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Frequency and duration of contacts between free-ranging raccoons: uncovering a hidden social system

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Raccoons (*Procyon lotor*), like most carnivores, are nocturnal and secretive and consequently difficult to observe. We used proximity-detecting collars to determine effects of sex, age, and season on contact rate and duration; document patterns of seasonal contact rates by dyad type and determine whether patterns were random; identify dyads that exhibited contact rates significantly greater than expected and document the persistence of these positive associations across seasons; and document frequency of den sharing as an additional measure of positive associations at an urban study site with a high-density raccoon population. Contact rate and duration were affected by dyad type, season, and their interaction. Male–male (MM) dyads exhibited higher contact values than male–female (MF) or female–female (FF) dyads, and contact parameters were greater during winter and spring than summer and autumn. Contact parameters for MM and FF dyads were not affected by age of dyad members, whereas those of MF dyads were affected by age and its interaction with season. MF dyads with older individuals exhibited greater contact parameters, and this effect was greatest during winter. For all dyad types and seasons, except FF dyads during winter, observed distributions of contact rates differed from expected. Males formed groups, with most positively associated dyads persisting across seasons, and females were associated almost exclusively with members of only 1 male group. Some positively associated MF dyads occurred during autumn and continued through spring. Positively associated FF dyads occurred at a lower rate and were ephemeral, seldom lasting more than 1 season. FF and MF dyads exhibited a greater proportion of low-frequency contacts with conspecifics than expected during all seasons, except winter, which may function to maintain amicable relationships between neighbors or reinforce dominance hierarchies and create a framework for more complex social behaviors. Raccoons appear to live in a fission–fusion society, with many short-term acquaintances and a few long-term associations.

Key words: Carnivora, contact duration, contact rate, fission–fusion, gregarious, *Procyon lotor*, raccoon, solitary

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Only 10–15% of all carnivore species are classified as gregarious, or those that occur in groups and exhibit cooperative behavior outside of the breeding season (Bekoff et al. 1984; Gittleman 1989); the remainder are classified as solitary (Sandell 1989). Solitary species often occupy habitats with dense vegetative cover, are nocturnal and secretive, and consequently are difficult to observe (Gittleman 1989; Wiens and Zitzmann 2003). These difficulties historically have limited the study of social behavior to more gregarious species (Cooper and Randall 2007; Gittleman 1989). As a result, the designation of solitary for some species could arise more from our inability to study them effectively than from the true nature of their social systems.

Raccoons (*Procyon lotor*) historically have been described as territorial (Fritzell 1978) or asocial and intolerant of conspecifics (Barash 1974; Ratnayeke et al. 2002; Sandell 1989; Sanderson 1987; Waser and Jones 1983). However,

mother–offspring and sibling bonds often continue until the next mating season (Fritzell 1977; Gehrt and Fritzell 1998a; Schneider et al. 1971), and family members can reestablish bonds after the next mating seasons ends (Gehrt and Fritzell 1998a). Neighbor recognition with apparent dominant–subordinate relationships in captive males (Barash 1974), communal denning (Gehrt and Fritzell 1998b; Mech and Turkowski 1966), and observable social hierarchies at feeding stations (Sharp and Sharp 1956; Totton et al. 2002) also lend support for a greater sociality in raccoons than commonly recognized.

Male behavior appears to range from territorial to social (Chamberlain and Leopold 2002; Fritzell 1978; Gehrt and



Fritzell 1998b). Fritzell (1978) documented nonoverlapping home ranges for males in a low-density population in North Dakota, with territorial males overlapping ranges with up to 3 females. Conversely, other radiotelemetry studies have documented male coalition formation, presumably for mate defense (Chamberlain and Leopold 2002; Gehrt and Fox 2004; Gehrt and Fritzell 1998b). Gehrt and Fritzell (1998b) reported that males in southern Texas formed spatial groups whose home ranges overlapped little with adjacent groups, suggesting territoriality among, but sociality within, groups. Home ranges of group males overlapped as many as 12 female home ranges, whereas home ranges of solitary males did not contain females. In Mississippi some males formed social groups; however, some males were solitary and maintained exclusive home ranges (Chamberlain and Leopold 2002). Home ranges of both group and solitary males overlapped those of 1–3 females. Chamberlain and Leopold (2002) noted that the density of females was lower than in the Texas study.

Differences in male sociality are likely due to differences in resource abundance and distribution. The effect of food resources can be direct, or indirect through the influence of food resources on the distribution of females (Sandell 1989). Population density also can have an effect on male sociality. High population density and an aggregated distribution of females are conducive to the formation of male groups (Caro 1994; Connor and Whitehead 2005; Gehrt and Fritzell 1998b; Wittenberger 1980). Furthermore, at low densities raccoons appear to be polygynous (Fritzell 1978), but at higher densities they switch between polygyny and promiscuity (Gehrt and Fritzell 1999; Roy Nielsen and Nielsen 2007).

With the exception of temporary relationships with kin, female raccoons consistently have been characterized as solitary, despite extensively overlapping home ranges (Chamberlain and Leopold 2002; Mech et al. 1966; Pitt et al. 2008; Ratnayeke et al. 2002; Schneider et al. 1971). Interactions between females, if they occur, can be extended mother–daughter relationships (enhancing learning), can occur in response to seasonal changes (e.g., communal winter denning for thermoregulation—Mech and Turkowski 1966), or can be limited interactions with neighbors to aid in neighbor recognition (Barash 1974) and increase their ability to share space amicably. Male–female interactions can occur for similar reasons or be limited to consortship during the breeding season (Gehrt and Fritzell 1999). Thus, raccoon social systems are likely complex and remain poorly understood.

Descriptions of raccoon social behavior have all been based on limited observations. In traditional radiotelemetry a contact typically is defined as occurring when 2 individuals are within 25–100 m because of positional error of locations (Atwood and Weeks 2003; Gehrt and Fritzell 1998b; Ramsey et al. 2002; White and Harris 1994; White et al. 2000). Furthermore, in terms of temporal accuracy, neither very-high-frequency (VHF) nor global positioning system collars currently are capable of providing continuous information regarding the proximity of individuals. Contacts between members of a free-ranging raccoon population have never been monitored

continuously for an entire annual period. Such intense monitoring might be required to illuminate subtle patterns of sociality.

We used proximity-detecting collars (Sirtrack Ltd., Have-lock North, New Zealand), which overcome many of the limitations of traditional VHF telemetry (Prange et al. 2006), to document dyadic relationships of a free-ranging raccoon population. Our overall goal was to clarify the social structure of raccoons. To accomplish this goal we monitored raccoons in a high-density population (75 raccoons/km²—Prange et al. 2003) in northeastern Illinois. We determined the effects of dyad type (male–male [MM], male–female [MF], or female–female [FF]), season, age of dyad members, and their interaction on contact rate (contacts/day) and duration (minutes of contact/day), documented overall patterns of seasonal contact rates by dyad type, determined whether observed patterns were random, determined which dyads exhibited contact rates that were significantly greater than expected based on a random distribution, documented the duration of significant contact rates for dyads across seasons, and documented frequency of den sharing as an additional measure of positive associations.

