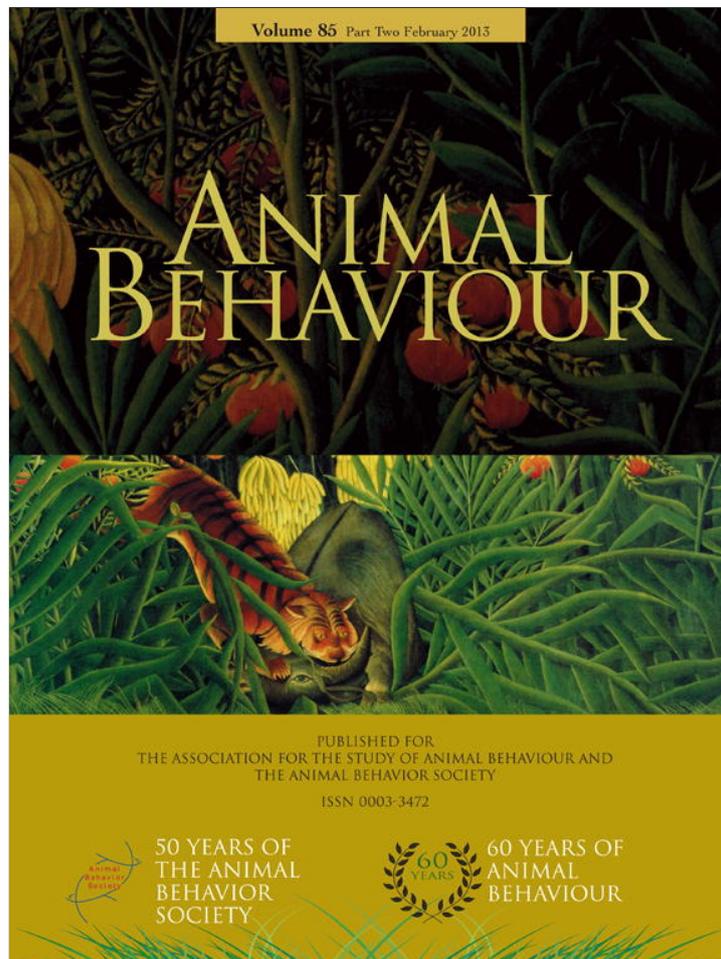


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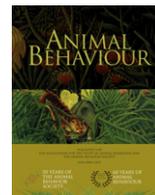
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Genetic relatedness does not predict racoon social network structure

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Social assortativity, preferentially associating with certain individuals, is a widespread behaviour among a diverse range of taxa. Animals often choose to associate with other individuals based on characteristics such as sex, age, body size, rank and genetic relatedness. These preferences can scale up to shape the overall social structure of an animal group or population. We investigated possible factors that might shape the social network structure of common racoons, *Procyon lotor*, in a high-density urban population in Cook County, Illinois, U.S.A. Racoon associations were recorded using proximity detecting radiocollars that recorded when individuals came within 1–1.5 m of each other. In addition, dyadic measures of home range overlap and genetic relatedness were calculated for all individuals included in our study. We used multiple regression quadratic assignment procedures to determine what factors influenced the structure of racoon association networks. The only variable that positively influenced racoon social structure was male–male homophily, which is consistent with previous studies that documented frequent social interactions between adult male racoons. Genetic relatedness had no effect on racoon social networks and there was no evidence that males or females preferentially associated with close relatives, despite the presence of kin in the population. This pattern, that kinship does not play a significant role in shaping social structure, is strikingly unusual among mammals and is not consistent with many socioecological models. Although racoon individuals showed strong social partner preferences, it is unclear what factors drove these choices. This unpredictability in partner choice shaped the structure of the racoon social networks and has important implications for disease transfer in this widespread animal vector.

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Accurately quantifying social structure and understanding the mechanisms that shape differences between animal societies is crucial for addressing many key questions in behavioural ecology, animal conservation and wildlife disease epidemiology. An individual's choice of social partners can greatly influence patterns of mating, coalition formation, predation risk and foraging success (Janson 1990; Krakauer 2005; Croft et al. 2006; Ohtsuki et al. 2006; Ryder et al. 2009). Social interactions also affect information and disease transmission between individuals (Altizer et al. 2003; Lusseau 2003). When animals choose to interact with particular individuals, these preferences can scale up to shape the overall social structure of the population or species (Krause et al. 2007). However, these social interactions rarely occur in isolation, and the behaviour of an individual is greatly influenced by its social and

physical environment (Sterck et al. 1997; Krause et al. 2009). To understand interactions between any two animals, it is necessary to consider the structure of the social network in which these interactions occur (Croft et al. 2005). Behavioural ecologists are increasingly using social network analyses to address these questions because these methods allow for the quantification of multiactor interactions, which provides a more realistic depiction of animal societies than traditional dyadic measures (Wey et al. 2007; Sih et al. 2009; Croft et al. 2011; Sueur et al. 2012).

