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BEHAVIORAL AND GENETIC ASPECTS OF MALE SOCIAL GROUPS IN RACCOONS

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Many mammalian species exhibit intersexual differences in sociospatial behavior; however, sociality of adult males in species with solitary females is relatively rare. Male raccoons (*Procyon lotor*) in southern Texas form social groups that have many similarities to male coalitions in other species, including spatially distinct home-range boundaries that are maintained year-round. Within these groups, males rest and travel together with varying frequencies. However, the length of social bonds and genetic relationships among group males are unknown. We quantify characteristics of male social groups for raccoons in southern Texas, examine the genetic structure of the population, and finally test whether variation in relatedness within groups is related to the frequency or length of association between males. Mean proportions of locations within 50 or 100 m for each dyad ranged from 0.04 to 0.48 for the duration of group membership, although most dyads had means between 0.20 and 0.30. Duration of dyads ranged from 6 to 39 months, with a mean of 18.4 months. Mean band-sharing coefficient for males within groups was not different (1-tailed $P = 0.376$) from males between groups. However, mean coefficient for males within groups was lower ($P < 0.01$) than that for litters, suggesting that male groups were not exclusively composed of close relatives. Genetic relatedness explained little of the variation of proportions of locations within 50 or 100 m within groups (1-tailed $P = 0.26$); however, band-sharing coefficients were positively related (1-tailed $P = 0.06$) to duration of associations within groups. Kin selection does not appear to explain male sociality in raccoons, but relatedness may be related to the length of associations between males within groups.

Key words: coalition, genetics, *Procyon lotor*, raccoon, relatedness, social behavior, Texas

For many mammalian species, males and females exhibit distinct differences in social behavior and spacing patterns. This pattern reflects differences in determinants of sociospatial systems between the sexes; the distribution of resources influences spacing patterns of females, and the distribution of females affects sociospacing systems of males (Clutton-Brock 2002; Macdonald 1983; Sandell 1989; Wrangham 1980). This relationship is particularly true for polygynous species, in which males do not assist in raising of young, and reproductive success of females is closely tied to efficient exploitation of resources (Clutton-Brock 1989; Rowell 1988; Silk 2007). Given that females of polygynous species typically are philopatric (Waser and Jones 1983), it is often the case that related females live in close proximity. Thus, assessments of social behavior among mammalian species typically focus on females (Silk 2007) because inclusive fitness or mutualism among relatives is generally considered to facilitate social bonds (Clutton-Brock 2002; Waser and Jones 1983).

Although philopatry provides a pathway for sociality among females via kin selection (Clutton-Brock 2002; Silk 2007), there are nevertheless a number of mammalian species with sociality among adult males. Male sociality in the form of alliances or coalitions has been observed for species representing a wide range of taxonomic groups, such as primates (baboons [*Papio cynocephalus*—Bercovitch 1988] and chimpanzees [*Pan troglodytes*—Watts 1998, 2004]), carnivores (lions [*Panthera leo*—Grinnell et al. 1995] and river otters [*Lontra Canadensis*—Blundell et al. 2002]), and cetaceans (dolphins [*Tursiops*—Connor et al. 1992]). However, nearly all of these species are considered social, with both sexes exhibiting social aggregations.

Relatively rare is the system in which males form coalitions or social bonds whereas females are solitary. Male coalitions have been described for few solitary species within Carnivora, including cheetahs (*Acinonyx jubatus*—Caro 1994), slender mongooses (*Herpestes sanguineus*—Waser et al. 1994), and kinkajous (*Potos flavus*—Kays and Gittleman 2001). For each of these species, male coalitions appear to be a response to the

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spatial distribution of females, in which male groups maintain exclusive access to females for mating opportunities.

Male coalitions within solitary species are something of a paradox because sociality is often assumed to derive from aggregations of closely related females (Silk 2007; Waser and Jones 1983). Because males of most species disperse from natal areas, close male relatives rarely are located near each other, which presumably limits the potential for sociality. However, in some mammals natal dispersal by males is nonrandom and relatives settle near each other (Cheney and Seyfarth 1983), or siblings disperse and settle together as cohesive units (Caro 1994), thereby providing an opportunity for inclusive fitness in male–male bonds.