We predicted that males would occur in groups and consequently MM dyads would exhibit higher contact parameters than dyad types containing females, but groups would not be spatially distinct due to the difficulty of defending a group territory in a high-density population. However, we predicted that members of male groups would exhibit greater overlap with each other than with members of other groups or solitary males (based on contact patterns), and group males would exhibit greater spatial overlap with females than solitary males. Because male group formation has been hypothesized to occur primarily for mate defense (Chamberlain and Leopold 2002; Gehrt and Fox 2004; Gehrt and Fritzell 1998b), we further predicted that contact parameters would be higher for MM and MF dyads containing an older male, due to a presumed increase in male reproductive success with age. In this case females would breed preferentially with older males, and younger males potentially could gain greater reproductive advantages by associating with an older male. At high densities raccoons tend toward a promiscuous mating system, and litters are sired by multiple males. Roy Nielsen and Nielsen (2007) found that 88% of litters in a high-density population were sired by >1 male. They concluded that high population densities led to the frequent inability of males to monopolize mating opportunities with females. Thus, younger group members might be able to maximize their chances of securing mating opportunities by associating with older males.

We predicted higher contact parameters for MM and MF dyads during winter (which includes the breeding season) and greater spatial overlap among group members and between group members and females due to consortship and increased cohesiveness within male groups to defend females. Thus, we expected MM and MF contact patterns to be nonrandom, with some dyads exhibiting higher contact rates than expected. We expected significant contact rates for MM dyads to persist

across seasons (indicative of relatively stable groups), whereas we expected significant contact rates for MF dyads only during winter. Although we expected substantial spatial overlap among females, based on the reported lack of sociality among female raccoons, we expected either random contact parameters or evidence of avoidance for FF dyads.

MATERIALS AND METHODS

We chose a 20-ha area within the 1,499-ha Ned Brown Forest Preserve in suburban Cook County, Illinois, as our core trapping area. The area is described in detail elsewhere (Prange et al. 2003). We placed 32 box traps (model 108, 25 × 30 × 81 cm; Tomahawk Live Trap Co., Tomahawk, Wisconsin) baited with cat food within the core area during May 2004 and maintained them for 4 weeks. Traps were set in areas to maximize raccoon capture, such as along creeks and near logs and active latrines. Trap sites were not static and were moved opportunistically when capture rate was poor. Trap density was 1.5 traps/ha, representing a minimum of approximately 38 traps/home range based on the minimum median of seasonal home ranges for females (home ranges smaller than those of males) at this study site (Prange et al. 2004). Consequently, we do not believe any raccoons were excluded spatially regardless of territoriality. During the last week 12 additional traps were placed within 200 m of the periphery of the core area. Captured raccoons were immobilized with an injection of Telazol (Fort Dodge Animal Health, Fort Dodge, Iowa—Gehrt et al. 2001), weighed, and sexed, and adults were placed into 1 of 5 age classes according to tooth wear (classes I–V—Grau et al. 1970). We noted reproductive condition by the length and pigmentation of teats in females and size of testes in males (Sanderson and Nalbandov 1973). All raccoons were marked with individually numbered ear tags (National Band and Tag Company, Newport, Kentucky), and all adults (>1 year old) were fitted with proximity-detecting collars (Prange et al. 2006). We used a similar protocol to recapture raccoons periodically to download data from their collars. Trapping and handling of raccoons conformed to guidelines of the American Society of Mammalogists (Sikes et al. 2011) and Ohio State University Animal Care and Use protocols (ILACUC#2003R0062).

The proximity-detector system consisted of radiocollars that communicated with each other over a short-range radio data link. Each transmitter broadcasted a unique identification code over an ultra-high-frequency (UHF) channel at 1.5-s intervals. When not broadcasting, the detector “listened” for other codes by sampling the UHF channel. In addition, proximity-detecting collars transmitted a standard pulsed VHF beacon (Prange et al. 2006). The collars allowed contact criteria to be set. We defined a contact as occurring when 2 individuals were within approximately 1.0–1.5 m of one another, and it terminated when the individuals moved out of this range for >45 s. At this point each collar recorded the identification number of the contacted collar, date, time contact was initiated, and contact duration (Prange et al. 2006). Variation

in contact distance among most collars ranged from 0.2 to 0.5 m. All collars communicated with one another, and each collar was capable of detecting and recording contacts with up to 8 others at any given time (Prange et al. 2006).

We used the smallest possible contact distance because the study was designed to obtain contact rates for disease transmission models, and close contact is more likely to result in disease transmission. This distance provided a conservative estimate of social contacts. Use of a larger distance would have provided a more liberal estimate of amicable contacts but also potentially would have introduced more error. For example, 2 raccoons foraging within a few meters of one another might be indicative of an amicable relationship, but it also could be the result of mere tolerance. Although we cannot associate a particular action with each contact, contacts within a short range, especially when repeated and of more than a brief duration, are likely to represent amicable contacts. This assumption is similar to that of radiotelemetry studies that use contact rates to identify positively associated dyads, although with much less resolution (contact usually defined as occurring if active locations are within 25–100 m—Atwood and Weeks 2003; Gehrt and Fritzell 1998b; Ramsey et al. 2002; White and Harris 1994; White et al. 2000).

We defined a dyad as 2 specific individuals whether or not they contacted one another. For example, 3 raccoons (A, B, and C) would result in 3 unique dyads (A–B, B–C, and A–C). We defined a group as ≥ 2 male raccoons that exhibited positive associations with one another, defined as contact rates (contacts/day) that were significantly greater than expected based on a random distribution. Groups of >2 males consisted of males all of which exhibited significant contact rates with one another. For example, if MM dyads A–B and B–C exhibited significant contact rates, raccoons A, B, and C were classified as a group only if dyad A–C also exhibited significant rates. We also used the occurrence of den sharing (defined as contacts lasting >4 h during the diurnal period) to corroborate that significant contact rates represented amicable interactions, and to strengthen our definition of male groups.

Typically, we downloaded collar information from both members of each dyad, which provided 2 records of the same set of contacts. Because of slight variation in detection distances between collars (0.2–0.5 m—Prange et al. 2006), however, these records were not always equivalent. Some variation in detection distance also can occur due to collar orientation. Other potential effects on detection distance, such as physical characteristics of the host and objects in the near field, require further study. Although these factors are expected to contribute to variation in detection distances, this variation is trivial compared to positional error of traditional radiotelemetry locations (Atwood and Weeks 2003; Gehrt and Fritzell 1998b; Ramsey et al. 2002; White and Harris 1994; White et al. 2000). To assess the extent of agreement between collars we selected 20 dyads from summer for correlation analyses. We restricted analyses to dyads for which we had an entire season of contact information and that exhibited contacts during at least 7 weeks (to avoid zero-driven

correlations). All dyads were highly correlated in terms of weekly number (Pearson correlation: $r \geq 0.85$, $n = 13$, $P < 0.001$ for all) and duration of contacts (Pearson correlation: $r \geq 0.91$, $n = 13$, $P < 0.001$ for all) based on data from both collars. Therefore, we randomly selected 1 dyad member to provide contact data for dyads for which both members had complete data. Regardless, positively associated dyads remained positively associated independent of the collar examined. For dyads with partial data for 1 or both members, or where data were lacking for 1 member, we used the most complete data set. To ensure data sets covered enough days to represent contact patterns for the season we censored dyads in which collar malfunctions or full memories prevented at least 21 days of data collection in that season (regardless of whether any contacts occurred on these days).

