

# **Raccoon Social Behavior in a Highly Urbanized Environment: A Genetic Investigation**

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When Darwin proposed his theory of natural selection (NS), he grappled with how sociality and the sharing of resources could evolve under such a system of individualized advancement (Darwin 1859). For decades, the field of animal behavior has conducted myriad investigations into this possible crux of NS, and has found that social associations do, in fact, benefit the individuals engaged. Sociality is thought to evolve from three main mechanisms: kin selection (Hamilton 1964), reciprocal altruism (Trivers 1971), and by-product mutualism (Connor 1986); kin selection predicts sociality between related individuals, while the other 2 theories deal with non-kin cooperation. Therefore, the first step in understanding the mechanism driving a species' social system is to examine if close associations are reserved for related individuals. It is also important to understand the mechanisms behind the social formations of species because management techniques may vary widely based on the social structure of an organism. Moreover, there is a particular impetus to know the sociality of species that exploit human dominated environs and transmit lethal zoonotic diseases. Raccoons (*Procyon lotor*), exemplify such a species.

Raccoons are a nocturnal, semi-arboreal, mid-sized Carnivore that inhabits much of North America. They are an intelligent species (Davis 1984, review Gehrt 2003) capable of neighbor recognition (Barash 1971) and obtain their highest densities in urban environments

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(Schinner and Cauley 1974, Riley et al. 1998, Prange et al. 2003) that are often rich with superabundant food resources. Raccoons are heavily studied due to their importance as transmitters of zoonotic diseases (Rupprecht and Smith 1994, Page et al. 1999), nest predators (Fritzell 1978a) and fur bearers (Sanderson 1951, Chamberlain et al. 1999), yet despite many investigations little is known of their social behavior. Raccoons are often described as solitary and intolerant of conspecifics (Bissonnette and Csech 1938, Fritzell 1978b), but instances of group foraging (Sharp and Sharp 1956), extended familial bonds (Gehrt and Fritzell 1998), den cohabitation (Mech and Turkowski 1966), and male coalition formation (Gehrt and Fritzell 1999, Chamberlain and Leopold 2002) have been documented.

One recent study (Prange and Gehrt unpublished data) was conducted to examine the frequency and duration of interactions between adult male and female raccoons such that a more complete picture of social behavior could be identified. They found the average contact rate between individuals was 0.4 contacts/day (range: 0-22.5) for an average of 1.5 minutes/day (range: 0-150.8). Additionally, they reported 11 male-male (MM) dyads that comprised 4 spatially and behaviorally distinct groups, nine female-female (FF) and 19 male-female (MF) pairs that exhibited higher contact rates than expected. It was suggested that these associations were the result of extended familial bonds. However, it is currently unknown how relatedness is involved in such social associations of raccoons. Therefore, the purpose of this study was to examine the variation and persistence of social associations between raccoons studied by Prange and Gehrt in regards to their degree of relatedness. I examined how relatedness affects percent home range overlap, distance between centroids (average location), contact rate, persistence of high contact rates, and instances of den sharing.

## METHODS

*Study Area and Capture:* This study was conducted in a section of the 1,499 ha Ned Brown Forest Preserve park approximately 30 km northwest of Chicago, IL. The area is comprised of 51% woodlands, 19% wetlands (including open water), 18% tall grasses, and 12% mowed lawns, picnic shelters and roads. The park section where trapping was concentrated, Busse Woods, is primarily used for picnicking which offers raccoons easy access to refuse for 8 months of the year that the park is open to the public (April to November). In May 2004, 32 tomahawk box traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin) were set in places thought to maximize raccoon capture success (i.e. along drainages, near snags, etc.) within a designated 20 ha core area. These traps were baited with commercial brand cat food and maintained for 3 weeks until no unmarked animals were captured. During the last week of May, 12 additional traps were placed outside the periphery of the core trapping area for a week until again no unmarked individuals were captured. This capture history coupled with nightly observations during telemetry rounds, led to the belief that most, if not all, raccoons residing within the core area had been identified.

Captured raccoons were sedated with an intramuscular injection of Telazol (Fort Dodge Laboratories, Fort Dodge, Iowa, USA). All individuals were sexed, weighed, and marked with individually numbered ear tags (Monel #3, National Brand and Tag Company, Newport, Kentucky, USA). Raccoons were aged by tooth wear (Grau et al. 1970); all adults were fitted with proximity detecting radio collars (see *contacts*) and sampled for genetic analysis. Unmarked individuals were processed and released on site, while marked animals were released without handling. All animals were processed in accordance with The Ohio State University's Animal Care and Use Protocol (ILACUC#2003R0062).