Male coalitions or social groups may evolve through 3 pathways: kin selection (Hamilton 1964), mutualism (Dugatkin 1997), or reciprocity (Trivers 1971). Each of these mechanisms may yield similar behavioral patterns, and each may involve close relatives; however, kin selection is separated from the others by the requirement that participants must be closely related. The other 2 mechanisms are discriminated by the nature of interactions between the participants, and whether cooperation is dependent on previous acts. Thus, these scenarios do not require associations with relatives (e.g., primates—Van Hooff and Van Schaik 1994). Indeed, ecological benefits through associations of nonkin have been observed for male coalitions of some species (e.g., chimpanzees [Mitani et al. 2000] and river otters [Blundell et al. 2004]).

Male raccoons (*Procyon lotor*) in southern Texas form social groups that have many similarities to male coalitions in other species. They form stable groups of 3–5 members that have little spatial overlap with other male groups, and group males form social bonds that include resting together during the day and traveling as a pair or group at night (Gehrt and Fritzell 1998a). Although group males have social bonds while resting and foraging through much of the year, there apparently is competition between males within groups and solitary males for access to estrous females during the mating season. During peak mating periods when females are in estrus, group males do not associate with each other and there is variation in success of consortships among males during the mating season (Gehrt and Fritzell 1999a), but group boundaries still are maintained. After the mating period, males resume their associations within the group or they may terminate associations and leave the group.

Male social groups have not been described for other raccoon populations, but may be more widespread than is currently recognized. Studies in Kansas (Gehrt and Fox 2004) and Mississippi (Chamberlain and Leopold 2002) have reported social bonds among adult males. Further, genetic relationships within raccoon coalitions are unknown. Published studies evaluating the ecological importance of kin relationships in raccoons are few, particularly those with a focus on genetic relatedness and social behavior. Recent studies of the spatial pattern of relatedness of raccoons have reported a relationship between spatial distance and genetic relatedness for females that was consistent with female natal philopatry, whereas there was little relationship between geographic distance and relatedness for males (Ratnayeke et al. 2002; Roy Nielsen and Nielsen 2007). However, no studies have determined the relationship between genetic relatedness and the sociospatial system of male raccoons.

Within our study population, females are philopatric, whereas males typically disperse from natal areas. Thus, adult females in a local population often are closely related and occur in a series of matrilines, whereas the relatedness of resident adult males is not known (Gehrt and Fritzell 1998b). Given that young males leave their natal areas and male groups are composed of different-aged males, it is unlikely that group males are closely related. However, if siblings disperse together or if direction and distance of dispersal are nonrandom, then the possibility exists that male groups are composed of related individuals.

In this paper, we provide a more detailed description of associations of male raccoons from the study of Gehrt and Fritzell (1998a) for comparisons with male coalitions from other carnivores. Although Gehrt and Fritzell (1998a) reported that group males associate with each other during the year, including denning and traveling together, they did not provide details on the length and frequency of the associations within groups. Intra- and interspecific comparisons of these characteristics of coalitions may provide important insight into the evolution of such social systems.

Materials and Methods

The study area was located on a portion of the 3,157-ha Welder Wildlife Refuge in southern Texas (28°8′N, 97°22′W). The refuge is located in a transitional zone between 2 major vegetational communities: the Gulf Prairies and Marshes and the South Texas Plains (Drawe et al. 1978). The climate is subtropical, and ambient temperatures rarely drop below freezing. The raccoon population had been protected from harvest since the early 1950s.