Because of the likelihood that 1-s contacts can occur spuriously or represent contacts beyond the preset contact distance (Prange et al. 2006), we censored these contacts. In addition to laboratory tests (Prange et al. 2006), dependability and accuracy also were tested in the field. We placed 2 proximity-detecting collars at feeding stations monitored with video cameras. The stationary proximity-detecting collars accurately identified collared raccoons visiting the station, with the exception of occasions when the raccoon was outside of the preset contact distance. In these cases brief, typically 1-s, contacts were recorded with inaccurate identification numbers. The use of feeding stations did not overlap the study presented herein.

We defined seasons based on raccoon biology and climatological changes—summer (June–August), autumn (September–November), winter (December–February), and spring (March–May). Pregnancy and parturition occur predominantly during spring (Sanderson and Nalbandov 1973), juveniles begin to move with their mother during summer, young are weaned and begin to move independently in autumn (Schneider et al. 1971), and winter is a period of greatly reduced activity. We standardized contact data by calculating the number of contacts/day (rate) and duration of contacts/day (duration) for each dyad by season. We defined dyad type based on sex of the dyad's members (i.e., MM, MF, and FF). We determined effects of age characteristics of dyads by classifying dyad members as old or young. We combined age classes I and II (hereafter referred to as young). Adults placed in age class I (0–14 months) became age class II (15–38 months—Grau et al. 1970) shortly after being captured during spring. Additionally, we lumped older age classes (age classes III–V: ≥ 39 months; hereafter referred to as old) because we had few age class IV or V individuals.

For all data we tested for the normality of residuals and used the modified Levene test to test for equality of variances before parametric statistics were conducted. The distribution of contact rate and duration departed significantly from normality; therefore, we added a constant (to account for zero values) and log-transformed these variables. Furthermore, because dyads were not independent data points (e.g., individual A could contact individuals B, C, and D), we used

generalized linear mixed models to determine effects of dyad type, age of members, season, and their interaction on contact rate and duration, and included the identity of each member of the dyad as a random factor. MM dyads had 3 age categories (young male–young male, old male–young male, and old male–old male), as did FF dyads. However, MF dyads had 4 age classes: young male–young female, old male–young female, young male–old female, and old male–old female. Therefore, the effect of age of members was examined separately by dyad type.

We assumed that random contact rates would conform to the Poisson distribution (Harper and Schulte 2005; Whitehall 2008) and compared observed with expected rates using a chi-square test. The Poisson distribution was used as the expected distribution because it is appropriate for modeling events occurring at random within a given interval of time or space and when the number of nonevents is nonsensical (i.e., number of noncontacts/day—Day et al. 2000). Because our data were continuous (i.e., were not a sampling at discrete intervals), tests of significance of association indices commonly used to determine positively associated dyads (e.g., Whitehall 2008) were inappropriate. Consequently, we defined positively associated dyads as those with a cumulative Poisson probability of occurrence ≤ 0.05 . Because the expected Poisson distribution was based on the mean of observed values, the distribution differed by dyad type and season, theoretically taking into account differences in random contact rates due to differences in movement rates between sexes and seasonal changes.

We collected radiolocations for spatial overlap analyses. We determined differences in spatial overlap within and between male groups using analysis of variance (ANOVA). Because we did not have data regarding male reproductive fitness, we used spatial overlap with females as a method of assessing the potential for increased reproductive fitness, and used ANOVAs to compare spatial overlap with females for group and nongroup males. We located diurnal rest site locations at least 2 times/week and obtained nocturnal locations at hourly intervals 2 or 3 times/week. A time interval of 60 min was sufficient to attain biological independence between locations (Gehrt and Fritzell 1997), because it allowed a raccoon time to travel to any part of its home range. To further ensure biological independence of locations nocturnal locations were not recorded if raccoons became inactive, as evidenced by signal modulation. Both diurnal and nocturnal locations were estimated by triangulation. Using a truck-mounted 4-element antenna, we established locations through triangulation of at least 2 bearings; however, due to the system of roads and drivable trails, the vast majority of locations were based on 3 bearings. Raccoon telemetry studies have been conducted at this site since 1995. Precision of bearings was 3.5° as estimated by a minimum of 360 bearings to 12 test collars. Mean ground distance from the location of test collars to estimated locations was 44 m ($SD = 29.8$ m—Prange et al. 2004). All pairwise comparisons were considered statistically significant at $P < 0.05$.

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 was the minimum number of locations needed to minimize bias and variance in fixed kernel home-range estimates (Seaman et al. 1999). We calculated 95% (home range) and 50% (core area) fixed kernel utilization distributions using the animal movement extension (Hooge and Eichenlaub 1997) in ArcView 3.3 (Environmental Systems Research Institute, Inc., Redlands, California). These contours were chosen because they commonly are used to define raccoon home ranges and core use areas (Barding and Nelson 2008; Beasley et al. 2007; Rosatte et al. 2010). We did not calculate home-range or core-area estimates for winter because of raccoon inactivity. We used Neil's Ute extension to calculate indices of overlap (Walls and Kenward 2001) for all dyads, where the coefficient of overlap = $2(\text{overlap area}_{1,2})/(\text{area}_1 + \text{area}_2)$.

RESULTS

During our initial trapping effort we captured 52 raccoons a total of 135 times. Of these, 42 (20 males and 22 females) were adults and were fitted with proximity-detecting collars. We did not collar juveniles. We captured most adult raccoons residing within the core trapping area during the initial session. We captured 3 uncollared raccoons during the 3rd trapping week and none during the final week. Although uncollared raccoons moved into the core area as the year progressed, based on our capture data, 100% of adult individuals using the core area were radiocollared during summer, 88% during autumn, and 82% during spring. We were able to verify that the great majority of raccoons within our core study area were radiocollared via visual observations during nocturnal telemetry sessions. No uncollared raccoons were observed during the initial season, and the number of uncollared individuals observed remained low throughout the study. However, the percentage of animals that were radiocollared, based on capture data alone, could be inflated slightly due to the potential presence of trap-shy individuals in the study area. Although we might have missed some positive associations due to uncollared raccoons, we believe that overall our data accurately depicted the social relationships of raccoons at this site.

We collected 77,543 records of contacts for analyses (summer: 21,845; autumn: 11,086; winter: 27,010; spring: 17,602 contacts). Our final data sets consisted of 32 (15 males and 17 females), 29 (13 males and 16 females), 24 (12 males and 12 females), and 26 (11 males and 15 females) individuals during summer, autumn, winter, and spring, respectively. The number of individuals available for analyses each season differed from the original number of 42 radiocollared adults due to mortality, lost signals, and collar malfunctions. Overall, 64%, 55%, 52%, and 55% of dyads exhibited at least 1 contact during summer, autumn, winter, and spring, respectively. Mean contact rates and durations were highly variable within dyad types (Fig. 1).