*Genetic analysis:* Blood samples collected from raccoons were taken to the Brookfield Zoo (Brookfield, IL) for processing. DNA was extracted using standard phenol-chloroform techniques (Sambrook 1989) and amplified with polymerase chain reaction (PCR) using an iCycler (Bio-Rad Laboratories, Hercules, California). Sixteen independent and highly variable microsatellite loci were employed from multiple published libraries (Paetkau et al 1995, Kays et al. 2000, Van De Busche et al. unpublished data, Cullingham et al. 2006). PCR reactions equaled a total volume of 12.5  $\mu$ L with 1.25  $\mu$ L of 10% 10X buffer (ProMega Corp.), 0.5 units *Taq* (Flexi-go), 0.2 mM dNTP, 8pmol primer, and 30-50 ng DNA.  $MgCl_2$  was adjusted to facilitate results, with concentrations ranging between 1.6 and 2.4 mM (Table 1.1). After PCR products were visually checked by running samples through a 1.5% agarose gel, successful reactions were sized by a Beckman-Coulter CEQ 8000XL automated capillary genotyping system (Beckman-Coulter, Inc., Fullerton, California). Fragments were analyzed using Genetic Analysis System Software, version 8.0 (Beckman-Coulter, Inc., Fullerton, California). Automated allele calls were visually assessed by manually graphing the distribution of fragment size and locating natural breaks, or bins, in the distribution.

Number of alleles per locus and allele frequencies, evidence of scoring errors, large allele drop out, and null alleles, and deviation from Hardy-Weinberg equilibrium were tested with Microsatellite Toolkit (Park 2001), Microchecker, (Van Oosterhout et al. 2004), and Genepop (Raymond and Rousset 1995) software respectively. Relatedness values ( $r$ ) were calculated using a log-likelihood ratio generated by the program Kinship 1.2 (Queller and Goodnight 1999). Relatedness ranges on a scale from -1 to 1, with a zero value indicating that the pair of individuals is as related as expected by chance alone, given the allelic frequencies in the population; positive values indicate the pair are more related than by chance alone.

*Spatial distribution:* All adult raccoons were fitted with proximity detecting radio collars that allowed for estimations of animal location via telemetry. Animal locations were obtained from either homing signals or triangulated from  $\geq 2$  bearings taken from a truck-mounted 3-element antenna. Nocturnal locations were obtained minimally once per week for each individual, once per hour for 5 hours beginning after sunset. Data were then partitioned into seasonal home ranges, using 30 or more locations per season. Fixed-kernel home ranges and core use areas (95% and 50% contours, respectively) were created using the Animal Movements extension in ArcView GIS 3.3 (Hooge and Eichenlaub 1997). Percent home range overlap between dyads was calculated using the Neil's Utility extension in ArcView GIS 3.3 using the formula:

$$\text{Coefficient of overlap} = 2(\text{Overlap Area}_{1,2}) / (\text{Area}_1 + \text{Area}_2).$$

Distance between centroids, or the average easting and northing coordinates for an individual within a season, (Moyer et al. 2006) was also calculated using the Neil's Utility extension in ArcView GIS 3.3.

*Contacts:* Proximity detecting radio collars (SIRTRACK ltd.) are a newly developed data logging technology and prototypes were first employed by this project. The proximity detecting radio collars are equipped with both VHF (very high frequency) and UHF (ultra high frequency) signals, which allow not only for traditional telemetry, but also for the detection of a “contact” between 2 or more individuals. A contact is defined as when two or more individuals come within 1 m of each other (Prange et al. 2006). The collars will also record the date and time contact was initiated, the duration of the contact (in seconds), and the id number of the contacted collar. Contacts are stored in the collar's internal memory until data can be downloaded via interface and a portable computer. Contact rates, duration of contact rates, and contacts indicative of den sharing were identified by Prange and Gehrt (unpublished data).

## RESULTS

**Genetics:** By the end of May 2004, 42 adult raccoons were captured and radio collared; all but one individual had blood samples removed and were successfully genotyped. Observed heterozygosity ranged by locus (Table 1.1), and was high overall at 0.742. Exact tests showed that 3 of 16 loci deviated from Hardy-Weinberg equilibrium (Table 1.1); there was a deficiency in the number of observed heterozygotes in each case. However, these aberrations are likely reflections of population substructure, whereby there may be an overrepresentation of closely related or inbred family groups (Marshall et al. 1998, Kitchen et al. 2005). Additionally, two studies conducted over large areas employed these loci and found no such deviations (Cullingham et al. 2006, Roy Nielson and Nielson 2007); therefore all 16 loci were included in analysis.

