Context-dependent social behaviour: testing the interplay between season and kinship with raccoons

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Abstract

Animals are organized in a wide range of social structures. Variability in sociality is found both within and among species and is influenced by extrinsic and intrinsic factors. Here we examine the interplay between social behaviour, social thermoregulation and kinship in shaping sociality. We do so for raccoon *Procyon lotor*, a species suggested to exhibit flexible sociality – from solitary to highly gregarious. We hypothesize that this variation in sociality is driven by environmental conditions, relatedness and their interaction. We used proximity-logging telemetry collars to quantify intraspecific encounters and infer social behaviour among female raccoons. We tested the effect of extrinsic (season and temperature) and intrinsic (pairwise relatedness) variables on proximity. We monitored 15 female raccoons from April 2010 to August 2011, which composed 120 dyads. Daily proximal encounter rate was eight times higher in winter (mean ± standard error: 24.1 ± 4.2) than in summer (3.0 ± 2.6) and daily encounter duration was 12 times longer in winter (558.8 ± 130.3 s) than in summer (43.4 ± 33.1 s). We also found a negative relationship between ambient temperature and proximal encounter rate, which suggested that female raccoons use social thermoregulation as a mechanism to reduce energetic costs in cold environments. Finally, we found that relatedness was positively correlated with encounter rate during summer and winter. Our results suggest that ecological factors, such as seasonality, may affect the evolution of sociality in temperate species, and that the evolution of social thermoregulation in raccoons is likely driven by kin selection.

Introduction

Animal social systems range from solitary to eusocial species. For decades, researchers have sought to identify the factors shaping sociality at the intra- and interspecific level (Lott, 1991; Schradin & Pillay, 2005) as well as quantifying the costs and benefits of social behaviours (Krause & Ruxton, 2002). As such, animal interactions can be used to explore how variation in sociality affects specific behaviours, such as mating (Clutton-Brock, 1989; Gehrt & Fritzell, 1999) and foraging (Beauchamp, 2005). Interactions that occur during proximal encounters are also very important factors in epidemiology (Lloyd-Smith *et al.*, 2005), as infectious diseases will spread more rapidly in gregarious species than in solitary ones (Begon *et al.*, 2002). Thus, understanding factors affecting encounter rate is crucial for both fundamental and applied research.

Environmental variability (Lott, 1991) and relatedness (Hamilton, 1964) have been posited to explain intraspecific variation in social systems. For endotherms, such as mammals, variable temperatures have been shown to influence social structure (Hwang, Larivière & Messier, 2007;

Willis & Brigham, 2007). Endotherms typically need to maintain a body temperature higher than their surroundings (McNab, 2002), a strategy that leads to consequent energy costs at low ambient temperatures. The cost of endothermy may be reduced by grouping with conspecifics (Hwang *et al.*, 2007; Willis & Brigham, 2007), a behavioural strategy known as social thermoregulation. For example, communal denning can lead to a reduction of thermal conduction and body fat loss (Merritt & Zegers, 2002; Hwang *et al.*, 2007). Therefore, in cold environments animals that den communally potentially save energy that can be allocated to survival and/or reproduction. The occurrence of communal denning should increase with a decrease of ambient temperature (Ebensperger, 2001). Thus, group formation of solitary species in cold temperature could be explained, at least partially, by social thermoregulation.

Kin selection theory predicts that relatedness is a major driver of the evolution of sociality (Hamilton, 1964). For sociality to persist both direct and indirect fitness benefits need to outweigh the costs of exhibiting social behaviours. Although more species of mammals are solitary than