Fieldwork was conducted between February 1990 and July 1992. Our trapping design was described in detail by Gehrt and Fritzell (1996, 1998a). Briefly, livetrapping with box live traps was focused on a 350-ha core area located near the center of the refuge. The goal of the trapping was to ensure that all raccoons that resided in the core area were radiocollared (Advanced Telemetry Systems, Inc., Isanti, Minnesota). Trapping sessions were conducted during each spring and autumn. In addition to trapping, offspring of radiocollared females were ear-tagged (#3 Monel; National Band and Tag Company, Newport, Kentucky) from natal dens and radiocollared when they reached a sufficient size (Gehrt and Fritzell 1998b). Our research protocol was approved by the University of Missouri Animal Care and Use Committee, and was conducted under Scientific Permits SPR0290-004 and SPR0191-333 from the Texas Parks and Wildlife Department. Research met guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Radiocollared raccoons were monitored continuously during the field portion of the study, and the monitoring protocol is described in detail elsewhere (Gehrt and Fritzell 1997, 1998a).

Locations of all radiocollared raccoons were obtained during diurnal hours by approaching each raccoon on foot with a portable receiver and handheld antenna once per day, usually 5 days/week throughout the year. Immediately before daytime tracking, raccoons were scanned with the receiver to determine activity based on signal modulation. Once raccoons became inactive after the previous night's foraging, they were approached to record rest sites and visual observations if possible. Raccoons were tracked at night via triangulation during 2–4 tracking shifts per week. All raccoons in the core area were located each hour during 6-h shifts. Each location also was recorded as active or inactive based on signal modulation (night locations) or visual observation (daytime locations). Peripheral raccoons captured outside the core area were monitored opportunistically at night. During 1990 and 1991, adult raccoons residing within and immediately adjacent to the core area were distributed into 2 spatial groups (Gehrt and Fritzell 1997). In 1992, home ranges of females were not as aggregated as in previous years and a 3rd group of males formed between the 2 groups.

Gehrt and Fritzell (1998a) identified male spatial groups and dynamic interaction among male dyads within those groups. We used results from that analysis to provide estimates of the frequency of associations between males and duration of male–male bonds. In that study, radiotelemetry data were partitioned into seasons (spring [March–May], summer [June–August], autumn [September–November], and winter [December–February]), and within each season the data were further partitioned into diurnal and nocturnal periods. For each dyad within a group we calculated the proportion of simultaneous locations that occurred within a critical distance during a season. Critical distance between simultaneous locations was 50 m for diurnal locations and 100 m for nocturnal locations, which encompassed our radiotelemetry error (Gehrt and Fritzell 1998a).

For analytical purposes, simultaneous locations were locations of 2 individuals recorded within 4 h of each other during the day when both animals were inactive, and within 20 min of each other at night when both animals were active, although in most instances the time interval was much less than 20 min (Gehrt and Fritzell 1998a). The longer time interval for diurnal locations was necessary because raccoons were located on foot, which provided important information on dyads through visual observations (Gehrt and Fritzell 1998a). However, this time interval should not have affected our results. The dynamic interaction test does not necessarily assume that paired locations truly are simultaneous, only that the length of time does not influence the probability of a dyad occurring within the critical distance. Thus, we only included locations for analysis of inactive raccoons during the day and only active locations during the night. Activity was determined by signal modulation, or visual sightings, at the onset, and during, a radiotracking shift.

The proportion of locations within 50 or 100 m (f_{ij}), or the number of simultaneous locations in which animals i and j were within the critical distance, divided by the total number of simultaneous locations for animal i or j (sample sizes were necessarily equal between animals), was initially determined separately for diurnal (50 m) and nocturnal (100 m) periods with a dynamic interaction test (Doncaster 1990) for each pair. This initial separation of data was necessary because of the differences in critical time intervals and distances between diurnal and nocturnal periods. We subsequently pooled data for both activity periods to provide a general proportion of locations within 50 or 100 m for each dyad within a season because patterns were similar between active periods for each dyad. Frequencies of significant dynamic interaction tests were not different between diurnal and nocturnal data (Gehrt and Fritzell 1998a), and seasonal proportions of locations within 50 or 100 m were highly correlated ($r = 0.78$, $n = 40$, $P < 0.001$) between activity periods. Seasonal estimates of proportions of locations within 50 or 100 m were used to determine an overall mean proportion of locations within 50 or 100 m for each dyad monitored for $\geq$2 seasons. All male pairs for which a proportion of locations within 50 or 100 m was determined exhibited high levels of home-range overlap (i.e., $>$80%) and significant positive dynamic interaction, which was reported elsewhere (Gehrt and Fritzell 1998a).