There are many factors that can influence the conspecifics with which an animal associates. One common pattern is the tendency for individuals to interact with similar individuals; a phenomenon termed 'homophily' (McPherson et al. 2001). Individuals of similar age, sex, body size or social status have been observed to associate with each other in a wide diversity of organisms (Pitcher et al. 1986; Janson 1990; Krause et al. 2000; Croft et al. 2005; Ruckstuhl 2007; Hirsch 2011). Even temporary physiological conditions can lead to homophily when hungry individuals preferentially associate with each other (Romey & Galbraith 2008). One of the most important variables that influences associative behaviour in animal species is

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genetic relatedness. In many animal societies, individuals preferentially associate with kin, direct affiliative behaviours towards close relatives and support close kin during agonistic interactions (Silk 2002). This support can result in numerous fitness benefits, such as increased food intake rates, longevity and reproductive success (Janson 1985; van Noordwijk & van Schaik 1999; Sapolsky 2005; Silk et al. 2010). Although the occurrence of kinship-based affiliative behaviour is commonly recorded in group-living and fission–fusion species, other species with less frequent social interactions may prefer to associate with kin as well.

The racoon, *Procyon lotor*, is an ideal species for testing hypotheses related to social structure formation. Racoons are geographically widespread and abundant in many habitat types ranging from relatively pristine forests to heavily urbanized areas (Anthony et al. 1990; Gehrt 2003). Although some studies have measured racoon social patterns, relatively little is known about racoon social interactions compared to diurnal mammals that are easier to observe. Because racoons live in such a wide diversity of habitats and local population density varies widely, racoons are a great study species with which to test socioecological theories relating ecology to social structure. In addition, racoons are common vectors of diseases that affect humans, thus quantifying and understanding the social patterns in this species has important implications for public health.

Racoons have often been considered a relatively solitary species (Ewer 1973; Barash 1974; Kaufmann 1982; Sandell 1989), yet several studies have reported varying degrees of racoon sociality (Gehrt & Fritzell 1998a; Chamberlain & Leopold 2002; Gehrt & Fox 2004; Pitt et al. 2008; Prange et al. 2011; Robert et al. 2012). Most studies have reported that adult females generally associate with their offspring and not with other adults, whereas adult males share dens and travel with other adult males for extended periods (Gehrt & Fritzell 1998a; Chamberlain & Leopold 2002; Gehrt & Fox 2004; Pitt et al. 2008). In some cases these male associates have exclusive territories that are defended from other adult males (Pitt et al. 2008). This variation in racoon sociality appears to be related to population density, with solitary males commonly exhibiting exclusive home ranges in low density populations (e.g. Gehrt & Fritzell 1997) and frequent male–male associations in medium- to high-density populations. If male racoons compete over resources such as feeding sites, dens or access to females, one could predict that associating and cooperating with close kin would result in increased fitness. Alternately, because racoons are commonly reported as exhibiting male-biased dispersal, male racoons may not have the opportunity to associate or form coalitions with kin (Urban 1970; Fritzell 1978; Clark et al. 1989; Gehrt & Fritzell 1998b). Although racoons are a relatively well-studied species, few studies have used molecular techniques to investigate racoon sociality, and it is unclear whether kinship affects male sociality (Ratnayeke et al. 2002; Gehrt et al. 2008). One recent study that used genetic analyses to investigate racoon parentage found that males that were more social did not sire a large percentage of offspring; thus, males probably do not cooperate or associate to gain access to females (Hauver et al. 2010).

Most studies of racoon sociality have used radiotelemetry to document spatial associations between individuals, which were then used as a proxy for social interactions. When racoons are actively moving through the environment, it is difficult to determine whether two racoons located near each other are actually interacting with each other. Two studies (Gehrt & Fritzell 1998a; Pitt et al. 2008) addressed this issue using dynamic interaction tests on simultaneous radiotelemetry fixes of multiple racoons (Doncaster 1990). In addition, Gehrt & Fritzell (1998a) reported numerous visual sightings of racoons travelling together. Although these techniques led to a better resolution of racoon social patterns,

some social interactions probably remained undetected. Quick or infrequent associations between individuals that do not coordinate travel are difficult to detect using radiotelemetry data. To precisely determine the number and duration of all associations between adult racoons, Prange et al. (2006, 2011) used proximity detecting collar technology that recorded when racoons came within 1–1.5 m of each other. While the exact nature of each association cannot be determined through contact data, individuals that spend a considerable time in close proximity are probably coordinating behaviours or, at a minimum, show a large degree of social tolerance towards each other. Prange et al. (2011) found that adult males associated with each other significantly more often than females, and these association rates increased during the winter.

In this study, we extend the work of Prange et al. (2011) to test hypotheses related to the formation and maintenance of sociality in racoons. We used proximity collar data to construct the first racoon social network ever reported and then used social network analyses to test whether these association networks were influenced by sex, age or genetic relatedness. Measures of spatial overlap and genetic relatedness in this population were previously calculated by Hauver et al. (2010). Through this combination of genetic, behavioural, demographic and spatial data, we are able to more precisely determine what factors influence the structure of racoon social networks, which in turn can shed light on the evolution of social behaviour and structure in this common mammal species.