**Home range overlap:** Home range sizes were typical of urban raccoons, and males had slightly larger home ranges than females (Table 1.2). I found no relationship between home range overlap and relatedness (all P-values > 0.05). Percent home range overlap was not significantly higher, or lower, among positively related dyads than negatively related individuals (Table 1.3). However, the average percent home range overlap between FF dyads was always  $\geq$  the average percent home range overlap of negatively related dyads (Figures 1.1-1.5).

**Distance between centroids:** Distance between centroids was not found to correlate with genetic relatedness for any dyad type during any season (Table 1.4), but ranged widely (Table 1.5). However, males and females exhibited different trends with their correlations as indicated by their corresponding Z-statistics. MM dyads demonstrated a positive relationship between increasing distance and relatedness, while females always showed an inverse relationship for all seasons (Table 1.4).

**Contacts:** When examining the contact rates between related and unrelated individuals I found that relatedness was not higher, or lower, among dyads with high contact rates. Moreover, highly social dyads were not often comprised of positively related individuals. In fact, MM dyads with significant rates of contact were overwhelmingly unrelated. Of the 11 MM dyads with high contact rates, 8 were negatively related (72.7%, Table 1.6). Relatedness was not a precursor to high contact rates between FF dyads either as nearly half (44.4%, n=9, Table 1.7) of the most social dyads were unrelated. Similarly for MF pairs, nearly half (47.3%, n=19, Table 1.8) of the most social dyads were negatively related.

**Persistence of associations:** Social associations between individuals were longer lasting in MM dyads than FF or MF dyads. Of 11 MM dyads that had higher contact rates than expected, 8 (72.7%) were social for all seasons in which data were available (Table 1.6). None of the 9 FF dyads or the 19 MF dyads had high contact rates for every season for which data were available (Tables 1.7 and 1.8 respectively). Five of the 8 (62.5%) MM dyads with high contact rates for more than 1 season were negatively related. Female-female dyads had higher contact rates than expected for more than 1 season only twice, and both of those dyads were negatively related. Eight MF dyads had higher contact rates than expected for more than 1 season and 7 (87.5%) of those were positively related. All of the 7 positively related MF dyads with high contact rates for more than 1 season occurred between females that were as old, or older, than the male involved, and 6 of these 7 dyads occurred with just 2 females.

**Den sharing:** Den sharing was not confined to highly related dyads, or in the case of MF den sharing in winter (the breeding season), reserved for negatively related dyads. Of 34 MF dyads that shared dens throughout the year, 18 dyads were negatively related (52.9%). These 34 dyads denned together a total of 219 times, of which 98 (44.7%) instances were between negatively

related dyads. Specifically during the breeding season, 17 of 31 MF dyads that denned together were negatively related (54.8%). Yet the majority of den sharing instances were between positively related individuals (98/173, 56.6%). Throughout the year, MM dyads most frequently shared dens (13/19, 68.4%) and instances of den sharing (182/317, 57.4%) between negatively related dyads. Conversely, the majority of FF dyads (6/11, 54.5%) and instances of den sharing among FF dyads (33/57, 57.8%) were between positively related dyads.

## DISCUSSION

Highly social behavior among Carnivora often occurs between related individuals. Kin-based groups are common among many canids (wolves (*Canis lupus*); Lehman et al. 1992, African wild dogs (*Lycaon pictus*); McNutt 1996, swift foxes (*Vulpes velox*); Kitchen et al. 2005, and San Joaquin kit foxes (*Vulpes macrotis mutica*); Ralls et al. 2001), while groups of highly related females are reported for lions (*Panthero leo*; Packer et al. 1991), coatis (*Nasua narica*; Gompper et al. 1998), and kinkajous (*Potos flavus*; Kays et al. 2000). It was expected, due to the reported philopatric nature of female raccoons (Ratnayeke et al. 2002) and length of familial bonds (Gehrt and Fritzell 1998), that relatedness would largely determine the social associations between raccoons. My results did not confirm this hypothesis, but rather, revealed an unexpected layer of social complexity, as many close and stable associations occurred between unrelated individuals.