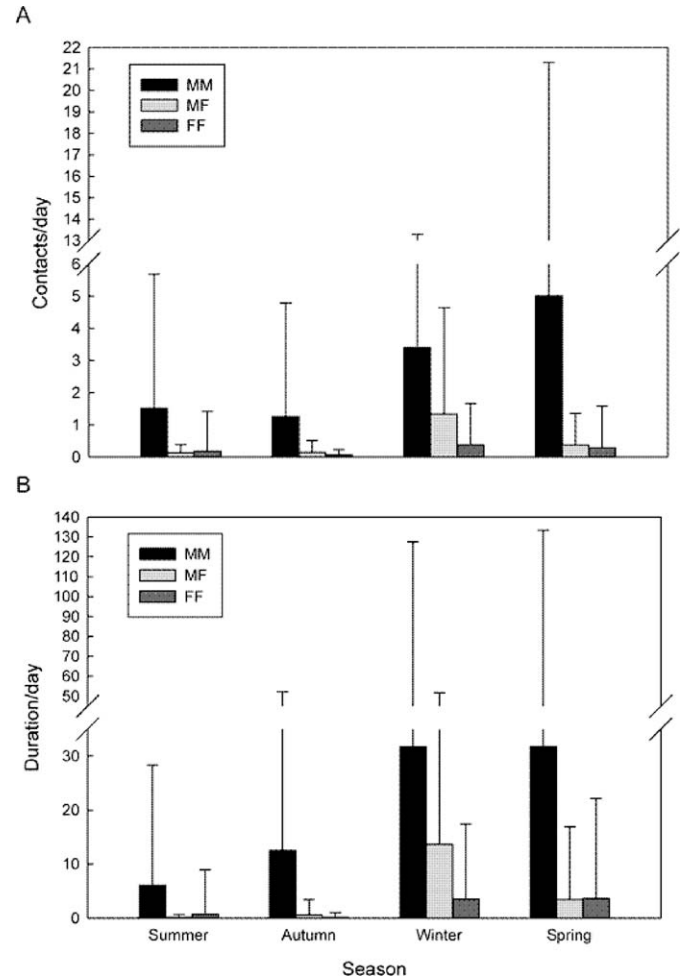


FIG. 1.—A) Mean (\pm SD) contacts per day by dyad type (M = male, F = female) and season, and B) mean (\pm SD) duration of contacts per day in minutes by dyad type and season from summer 2004 to spring 2005 at the Ned Brown Forest Preserve in Cook County, Illinois.

Contact rate differed by dyad type ($F_{2,1,401} = 25.93$, $P < 0.001$), season ($F_{3,1,401} = 8.82$, $P < 0.001$), and their interaction ($F_{6,1,401} = 3.92$, $P = 0.001$). MM dyads exhibited greater contact rates than did MF or FF dyads, and contact rates were greater in winter and spring than summer and autumn. Contact rates were greater for MM and MF than FF dyads during winter, and greater for MM than either MF or FF dyads during spring (Fig. 1). Contact rates for neither MM nor FF dyads varied by age (MM: $F_{2,247} = 2.71$, $P = 0.069$; FF: $F_{2,413} = 0.57$, $P = 0.567$) or the interaction of age and season (MM: $F_{6,247} = 0.52$, $P = 0.792$; FF: $F_{6,413} = 1.09$, $P = 0.368$). Conversely, age ($F_{3,713} = 4.33$, $P = 0.005$) and the interaction of age and season ($F_{9,713} = 2.46$, $P = 0.009$) significantly affected contact rates for MF dyads. Old-old dyads and those in which the female member was old exhibited greater contact rates than young-young dyads. The interaction of season and age was greatest during winter, when contact rates for the old-old age type increased disproportionately (Fig. 2).

Contact duration differed by dyad type ($F_{2,1,401} = 20.81$, $P < 0.001$), season ($F_{3,1,401} = 12.26$, $P < 0.001$), and their

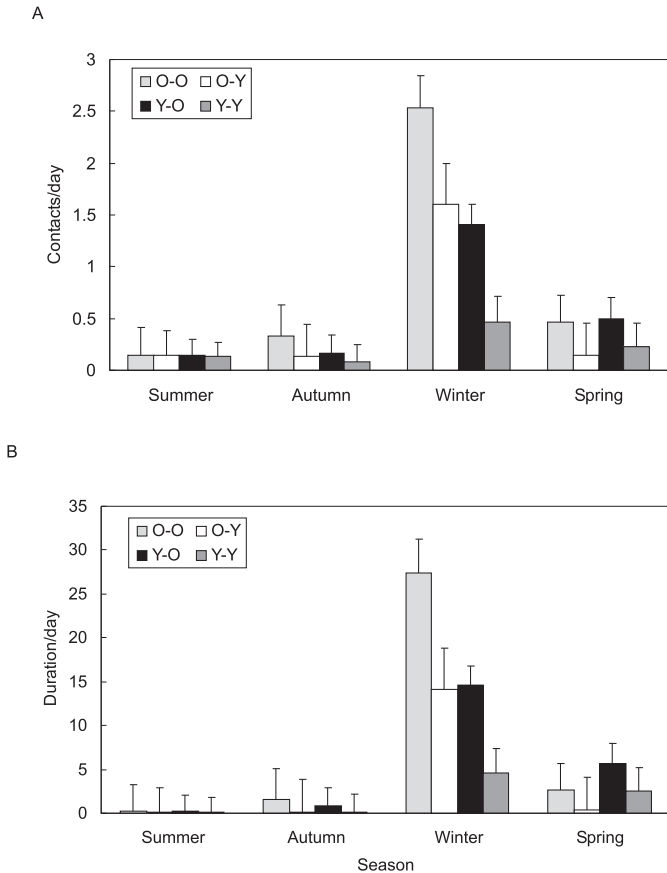


FIG. 2.—A) Mean ($\pm SD$) contacts per day by age type (O-O = old-old; O-Y = old male-young female; Y-O = young male-old female; and Y-Y = young-young) and season, and B) mean ($\pm SD$) duration of contacts per day in minutes by age type and season from summer 2004 to spring 2005 for MF dyads at the Ned Brown Forest Preserve in Cook County, Illinois.

interaction ($F_{6,1401} = 3.29, P = 0.003$). Contact duration was greater for MM dyads than either dyad type containing females. Seasonally, contact duration was greater during winter and spring than summer and autumn. Interactions of dyad type and season were similar to those observed for contact rate (Fig. 1). Also similar to contact rates, contact duration for MM and FF dyads did not vary by age (MM: $F_{2,247} = 1.86, P = 0.158$; FF: $F_{2,413} = 0.76, P = 0.466$) or the interaction of age and season (MM: $F_{6,247} = 0.45, P = 0.842$; FF: $F_{6,413} = 1.09, P = 0.365$), whereas age ($F_{3,713} = 2.56, P = 0.050$) and the interaction of age and season ($F_{9,713} = 18.46, P < 0.001$) significantly affected contact duration for MF dyads. Old-old dyads exhibited longer contact duration than young-young ones. Interaction of season and age was greatest during winter, with the old-old age type exhibiting a disproportionate increase in duration (Fig. 2).

