Six of the adults (4 males, 2 females) were radiocollared, and an average of 20.5 locations was obtained for these hares (range, 18–25, trapping plus telemetry). Low sample size on this grid prevented statistical analyses by sex and age class.

The number of distinct alleles and the observed and expected heterozygosities for each microsatellite locus are shown in Table 1. There were no significant deviations from Hardy–Weinberg equilibrium in either the Flint or the Chitty samples when loci were considered both separately ($P > 0.05$ after Bonferroni correction) and in combination (Flint $\chi^2 = 7.6$, *d.f.* = 14, $P = 0.91$; Chitty $\chi^2 = 16.3$, *d.f.* = 14, $P = 0.30$), suggesting that the populations were mating randomly. All pairs of loci were also in genotypic linkage equilibrium ($P > 0.05$), in-

TABLE 1.—Number of alleles and expected (H_E) and observed (H_O) heterozygosity at each locus for hares sampled from the Flint ($n = 56$) and Chitty ($n = 12$) grids in Yukon Territory, Canada.

			Heterozygosity			
	Number of alleles		Flint		Chitty	
Locus	Flint grid	Chitty grid	H_E	H_O	H_E	H_O
Sol03	6	4	0.40	0.41	0.72	0.67
Sol33	6	8	0.76	0.80	0.77	0.75
Sat2	20	15	0.93	0.93	0.95	1.00
Sat3	7	3	0.61	0.64	0.56	0.58
Sat12	7	7	0.59	0.63	0.80	0.92
Sat13	3	3	0.18	0.20	0.47	0.17
Sat16	8	6	0.82	0.82	0.77	0.92

dicating that they were segregating independently.

Relatedness.—The estimated degree of relatedness (r) between any pair of adult hares on the Flint grid ranged from −0.66 to 0.87 with an overall mean of −0.027 (±0.24; Table 2), which was significantly less than 0 (randomization $P < 0.001$). The distribution of r values was significantly different from the distribution for 1,000 simulated, unrelated pairs (test for goodness of fit, $\chi^2 = 74.3$, *d.f.* = 15, $P < 0.001$), with the Flint mean falling below the lower 95% confidence limit (−0.010) of the simulated mean. This suggests that adults on the grid may have been less related than expected by chance, although the slight difference may not be biologically significant. Only 4.6% of the adult relationships on Flint were classified as either full or half siblings by program KINSHIP (36 of 780 pairwise comparisons, $P < 0.05$). There was no significant difference in mean pairwise relatedness between adult males and adult females (randomization $P = 0.95$). However, juveniles on the grid were more related than adults (randomization $P = 0.023$).

TABLE 2.—Pairwise relatedness (r) of snowshoe hares on the Flint and Chitty grids in Yukon Territory, Canada. Percentage of pairwise relationships classified as full sibling or half sibling by program KINSHIP ($P < 0.05$) is also shown. Results considering only the radiocollared hares are also given because it is possible that some of the noncollared hares were not residents on the grids.

		r		Full–half sibling relationships (%)		r		Full–half sibling relationships (%)
Group	n total	$\bar{X}$	*SD*[a]		n radiocollared	$\bar{X}$	*SD*[a]	
Flint								
All adults	40	−0.027[b]	0.24	4.6	21	0.025	0.24	4.8
Males	16	−0.032	0.26	3.3	7	−0.032	0.25	9.5
Females	24	−0.034	0.23	5.1	14	0.037	0.23	6.6
Juveniles	16	0.019[c]	0.25	8.3				
Chitty								
All adults	8	−0.080	0.27	0	6	−0.073	0.27	0
Males	5	−0.094	0.28	0	4	0.050	0.25	0
Females	3	0.091	0.27	0	2	−0.19		0
Juveniles	4	0.074	0.15	0				

[a] *SD*s calculated over all pairwise comparisons, with the number of comparisons equal to $n(n - 1)/2$.

[b] Mean r for Flint grid adults was significantly <0 (randomization $P < 0.001$).

[c] Mean r for Flint grid juveniles was significantly greater than for Flint grid adults (randomization $P = 0.023$).

TABLE 3.—Summary of spacing behavior among snowshoe hares on the Flint and Chitty grids in Yukon Territory, Canada, showing distance between activity centers, home-range size, home-range overlap, and dynamic interaction (*J*). Distance between snowshoe hares was calculated for all trapped individuals, whereas other measures were based only on radiocollared hares.