METHODS

Study Area

Fieldwork was conducted in a 20 ha area within the 1499 ha Ned Brown Forest Preserve in suburban Cook County, IL, U.S.A. (for further details, see Prange et al. 2003). The size of the study area was determined by the local density of racoons, as it was important to monitor all, or nearly all, resident racoons (Prange et al. 2011). The high densities of racoons found at this site (40–70 racoons/km²) were likely due to an abundance of artificial food sources available from garbage cans (Prange et al. 2003, 2004). From May 2004 to December 2005, racoons were trapped in box traps (Model 108, Tomahawk Live Trap Co., Tomahawk, WI, U.S.A.), immobilized with an injection of Telazol (as in Gehrt et al. 2001), weighed, sexed and individually tagged. Traps were checked twice per day, and food inside the traps was available to the racoons. Trapping and handling of racoons conformed to ASAB/ABS guidelines and The Ohio State University Animal Care and Use protocols (IACUC no. 2003R0062). Racoons were aged according to tooth wear (Grau et al. 1970). All racoons older than 12 months of age were fitted with proximity logging radiocollars (SirTrack Ltd, Havelock North, New Zealand), which recorded the identity of the contacted collar and the length of contact when two radiotracked racoons were within 1–1.5 m proximity (for details see Prange et al. 2006). In accordance with standard wildlife handling practices (Amlaner & MacDonald 1980), the 125 g collars were below 5% of the body weight of all collared racoons in this study. We condensed age classes for use in the social network analyses: collared adults racoons were either classified as young adults (12–38 months) or old adults (≥ 39 months) following Prange et al. (2011). We collared 42 adults (20 males and 22 females), and these individuals represented close to 100% of all adult racoons living in the core area (Prange et al. 2011). Racoons in this population were retrapped repeatedly to replace malfunctioning collars and to maintain a high population of marked individuals in the population. Radiocollars from animals that were retrapped at the end of the study were removed.

Home Range

Raccoon space use was calculated using traditional wildlife telemetry techniques. Raccoon locations were obtained by triangulation of at least two bearings from a truck-mounted three-element antenna. Telemetry error, the average \pm SD distance between the estimated and true location, was 25.5 ± 30.2 m for 300 bearings from 10 test collars (Hauver 2008). Each raccoon was located at least once per week from April through November, and a telemetry fix was recorded. To conform to assumptions of statistical independence, samples from the same individual (up to six per night) were always recorded at least 1 h apart and were not recorded if the raccoon became inactive during the night (Gehrt & Fritzell 1997). If raccoons were opportunistically sighted, their location was recorded using a hand-held GPS receiver (Garmin Automotive III). We used a minimum of 30 locations as the criterion for home range estimation. Based on simulated home ranges varying from simple to complex shapes created by mixing bivariate normal distributions, 30 is the minimum number of locations needed to minimize bias and variance in fixed kernel home range estimates (Seaman et al. 1999). Home range overlap indices based on radiotracking locations were constructed for each season except winter, when raccoons are less active and thus difficult to observe outside of their dens. In this study population, raccoon home ranges are relatively stable over time and across seasons (Prange et al. 2004), thus the winter home range overlap was based on observed home range overlap recorded during either autumn (used for December–January) or spring (used for February–March). We calculated 95% fixed kernel utilization distributions using the animal movement extension (Hooge & Eichenlaub 1997) in ArcView 3.3 (Environmental Systems Research Institute, Inc., Redlands, CA, U.S.A.). These contours were chosen because they are commonly used to define raccoon home ranges and core use areas (Beasley et al. 2007; Barding & Nelson 2008; Rosatte et al. 2010). We used Neil's Ute extension to calculate indices of overlap (Walls & Kenward 2001) for all dyads, where the coefficient of overlap was equal to $2(\text{overlap area}_{1,2})/(\text{area}_1 + \text{area}_2)$.

Genetics

We collected at least 0.1 ml of blood from all adults included in this study. DNA was extracted using standard phenol–chloroform techniques (Sambrook et al. 1989). Each individual was genotyped at 15 highly variable microsatellite loci with an average of 12.8 alleles per loci (range 4–24; Hauver et al. 2010). Further details of reaction volume and primer optimization are detailed in Hauver et al. (2010). Polymerase chain reaction products were screened using a Beckman-Coulter CEQ 8000XL automated capillary genotyping system (Beckman-Coulter, Inc.), and allele sizes were determined using Genetic Analysis System Software, v.8.0 (Beckman-Coulter, Inc.). Individual genotypes were based on allele fragment sizes estimated by running a known-size standard (400 kb ladder; Promega Corp.) with each sample. The number of alleles and allele frequencies for each locus were calculated using the Microsatellite toolkit (Park 2001). We used the program MICRO-CHECKER to screen data for evidence of scoring errors, allelic drop out and null alleles (Van Oosterhout et al. 2004). Linkage disequilibrium and deviations from Hardy–Weinberg equilibrium were assessed using GENEPOP v.3.4 (Raymond & Rousset 1995), and we found no evidence of linkage disequilibrium (Hauver et al. 2010). Coefficients of relatedness (r) were calculated using a log-likelihood ratio generated with the program Kinship v.1.2 (Queller & Goodnight 1999). We then used these r values to construct matrices of genetic relatedness between pairs of raccoons.