One previous study conducted within a low-density area found a significant relationship between relatedness and spatial proximity of female raccoons, (Ratnayeke et al. 2002) however this trend was not observed within my urban study site. I did not find that percent home range overlap or distance between centroids of related females and unrelated females were significantly different. However, for every season home range overlap was slightly greater among related



females. Additionally, females always exhibited an inverse relationship of increasing relatedness and decreasing distance between centroids. Contacts rates and instances of den sharing were not found to be significantly greater among related females, but still, social associations were slightly more common among related females. These results offer tenuous, but consistent, evidence that relatedness may be responsible for underlying association patterns of female raccoons, but it is not the ultimate factor influencing female raccoon sociality.

Another surprising result from this study was the prevalence of MF associations outside of the breeding season. Male and female raccoons were thought to associate only for breeding purposes (Gehrt and Fritzell 1999, Gehrt 2003). Some reports of extended familial bonds do exist (Gehrt and Fritzell 1998), and the persistence of high contact rates for MF dyads in our study was heavily influenced by relatedness. Of the MF dyads that exhibited high contact rates for more than 1 season, 87.5% of were positively related. However, these persistent high contact rates were exhibited by only 2 females and the relatedness values were never indicative of a parent-offspring relationship. Therefore, these data do not support the theory that associations outside of the mating period are suggestive of extended familial bonds.

Relatedness did not positively impact the spatial distribution of male raccoons within my study site, nor their contact rates. Nearly 73% of highly social MM dyads were comprised of unrelated individuals, and these negatively related dyads with high contact rates were very stable throughout the study duration. Of the 4 male groups identified by Prange and Gehrt (unpublished data), only 1 contained related males, which was the largest group with 4 members. Den sharing between males and females were recorded for all group males, except in the case of the largest group where 1 male failed to den share with any female. This finding provides support for the hypothesis that male raccoons form coalitions for access to mates; breeding

access is more equitable among small groups so relatedness among members need not be high, while large groups do not share mating opportunities equally and must be comprised of related individuals (Packer et al. 1991).

In conclusion, my results indicate that genetic relatedness cannot solely explain the formation and variation of social associations of adult raccoons. Perhaps in low density environs with limited food resources, relatedness plays a much greater role in the formation and maintenance of social associations than what was observed here. Although raccoons are classically defined as solitary and intolerant of conspecifics, fierce defense of space or resources in a high density environment with superabundant food, would likely be disadvantageous. The benefits, however, of social tolerance (i.e. sharing home ranges and food sources) in such an environment would theoretically be great. Raccoons are well known for their highly adaptable nature, and are expert exploiters of their environment. That flexibility may be the principal key to their social tolerance, and in turn, their successful expansion into urbanized systems.

This is the first study to examine contact rates for any free-ranging species that has not been habituated to human observation, and the results contribute to a growing list of species that associate with non-kin. Within Carnivora, hyenas (*Crocuta sp.*; Van Horn et al. 2004, Wagner et al. 2007), wolves (Vucetich et al. 2003), costal river otters (*Lontra canadensis*; Blundell et al. 2002), and male lions (Packer et al. 1991), kinkajous (Kays et al. 2000), and dwarf mongooses (*Helogale parvula*; Creel and Waser 1993) have all demonstrated cooperation among non-kin. These results yield important empirical evidence for the theoretical study of how social behavior evolves. As data logging and molecular technologies improve and become more cost effective, it is likely that our current views of social behavior will continue to change as more complex social systems are revealed.

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## TABLES AND FIGURES

Locus	Annealing temp (°C)	MgCl <sub>2</sub> (mM)	Number of alleles	H <sub>e</sub>	H <sub>o</sub>	P-value
M2	56	2.4	12	0.860	0.825	0.822
M3	56	2.4	7	0.765	0.873	0.125
M14	68	1.6	18	0.878	0.857	0.373
M15	56	2.4	12	0.859	0.778	0.267
M17	56	1.6	8	0.780	0.714	0.535
M20	56	2.4	12	0.863	0.794	0.001
M71	56	2.4	12	0.767	0.714	0.158
M117	56	2.0	18	0.880	0.841	0.145
M117X	64	2.0	7	0.770	0.429	0.000
M86	56	2.0	24	0.901	0.921	0.013
M123	68	2.4	12	0.866	0.825	0.813
G10C	56	2.4	4	0.414	0.492	0.401
P140	52	1.6	8	0.754	0.698	0.107
P161	68	2.4	8	0.491	0.508	0.822
PFL9	54	2.0	10	0.828	0.794	0.183
PFL11	62	1.6	15	0.873	0.810	0.098

Table 1.1. Annealing temperature (°C), concentration of Mg Cl<sub>2</sub> (mM), number of alleles, expected and observed heterozygosity levels by locus, where H<sub>e</sub> is expected and H<sub>o</sub> is observed heterozygosity.