We also tabulated the number of months each male remained within a particular social group. A follow-up study was conducted in 1993, in which the core group of males was radiotracked from January to July (Clark 1994). Because the monitoring protocol essentially was identical to that of the original study, we used data from this follow-up study to assess the duration of male associations within groups. Our measures of duration are underestimates because many associations had begun before the initiation of the original study, and the study ended before some associations broke up.

Preparation of DNA profiles.—Blood or tissue samples were collected for genetic analysis from most (9 of 12) radiocollared male raccoons and from offspring of radiocollared females that were collected from natal dens or as juveniles traveling with the mother. Tissue was obtained from ear punches of some radiocollared raccoons, and a portion of a liver or kidney for some females collected as part of a study that continued after our fieldwork (Clark 1994). DNA profile tests were performed by Therion Corporation (now Therion International, LLC, Saratoga Springs, New York) using the following procedures: DNA was extracted from each sample using a standard organic (phenol—phenol–chloroform) extraction protocol and DNA quality was examined with an agarose yield gel. The DNA was then cleaved (conditions specified by supplier) with 20 units of restriction enzyme Bstn I (BRL, Bethesda, Maryland) per microgram of DNA. Completeness of digestion was monitored by comparison to controls on an agarose gel. One microgram of digested DNA from each individual was loaded onto a 1% agarose analytical gel. Molecular weight sizing standards were loaded in up to 3 lanes so that samples were bracketed by molecular weight sizing standards. The set of standard DNA fragments of known molecular size was composed of 48 bands ranging from 0.504 to 34.679 kilobase pairs. Gels were run in 40 mM Tris (pH 7.8) and 1 mM ethylenediaminetetraacetic acid for a total of 1,200 V·h. DNA was transferred from the gel to a nylon membrane (Biodyne B; Pall Corporation, East Hill,

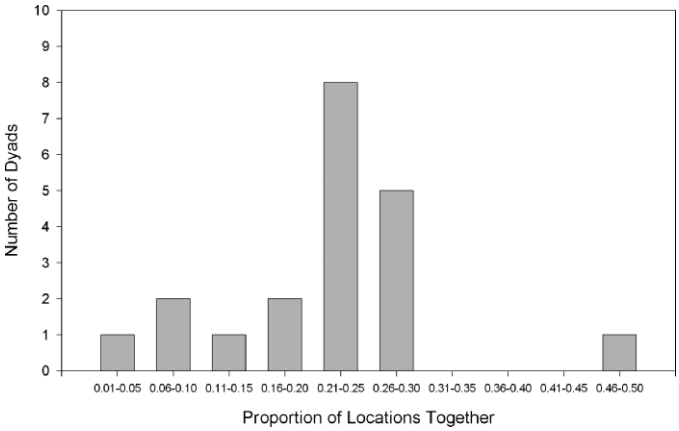

FIG. 1.—Distribution of mean seasonal proportions of locations within 50 or 100 m for members of male dyads of raccoons (*Procyon lotor*) in southern Texas during 1990–1993. Proportions were calculated as the number of simultaneous locations in which animals *i* and *j* were within a critical distance of each other (50 m for daytime locations and 100 m for nighttime locations), divided by the total number of simultaneous locations for animal *i* or *j*. Means were derived for each dyad monitored for >2 concurrent seasons.

New York) using an alkaline transfer technique described by the manufacturer.