Statistical Methods

We analysed data from 30 raccoons (11 male, 19 female) in our study population, and the monthly social network matrices were composed of an average of 16.2 individuals per month (range 10–24). The number of raccoons with contact data decreased over time because animals died ($N = 4$) or proximity collars expired. Because individuals with working proximity collars entered and exited our study over time, creating social networks over long time periods (3 months or more) was problematic. We instead partitioned the association data into 1-month increments, which allowed us to maximize the number of individuals included in the analyses and to compare social patterns during the mating season (December–March) with months when mating did not occur. Any individuals without a functioning radiocollar or that were dead for at least 10 days during a particular month were censored from the monthly association matrix. Association matrices were constructed using the total amount of time that two individuals spent in close proximity (1–1.5 m) during that month (divided by the total number of days in the month). Monthly matrices of home range overlap, genetic relatedness, age homophily (young adults versus older adults), and male and female homophily were constructed using the same individuals present in the association matrices. For the homophily matrices, similar dyads received a value of 1 and dissimilar dyads received a value of 0.

We used multiple regression quadratic assignment procedures (MRQAP) with the double dekker semipartialing permutation method to determine what factors influenced the structure of the raccoon association networks (Dekker et al. 2007). The MRQAP is an extension of the Mantel test that allows for a dependent matrix to be regressed against multiple independent matrices. MRQAP regressions were run in UCINET v.6.3. For each month, we entered matrices of genetic relatedness, home range overlap, male and female homophily, and age homophily as independent variables with the association matrix as the dependent variable. Because we repeated statistical tests on the same population, we present Bonferroni corrections for P values. Because the factors that drive sociality may differ by sex, we also repeated all MRQAP analyses using sex-segregated networks. For example, if males preferentially associate with relatives but females do not, we would expect that genetic relatedness would only be a significant variable in the male-specific analyses.

Although raccoons in our study area had home ranges that overlapped with several other individuals, not all individuals in the population had overlapping home ranges. For this reason, it would not have been possible for some raccoons to interact with every other individual in the population without leaving their home range. To correct for this potential complication, we entered monthly matrices of home range overlap into the MRQAP regressions (cf. Mann et al. 2012). Although we expected that the home range overlap variable would be highly correlated with the association matrixes (as in Robert et al. 2012), this does not have to be the case. Even if two raccoons have a high degree of home range overlap, they still might not interact with each other. By entering the home range overlap variable into the MRQAP regressions, we were better able to determine what factors drive individuals to have social interactions (Mann et al. 2012).

Social network metrics were calculated for all individuals in our networks. In particular, we calculated two measures of network centrality: normalized degree and betweenness. Average normalized degree was calculated by dividing the number of conspecifics that an individual associated with during the month by the network size minus one. This measure provides a relative measure of social network size for individuals (0 = no associates, 1 = associations recorded with every individual in the network).

Normalized Freeman node betweenness values were calculated using UCINET v.6.3. Betweenness is a measure of where an individual is located within the social network. If an individual is frequently part of the shortest path linking two other individuals, this individual will have high betweenness values. All monthly normalized degree and betweenness values were averaged by individual. Individuals that were present in the social networks for less than 5 months ($N = 5$ females) were removed from the centrality measure comparisons (average number of months per individual = 11.5, range 5–18). Generalized linear models were run in STATISTICA v.6.1 with sex, age and home range overlap as independent variables, and normalized degree, betweenness and total time spent in association with conspecifics entered as dependent variables.

RESULTS

Racoons spent an average \pm SD of 96.58 ± 159.77 min per day in close proximity to other racoons (range 0–936 min). The average \pm SD pairwise home range overlap between racoons in our social networks was $23 \pm 21.01\%$ (range 0–80%), and racoon home ranges in our study area ranged from 25.2 to 52.8 ha (Prange et al. 2004). The average \pm SD pairwise genetic relatedness between racoons was 0.011 ± 0.134 , and 16% of dyads were closely related ($r > 0.125$). Average pairwise relatedness did not differ significantly with age class categories (female–female: $r = 0.015 \pm 0.143$; female–male: $r = 0.010 \pm 0.129$; male–male: $r = 0.009 \pm 0.129$; all pairwise t tests: $P > 0.69$).

There were no significant correlations between home range overlap and genetic relatedness (Pearson correlations: all P values > 0.05). No significant differences between the sexes were found in the relationship between home range overlap and genetic relatedness (average slope value; females = -0.001 , males = -0.017 ; paired t test: $t_{18} = 0.25$, $P = 0.807$). Genetic relatedness was never a significant predictor of racoon association structure in the monthly MRQAP regressions (all P values > 0.05). Similar results were found in the sex-specific analyses (Table 1), and any statistically significant relationship between genetic relatedness and association was negative (i.e. closely related individuals were less likely to associate with each other than non-related individuals). Age homophily was also not a good predictor of racoon association network structure for the entire population (17 out of 18 P values > 0.05 , all P values > 0.0028) and for sex specific networks (all 36 P values > 0.0028). Home range overlap was frequently a significant predictor variable that shaped association network structure (Table 1). Male homophily was a significant predictor of network structure during some months ($P < 0.0028$ during 5 out of 18 months). All months with significant P values ($P < 0.0028$) occurred outside the mating season, and the average effect of male–male homophily on the racoon association networks was greater outside the mating season than during the mating season (average standardized effect: mating season = 0.046 , non-mating season = 0.257 ; ANOVA: $F_{1,17} = 23.44$, $P < 0.001$). This is consistent with the pattern that males associate with females more frequently during the mating season (Fig. 1a, b).