	Summer 04		Fall 04		Spring 05		Summer 05		Fall 05	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Male	48.5	14.8	58.4	47.2	66.9	22.5	69.5	22.6	55.2	51.5
Female	44.0	52.6	46.5	28.1	16.9	15.2	43.1	18.4	44.4	16.4

Table 1.2. Average size and standard deviation (Ha) of 95% fixed-kernel home range for male and female adult raccoons by season in Busse Woods, IL between summer 2004 and fall 2005.

	<u>MM</u>	<u>FF</u>	<u>MF</u>
Summer 04	0.928	0.948	0.669
Fall 04	0.394	0.486	0.715
Spring 05	0.801	0.862	0.228
Summer 05	0.283	0.969	0.271
Fall 05	0.876	0.896	0.182

Table 1.3. P-values of 2-Sample permutation tests comparing percent home range overlap among positively and negatively related adult raccoon dyads within Busse Woods, Il between summer 2004 and fall 2005.

	<u>MM</u>			<u>FF</u>			<u>MF</u>		
	g stat	Z-stat	r	g stat	Z-stat	r	g stat	Z-stat	r
Summer 04	1.568	453.61	0.182	1.378	-26.79	0.196	-2.206	2296.02	-0.252
Fall 04	0.338	67.59	0.036	0.476	-3302.28	0.065	-0.896	-175.60	-0.094
Spring 05	0.269	3.35	0.040	1.640	-26.38	0.202	-0.045	-226.02	-0.010
Summer 05	0.102	154.65	0.017	1.294	-31.09	0.161	-0.148	-837.21	-0.029
Fall 05	0.014	160.57	0.003	1.243	-2379.26	0.189	0.108	1713.01	0.020

Table 1.4. Standard normal variate (g) statistic, Z-statistic, and standardized Mantel correlation coefficients of Mantel test comparing genetic relatedness and distance between centroids of adult raccoons in Busse Woods, Il between summer 2004 and fall 2005. Value of g must be higher than the critical value of 1.645 to be significant at the 0.05 level.

Season	<i>N</i>	Mean (m)	Range (m)	SD
<b>Summer 04</b>				
FF	153	761.30	18.5 - 2774.9	568.1
MF	234	674.42	34.6 - 2742.7	488.2
MM	78	597.28	54.6 - 1246.3	310.7
<b>Fall 04</b>				
FF	105	840.72	34.0 - 2412.6	517.1

MF	210	726.09	37.5 - 2592.3	472.2
MM	91	637.72	43.3 - 1259.9	335.6
<b>Spring 05</b>				
FF	120	391.32	18.6 - 752.3	219.2
MF	160	510.72	17.5 - 1064.1	274.4
MM	45	587.27	13.5 - 1095.4	322.4
<b>Summer 05</b>				
FF	78	477.67	42.2 - 971.9	225.7
MF	117	517.84	58.1 - 1249.8	275.1
MM	36	585.94	10.42 - 1231.2	341.3
<b>Fall 05</b>				
FF	79	451.99	55.5 - 1218.2	240.7
MF	104	432.65	19.4 - 1228.9	250.3
MM	27	458.98	39.5 - 912.0	270.2

Table 1.5. Average distance between centroids (m), range, and standard deviation by season and dyad type of adult raccoons in Busse Woods, IL.

Group	Relatedness	Ear Tags		Age		# of seasons
		A	B	A	B	
1	-0.16009	6308	6407	II	II	2/4
2	-0.00035	6328	6424	II	II	2/2
3	-0.00375	6453	6462	III	IV	3/3
3	-0.04246	6482	6453	I	III	2/3
3	-0.10421	6482	6462	I	IV	3/3
4	0.21724	6468	6485	I	III	2/3
4	0.15107	6488	6468	II	I	3/3
4	0.05504	6488	6485	II	III	3/3
4	-0.05101	6488	6490	II	III	1/1
4	-0.09622	6485	6490	III	III	1/1
4	-0.08776	6468	6490	I	III	1/1

Table 1.6. Group number, relatedness value, dyad members (A, B), age class, and number of seasons with significant contact rate out of total seasons data was available for male dyads in Busse Woods, IL.