The resulting Southern blot membranes were then hybridized sequentially with 2 unrelated multilocus probes, OPT-02 and OPT-03. In a pilot study, these 2 probe–enzyme combinations gave highly variable DNA profile patterns among 6 unrelated raccoon individuals. Probes were labeled with 32P (NEN, Boston, Massachusetts) by primer extension and unincorporated nucleotide was removed on a Nuc-Trap column (Stratagene, La Jolla, California). Hybridizations were carried out at 50°C in 5× SSPE (1× = 150 mM NaCl, 10 mM sodium phosphate, and 1 mM ethylenediaminetetraacetic acid), 2% sodium dodecyl sulfate, 1 mg/ml herring testes DNA, and 1% polyethylene glycol for 18 h. Membranes were washed at 55°C in 2× SSPE and 1% sodium dodecyl sulfate, covered with plastic, and exposed to X-ray film at −70°C for 1–5 days.

DNA fragment scoring and data analyses.—Both sets of DNA profiles and each DNA fragment (band) were independently scored by 2 investigators. We visually compared offspring bands with putative parents to confirm parentage. To calculate band-sharing (an estimate of genetic similarity) among individuals on all gels, band sizes also were hand-digitized and the resulting data entered into computer programs designed at Therion. The ability to estimate relatedness from multilocus DNA probe profiles using band-sharing coefficients (and the analysis techniques developed at Therion) has been established previously by Casna et al. (1997), Collins et al. (1990), Gergits et al. (2002), and Haig et al. (1994, 1995). Bands that were lighter than the lightest, easily detected molecular weight sizing standards were not scored. Band sizes for each individual were determined by comparison to the molecular weight sizing standards within the range of 13.823–3.222 kilobases. Using this method, the sizing error within and between gels is estimated to be 0.6% of band size (Balazs et al. 1989, 1990; Risch and Devlin 1992). Therefore, during comparisons to determine band-sharing between individuals, bands were considered to be a match when their respective sizes overlapped within a range of ±0.9% of each band size (i.e., the total range is equal to 3 *SD* or 1.8% of band size). These values are consistent with those of Galbraith et al. (1991), who suggest that the distance between bands be at least 2.8 *SD* before they are declared different at the 0.05 level. Similarity was then calculated for all pairs of individuals sampled by combining the band-sharing coefficients for both probe–enzyme combinations.

The sibling group represents related or genetically similar individuals, whereas the other group represents ''background'' (or unknown) relatedness in the population (throughout this paper close relatedness or genetic similarity represents $r = 0.25–0.5$). The statistical significance of this comparison was assessed using the nonparametric Mantel test, which compares 2 distance matrices (Fortin and Gurevitch 1993). The null distribution consisted of 10,000 permutations of the band-sharing data. One female was the mother of 2 litters, which we considered independent because she consorted with different males each year.

Second, we addressed the question: Are male groups composed of close relatives? Again, we constructed 2 distance matrices, 1 composed of the band-sharing coefficients, and another constructed with a ''1'' for intragroup males and a ''0'' for intergroup males. As before, we compared group matrices with the Mantel test. A significant correlation between matrices is expected if groups are composed of closely related (or genetically similar) individuals and males between groups are distantly related or unrelated (or less genetically similar). We used a 1-tailed probability because we expected higher band-sharing coefficients for intragroup males than for intergroup males. We also compared mean band-sharing coefficients derived for within and between male groups to those of litters with known close relatives. We used *t*-tests with 1-tailed distribution, for significance; however, significance must be considered with caution because of nonindependence within the samples.

Finally, we also used Mantel tests to determine if genetic similarity, as estimated by band-sharing coefficients, explained variations in duration and frequency of male associations within male groups. Again, we used Mantel tests to assess statistical significance rather than typical parametric tests because pairs of raccoons often shared a member with another dyad, with resulting nonindependence. However, for comparisons with other studies we summarized data with means (± *SD*).

RESULTS

Male associations.—Male associations were determined for 12 adult males from 3 groups residing in or adjacent to the core area, which resulted in 20 dyads that were monitored for ≥2 seasons. Mean proportions of locations within 50 or 100 m for each dyad ranged from 0.04 to 0.48 for the duration of group membership. Most (15 of 20) dyads had mean proportions of locations within 50 or 100 m between 0.20 and 0.30 (Fig. 1),

and proportions of locations within 50 or 100 m within a season ranged between 0.00 and 0.67.