gregarious (Jarman & Kruuk, 1996), group-living mammals have been the focus of most studies of social behaviours (Alexander, 1974; Dunbar, 1988). The aim of this paper was to investigate extrinsic and intrinsic factors affecting social interactions (described by proximal encounters), in a socially flexible mesocarnivore (Gehrt, 2003). Raccoon *Procyon lotor* foraging is thought to involve infrequent encounters with other adult conspecifics (Waser & Jones, 1983). However, evidence from exclusive male coalitions in raccoons (Gehrt & Fritzell, 1998*a*; Pitt, Larivière & Messier, 2008) suggests that raccoon social structure is more complicated than previously reported (see also Hirsch *et al.,* 2013). Furthermore, recent research on raccoons in the centre of their geographic distribution has highlighted that they have variable social behaviours (e.g. encounter rates; see Prange, Gehrt & Hauver, 2011). This suggests that in northern climates sociality might be exacerbated due to the increased importance of social denning. We extend research by Prange *et al.* (2011) to assess the role of relatedness (see also Hirsch *et al.,* 2013), both within and beyond the family groups, in social encounters and social denning. Raccoons are known to form family groups consisting of a female and her yearlings (Gehrt, 2003); however, to what extent related family groups interact and socially den over extended periods of time merits further exploration.

In this study, we assess the social flexibility of female raccoons by investigating factors affecting their encounter rates and durations described by fine-scale proximity of both individuals in a dyad between seasons and by assessing their kinship. The interactions that arise from these dyadic encounters are the building blocks of social structure within animal societies (Krause & Ruxton, 2002; Whitehead, 2008, 2009). We employ a recent technology, proximity-based data-logging telemetry collars, as an objective method to quantify proximal encounter rate at a very fine spatial scale. As raccoons den communally at low temperatures, we expected to find higher proximal encounter rates during winter than summer. Because temperature is variable during winter, we also predicted that encounter rate will vary within that season, increasing at lower temperatures. Given the probability of kin-based social groups, we further predicted that encounter rate will be higher among relatives than non-relatives, particularly during winter. As raccoons are solitary during summer, however, we expected no correlation to relatedness.

Methods

Study area and captures

We radiotracked adult female raccoons from April 2010 to April 2011 on a 58-km² study site in Mont-Orford Provincial Park, Québec, Canada (45°21′39′′N, 72°14′18′′W). All animal handling was approved by the University of Sherbrooke's Animal Care Committee (FP2008-02). Captures occurred in spring (April 2010 and 2011) and autumn (October 2010). During each 20-day trapping session, 66 traps were set 100 m apart over a 1000 m × 500 m grid (see Robert, Garant & Pelletier, 2012*a* for trapping details).

Captured raccoons were weighed in the trap and then immobilized. For details on immobilization see Robert, Garant & Pelletier (2012*b*). No long-term behavioural or physiological effects of anaesthesia have been detected (see Robert *et al.*, 2012*b*). Adult female raccoons (>5 kg) were fitted with proximity data-logging telemetry collars (≈110g, hereafter, proximity collars; Sirtrack©, Havelock North, Hawkes Bay, New Zealand). We retrieved radio-collars following raccoon mortality or at the end of the study. During the anaesthesia, ear tissue was taken from all individuals for genetics analyses with a 2-mm-diameter punch pliers (Maun Industries, Notts, UK) and kept in ethanol 95% until genetic analysis.

Adult male raccoons occurred as incidental capture and were not fitted with proximity collars. Mixed-sex groups occur predominantly in winter and typically consist of only one adult male per multi-female den site (Prange *et al.*, 2011). Thus, we chose to focus exclusively on females as they are also known to be the more philopatric sex (Gehrt & Fritzell, 1998*a*; Pitt *et al.*, 2008) and are expected to comprise the majority of co-denning individuals.