Because contact rate and duration exhibited similar influences from dyad type, season, and age, and because of their correlation for individual dyads (Pearson correlation: $r^2 \geq 0.96, P < 0.001$), we used 1 variable, contact rate, to examine contact patterns. Distribution of contacts/day did not fit the expected Poisson distribution for any dyad type ($\chi^2_2 \geq$

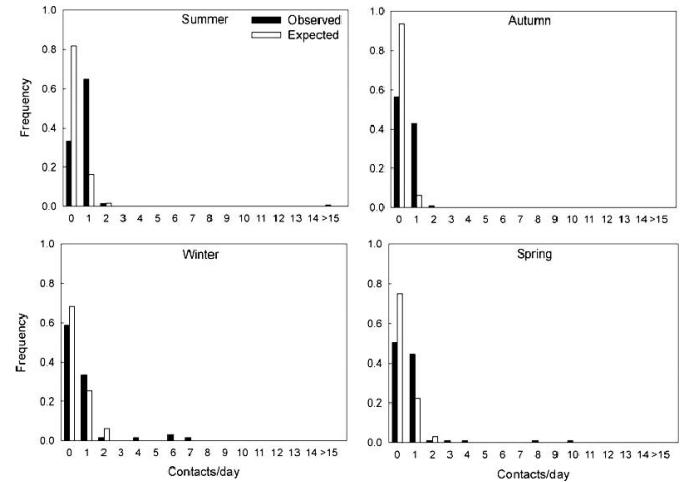


FIG. 3.—Expected and observed distribution of contacts for female-female dyads during summer, autumn, winter, and spring at the Ned Brown Forest Preserve in Cook County, Illinois.

12.50, $P \leq 0.002$), except FF dyads during winter ($\chi^2_2 = 1.24, P = 0.539$; Fig. 3). Although overall FF contact rates were random during winter, some dyads had values beyond the upper end of the expected distribution. FF dyads diverged from a random distribution by having fewer zero values and a greater number of intermediate values than expected (Fig. 3), MM dyads exhibited greater than expected contact rates at the upper and lower ends of the distribution (Fig. 4), and the distribution of MF contact rates was similar to that of FF dyads, except during winter when their distribution resembled that of MM dyads (Fig. 5).

During all seasons the majority of males (54–77%) exhibited a positive association with at least 1 other male. Nine, 8, 7, and 5 MM dyads exhibited positive associations during summer, autumn, winter, and spring, respectively. Based on patterns of contacts during summer, we identified 4 MM groups (Table 1). Two were single dyads (groups 1 and 2), whereas 2 were larger groups of 3 and 4 raccoons (groups 3

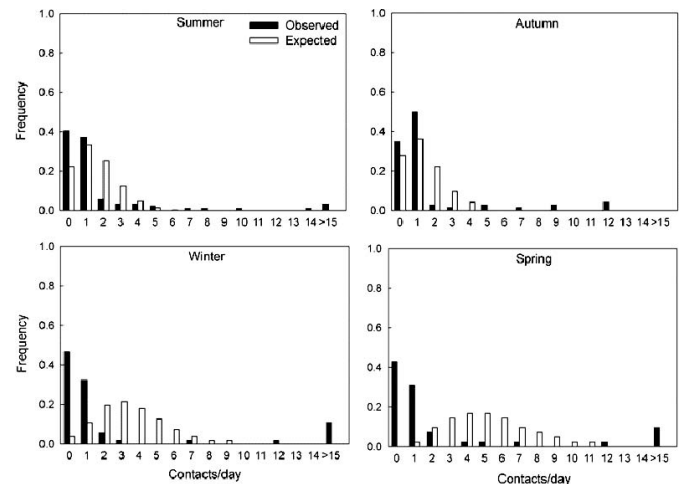


FIG. 4.—Expected and observed distribution of contacts for male-male dyads during summer, autumn, winter, and spring at the Ned Brown Forest Preserve in Cook County, Illinois.

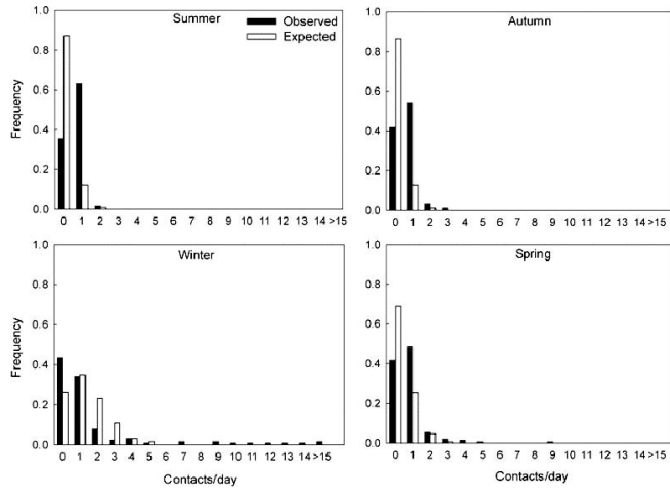


FIG. 5.—Expected and observed distribution of contacts for male–female dyads during summer, autumn, winter, and spring at the Ned Brown Forest Preserve in Cook County, Illinois.

and 4, respectively). By winter, dyads in groups 3 and 4 continued to exhibit positive associations, whereas the group 1 dyad did not, and 1 member of group 2 was lost, presumably due to dispersal. By spring group 1 disbanded, and each member exhibited a positive association with 1 or more members of either group 3 or 4 (Table 2). Four young males failed to exhibit a positive association with another male during any season monitored.

Seven MM dyads shared dens on 24 occasions, 8 on 106 occasions, 10 on 99 occasions, and 9 on 89 occasions during summer, autumn, winter, and spring, respectively. All group members shared dens at some point, and all den sharing was between group members, except for several instances of solitary male 6491 sharing a den with 1 member of group 3 during winter and spring. More than 2 males shared the same den simultaneously during autumn (3 together 8 times), winter (3 together on 13 occasions), and spring (3 raccoons together 14 times, with 4 sharing a den on 1 occasion).

Because of collar malfunctions and full memory banks, especially during winter, we had insufficient data to establish contact rates for all MM dyads during all seasons. Based on available data, it appeared that most positive associations between group 3 and 4 members persisted across seasons (Table 1). However, although all group members were positively associated with one another, they were seldom all together at the same time. Pairs of males formed, separated, and reformed over the course of hours or days (Fig. 6).

Home-range overlap was greater within (summer, $\bar{X} \pm SD = 72.0\% \pm 5.5\%$; autumn, $57.9\% \pm 7.1\%$; spring, $43.9\% \pm 21.1\%$) than between group members (summer, $11.5\% \pm 9.0\%$; autumn, $9.4\% \pm 11.6\%$; spring, $17.0\% \pm 14.9\%$) during all seasons (summer: $F_{1,34} = 83.56, P < 0.001$; autumn: $F_{1,43} = 128.81, P < 0.001$; spring: $F_{1,26} = 25.97, P < 0.001$). Additionally, all MM dyads with significant contact rates exhibited core-area overlap (summer, $33.9\% \pm 17.0\%$; autumn, $35.1\% \pm 22.7\%$; spring, $13.8\% \pm 20.0\%$), whereas no core-area overlap occurred between males in different groups during summer, and core areas of members of groups 3 and 4 remained exclusive during all seasons. Home-range and core-area overlap of solitary males with group members were variable, but all solitary males exhibited core-area overlap (summer, $12.7\% \pm 16.1\%$; autumn, $25.6\% \pm 30.0\%$; spring, $31.4\% \pm 12.8\%$) with members of only 1 of the 2 larger groups.