Relatedness	Ear Tags		Age		# of seasons
	A	B	A	B	
0.35383	6456	3625	II	V	1/4
0.18345	6115	6473	III	I	1/3
0.10819	4014	6473	V	I	1/3
0.27777	6456	4047	II	IV	1/4
-0.05448	6425	6326	IV	III	2/4
0.00815	4005	6115	III	III	1/4
-0.04594	4005	4014	III	V	2/4
-0.10538	6456	6493	II	I	1/4
-0.04185	6416	3625	II	V	1/3

Table 1.7. Group number, relatedness value, dyad members (A, B), age class, and number of seasons with significant contact rate out of total seasons data was available for female dyads in Busse Woods, IL.

Relatedness	Ear Tags		Sex		Age		# of seasons
	A	B	A	B	A	B	
-0.02564	6407	3625	M	F	II	V	1/4
0.44848	6468	4047	M	F	I	IV	1/4
0.06462	6485	4005	M	F	III	III	3/4
0.28867	6485	4014	M	F	III	V	2/4
0.07418	6488	4005	M	F	II	III	2/3
0.12714	6488	4014	M	F	II	V	2/3
-0.12693	6482	6115	M	F	I	III	1/4
-0.14128	6453	6115	M	F	III	III	1/4
0.04844	6468	4005	M	F	I	III	3/4
-0.06686	6453	6456	M	F	I	II	1/4
-0.12209	6482	4047	M	F	I	IV	1/4
0.07959	6488	6115	M	F	II	III	1/3
0.04695	6462	4047	M	F	IV	IV	2/4
-0.13049	6308	4047	M	F	II	IV	1/4
0.08616	6407	4014	M	F	II	V	2/4
-0.06074	6308	6456	M	F	II	II	2/4
0.06588	6453	4047	M	F	I	IV	1/4
-0.19184	6407	4005	M	F	II	III	1/4
-0.01674	6308	3625	M	F	II	V	1/4

Table 1.8. Group number, relatedness value, dyad members (A, B), sex of dyad members, age class, and number of seasons with significant contact rate out of total seasons data was available for male-female dyads in Busse Woods, IL.

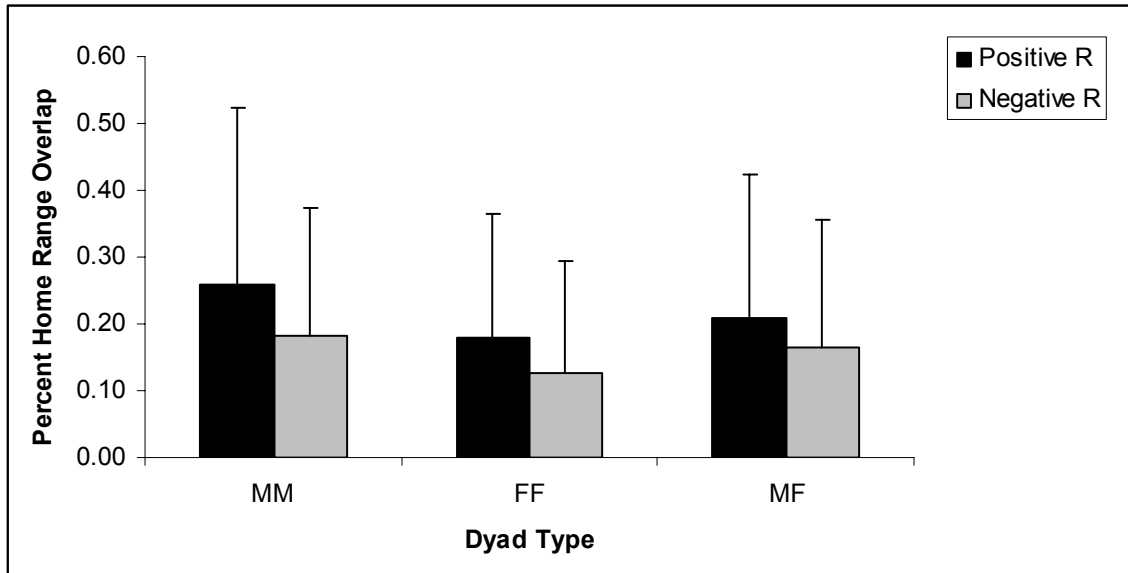


Figure 1.1. Average home range overlap between positively and negatively related MM, FF, and MF dyads (+SD) of adult raccoons from during summer 2004 in Busse Woods, IL.