Encounter rates and durations

We used proximity collars to collect data on encounter rates and durations. Proximity collars have been successfully employed on various species (e.g. raccoons, Prange *et al.*, 2011; badgers *Meles meles*, Goodman, 2007; white-tailed deer *Odocoileus virginianus,* Walrath, Van Deelen & Vercauteren, 2011; elk *Cervus canadensis*, Vander Wal, Yip & McLoughlin, 2012) and provide a valuable tool to answer questions linked to animal sociality (see Cross *et al.,* 2012 for review). We programmed the proximity collars to register data (i.e. encounters) every time an animal was within 1.85 m [±0.14 standard deviation (SD), Goodman, 2007] of another conspecific fitted with a proximity collar. We ensured that all collars were programmed similarly to guarantee consistency among comparisons of individuals. The separation distance chosen to record encounters was a technical and biological trade-off. First, we assumed that raccoons can detect conspecifics in a forest environment at ≤ 2 body lengths. Second, using this range prevented recording small movements within a den during winter, thus avoiding overloading the collar's memory and allowing us to collect data throughout the year. Technical challenges included that collars have been shown to fail to record encounters if set to *c*. 1 m or less (Goodman, 2007). Proximity collars do not disengage at the same distance they engage (see Goodman, 2007 for details); thus, a new encounter was logged every time two units were separated for at least 30 s at a distance > 3.15 m (±0.17 SD, Goodman, 2007). When the loggers were within this range, the logger recorded the other collar identity, date, time and duration of the encounter. See Supporting Information Appendix SA: Supplementary Methods for further discussion regarding proximity collars.

Encounter rate was defined as the number of encounters per day for each dyad by season. Also, since most raccoons had their collars installed on different days, the total number of

encounters of a given dyad was divided by the number of days during which both individuals simultaneously had an active collar. As such, $\text{encounter rate} = \frac{\sum E_{(i,j)}}{\sum D_{(i,j)}}$, where i and j are two collared individuals, E is the encounter, and $D_{(i,j)}$ is the total number of days collars were simultaneously deployed on i and j. Encounter duration was defined as the total duration of the encounters per day for each dyad (i.e. $\frac{\sum\sum ED_{(i,j)}}{\sum D_{(i,j)}}$, ED is the encounter duration per day). See also Robert *et al.* (2012*a*) for details. We defined two principal seasons based on local climate, raccoon biology and radio-tracking constraints: snow-free (April–August, approximating 'summer') and snow-present (November–March, approximating 'winter').

Daily temperature

We used temperature data loggers (Thermochron iButton DS1921, Dallas Semiconductor, Dallas, TX, USA; accuracy $\pm 0.5°C$; 17 mm × 6 mm, 3·0 g) to record ambient temperatures at our study site every 4 h. We placed temperature-loggers ($n = 20$) at five recording sites randomly selected on our trap grid. At each recording site two temperature-loggers were installed in a tree cavity and two were attached on the exterior of the tree to account for potential differences within and outside den sites. We determined the average daily temperature by calculating the mean for all loggers per day.

Home range

In addition to an ultra-high frequency feature that recorded encounters, proximity collars were equipped with a very high frequency transmitter used to relocate the animals (see Robert *et al.*, 2012*a* for details on relocation methods). We obtained estimates of the summer and winter home range via fixed kernel analysis (h_{ref}; Worton, 1989). Home ranges were calculated with a minimum of 19 locations in winter and 30 locations in summer (see Robert *et al.*, 2012*a* for details). According to Börger *et al.* (2006), this method is accurate, robust and does not overestimate home range size for studies with a low (i.e. < 10) number of relocations. Home ranges were calculated as 95% isopleths with the adehabitat package (Calenge, 2006) for R software (version 2.10.0, R Development Core Team, 2009). Home range overlap was calculated using the utilization distribution overlap index, which quantifies overlap based on the product of the utilization distribution (UD) of two individuals. It generally ranges between 0 (no overlap) and 1 (100 % uniform distribution), but it can be >1 if the UDs of the two individuals are not uniform in space and have considerable overlap (Fieberg & Kochanny, 2005; see also Robert *et al.*, 2012*a* for details).