Because groups 1 and 2 were short lived and did not persist into the breeding season, we compared the number of females' home ranges and core areas overlapped for large group members with that of single dyads and solitary males combined. During summer, members of larger groups did not overlap more female home ranges ($\bar{X} \pm SD = 14.2 \pm 1.5$) than solitary males and single dyad group members ($13.8 \pm 1.6; F_{1,11} = 0.26, P = 0.620$); however, members of larger groups did overlap a significantly greater number of female core areas (5.6 ± 0.5 versus $2.0 \pm 1.8; F_{1,11} = 17.41, P = 0.002$). This relationship did not hold during autumn; members of larger groups did not share home ranges or core areas with more females (home range, 10.5 ± 2.2 ; core area, 3.7 ± 2.3)

TABLE 1.—Group, dyad members (A and B), age class (see “Materials and Methods” for definitions), mean contacts/day (rate), probability of mean contact rate (*P*), and mean duration of contacts/day in minutes (duration) for positively associated male–male dyads by season (summer 2004–spring 2005) at the Ned Brown Forest Preserve in Cook County, Illinois. Groups are based on summer 2004 contact rates. Significant *P*-values are in boldface type.

Group	Dyad members		Age class		Summer			Autumn			Winter			Spring		
	A	B	A	B	Rate	<i>P</i>	Duration	Rate	<i>P</i>	Duration	Rate	<i>P</i>	Duration	Rate	<i>P</i>	Duration
1	6308	6407	II	II	22.1	<0.001	151	11.9	<0.001	119	0.8	0.979	6	0.04	0.999	<1
2	6328	6424	II	II	10.0	<0.001	64	8.9	<0.001	81						
3	6453	6462	III	IV	13.4	<0.001	20	6.8	<0.001	35	21.8	<0.001	163			
3	6453	6482	III	I	4.6	0.031	8	2.9	0.149	8	11.0	<0.001	97			
3	6462	6482	IV	I	7.7	<0.001	36	14.4	<0.001	157	15.5	<0.001	163			
4	6468	6485	I	III	6.4	0.002	7	4.8	0.013	38				4.6	0.632	7
4	6468	6488	I	II	4.3	0.046	28	8.3	<0.001	119	28.2	<0.001	334			
4	6485	6488	III	II	16.0	<0.001	40	19.9	<0.001	216	60.3	<0.001	545			
4	6488	6490	II	III	22.5	<0.001	124									
4	6468	6490	I	III										36.1	<0.001	238
4	6485	6490	III	III										12.1	0.005	125

TABLE 2.—Dyad members (A and B), age class (see “Materials and Methods” for definitions), mean contacts/day (rate), probability of mean contact rate (*P*), and mean duration of contacts/day in minutes (duration) by season (summer 2004–spring 2005) for males from group 1 (member A) with those from groups 3 or 4 (member B) at the Ned Brown Forest Preserve in Cook County, Illinois. Groups are based on summer 2004 contact rates. Significant *P*-values are in boldface type.

Dyad members		Age class		Summer			Autumn			Winter			Spring		
A	B	A	B	Rate	<i>P</i>	Duration	Rate	<i>P</i>	Duration	Rate	<i>P</i>	Duration	Rate	<i>P</i>	Duration
6308	6453	II	III	2.1	0.402	<1	0.2	0.964	<1	2.01	0.852	4			
6308	6462	II	IV	0.1	0.989	<1	1	0.753	3	17.0	<0.001	150	15.6	<0.001	178
6308	6482	II	I	3.7	0.092	22	45	0.013	118	20.4	<0.001	255	1.3	0.987	2
6407	6468	II	I	0.1	0.988	<1	0.01	0.998	<1	1.2	0.951	384	30.9	<0.001	170
6407	6485	II	III	0.02	0.998	<1	0	1.000	0	0.1	0.999	7	0.6	0.998	1
6407	6488	II	II	0.02	0.998	<1	0.01	0.998	<1	0.5	0.991	79	6.2	0.352	13
6407	6490	II	III	0	1.000	0							9.6	<0.001	576

than single dyad members and solitary males (home range, 11.6 ± 2.5 , $F_{1,11} = 0.47$, $P = 0.507$; core area, 4.4 ± 1.4 , $F_{1,11} = 0.12$, $P = 0.737$). However, members of larger groups exhibited a greater degree of spatial overlap with females than did other males ($39.4\% \pm 20.8\%$ versus $26.8\% \pm 16.9\%$, $F_{1,48} = 4.27$, $P = 0.044$).

The number of positive associations for MF dyads peaked during winter, but positive associations were observed during all seasons. Two, 6, 13, and 7 MF dyads exhibited positive associations during summer, autumn, winter, and spring, respectively (Table 3). Females associated with up to 5 different males, and they almost always (93%) associated only with males from 1 of the larger groups. We collected data for all seasons for 16 of 19 dyads with positive associations. Of these, none persisted across all seasons, 2 exhibited positive associations during 3 seasons, 4 during 2 seasons, and 10 during 1 season only (Table 3). In some cases females essentially became temporary members of 1 of the 2 larger groups. As with MM groups, subgroups formed, separated, and reformed within hours or days.

One MF dyad shared a den site on 1 occasion, 5 on 9 occasions, 31 on 173 occasions, and 13 on 36 occasions, during summer, autumn, winter, and spring, respectively. Two males denned simultaneously with the same female on 1 occasion, ≥ 2 males on 17 occasions (2 males 16 times and 3 males 7 times), and 2 males 6 times during autumn, winter, and spring, respectively. Females denned almost exclusively with members of only 1 male group. Not all MF dyads

with significant interactions shared dens during summer and autumn, but all positively associated dyads during winter and spring did. However, most MF dyads that shared a den during the breeding season (i.e., winter) did not contact one another enough for their overall contact rate to be significantly greater than expected. Thirteen MF dyads exhibited significant contacts during winter, but 31 MF dyads denned together at least once.

Positive associations between females were observed during all seasons except autumn, and $\geq 50\%$ of females exhibited a positive association with at least 1 other female during winter and spring. Three, 7, and 4 FF dyads exhibited positive associations during summer, winter, and spring, respectively (Table 4). We had complete seasonal data for 7 of 9 positively associated dyads. Positive associations for only 2 dyads lasted for 2 seasons, with the remaining lasting 1 season only (Table 4). One FF dyad shared a den site on 10 occasions, 1 on 1 occasion, 5 on 28 occasions, and 6 on 29 occasions during summer, autumn, winter, and spring, respectively. Den sharing was not confined to dyads with significant positive associations, although all dyads with significant contact rates during winter and spring shared dens.