Group	Sample size (total/ radiocollared)	Distance (m)		Home range: Size (ha)		Home range: % overlap		*J*	
		$\bar{X}$	*SD*[a]	$\bar{X}$	*SD*[a]	$\bar{X}$	SD[a]	$\bar{X}$	*SD*[a]
Flint									
All adults	40/21	185.2	97.2[b]	3.4	3.1	24.2	25.9	0.04	0.11[c]
Males	16/7	209.3	102.0[b]	3.4	1.5	27.0	24.1	0.01	0.09
Females	21/14	173.8	91.1[b]	3.5	3.8	20.7	25.1	0.06	0.12[c]
Juveniles	16	151.7	70.4[b]						
Chitty									
All adults	12/8	231.5	131.9	5.7	3.3	25.3	23.4	0.03	0.12
Males	5/4	246.9	131.7	6.3	4.1	22.8	27.9	−0.02	0.05
Females	3/2	236.8	102.0	4.6	0.8	21.0	3.3	−0.07	
Juveniles	4	356.4	167.1						

[a] *SD*s calculated over all pairwise comparisons, as $n(n - 1)/2$, except for the dynamic interactions where the number of comparisons for all adults, males, and females on the Flint and Chitty grids were 168, 17, 74, and 15, 6, 1, respectively.

[b] On the Flint grid, adults were significantly farther apart than juveniles and males were farther apart than females (randomization $P < 0.001$).

[c] Mean *J* for Flint grid adults and adult females was significantly >0 (randomization $P < 0.001$).

Results were similar for the Chitty grid: pairwise relatedness values ranged from −0.59 to 0.50, and the mean pairwise *r* for all 12 individuals was significantly less than 0 (−0.088 ± 0.26, randomization $P = 0.003$; Table 2). The mean *r* for Chitty adults (−0.080 ± 0.27) was not significantly less than 0 (randomization $P = 0.065$), and the distribution of adult *r* values did not differ significantly from the randomly generated distribution ($\chi^2 = 19.3$, *d.f.* = 12, $P = 0.081$). The adult mean, however, fell below the lower 95% confidence limit (−0.015) of the simulated mean. None of the 66 pairwise comparisons among Chitty individuals were classified as statistically significant ($P < 0.05$) full sibling or half sibling relationships.

When only the Flint radiocollared adults were considered, the mean *r* increased to 0.025 (Table 2). This was not statistically greater than 0 (randomization $P = 0.059$); however, it was above the upper confidence limit (0.019) for the mean of the random distribution. The difference can be attributed to higher relatedness among females due to the exclusion of several noncollared females who had very low *r* values. These latter females were trapped only 1–3 times each, and it is possible that they were transients on the grid. Although the mean *r* for radiocollared females was not statistically greater than 0 (randomization $P = 0.058$) or different from the male mean (randomization $P = 0.11$), it suggests that there might have been slightly higher relatedness among resident females.

Spacing behavior.—The average distance between adult activity centers on the Flint grid was 185.2 m (range, 6.5–496.9 m; Table 3). Males were located significantly farther apart than females (randomization $P < 0.001$), and adults were significantly farther apart than juveniles (randomization $P < 0.001$). There was no association between relatedness and distance between activity centers for all adult hares on Flint (Mantel $Z = 299{,}029$, $P = 0.16$; Fig. 1). Similarly, there were no significant correlations for adult males ($Z = 52{,}308$, $P = 0.26$), adult females ($Z = 99{,}782$, $P = 0.29$), or juveniles ($Z = 35{,}865$, $P = 0.33$).