Genetic data

We performed DNA extraction on 75 individuals ($n = 38$ females, 37 males; captured between 2008 and 2010) using a modified version of the salting-out method as described by Chambers & Garant (2010). See Côté *et al.* (2012) for detailed methods. See Supporting Information Appendix SA: Supplementary Methods for details on microsatellites used. Amplifications were performed in a GeneAmp PCR System 9700 thermocycler (Life Technologies, Rockville, MD, USA). Amplification products were visualized using an AB 3130 capillary DNA sequencer (Life Technologies).

Microsatellites polymorphism and relatedness coefficients

We tested all loci for departure from Hardy-Weinberg equilibrium and linkage disequilibrium using the software GENEPOP version 4.0 (Raymond & Rousset, 1995). We used CERVUS version 3.0.3 (Marshall *et al.*, 1998; Kalinowski, Taper & Marshall, 2007) to assess the presence of null alleles. Finally, we used SPaGEDi version 1.3 (Hardy & Vekemans, 2002) to estimate pairwise genetic relatedness (Rxy) for all captured raccoons using Wang's estimator (Wang, 2002).

Statistical analyses

Extrinsic determinants

We assessed the correlation between mean daily encounter rate and mean summed daily duration using a Pearson correlation. Daily encounter data were right-skewed and zero-inflated, thus we ran the analyses in two steps. First, we tested whether the independent variable affected the probability of an encounter occurring (defined as 0, no encounter per day; and 1, having at least one encounter per day) using generalized linear models with a binomial error distribution. Then, for animals that experienced at least one encounter, we tested whether the independent variable affected the incidence at which individuals had encounters. These generalized linear models were fitted on data rounded to the nearest integer with a Poisson distribution adjusted for over-dispersion.

Following from our hypotheses on social thermoregulation, we first tested the effect of season on encounter rate. Then, we tested the effect of ambient temperature on winter encounter rate in a separate model. We did not consider the relationship between ambient temperature and encounters during the snow-free period, as raccoons were not expected to den socially in the summer. All linear mixed-effects models were performed in R (v.2.10.0). As dyads are non-independent, we included dyad identity as a random effect in each model. Additionally, we controlled for over-dispersion in the Poisson models following the technique described by Atkins *et al.* (2012).

Intrinsic determinants

We used mean encounter rate and mean summed duration per dyad in multiple regression matrices (MRM; Lichstein, 2007) to assess the correlations between encounter rate, home range overlap and relatedness for each season. We also used MRM

to assess the relationship between home range overlap and pairwise relatedness. All the MRM analyses were conducted in R (v. 2.10.0).

Results

We fitted 15 females with proximity collars for 2 years. We estimated that 92% of the females were marked in our study area [≈2.6–4 raccoons km^{-2} (Massé, 2010)] and each had a collar (Robert *et al.*, 2012*a*). During the study, all 15 collared females had an encounter with at least two other females. Mean [±standard error (SE)] number of encounters was 9799 (±2376) with a mean duration of 25 ± 0.4 s. There was a strong correlation between encounter rate and duration (r = 0.83; Supporting Information Appendix SB: Supplementary Results Fig. S1). The sampled raccoons were genotyped at 11 microsatellites. No significant deviation from Hardy–Weinberg equilibrium or linkage disequilibrium was detected after Bonferroni correction. Null alleles were found at low frequencies within our data (<5%). The relatedness among members of dyads had a near normal distribution (mean ± SD: 0.008 ± 0.183; Fig. 1).