No significant differences in network centrality measures were found between males and females (Table 2). While males had greater normalized degree (mean \pm SD: females = 0.419 ± 0.113 , males = 0.479 ± 0.152) and betweenness values (mean \pm SD: females = 3.13 ± 2.41 , males = 4.30 ± 3.01), these differences were not significant in univariate ANOVA or multivariate GLM models with age and home range overlap entered as covariates (all P values > 0.26). Males differed from females in the average \pm SD amount of time spent with conspecifics per day (females = 52.7 ± 56.1 min, males = 156.7 ± 88.3). Home range overlap

Table 1

Results from the monthly MRQAP analyses relating racoon social network structure to four independent variables: male–male homophily, age (young versus old), home range overlap and genetic relatedness

Month	Total network		Female network		Male network	
	Slope	<i>P</i>	Slope	<i>P</i>	Slope	<i>P</i>
Jul 2004 N=24						
Male–Male	0.1711	0.0060				
Female–Female	0.0330	0.3473				
Age	0.0187	0.4603	–0.1201	0.0530	0.1402	0.1974
Home range overlap	0.2083	0.0005*	0.2622	0.0085	0.4702	0.0030
Relatedness	–0.0666	0.0975	–0.0100	0.4918	–0.1429	0.1979
Aug 2004 N=22						
Male–Male	0.2148	0.0005*				
Female–Female	0.0269	0.3428				
Age	0.0587	0.2154	–0.1253	0.1184	0.2294	0.0330
Home range overlap	0.2376	0.0005*	0.3635	0.0030	0.5200	0.0005*
Relatedness	–0.0482	0.2119	0.0258	0.3408	–0.1014	0.2234
Sep 2004 N=19						
Male–Male	0.2118	0.0030				
Female–Female	–0.0055	0.5217				
Age	0.0273	0.4238	0.1522	0.1629	0.1134	0.1499
Home range overlap	0.2204	0.0010*	0.3285	0.0150	0.4267	0.0110
Relatedness	–0.0574	0.1994	–0.1747	0.0755	–0.1622	0.1559
Oct 2004 N=18						
Male–Male	0.2719	0.0015*				
Female–Female	–0.0001	0.5142				
Age	0.0876	0.1449	0.2227	0.1199	0.2089	0.0870
Home range overlap	0.2503	0.0005*	0.3177	0.0425	0.4652	0.0055
Relatedness	–0.0541	0.2349	–0.1440	0.1409	–0.1278	0.1944
Nov 2004 N=19						
Male–Male	0.2033	0.0075				
Female–Female	–0.0084	0.4943				
Age	0.1105	0.0385	0.1834	0.1429	0.2089	0.0830
Home range overlap	0.2471	0.0005*	0.3274	0.0200	0.4652	0.0070
Relatedness	–0.0475	0.1969	–0.1084	0.1654	–0.1278	0.1944
Dec 2004 N=15						
Male–Male	0.0669	0.2134				
Female–Female	–0.1053	0.1329				
Age	–0.1175	0.0855	0.1025	0.2614	–0.1268	0.2509
Home range overlap	0.2069	0.0150	0.4939	0.0035	0.2690	0.1014
Relatedness	0.0106	0.3973	–0.1393	0.1954	0.0120	0.4608
Jan 2005 N=15						
Male–Male	0.1472	0.1010				
Female–Female	0.0450	0.3298				
Age	0.1163	0.1319	0.1704	0.2854	0.2751	0.1304
Home range overlap	0.2293	0.0225	0.2118	0.1839	0.2272	0.2074
Relatedness	–0.0159	0.4718	–0.0297	0.4433	–0.0235	0.4733
Feb 2005 N=13						
Male–Male	0.1743	0.0690				
Female–Female	–0.1523	0.0955				
Age	0.0352	0.3633	0.2402	0.1264	–0.1310	0.3138
Home range overlap	0.2929	0.0075	0.1001	0.2769	0.1561	0.4443
Relatedness	–0.0356	0.3663	–0.0842	0.3343	–0.2679	0.2549
Mar 2005 N=15						
Male–Male	–0.0734	0.2874				
Female–Female	0.0924	0.1674				
Age	0.0702	0.2699	0.1655	0.2114	0.3563	0.1419
Home range overlap	0.1049	0.1414	0.0445	0.2479	0.4404	0.0235
Relatedness	–0.0890	0.1569	–0.0830	0.3173	0.2033	0.1329
Apr 2005 N=18						
Male–Male	0.2726	0.0080				
Female–Female	0.0595	0.2349				
Age	–0.0177	0.3953	–0.1218	0.3323	–0.0523	0.2349
Home range overlap	0.3466	0.0005*	0.0593	0.1964	0.6809	0.0070
Relatedness	0.0539	0.2174	–0.0580	0.3698	0.1081	0.2509
May 2005 N=17						
Male–Male	0.1664	0.1040				
Female–Female	0.0351	0.3698				
Age	–0.0721	0.3024	0.2234	0.0855	–0.2877	0.0165
Home range overlap	0.2222	0.0135	0.2225	0.0805	0.5740	0.0070
Relatedness	–0.0225	0.4358	–0.0483	0.3958	–0.0320	0.4408
Jun 2005 N=16						
Male–Male	0.3149	0.0005*				
Female–Female	0.0310	0.3348				
Age	0.0096	0.4433	–0.0177	0.4448	–0.0881	0.3763
Home range overlap	0.3452	0.0005*	0.5911	0.0030	0.7504	0.0030