Low proportions (<0.15) of locations within 50 or 100 m between 2 raccoons during a season were indicative of either a new male entering the group or the dissolution of group membership for 1 of the raccoons. For example, 2 young adult males entered the territory of a male group within a month of the death of a resident male (that had been a member of the group for ≥18 months). Initially, the immigrant pair was closely associated together, but over the next 9 months their association dissolved (Fig. 2) as 1 of them formed associations with resident group members and the other eventually left and became solitary (Gehrt 1994).

Duration of dyads ranged from 6 to 39 months, with a mean of 18.4 ($SD = 8.95$, median = 18). Dyads were terminated by a death ($n = 4$) or emigration ($n = 9$) of 1 of the group members, and 7 dyads were essentially truncated by the end of fieldwork.

Genetic structure.—Genetic analyses were conducted for 22 individuals representing mothers ($n = 6$) and offspring ($n = 7$ litters; 1 female was mother to 2 litters), and 9 adult males that comprised 3 social groups. Mean "within litter" coefficients of band-sharing was 54.0 ± 8.6 ($n = 10$), which was higher than the mean coefficient (40.2 ± 7.8, $n = 10$) for "between litters." The Mantel correlation between matrices ($r = 0.437$) was significant ($P < 0.001$). Coefficients of band sharing within all litters ranged between 38 and 69.

Mean band-sharing coefficient for males within groups (45.5 ± 11.1, $n = 13$) was similar to that for males between groups (44.9 ± 7.6, $n = 16$). Consequently, there was no relationship ($r = 0.052$, 1-tailed $P = 0.376$) between matrices. Coefficients of band sharing among all male dyads ranged between 26 and 61. Mean band-sharing coefficients for males within and between groups were lower than that of within litters (within male groups versus known siblings, $t = 2.00$, $d.f. = 21$, 1-tailed $P = 0.029$; and between male groups versus known siblings, $t = 2.83$, $d.f. = 24$, 1-tailed $P < 0.001$).

There were 13 male dyads with genetic data and sufficient radiotelemetry data to characterize associations within groups. Genetic similarity had no ($r = 0.11$, 1-tailed $P = 0.26$) relationship to mean proportions of locations within 50 or 100 m within groups. However, band-sharing coefficients were positively ($r = 0.31$, 1-tailed $P = 0.06$) related to duration of associations within groups, although the test only approached significance.