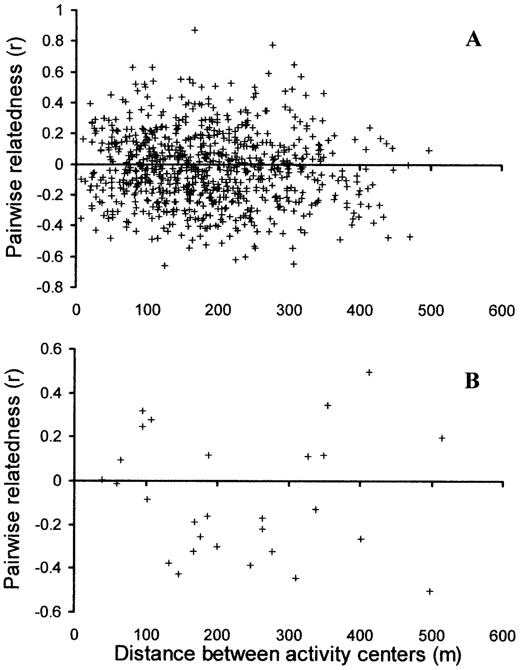

FIG. 1.—Relatedness (r) versus distance between activity centers for all pairs of adult snowshoe hares trapped on A) Flint and B) Chitty grids in Yukon Territory, Canada. There was no correlation between the 2 variables for either grid (Flint: Mantel $Z = 299{,}029$, $r = 0.067$, $P = 0.16$, $n = 40$, 780 pairwise comparisons; Chitty: $Z = 14{,}061$, $r = 0.031$, $P = 0.43$, $n = 8$, 28 pairwise comparisons).

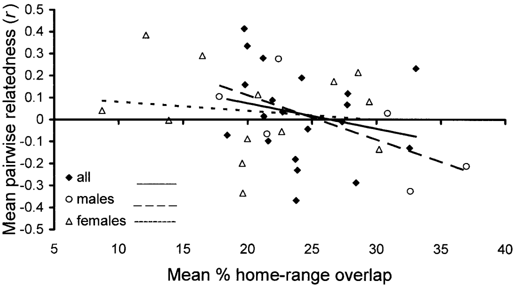

FIG. 2.—Relationship between mean of the ranked pairwise relatedness values (r) and corresponding mean percent home-range overlap for radiocollared snowshoe hares captured on the Flint grid in Yukon Territory, Canada. The variables were not significantly correlated (overall $r^2 = 0.052$, $P = 0.33$, $n = 20$; males $r^2 = 0.49$, $P = 0.12$, $n = 6$; females $r^2 = 0.019$, $P = 0.65$, $n = 13$).

Results were similar for the Chitty grid: the distance between activity centers varied from 30.4 to 568.6 m (Table 3), and the distance between individuals' activity centers was not correlated with their relatedness ($Z = 14{,}061$, $P = 0.43$; Fig. 1).

Hares on both grids showed considerable variation in home-range size and overlap (Table 3). On Flint, the average home-range size was 3.43 ha (range, 1.19–15.83) and did not differ significantly between males and females (Wilcoxon 2-sample test, $z = 0.93$, $P = 0.35$). Most hares overlapped to some extent (82.6% of 420 pairwise comparisons), and the mean degree to which 1 individual's home range was overlapped by each of the others was 24.2% (range, 0.1–99.8%). The overlap among females was not significantly different from that among males (randomization $P = 0.071$; Table 3) but was significantly less than between males and females (mean = 27.6%, $P = 0.010$). On the Chitty grid, the average home-range size for the 6 radiocollared hares was 5.73 ha (range, 3.05–12.11 ha; Table 3), and the mean degree of overlap was 25.3% (range, 0.3–74.7%).

None of the slopes (b) of the individual regressions of relatedness on overlap were significantly different from 0 for hares on either grid ($P > 0.15$; Flint: mean $b = -0.001 \pm 0.002$; Chitty: mean $b = -0.002 \pm 0.012$). Similarly, the regression of the mean ranked relatedness on the corresponding percent overlap over all individuals was nonsignificant (Flint: $r^2 = 0.052$, $P = 0.33$; Fig. 2; Chitty: $r^2 = 0.13$, $P = 0.54$; not shown). Six of the 7 radiocollared Flint males had negative slopes for the individual regressions between males. None of the regressions were statistically significant after Bonferroni correction ($\alpha = 0.05$); however, the mean of the individual slopes (−0.004) was significantly less than 0 (Wilcoxon signed rank = −11.5, $P = 0.031$). The relationship between mean ranked relatedness and overlap was not statistically significant for the males ($r^2 = 0.49$, $P = 0.12$; Fig. 2).

Among the Flint radiocollared females, none of the individual regressions were significant, nor was the mean slope over all regressions (−0.001) significantly different from 0 (Wilcoxon signed rank = −21.5, $P = 0.19$). Regressions of the mean ranked relatedness and overlap values were not significant among these females ($r^2 = 0.019$, $P = 0.65$; Fig. 2) or between Flint males and females ($r^2 = 0.006$, $P = 0.74$). There were also no significant differences between males and females in the slopes of the individual regression lines (Wilcoxon $z = 1.34$, $P = 0.18$).