Extrinsic determinants

Daily encounter rate differed significantly between seasons, being eight times higher during winter (mean ± SE: 24.07 ± 4.21) than summer (mean ± SE: 3.02 ± 2.58; Fig. 2a). Similarly, duration of encounters was greater during winter (mean ± SE: 558.07 s ± 130.29) than in summer (mean ± SE: 43.35 s ± 33.82). The odds ratios from the binary model predict that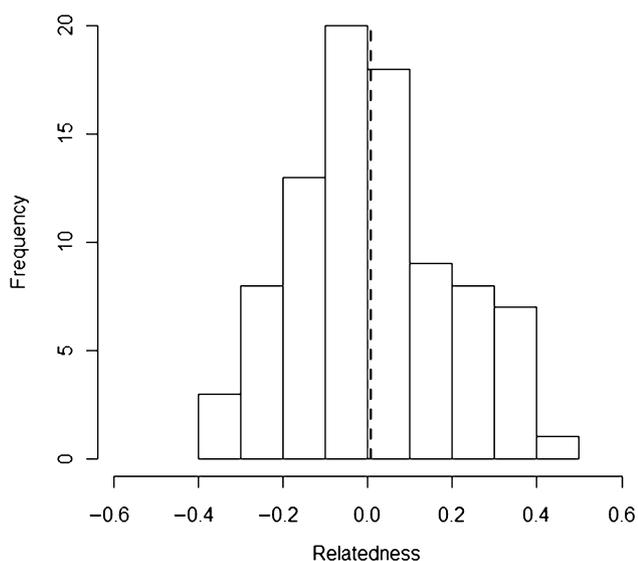 raccoons were 2.15 times more likely to have had encounters when snow was present than absent (P < 0.001; Table 1a, $e^{\beta winter}/e^{\beta summer}$). Dyads with at least one encounter had more (incidence rate ratio = 43.60, Table 1b) encounters when snow was present than absent (P < 0.001; Table 1b). Similarly, encounter durations were greater in winter than summer (P < 0.05; Table 1b).

During the snow-present period, the daily odds that raccoons would interact increased by 1.05 per decrease of 1°C in ambient temperature (P < 0.001; Table 2a). However, when only dyads with encounters were considered, there was no effect on rate or duration of encounters (P > 0.35; Table 2b).

Intrinsic determinants

Female raccoon home ranges overlapped 17 ± 23% (mean ± SD) and 37 ± 27% in summer (2010 and 2011, respectively) and 66 ± 46% (n = 210 dyads) in winter. MRM analysis revealed a positive correlation between home range overlap and relatedness during summer and winter (P < 0.05; Table 3, Fig. 3). During all seasons female raccoons had more encounters with related females (P < 0.01; Table 4). In MRM models that account for relatedness, home range overlap has a significant (P < 0.01), albeit weak (β = 0.003), effect on encounter rate during the snow-present period (Table 4). Results were qualitatively similar for encounter duration (Table 4).

Discussion

Here we report a clear link between home range overlap, relatedness and encounter rates. When female raccoons associate (e.g. denning and travelling together; Gehrt & Fritzell, 1998b), home range overlap occurs (Pitt *et al.*, 2008; Robert *et al.*, 2012*a*) and encounter rates increase (Hirsch *et al.*, 2013). We show that the effect of overlap on pairwise encounters is explained by relatedness, suggesting a role for kin
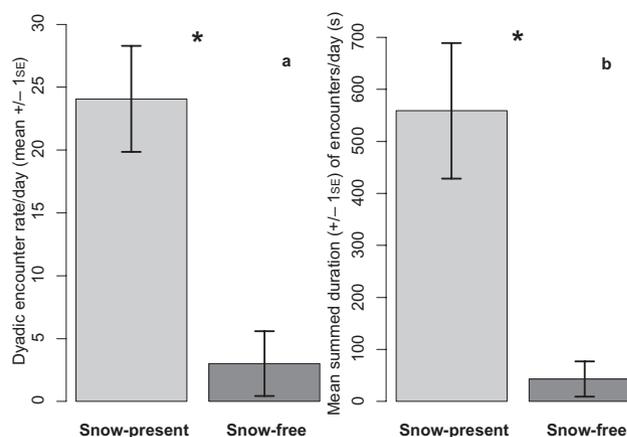

Figure 1 Distribution of estimates of pairwise relatedness among raccoons *Procyon lotor* (*n* = 75) sampled from April 2008 to April 2010 in the Mont-Orford Provincial Park, Québec, Canada. Mean relatedness is represented by the dashed line.