Table 1 (continued)

Month	Total network		Female network		Male network	
	Slope	P	Slope	P	Slope	P
Relatedness	-0.0344	0.3623	-0.2042	0.0780	0.0157	0.4418
Jul 2005 N=15						
Male–Male	0.3265	0.0015*				
Female–Female	0.0260	0.3758				
Age	-0.0380	0.3468	0.2122	0.0400	-0.1563	0.0480
Home range overlap	0.3392	0.0005*	0.6930	0.0005*	0.9004	0.0070
Relatedness	-0.0182	0.4378	-0.3062	0.0020*	-0.1375	0.1629
Aug 2005 N=16						
Male–Male	0.2555	0.0035				
Female–Female	0.1408	0.0490				
Age	0.0731	0.2049	0.1169	0.3193	-0.0888	0.1294
Home range overlap	0.4292	0.0005*	0.3765	0.0220	0.9317	0.0005*
Relatedness	-0.0959	0.0815	-0.1623	0.1329	-0.0433	0.2974
Sep 2005 N=15						
Male–Male	0.2402	0.0115				
Female–Female	0.0698	0.2509				
Age	0.1051	0.1629	0.1864	0.1759	0.2391	0.0190
Home range overlap	0.3293	0.0005*	0.3246	0.0190	0.8803	0.0145
Relatedness	-0.0984	0.1304	-0.1328	0.1629	-0.1571	0.1154
Oct 2005 N=13						
Male–Male	0.3918	0.0005*				
Female–Female	-0.0869	0.1584				
Age	0.1150	0.1664	-0.1574	0.2619	0.2263	0.0820
Home range overlap	0.4095	0.0005*	0.3932	0.0500	0.8427	0.0025*
Relatedness	-0.1322	0.0710	-0.0776	0.4043	-0.1930	0.0315
Nov 2005 N=12						
Male–Male	0.2962	0.0140				
Female–Female	-0.0662	0.2914				
Age	0.1058	0.2724	0.1885	0.1079	0.1593	0.4188
Home range overlap	0.3220	0.0125	0.6825	0.0055	0.5781	0.0515
Relatedness	-0.0701	0.2844	-0.2840	0.0705	-0.0879	0.3593
Dec 2005 N=10						
Male–Male	-0.0841	0.3258				
Female–Female	0.0925	0.2464				
Age	0.1611	0.1894	0.0534	0.2899	1.2534	0.1779
Home range overlap	-0.0932	0.2874	0.6825	0.0155	0.8321	0.2109
Relatedness	0.0355	0.3363	0.0719	0.4448	-0.9746	0.1334

Network types analysed: total network (all available individuals) and sex-specific networks (female and male). Slope values represent the strength and direction of the effect. Bold values are significant to $P < 0.05$, and values that were significant after Bonferroni corrections are indicated by an asterisk.

was positively correlated with both network centrality measures (degree: $R^2 = 0.674$, $F_{1,14} = 47.45$, $P < 0.001$; betweenness: $R^2 = 0.452$, $F_{1,14} = 18.97$, $P < 0.001$).

DISCUSSION

In general, very few of the factors that we measured affected the structure of racoon social networks. We found that racoon social network structure was not influenced by genetic relatedness or age. During some months outside the mating season, male–male homophily was a significant predictor of racoon network structure. Neither age nor genetic relatedness was a significant predictor variable shaping these male–male interactions. This result is consistent with Gehrt et al. (2008), who found that male–male associations frequently occurred between nonrelated individuals. During the mating season, males and females interacted with each other more frequently, and these increased association patterns were presumably driven by reproduction. We also found that adult females frequently interacted with other females and associated with similar numbers of conspecifics as males (as measured by normalized degree). These female associative behaviours remain undocumented in most racoon populations (but see Robert et al. 2012). Female–female associations were also not influenced by age or genetic relatedness. These results leave two major questions unresolved: (1) why do racoons associate with each other, and (2) why are racoons not associating with kin?