The mean level of dynamic interaction between all pairs of overlapping hares on the Flint grid was small but significantly greater than 0 (Jacob's index = 0.041 ± 0.11, randomization $P < 0.001$; Table 3). There was no significant difference between males and females in the mean level of interaction (randomization $P = 0.066$), nor was interaction between the sexes (0.031 ± 0.11, $n = 77$ pairs) significantly different from that within the sexes (randomization $P > 0.068$). As with the other measures of spacing, there was no correlation between the degree of interaction among Flint hares and their estimated relatedness ($r^2 = 0.008$, $P = 0.26$). On the Chitty grid, coefficients of interaction (Jacob's index) between overlapping hares ranged from −0.1 to 0.3 with a mean value of 0.031 (Table 3), and there was also no relationship between interaction and relatedness ($r^2 = 0.012$, $P = 0.70$).

DISCUSSION

Our results suggest that interactions between kin do not play an important role in snowshoe hare spacing behavior. There were few closely related hares on either grid, and the overall degree of relatedness among individuals was equal to or less than that expected by chance. The location of an individual hare on a grid did not seem to be affected by the relatedness of neighboring hares. Furthermore, these results were generally not different between males and females or adults and juveniles. There was an indication that resident adult females and juveniles may be more related than adult males; however, the observed differences were slight.

TABLE 4.—Pairwise relatedness (r) values for hares of known relatedness from a concurrent paternity study (Burton 2002), with number of pairwise comparisons (n) and theoretically expected values for each relationship (Blouin et al. 1996; Queller and Goodnight 1989).

		r		
Relationship	n	Expected	$\bar{X}$	SD
Full sibling	39	0.5	0.52	0.17
Half sibling	35	0.25	0.22	0.22
Mother–offspring	65	0.5	0.50	0.16
Unrelated	65	0	−0.02	0.23

A few limitations should be noted with regard to the interpretation of the degree of relatedness among hares in this study. First, it is possible that the spatial scale at which we sampled (7.3-ha grids) was too small to detect clusters of related individuals. Hares show some genetic structuring at larger spatial scales (Burton et al. 2002); however, the degree of structuring is low and appears unlikely to be caused by local kin clusters. Second, we made the assumption that the individual and mean r values are good estimates of the true relatedness between hares. Queller and Goodnight (1989) caution that individual pairwise relatedness estimates may not always reliably represent true pedigree relationships and are best used in aggregate. The considerable variation in relatedness values that we observed on each grid also calls into question the usefulness of group means. To test our assumptions, we examined r values between individuals of known relatedness from a concurrent paternity study (Burton 2002). This analysis illustrates the potential variation in r values but confirms that the means accurately represented the true relationship among group members (Table 4). The conclusions in the current study are based on multiple pairwise comparisons of relatedness and should therefore be robust to variation in *r* values. Data from the paternity analysis also confirm that program KINSHIP is generally reliable at identifying full or half-siblings, although occasionally both type I and type II errors were made (i.e., classifying unrelated individuals as siblings or vice versa). It is thus possible that the number of siblings is slightly misestimated in this study. However, the general conclusions based on these estimates are valid.

Our finding of low group relatedness is consistent with previous observations of high juvenile dispersal (Gillis and Krebs 1999) coupled with low survival in snowshoe hares of both sexes (Gillis 1998; Krebs et al. 1995; O'Donoghue 1994). It is also consistent with the patterns of mating structure observed in our concurrent study (Burton 2002): multiple paternity and widespread reproductive success among males likely decrease the chances that neighboring juveniles will be closely related. Previous observations of limited parental care and short-term associations among littermates (Graf and Sinclair 1987; O'Donoghue and Bergman 1992) corroborate the suggestion that social relationships among kin are not important in hares.

Although our results suggest that some individuals on the grids were related, the degree of relatedness did not explain the considerable variation in spacing behavior among hares. The fact that most of the radiocollared hares on both grids had overlapping home ranges confirms previous results (Boutin 1979) and is consistent with the idea that there is considerable potential for social interactions among hares (Graf 1985). Nevertheless, the average amount of overlap was low, as was the mean level of dynamic interaction. Measures of the latter (Jacob's index) indicated that most interactions were weak but that in general hares of both sexes were more likely to associate (positive interaction) than to avoid each other (negative interaction). This pattern contrasts with Boutin's (1980) observation that during an increase phase of the population cycle, females used their home ranges in such a manner as to reduce interaction. Further investigation is needed to test for other possible mechanisms underlying the observed variation in snowshoe hare social interactions and spacing behavior.