Figure 2 Daily mean (±1 SE) for dyadic encounter rate (a) and duration (b) for *n* = 15 raccoons *Procyon lotor* in Mont-Orford Provincial Park (Québec, Canada) by season between 2010 and 2011. Asterisks denote significant differences between season for both encounter rate and duration. SE, standard error.
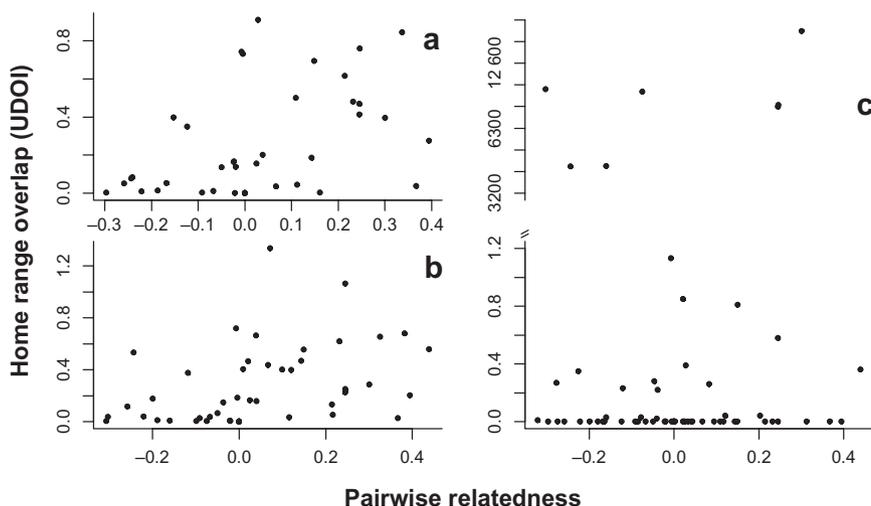
Figure 3 The relationship between home range overlap (according the utilization distribution overlap index, UDOI) and pairwise relatedness for 15 female raccoons *Procyon lotor* in Mont-Orford Provincial Park (Québec, Canada) during the snow-free period of 2010 (a), 2011 (b) and snow-present period of 2010–11 (c). Note that high values for the UDOI index in winter correspond to individuals that are clumped in space (i.e. animals use the same winter dens) and have high home range overlap. Conversely, summer home range use is more uniformly distributed.

Table 1 General linear mixed models for the daily mean encounter rate and mean daily summed duration by season (snow-free vs. snow-present period) for female raccoon *Procyon lotor* dyads sampled in Mont-Orford Provincial Park, Québec, Canada

	(a) Binomial					(b) Poisson (quasi)				
Model	Coefficient	SE	OR[a]	z	P	Coefficient	SE	IRR[b]	z	P
Mean encounter rate	β_1[c] = −6.554	0.389	0.519	−16.860	**<0.001**	β_1 = −3.034	0.517	–	−5.857	**<0.001**
(per day) ~ season	β_2[d] = 3.690	0.111	1.117	33.180	**<0.001**	β_2 = 3.775	0.436	43.597	8.649	**<0.001**
Mean summed encounter	–	–	–	–	–	β_1 = −1.138	0.485	–	−2.348	**0.019**
duration (per day) ~ season						β_2 = 4.079	0.505	59.086	8.078	**<0.001**

Due to zero-inflated and skewed data, two sets of models were analysed: (a) binomial quantifying the probability of encounters (0, 1) and (b) Poisson (over-dispersed) quantifying whether rate or duration of encounter changed for animals that had at least one encounter. Probability of encounter and frequency of encounter increased in winter. Note that the binary model for rate and duration are identical.

P-values in bold are statistically significant (i.e., α < 0.05).

[a]Odds ratio (i.e. e^{β_i}).

[b]Incidence rate ratio (i.e. e^{β_i}).

[c]Reference category (snow-free).