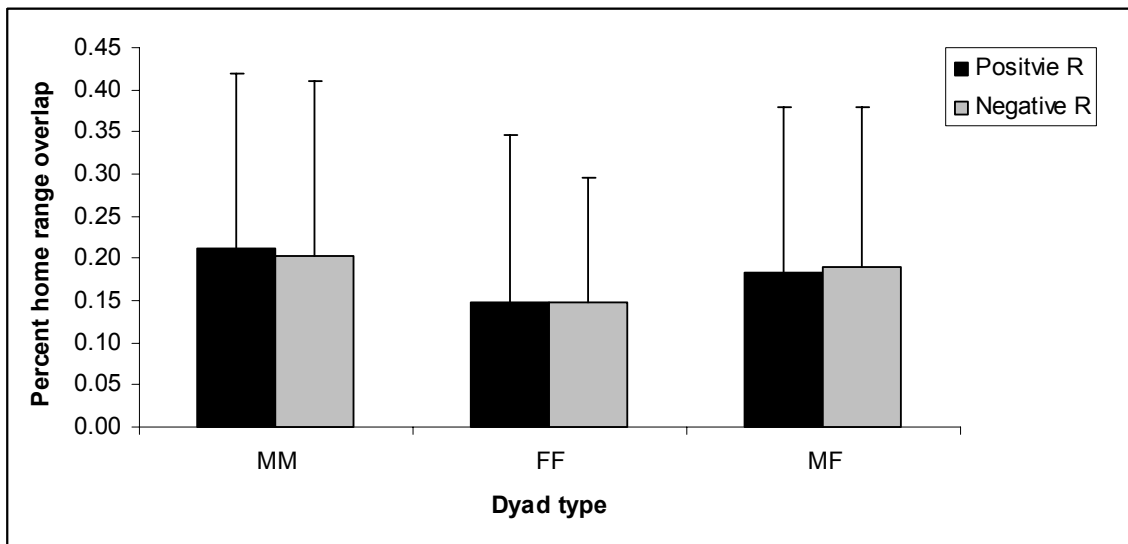


Figure 1.2. Average home range overlap between positively and negatively related MM, FF, and MF dyads (+SD) of adult raccoons from during fall 2004 in Busse Woods, IL.

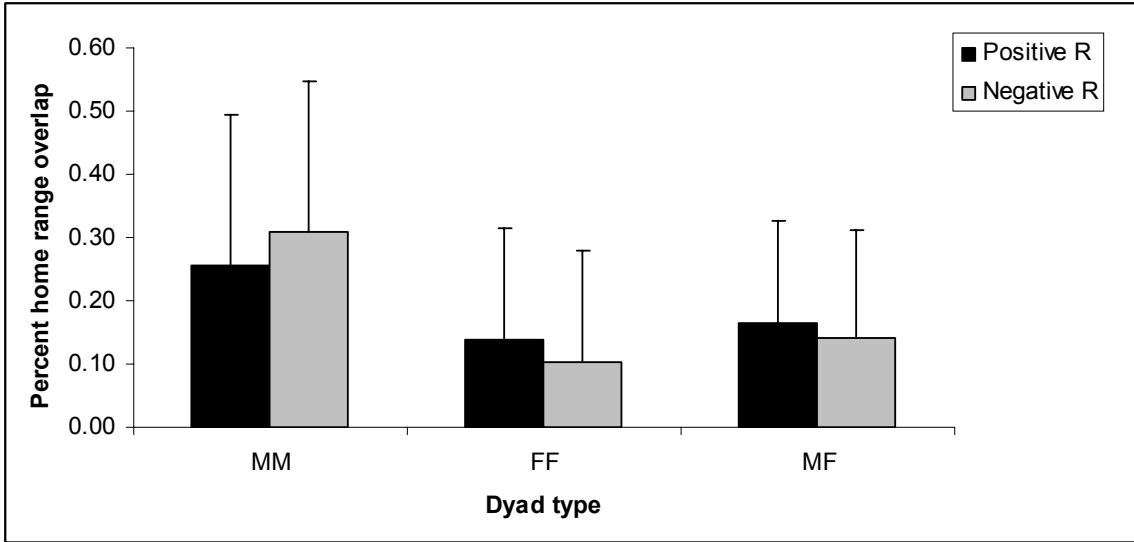


Figure 1.3. Average home range overlap between positively and negatively related MM, FF, and MF dyads (+SD) of adult raccoons from during spring 2005 in Busse Woods, IL.