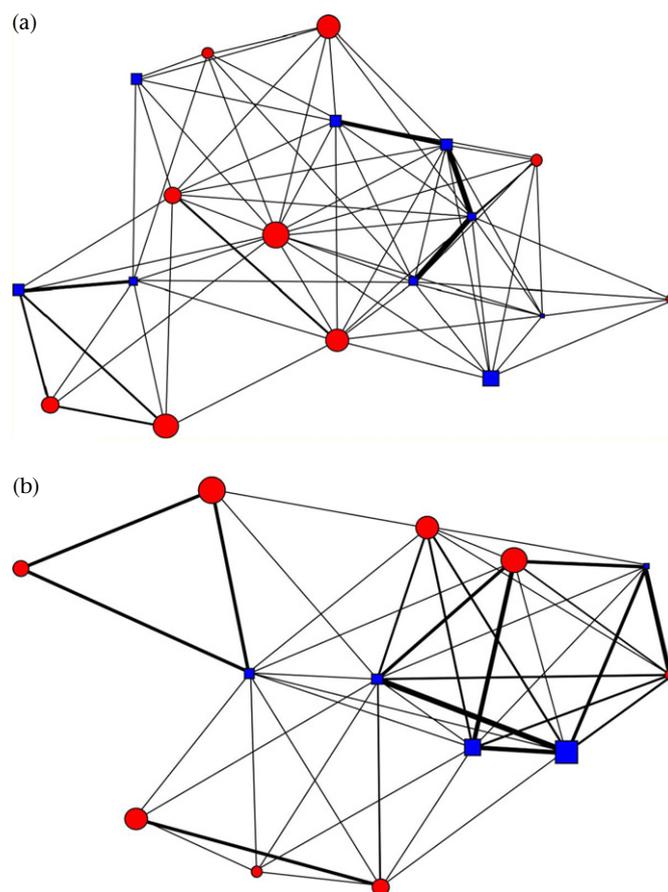


Figure 1. Social network diagram of association rates between individual racoons in (a) October 2004 and (b) February 2005. Red circles: females; blue squares: males. Node size scales to age, with the largest circle/square indicating the oldest racoons. Lines between individuals scale to contact rates, with the thickest lines indicating more time spent in proximity. Note that strong male–male associations were common in October, while several strong male–female associations were present during the February mating season.

Previous studies have documented racoons resting together in the same dens (Gehrt et al. 1990; Enders & Smith 1993; Gehrt & Fritzell 1998a). Den sharing most commonly occurs between adult females and their offspring, or between pairs of adult males.

Table 2

Generalized linear models testing the effect of sex, age and home range overlap on two network statistics (normalized degree and normalized betweenness) and the amount of time spent associating with other racoons per month

Variable	Wald	Df	P
Normalized degree			
Sex	1.533	1	0.216
Age	0.001	1	0.974
Home range overlap	41.024	1	<0.001
Normalized betweenness			
Sex	2.888	1	0.089
Age	0.759	1	0.384
Home range overlap	14.621	1	<0.001
Association time			
Sex	10.375	1	0.001
Age	0.086	1	0.769
Home range overlap	5.343		0.021

Individuals that had home ranges near the centre of the study area had higher network centrality measures, even if they spent little time with others. Males spent more time with other racoons, but were not necessarily central in the social network.

These denning behaviours could explain some of the association patterns found in our study population. For example, the amount of time spent in close proximity increased during cold winter months when racoons were less active (Prange et al. 2011). This would increase the amount of time adult males spent in close proximity to other males, while adult females would be in close proximity to their noncollared offspring. Interestingly, the relatively large amount of time that adult males spent together did not translate into significantly greater centrality or degree network measures in males.

Although we predict that den sharing plays a role in shaping the affiliative social networks of racoons, adult racoons also associate with others during travelling and foraging. For example, Gehrt & Fritzell (1998a) found that pairs of adult males travelled together more frequently than adult females, and the few occasions of adult female associations were between close relatives (Gehrt & Fritzell 1998b). Several authors have also observed racoons travelling or feeding together at concentrated food resources (Gehrt & Fritzell 1998a; Totton et al. 2002; Bozek et al. 2007). This behaviour may be particularly common in areas where racoons have access to concentrated anthropogenic food sources (Prange et al. 2004; Hauver 2008). In the Ned Brown Forest Reserve, access to these food sources is highly seasonal, and racoons commonly lose weight during the winter (Prange et al. 2003). Cameras placed at anthropogenic food sources in our study area indicated that racoons arrived at the food site with at least one other individual during 18.6% of all visits (total $N = 2943$; S. Hauver, B. T. Hirsch, S. Prange, J. Dubach & S. D. Gehrt, unpublished data). This pattern leads us to conclude that racoons in our study population travel and forage with conspecifics, and that these associations were not solely the result of den sharing. In future studies, this issue could be more thoroughly addressed through the use of collar-mounted accelerometer sensors, which can be used to distinguish resting from other activities (Wilson et al. 2008; Halsey et al. 2009; Brown et al. 2012). Additionally, data from accelerometer sensors and remote cameras could yield additional insights into the nature of these racoon associations. While we have used spatial proximity as a proxy for social affiliation, it is currently unclear how many of these associations were affiliative versus antagonistic interactions. To fully understand racoon social behaviour, it would be ideal to determine which associations were the result of fighting, passive tolerance of nearby racoons, or intentional prosocial contacts.