[d]Snow-present period.

selection in the evolution of social bonds in raccoons. This effect is critical in winter when raccoons co-den (i.e. social thermoregulation). Our results highlight that the probability and frequency of encounters increase during the snow-present period. Some of our results are also consistent with recent studies by Prange *et al.* (2011) and Hirsch *et al.* (2013), which showed that encounters were affected by seasons and were higher in winter than summer. However, female encounter rates during winter in our study were much higher than those reported in Prange *et al.* (2011). Prange *et al.* (2011) observed less than one encounter per day among female dyads, whereas we recorded over 24 encounters per day.

Similar discrepancies exist between our results and Hirsch *et al.* (2013). Indeed, while Hirsch *et al.* (2013) found no significant effect of relatedness on encounter rate, our results suggest an effect across seasons, which is ≈24–400 times greater in the winter than summer [i.e. MRM $\beta_{(snow-present)}/\beta_{(snow-free)}$; Table 4]; highlighting that climate may be playing a role and may be an important determinant for the evolution of

social behaviours via kin selection. Variation between populations in encounter rate could also be explained by differences in climatic constraints between study sites. Our study was conducted in southern Québec – at the northern edge of the raccoon distribution – whereas the Prange *et al.* (2011) and Hirsch *et al.* (2013) studies were performed in northern Illinois, which is located farther south (>3° latitude) and at a lower altitude. In southern Québec winters are relatively long and cold, with a mean low temperature of −13.4°C in January (Environment Canada, 2011). In contrast, mean January low temperature in Illinois is −2.9°C (National Climatic Data Center, 2012). As the climate is colder in our study site it could be more advantageous for individuals to share dens with several raccoons to keep a warmer body temperature. Our results suggest that the covariance of colder temperatures and seasonality affect the propensity to form social clusters within which encounter rates increase. Thus, the social thermoregulation hypothesis (Ebensperger, 2001) may explain the apparent variation in social behaviours observed among study sites.

Table 2 General linear mixed models for the daily mean encounter rate and mean daily summed duration by daily ambient temperature for female raccoon *Procyon lotor* dyads sampled in Mont-Orford Provincial Park, Québec, Canada

Model	(a) Binomial					(b) Poisson (quasi)				
	β	SE	OR[a]	z	P	β	SE	IRR[b]	z	P
Mean encounter rate (per day) ~ temperature	−0.049	0.008	0.95	−5.909	**<0.001**	−0.005	0.005	0.995	−0.916	0.36
Mean summed encounter duration (per day) ~ temperature	–	–	–	–	–	0.0005	0.008	1.005	0.062	0.95

Due to zero-inflated and skewed data, two sets of models were analysed: (a) binomial quantifying the probability of encounters (0, 1) and (b) Poisson (over-dispersed) quantifying whether rate or duration of encounter changed for animals that had at least one encounter. Probability of encounter was inversely related to temperature (a), but encounter frequency was unaffected (b). Note that the binary model for rate and duration are identical. *P*-value in bold is statistically significant (i.e., α < 0.05).
[a]Odds ratio (i.e. e^{β}).
[b]Incidence rate ratio (i.e. e^{β}).

Table 3 Multiple regression matrices results for the correlations between relatedness and home range overlap among female raccoons *Procyon lotor* sampled in the Mont-Orford Provincial Park, Québec, Canada

Season (year)	Independent variable	β	P	R^2
Snow-free (2010)	Relatedness	0.049	**0.001**	0.338
Snow-free (2011)	Relatedness	0.719	**0.020**	0.120
Snow-present (2010–2011)	Relatedness	23.103	**0.028**	0.079

P-values in bold are statistically significant (i.e., α < 0.05).