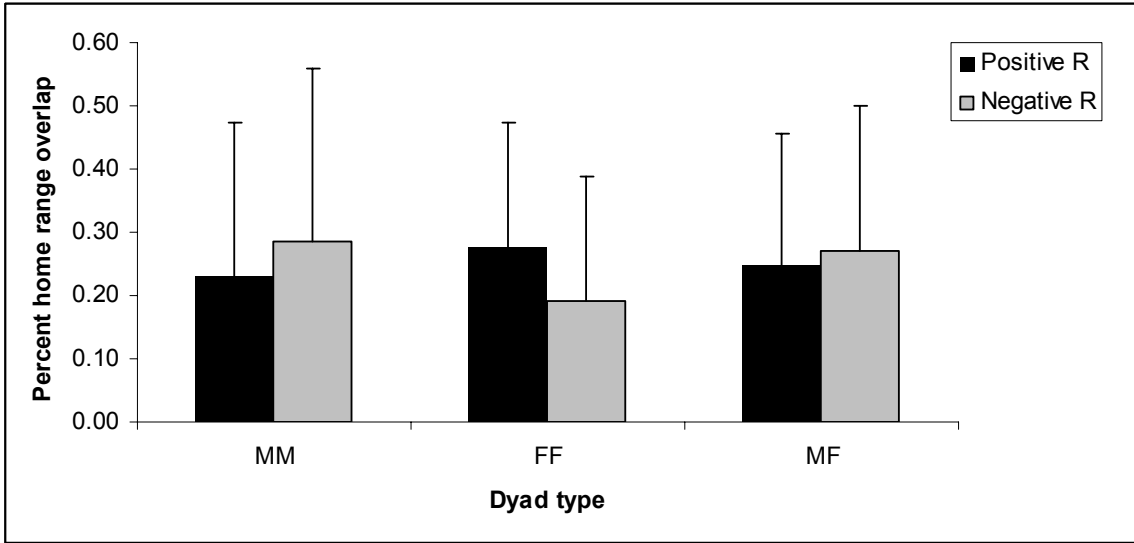


Figure 1.4. Average home range overlap between positively and negatively related MM, FF, and MF dyads (+SD) of adult raccoons from during summer 2005 in Busse Woods, IL.

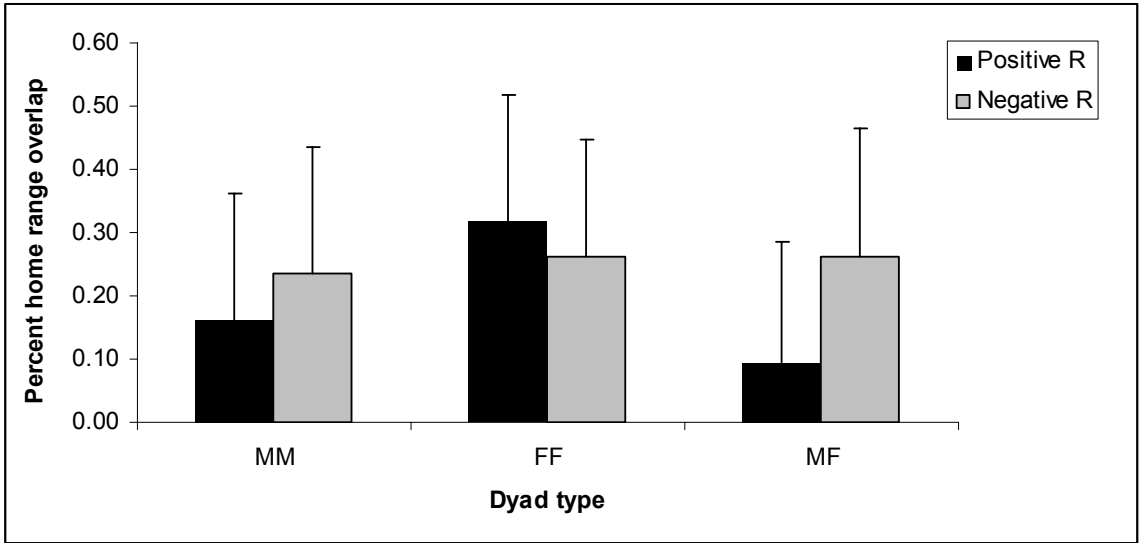


Figure 1.5. Average home range overlap between positively and negatively related MM, FF, and MF dyads (+SD) of adult raccoons from during fall 2005 in Busse Woods, IL.