The lack of strong differences in kin structure between males and females confirms that snowshoe hares are unusual among mammals in not exhibiting sex-biased dispersal (typically male) or philopatry (typically female—Greenwood 1980). We found weak evidence that male hares may avoid other related males. This is not consistent with inbreeding avoidance because there was no similar negative correlation of relatedness and spacing between males and females. It is, however, consistent with the idea of kin competition. Males on a grid would be competing for access to neighboring females, and less competition among related males should be favored. The effect may be weak because the overall relatedness among males was low. Furthermore, the results from our concurrent study (Burton 2002) suggest that there is a relatively low variance in male reproductive success, thus limiting the severity of competition.

The failure to detect kin structuring for either sex in snowshoe hares contrasts with recent findings in other small mammal species. Clusters of related females have been reported in voles (Ishibashi et al. 1997), rabbits (Surridge et al. 1999), and ground squirrels (van Staaden et al. 1996), and male kin clusters have been detected in shrews (Balloux et al. 1998). It is possible that in hares, selective benefits of kin association are outweighed by the costs of competition among kin or overwhelmed by selective pressures on individuals to avoid predation (i.e., predation risk determines spacing). Low survival and the lack of territoriality in hares may weaken any benefits of strategies that increase kin association or decrease the risk of inbreeding (such as female philopatry and male-biased dispersal). Regardless of underlying reasons, lack of kin clustering is consistent with the belief that spacing behavior is relatively unimportant in snowshoe hare population regulation (Krebs 1996).

It is important to consider how spacing among kin might be affected by changes in density, predation, and food associated with the snowshoe hare population cycle. For example, in their hypothesis to explain the dynamics of vole cycles, Charnov and Finerty (1980) predict low relatedness during the high-density peak phase of the cycle and high relatedness during the low phase. The low relatedness observed among snowshoe hares during this peak phase is consistent with this prediction; however, the lack of any significant correlation between relatedness and spacing suggests that it is unlikely that kin interactions play a role during any phase of the hare cycle. Furthermore, the density on the Flint grid was approximately 5 times that on the Chitty grid, yet there were no significant differences in the kin-spacing results for the 2 grids (although the small sample on Chitty might limit the generality of such comparisons). There was some indication that the mean relatedness and proportion of putative siblings was lower on the Chitty grid, implying that relatedness might increase with density. This is contrary to the Charnov and Finerty (1980) prediction but consistent with those made by Lambin and Krebs (1991) for cycles in microtines. The average home-range size and distance between hares were significantly larger on the Chitty grid, suggesting that density may have an effect on hare spacing behavior. Temporal and manipulative investigation into the effects of changes in density on relatedness and spacing in hares would be useful to expand on these results.

Sinclair (1986) and Ferron (1993) suggest that spacing behavior may be important in hare regulation only when food is limiting. It is possible that food was not limiting on either grid during this study and that social interactions were therefore of low importance. However, if food shortage is ever an important factor in snowshoe hare cycles, it is most likely to be during the peak phase (Hodges 2000; Keith 1990) and would thus have been most pronounced during this study. Predation risk should also be high during this phase (Hik 1995), and associated predator-sensitive behavior may be much more important than social spacing behavior. The latter may be important only when predation risk is reduced, such as during the low phase (Hodges et al. 1999). We do not have any quantitative data on food availability or predation risk for the sampling grids used in this study. However, our qualitative observations suggest that food and cover were more plentiful on Flint than on Chitty, which is consistent with the lower hare density on Chitty. If these observations correspond to actual differences in food and predation experienced by the hares, then our results suggest that these factors did not affect patterns of kin interaction. It would be desirable to repeat this study during different phases of the hare cycle and under different manipulations of food and predation to confirm these speculations. Similarly, a direct experimental test of behavior between related and unrelated hares would be important to confirm the suggestion that degree of relatedness does not affect hare interactions.

In summary, relatedness is not a good predictor of spacing behavior for either male or female snowshoe hares during the peak phase of the population cycle. In general, there is low relatedness among hares in a group, and related individuals associate more or less randomly. This is in contrast to other small mammals, such as voles and rabbits, in which clusters of related individuals have been detected, and lends further support to the belief that spacing behavior is relatively unimportant in regulation of snowshoe hare populations.

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