Table 4 Multiple regression matrices results for the correlations between relatedness and home range overlap with the mean encounter rate and mean summed duration for female raccoon *Procyon lotor* dyads sampled in the Mont-Orford Provincial Park, Québec, Canada (2010–2011)

Season (year)	Covariates	Encounter rate (per day)			Summed encounter duration (per day)		
		β	P	R^2	β	P	R^2
Snow-free (2010)s	Relatedness	0.041	**0.003**	0.373	0.074	0.565	0.027
	Home range overlap	0.012	0.201		0.072	0.714	
Snow-free (2011)	Relatedness	0.734	**0.026**	0.121	31.91	**0.03**	0.099
	Home range overlap	−0.027	0.874		−4.119	0.67	
Snow-present (2010–2011)	Relatedness	17.933	**0.021**	0.491	483.642	0.071	0.514
	Home range overlap	0.003	**0.004**		0.121	**0.003**	

P-values in bold are statistically significant (i.e., α < 0.05).

According to this hypothesis, winter aggregations should occur in cold environments and the frequency of groupings should show a negative relationship with ambient temperature (Ebensperger, 2001).

Social thermoregulation has been observed in other species: for example, agile antechinus *Antechinus agilis* (Fisher *et al.,* 2011), Abert's squirrels *Sciurus aberti* (Edelman & Koprowski, 2007) and big brown bats *Eptesicus fuscus* (Willis & Brigham, 2007). Social thermoregulation results in decreased water loss and energy costs associated with thermoregulation (Merritt & Zegers, 2002; Hwang *et al.,* 2007). For example, in skunks *Mephitis mephitis*, individuals that participated in social thermoregulation during winter had a higher percentage of fat reserves at den emergence than solitary individuals (Hwang *et al.,* 2007). The percentage of fat at den emergence is also important for raccoons as their food resources are scarce during that period. It might be especially

important for females because of high reproductive costs during gestation. Our results suggest the social thermoregulation hypothesis may have shaped the evolution of sociality among female raccoons at the northern range of their distribution.

Our results are consistent with findings that female raccoons are philopatric (Gehrt, 2003). Molecular evidence has revealed that females who were proximally located were closely related (Ratnayeke, Tuskan & Pelton, 2002; Côté *et al.,* 2012; but see Hirsch *et al.,* 2013). According to the kin selection theory (Hamilton, 1964), it is beneficial for an individual's fitness to share food resources or shelter, for example, with related individuals rather than unrelated individuals. This was evident in our study due to the positive effect of relatedness on encounters during the snow-present period. Although encounters were infrequent during the snow-free period, they were positively affected by relatedness. These

results suggested a higher tolerance for kin, which is reinforced by philopatry as we observed that kin were more aggregated in space. Our results suggest that raccoons are denning primarily with individuals in their kin pool (i.e. individuals with $r > 0$). As such, the benefits (b) of kin-based social groups must outweigh the costs (c) incurred [$r*b–c > 0$ (Charnov, 1977)] by increased competition or probability of contracting infectious diseases during social denning and thermoregulation. However, further research into the number of available den sites and timing of use is necessary to better understand the relationship between home range overlap and encounter rate in winter.

Our results suggest that ecological factors, such as seasonality, may affect the evolution of sociality in female raccoons; and that the evolution of social thermoregulation in raccoons is likely driven by kin selection. They also suggest that female raccoons are socially flexible (Lott, 1991) as observed in a wide range of species. In carnivores, it has been suggested that sociality has evolved from socially flexible solitary ancestors (Dalerum, Creel & Hall, 2006). Thus, studies on solitary species that show context-dependent social flexibility, such as raccoons, provide insights into factors that shape the evolution of sociality in more gregarious species. Finally, as the benefits and constraints of sociality might be mediated by environmental conditions, it is important to consider environmental heterogeneity in behavioural ecology studies.

Acknowledgements

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix SA. Supplementary methods.
Appendix SB. Supplementary results.

Figure S1. Relationship between encounter rate (per day) and summed daily duration (per day in second) among 120 dyads of female raccoons sampled in the Mont-Orford Provincial Park, Québec, Canada in 2010 and 2011.