These frequent associations between adult racoons would not be predicted by current socioecological theory. Diurnal animals typically live in groups as a mechanism to reduce predation risk, and the benefits of increased group size in relation to predator detection and dilution effects are well documented (Krause & Ruxton 2002; Caro 2005). Because predation has repeatedly been reported as a minor cause of mortality in this and other racoon populations, there is no evidence that racoon sociality leads to significant antipredation benefits (Clark et al. 1989; Chamberlain et al. 1999; Mankin et al. 1999; Gehrt & Clark 2003; Prange et al. 2003). On the other hand, the most frequent cost of living in a group is an increase in feeding competition. If racoons consume patchy, defensible resources, this increase in contest feeding competition may lead to decreased food intake rates for subordinate social racoons (Janson & van Schaik 1988). The presence of conspecifics may also interfere with hunting, especially if prey species can detect groups of predatory racoons more easily than solitary racoons. In The Ned Brown Forest Reserve, anthropogenic sources of food such as refuse bins play an important role in the foraging ecology of the racoon population (Prange et al. 2004). Previous studies have demonstrated that anthropogenic resources can lead to an increase in racoon social interactions (Gompper & Wright 2005; Wright & Gompper 2005), but the exact costs and

benefits of sociality in racoons are still poorly understood. If these refuse bins are large enough for multiple racoons to feed simultaneously without appreciable declines in individual foraging rates, there may be very little cost of travelling and foraging with other racoons in this population. In this case, an increase in associations among racoons could facilitate information transfer between individuals, which may improve the detection of new food resources.

Even if racoons can defend concentrated resources from other individuals, if individuals feeding on the same resource are closely related, these racoons may be more likely to cooperate and feed near each other without fighting. If racoons preferentially associate with close relatives, this should lead to a reduction in contest competition for food resources. We found no evidence that males or females preferentially associated with relatives. Indeed, the apparent tolerance of nonrelatives at concentrated food resources is an unusual social pattern in mammals. In some species, similar patterns are driven by immigration and other demographic patterns that reduce the likelihood of individuals living in proximity of close relatives. For example, in species with sex-biased dispersal, the philopatric sex typically associates with relatives while individuals that emigrate from their natal territory do not have close relatives with which to associate (Pusey 1987). In the case of racoons, dispersal is typically male biased (Gehrt & Fritzell 1998b; Ratnayake et al. 2002), which may lead to relatedness-based associations in females but not in males. We found no conclusive evidence of male-biased dispersal in this population. If males dispersed significantly longer distances than females, we would have expected a strong negative relationship between genetic relatedness and home range overlap in males and a possible positive relationship in females. Neither pattern was found, and it appears that both adult males and females have home ranges that overlap with multiple relatives and nonrelatives.

We found no evidence that adult females preferentially associated with adult relatives. In fact, the average effect slope of relatedness in our MRQAP analyses of female social networks was negative, although this effect was only significant during one month (Table 1). This suggests that if females do choose to associate with other racoons based on the degree of relatedness, they are in fact avoiding associating with relatives. This result somewhat contrasts to a Texas racoon population where infrequent female associations were typically observed among related individuals (Gehrt & Fritzell 1998b). In some species such as chimpanzees, *Pan troglodytes*, long interbirth intervals result in demographic patterns that greatly reduce the probability that individuals have same-sex close relatives available for associating with (Mitani et al. 2002). In our population, 16% of racoon dyads were close relatives ($r > 0.0125$); thus, there appeared to be ample opportunities for individuals to preferentially associate with relatives. We also found no evidence that racoons were spatially segregated from relatives, as this would have resulted in a strong negative correlation between home range overlap and genetic relatedness. This pattern of racoons not preferentially associating with close relatives, despite their ability to do so, contrasts strongly with other animal social systems (Widdig et al. 2001; Griffiths & Armstrong 2002; Archie et al. 2006; Wiszniewski et al. 2010; Holekamp et al. 2011; Davis 2012; Hirsch et al. 2012). We posit that kinship is not a significant mechanism driving sociality in this racoon population.

One fascinating aspect of this study is that our results partially mirror those of Gehrt et al. (2008), who found that adult male racoon social partners in Texas were typically nonrelatives. Racoon population density in the Texas study site was considerably lower than that in Illinois, and few anthropogenic food sources were available in the Texas population (Gehrt & Fritzell 1998a; Gehrt et al. 2008). Adult males in Texas had partially exclusive home

ranges that they shared with females and male social partners. In Illinois, the home ranges of individual raccoons overlapped with multiple other individuals in the population. In many cases, mammal species that are widely distributed and occur in different habitat types have drastically different social structure depending on their local environment (Barton 2000). The observation that nonkin-based male association patterns were found in both racoon populations suggests that this behaviour may have little relation to local environmental variables. Ideally, future studies should record information on racoon associations during foraging and travel, aggressive interactions between racoons, and quantify the size and distribution of racoon food resources. If these pieces of information were gathered from a variety of habitats, it may be possible to determine when and why adult racoons associate with each other, and racoons could be an ideal species to test broad socioecological questions. In addition, if it is possible to predict racoon association rates based on population density and local ecological variables, this would be extremely beneficial for scientists and wildlife officials who are trying to reduce disease spread from racoons to humans.

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