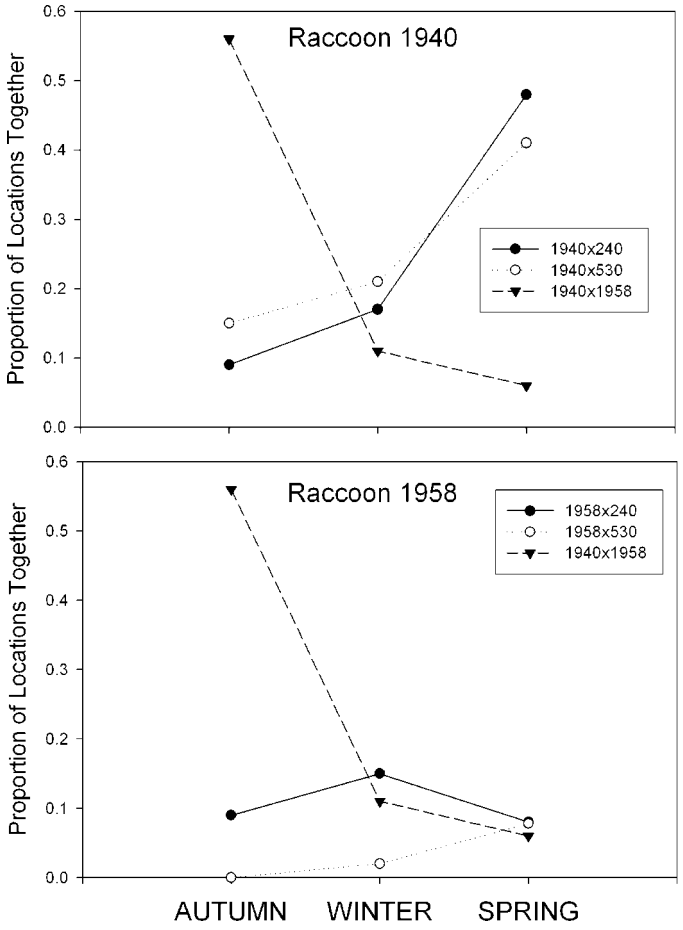

Fig. 2.—Proportion of time 2 members of dyads of adult male raccoons (*Procyon lotor*) were located within a critical distance (<50 m during day and ≤100 m during night) of each other during 1991–1992 on the Welder Wildlife Refuge, Texas. Raccoons 1940 and 1958 moved into the area of a male group during autumn, and initially were located together >50% of the time while spending relatively little time with resident males (240 and 530). As the season and year progressed, 1940 increased associations with residents and decreased his association with 1958, and 1958 eventually left the group by the end of spring after the peak mating period and became a solitary male.

Discussion

Our genetic analysis supported the expectation, derived from field data, that male social groups generally are not composed of close kin. However, this pattern was not exclusive because there was evidence of genetically similar individuals within groups. Our results are consistent with other studies of raccoons that reported no correlation with geographic distance between individual males and genetic relatedness (Ratnayeke et al. 2002; Roy Nielsen and Nielsen 2007), indicating that some males in close proximity are not closely related. These earlier studies did not report home-range overlap or measures of social behavior and our results suggest that social organization of males cannot necessarily be inferred from genetic surveys.

Intraspecific patterns of sociality in raccoons suggests that male social groups are a response to the distribution of females and, consequently, mating opportunities (Gehrt and Fritzell 1998a). However, it is important to note the only period during the year that no group males associated together was during the peak estrous period, when all resident females came into estrus within a short time interval, and group males apparently competed among each other for mating opportunities (Gehrt and Fritzell 1999a). If cooperation occurs within male groups, as required by models of reciprocity and mutualism, it likely occurs outside the peak mating period or it is subtle during this critical time. Establishing social bonds outside of the mating season and developing a dominance hierarchy may reduce the severity of conflict during the peak mating period.

Male coalitions or social groups of other species vary in the composition of close relatives. Kinkajous are procyonids with coalitions consisting of 2 adults, but they also occur as part of family groups that include an adult female and 1 or 2 subadults (Kays and Gittleman 2001). It is unclear as to whether kinship is an important factor for coalitions of male kinkajous, because genetic relatedness was determined for only 2 coalitions, with 1 pair closely related (father–son or full sibs) and the other a pair composed of unrelated males (Kays et al. 2000).

Coastal river otters showed no relationship between frequency of association (or proportions of locations observed together) and close relatedness within male social groups (Blundell et al. 2004). In this species, sociality is apparently driven by ecological factors rather than kin selection. However, in contrast to our study, males did not maintain stable, exclusive groups, but rather formed loose associations that resembled fission–fusion systems, and sometimes included females (Blundell et al. 2002). Likewise, short-term associations among male grizzly bears (*Ursus arctos*) determined from global positioning system data were not explained by relatedness (Stenhouse et al. 2005).

Loosely structured male aggregations, sometimes termed bachelor herds, have been observed in nearly every ungulate species (Ruckstuhl and Kokko 2002), as well as elephants, whales, and some primates (Ruckstuhl and Neuhaus 2000). In many of these species, these are groups that form outside the mating season and may consist of subadult, or young, individuals, with older, dominant individuals maintaining a solitary status. In many cases, particularly among ungulates, bachelor herds probably are a result of predation pressure (e.g., red deer [*Cervus elaphus*]—Clutton-Brock et al. 1982).

