Genetic relatedness does not predict racoon social network structure

Ben T. Hirsch [a,b,*], Suzanne Prange [c], Stephanie A. Hauver [d], Stanley D. Gehrt [a]

[a] School of Environment and Natural Resources, Ohio State University, Columbus, OH, U.S.A.
[b] Smithsonian Tropical Research Institute (STRI), Balboa, Panama
[c] Ohio Division of Wildlife, Athens, OH, U.S.A.
[d] School of Education, Binghamton University, Binghamton, NY, U.S.A.

ARTICLE INFO

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

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Accurately quantifying social structure and understanding the mechanisms that shape differences between animal societies is crucial for addressing many key questions in behavioural ecology, animal conservation and wildlife disease epidemiology. An individual's choice of social partners can greatly influence patterns of mating, coalition formation, predation risk and foraging success (Janson 1990; Krakauer 2005; Croft et al. 2006; Ohtsuki et al. 2006; Ryder et al. 2009). Social interactions also affect information and disease transmission between individuals (Altizer et al. 2003; Lusseau 2003). When animals choose to interact with particular individuals, these preferences can scale up to shape the overall social structure of the population or species (Krause et al. 2007). However, these social interactions rarely occur in isolation, and the behaviour of an individual is greatly influenced by its social and physical environment (Sterck et al. 1997; Krause et al. 2009). To understand interactions between any two animals, it is necessary to consider the structure of the social network in which these interactions occur (Croft et al. 2005). Behavioural ecologists are increasingly using social network analyses to address these questions because these methods allow for the quantification of multiactor interactions, which provides a more realistic depiction of animal societies than traditional dyadic measures (Wey et al. 2007; Sih et al. 2009; Croft et al. 2011; Sueur et al. 2012).

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

* Correspondence and present address: B. T. Hirsch, School of Environment and Natural Resources, The Ohio State University, 2021 Coffey Rd, Columbus, OH 43210, U.S.A.
E-mail address: hirschb@si.edu (B. T. Hirsch).

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

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

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

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

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

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

METHODS

Study Area

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