DISCUSSION

Contact rate and duration were greater for MM dyads, in agreement with our predictions and previous studies (Chamberlain and Leopold 2002; Gehrt and Fritzell 1998b). Previous studies also documented male groups ranging in size from 2 to 5, which is similar to that observed during our study (Chamberlain and Leopold 2002; Gehrt and Fritzell 1998b; Pitt et al. 2008). The groups we observed, in contrast to previous studies, did not exhibit largely exclusive home ranges, but group core use areas were exclusive for the 2 larger male groups during all seasons, lending support to our definition of groups based on contact rates. Group membership also did not confer benefits in the form of exclusive overlap of female home ranges. However, members of larger groups were potentially able to access a greater number of females through greater core-area overlap. The reason for differences between studies could be related to population density. Our study area was an urban forest preserve; raccoon density was high (up to approximately

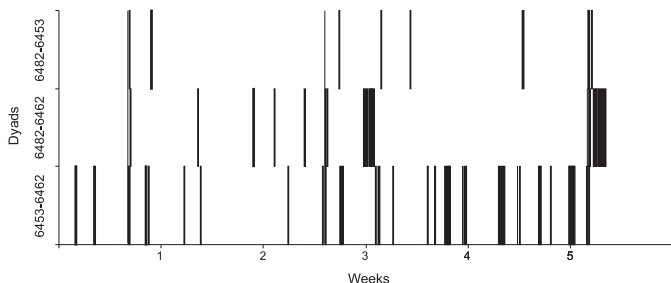


FIG. 6.—Example of male–male (MM) group dynamics: time spent together (indicated by black bars) for each dyad within MM group 3 during August 2004 at the Ned Brown Forest Preserve in Cook County, Illinois.

TABLE 3.—Dyad members (A and B), age class (see “Materials and Methods” for definitions), sex, contacts/day (rate), probability of contact rate (*P*), and mean duration of contacts/day in minutes (duration) for male–female dyads that were positively associated during any season (summer 2004–spring 2005) at the Ned Brown Forest Preserve in Cook County, Illinois. Significant *P*-values are in boldface type. M = male; F = female.

Dyad members		Age class		Sex		Summer			Autumn			Winter			Spring		
A	B	A	B	A	B	Rate	<i>P</i>	Duration	Rate	<i>P</i>	Duration	Rate	<i>P</i>	Duration	Rate	<i>P</i>	Duration
6407	3625	II	V	M	F	1.4	0.050	4	0.2	0.727	<1	0.2	0.968	<1	0.05	0.961	<1
6468	4047	I	IV	M	F	1.7	0.023	6	0.01	0.985	<1	0.04	0.994	<1	0.2	0.842	<1
6453	6115	III	III	M	F	0.1	0.853	<1	1.4	0.049	3	0	1.000	0	0	1.000	0
6482	6115	I	III	M	F	0.3	0.599	<1	1.5	0.040	4	0	1.000	0	0	1.000	0
6485	4005	III	III	M	F	1.1	0.102	1	2.5	0.002	8	12.3	<0.001	143	2.9	0.008	27
6485	4014	III	V	M	F	0.8	0.209	3	2.3	0.004	23	19.9	<0.001	136	0.1	0.922	<1
6488	4005	II	III	M	F	0.6	0.327	<1	1.6	0.031	25	10.8	<0.001	90			
6488	4014	II	V	M	F	0.4	0.493	<1	1.6	0.031	16	11.5	<0.001	57			
6308	4047	II	IV	M	F	0.2	0.718	<1	0.2	0.727	<1	7.0	<0.001	87	1.6	0.114	13
6407	4014	II	V	M	F	0.1	0.853	<1	0.04	0.942	<1	6.2	0.022	43	2.9	0.008	20
6453	4047	I	IV	M	F	0.1	0.853	<1	0.1	0.858	<1	4.0	0.043	37	1.0	0.309	4
6462	4047	IV	IV	M	F	0.5	0.403	<1	0.3	0.610	<1	8.2	<0.001	165	3.6	0.002	22
6468	4005	I	III	M	F	0.5	0.403	<1	1.2	0.086	8	13.8	<0.001	149	4.2	<0.001	90
6482	4047	I	IV	M	F	0.5	0.403	<1	0.6	0.339	<1	9.8	<0.001	250	0.7	0.474	4
6488	6115	II	III	M	F	0.1	0.853	<1	0.1	0.858	<1	8.6	<0.001	54			
6308	6456	II	II	M	F	0.1	0.853	<1	0	1.000	0	4.2	0.033	86	4.0	<0.001	82
6453	6456	I	II	M	F	0.7	0.263	<1	0.1	0.858	<1	14.3	<0.001	143	0.3	0.763	<1
6308	3625	II	V	M	F	0.6	0.327	<1	0.1	0.858	<1	3.4	0.096	39	2.5	0.019	63
6407	4005	II	III	M	F	0.04	0.940	<1	0.01	0.985	<1	1.4	0.589	12	8.3	<0.001	81

75 raccoons/km²—Prange et al. 2004), and spatial distribution of females was aggregated during most seasons. High density and an aggregated distribution of females are conducive to the formation of male groups (Caro 1994; Connor and Whitehead 2005; Gehrt and Fritzell 1998b; Wittenberger 1980); however, at some density the maintenance of exclusive home ranges and the complete sequestering of females might no longer be energetically beneficial.

Solitary males were young, primarily yearlings, and may have been in the process of attempting to incorporate themselves into a group. In support of this, solitary male 6491 increased his spatial overlap with members of group 3 and denned with a member of group 3 during winter and spring. The effect of age on contact rates of MM dyads was marginally nonsignificant, with dyads containing older males having greater rates. This might be indicative of a weak effect of age or an effect that would have been evident given a larger sample

size. Pitt et al. (2008) noted that in all cases where only 1 male of an original coalition remained (due to the death or emigration of others) the remaining male formed a new coalition with a young, solitary male.

Results of seasonal analyses suggested that most MM dyads with positive associations maintained them year-round, similar to previous observations (Chamberlain and Leopold 2002; Gehrt and Fritzell 1998b). However, during winter a single dyad group dissolved, and each member joined 1 of the 2 larger groups. The shift occurred prior to or during the breeding season, when benefits of membership in larger groups would presumably be greatest. Small groups might be less stable than larger ones, and Waser et al. (1994) found that smaller groups of slender mongooses (*Galerella sanguinea*) had the shortest tenure.

We observed more long-term positive associations for MF dyads than expected. Some females essentially became tem-

TABLE 4.—Dyad members (A and B), age class (see “Materials and Methods” for definitions), contacts/day (rate), probability of contact rate (*P*), and mean duration of contacts/day in minutes (duration) for female–female dyads that were positively associated during any season (summer 2004–spring 2005) at the Ned Brown Forest Preserve in Cook County, Illinois. Significant *P*-values are in boldface type.

Dyad members		Age class		Summer			Autumn			Winter			Spring		
A	B	A	B	Rate	<i>P</i>	Duration	Rate	<i>P</i>	Duration	Rate	<i>P</i>	Duration	Rate	<i>P</i>	Duration
3625	6456	V	II	1.6	0.047	2	0.3	0.494	<1	0.3	0.767	<1	1.3	0.146	4
4014	6473	V	I	15.1	<0.001	102	0	1.000	0				0.1	0.906	<1
6115	6473	III	I	1.9	0.022	5	0.3	0.494	<1				0.05	0.953	<1
4005	4014	III	V	0.4	0.560	<1	0.6	0.221	5	3.7	0.001	23	7.3	<0.001	66
4005	6115	III	III	0.04	0.951	<1	0.1	0.800	<1	5.2	<0.001	37	0.02	0.981	<1
6425	6326	IV	III	0.3	0.657	<1	0.1	0.800	<1	5.3	<0.001	64	3.9	<0.001	83
6456	4047	II	IV	0.3	0.657	<1	0	1.000	0	6.5	<0.001	82	0.2	0.812	<1
6416	3625	II	V	0.2	0.764	<1	0.3	0.494	<1	0.4	0.690	3	3.0	0.003	28
6456	6493	II	I	0.1	0.879	<1	0	1.000	0	0.1	0.924	<1	9.5	<0.001	146

porary members of male groups. In support of this, the distribution of contact rates for MF dyads during winter differed from that of other seasons and was similar to that of MM dyads, indicative of selectivity in terms of contacts and possible group formation. MM and MF contact rates were greatest during winter, as predicted; however, in some cases significant positive associations occurred prior to or following the breeding season, or both. Although we predicted older males would be more likely to form positive associations with females, we also found that males exhibited positive associations primarily with older females. These females might have been guarded preferentially because of the greater likelihood of their successfully rearing a litter, or males might have established relationships with them over time.