We do not believe the social system of male raccoons in this population is consistent with classic bachelor herds of other species, especially ungulates. Male groups of raccoons are composed only of mature adults that compete for females during the mating season, which differs from bachelor herds of many ungulates (e.g., pronghorns [*Antilocapra americana*—Byers 1997] and bison [*Bison bison*—Berger and Cunningham 1994]) and elephants (e.g., *Loxodonta africana*—Nyakaana et al. 2001) that consist primarily of younger, prereproductive males. Juvenile or yearling male raccoons were never observed associated with male groups, despite occurring within group territories. The stable membership of groups of male raccoons, maintaining exclusive group territories (Gehrt and Fritzell 1998a), also is inconsistent with bachelor herds. Home ranges of males exhibited nearly complete overlap within groups, home-range size did not change with seasons (boundaries were stable), and the sizes of home ranges of males were larger than would be predicted based on energetic demands (Gehrt and Fritzell 1997). We are unaware of bachelor herds of any species maintaining exclusive territories, and typically membership is fluid across different groups (Clutton-Brock et al. 1982). Unlike river otters (Blundell et al. 2002), we did not observe male raccoons extending associations beyond their group, given the exclusivity of their home ranges. If a male left a group, it was a permanent exit and it did not return to the original group (Gehrt and Fritzell 1998a).

Male groups of raccoons also differ from the typical bachelor herd system in other ways. In many species with bachelor herds, there is spatial segregation between the males and adult females. This segregation is especially notable in ungulates, and has spawned considerable attention as to the reasons for this separation (Ruckstuhl and Kokko 2002). In our study population of raccoons, there was no spatial segregation between male groups and females. To the contrary, the orientation and size of group territories was such that they centered on groups of home ranges of females (Gehrt and Fritzell 1997, 1998a). Most importantly, species with bachelor herds tend to be species with a propensity for aggregation of both sexes, with social bonds often stronger among females in female herds than among males in bachelor herds (Clutton-Brock et al. 1982). As mentioned previously, it is notable that social groups of males have developed in raccoons despite the lack of sociality among females. Many species with bachelor herds have social systems shaped through the pressure from predation, and the development of bachelor herds is likely a response to the threat from predators (Clutton-Brock et al. 1982). Predation is an unlikely explanation for male coalitions in our study population (Gehrt 1994). Despite a considerable predator community on the study area, predation was not common and annual survival was consistently >0.80 for both social males and solitary females (Gehrt and Fritzell 1999b). Furthermore, natural predation has consistently been low in studies of raccoon populations from other areas (see Gehrt [2003] and Gehrt and Clark [2003] for reviews).

We determined that male groups were not generally composed of close kin based on genetic similarity; however, there appeared to be some intragroup variation in relatedness, with a few male dyads having levels of band-sharing equivalent to closely related females. If our measures of band-sharing reflected relatedness, then genetic relatedness was not related to mean proportions of locations within 50 and 100 m within male groups, but may be related to the duration of social bonds. Although the correlation between duration of association and relatedness was only marginally significant, this may have been affected by our inability to follow all relationships through to completion and small sample size.

Raccoons conform to the general mammalian pattern in which ecological factors influence the sociospatial pattern of females, and males respond to those female patterns through their own sociospatial patterns (Van Hooff and Van Schaik 1994). Although quite rare among mammalian species, males can develop social groups in a population with solitary females, and kinship does not appear to be a necessary factor for the development of male social groups in raccoons. Similarly, other mechanisms, such as mutualism or reciprocal benefits, have been suggested as likely mechanisms for the formation of male coalitions or associations in other species, despite the fact that some coalitions are formed primarily by close kin (Grinnell et al. 1995; Van Hooff and Van Schaik 1994). However, genetic relatedness may influence the duration of social bonds, which may in turn affect the tenure of social groups. Duration of social bonds among males was associated with high genetic similarity, despite our inability to follow all dyads to their termination.

Few studies have focused on male sociality in raccoons, thus the full role of relatedness in influencing raccoon social dynamics, and the possible roles of other mechanisms in the development of social groups, remain to be determined.

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