At high densities raccoons exhibit a promiscuous mating system, and multiple paternity of litters appears to be common (Roy Nielsen and Nielsen 2007). Furthermore, Gehrt and Fritzell (1999) believed males formed breeding hierarchies within groups. These facts support the contention that increased MM contact rates during winter occurred due to increased mate guarding. Additionally, group males continued to share den sites during winter, even in the absence of a female, which suggests a lack of antagonistic behavior. However, the possibility remains that the apparent increase in male group cohesiveness during the breeding season resulted from increased competition among group males for females.

Female raccoons consistently have been characterized as solitary (Pitt et al. 2008). However, contrary to our predictions, we observed positive MF associations that did not appear to be related to securing breeding opportunities (e.g., those occurring during summer). We also observed positive FF associations. One FF dyad traveled and denned together often during summer. Furthermore, we found that >50% of females during winter and spring formed positive associations with other females. Positive FF associations, however, were ephemeral, typically forming and dissolving over the course of 1 season. Benefits of these associations were unclear. Extended familial bonds that enhance transfer of knowledge, such as locations of food sources, could explain summer associations, because 1 member of each dyad was relatively young (age class I or II). However, the age of members of most dyads with significant contact rates during winter and spring suggested that these associations did not represent extended familial bonds, unless these bonds are capable of lasting throughout life. Benefits of associations during winter and early spring likely include denning together to decrease the thermoregulatory stress of cold weather. It is also possible that benefits of FF associations vary seasonally. In support of this, all FF dyads with significant positive interactions during winter and spring shared den sites on multiple occasions, whereas only 1 of 3 positively associated dyads shared dens during summer.

A greater proportion of low-frequency contacts (approximately 1 contact/day) than expected occurred for dyads containing females during all seasons except winter. The fact that FF contact rates did not fit the predicted random Poisson

distribution during most seasons, with fewer near-zero contact rates than expected, suggests that females were not completely avoiding one another. Low-frequency contacts might reinforce social hierarchies or friendly relationships with neighbors and contribute to the raccoon's ability to share space in dense populations with highly overlapping home ranges. For MF dyads low-frequency contacts might serve to maintain relationships and increase subsequent mating success. Low-frequency contacts, along with positive, albeit ephemeral, associations between females might set the stage for more complex social relationships should conditions arise where their benefits outweigh costs. Alternatively, low-frequency contacts among females might constitute antagonistic behavior, such as the enforcement of boundaries. Additional research is needed to clarify the nature of these contacts, which will enhance our understanding of social interactions among female raccoons. The absence of this pattern during winter for FF dyads might have been due to decreased activity during extended periods of cold temperatures.

Individual association patterns can be used to characterize a species' social system. If the association of individuals is not random, the society is structured (Smolker et al. 1992). Fission–fusion is a social system in which the entire group rarely coalesces, but subgroups exist with variable membership (Connor and Whitehead 2005; Rhodes 2007). The fission–fusion social system has been described with increasing frequency in a variety of mammalian taxa (Connor and Whitehead 2005; Rhodes 2007; Wittemyer et al. 2005). Within Procyonidae kinkajous (*Potos flavus*) exhibit a fission–fusion social system that might have evolved in response to both predation risk and resource availability (Kays and Gittleman 2001).

The social system of raccoons is more complex than previously recognized. Raccoons at our study site appeared to live in a fission–fusion society made up of short-term casual acquaintances and a smaller number of long-term positive associations. Females temporarily fused with male groups, possibly for mating purposes, and positively associated FF dyads formed and dissolved fairly rapidly. van Schaik (1999) defined 2 types of fission–fusion societies, those that live in permanent social groups and tend to fission into smaller parties (group-based fission–fusion; e.g., long-tailed macaques [*Macaca fascicularis*]—van Schaik and van Noordwijk 1988), and those that live in social units that are only recognizable through the analysis of association patterns, with individuals that are often solitary (individual-based fission–fusion; e.g., orangutans [*Pongo pygmaeus*]—van Schaik 1999). Clearly, raccoons fall into the latter category. In individual-based fission–fusion, groups tend to be small and benefits tend to be social rather than ecological (e.g., food access—van Schaik 1999).

Aureli et al. (2008) further classified “lower” and “higher” fission–fusion dynamics that represented relative points within a multidimensional fission–fusion space consisting of variation in spatial cohesion, party size, and party composition. Systems characterized as lower fission–fusion

have relatively greater temporal stability in membership and cohesion. MM dyads exhibited lower fission–fusion dynamics than MF or FF dyads. Although party size and composition changed frequently, overall group membership appeared to be relatively stable across the course of a year.

Females essentially fused into MM groups beginning in autumn and continuing into spring. As in MM groups, individual subgroups of 1 female and 1–3 males formed, dissolved, and reformed quickly over time, with overall groups being stable for 1 or more seasons. FF dyads exhibited transient positive associations and a greater than expected number of short-duration contacts with conspecifics. Larger groups, if they existed, were not apparent from our analyses but might involve a loose network of associations with stronger, yet transient, positive associations forming among dyads. Similarly, Smolker et al. (1992) described sexual differences in patterns of associations for bottlenose dolphins (*Tursiops truncatus*) and found male groups but concluded that FF associations were better described as a network than discrete groups. The evolutionary route from solitary to higher fission–fusion groups might begin with associations that are short-lived and opportunistic (Aureli et al. 2008), and it may be easier to form these associations with familiar conspecifics. Low-level contacts among female raccoons might serve to maintain familiarity and facilitate these associations.

Overall, raccoons at our study site exhibited considerably high fission–fusion dynamics in comparison with more gregarious species. Both males and females spent the majority of their time alone, with frequent fission and fusion events occurring among group members. An important aspect of fission–fusion dynamics is their apparent flexibility; they can differ between populations within a species or within a population between sexes or over time (Connor et al. 2000; Strier 2003). Dalerum et al. (2006) suggested that social flexibility, rather than a strictly solitary existence, was the original state from which all social systems in Carnivora evolved. Examination of the social system of socially flexible species, such as the raccoon, under a variety of ecological constraints might provide insight into the evolution of social systems in other species. In particular, additional work using proximity-detecting collars or similar technology is needed for raccoons occupying more rural landscapes, including both agricultural landscapes where edges might concentrate raccoon activity and large blocks of contiguous forest where activity should be more dispersed. Because of the apparent flexibility of raccoon behavior, thorough analyses of behaviors in a variety of landscapes supporting different densities of raccoons and differing in the abundance and spatial distribution of resources are necessary before a clear picture of raccoon sociality and its driving forces can emerge.

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