

# Communal nesting in an ‘asocial’ mammal: social thermoregulation among spatially dispersed kin

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**Abstract** Communal nesting can help defray the high cost of endothermic heat production in cold environments, but such social behavior is generally thought to be incompatible with the persistent defense of exclusive territories in typically ‘asocial’ animals. We examined the propensity for communal nesting in female red squirrels (*Tamiasciurus hudsonicus*), which maintain individual year-round territories, through intensive monitoring of litters over 22 years and by radio-tracking females during 3 years in late winter/early spring. Communal nesting was exceptionally rare during lactation: of 1,381 litters tracked to emergence, we observed a single instance in which two closely related ( $r=0.5$ ) females pooled their litters into a single nest. In contrast, nest sharing between 2–3 females was relatively common in the late winter/early spring, prior to mating; at least 12 of 63 females (19 %) engaged in communal nesting during a year of systematic tracking of radio-collared females from late February to April. Communal nesting occurred more frequently when temperatures were colder, suggesting that such aggregations might function to reduce

thermoregulatory costs. These social associations were typically, though not exclusively, between closely related individuals ( $r \geq 0.25$  for seven of eight cases; mother–daughter dyads: four of eight), suggesting this cooperative behavior might evolve through kin selection and/or may reflect extended parental care. Our results demonstrate that female red squirrels engage in communal nesting, typically with closely related kin, despite a dispersed population structure that stems from the persistent defense of individual territories.

**Keywords** Cooperation · Kin selection · Parental care · Red squirrels · Social thermoregulation · Territoriality

## Introduction

Social structure within a population constitutes the framework through which all conspecific interactions take place and is shaped by the spatial and temporal dispersion of resources and the cost of their defense (Axelrod and Hamilton 1981; Ostfeld 1985). The population biology of a species, in turn, is affected by its underlying social structure because of the role that intraspecific interactions play in gene flow and genetic structure (Altmann et al. 1996). Given the fundamental role of cooperation in the evolution of biological organization (Nowak 2006), mutually beneficial interactions have been the focus of intensive study for decades, although much of this effort has focused on the co-evolution of social structure and cooperation in highly social species (e.g., Voelkl and Kasper 2009; Olson and Blumstein 2010). When food is economically defensible, however, it can lead to the evolution of territoriality, agonistic intraspecific interactions, and a dispersed population structure (Brown 1964). Kin selection plays an important role in the evolution and maintenance of cooperative behavior in species where members of a group live/breed communally on a

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shared territory, but, by definition, ‘asocial’ species are assumed to rarely cooperate.

Communal nesting, which involves sharing of a common place of refuge, is taxonomically widespread and can involve aggregations of individuals that form for the purposes of thermoregulation or to collectively raise one or more litters or broods (Hayes 2000, Riehl 2010). Although the behavior is typically described as cooperative, as two or more individuals must be complicit for the activity to occur, interactions within a nest may also be antagonistic, particularly when caring for eggs or offspring. In the greater ani (*Crotophaga major*), for example, communally nesting females compete for reproduction by ejecting each other's eggs from the nest (Riehl 2010). Communal nesting that does not involve the collective rearing of young is often construed as a thermoregulatory mechanism; metabolic rate of captive individuals forced to nest or roost singly is higher than when two or more individuals are permitted to huddle within a nest or cavity with metabolic savings increasing with group size (e.g., southern flying squirrels *Glaucomys volans* (Stapp et al. 1991), sugar gliders *Petaurus breviceps* (Fleming 1980), pygmy possums *Cercartetus nanus* (Namekata and Geiser 2009), and mousebirds *Colius colius* (McKechnie and Lovegrove 2001)).

Communal nesting is frequently observed during winter in tree squirrels, but this behavior is thought to be restricted to species that are not territorial or where territoriality dissolves seasonally (Layne and Raymond 1994; Koprowski 1996; Koprowski 1998). Red squirrels (*Tamiasciurus hudsonicus*) found throughout the boreal forest of North America, however, are aggressive toward conspecifics throughout the year as individuals defend a solitary territory containing a stored food cache (Smith 1968; Price et al. 1990). Year-round individual territorial behavior results in a dispersed population distribution although natal dispersal distances are short, such that most offspring could potentially interact with their mothers (Larsen and Boutin 1994). The resultant spatial relatedness structure provides the opportunity for the evolution of cooperative behavior via kin selection but cooperation among neighboring territory holders has not previously been reported. In fact, adjacent territory holders rarely physically interact, and when they do, observed interactions are agonistic; Gorrell et al. (2010) found that only 307 of 54,785 (0.6%) behavioral observations of territorial red squirrels involved physical interactions between adults (excluding male–female matings), and all of these interactions were aggressive territorial chases against intruders. However, Gorrell et al. (2010) also reported that female red squirrels will adopt orphaned kin, thereby enhancing their inclusive fitness, which suggests that some level of social connectivity among neighboring kin is maintained.

Here, we examine whether the persistence of individual food-based territories throughout the year precludes the establishment of communal nesting groups in red squirrels, as

previously assumed. We hypothesized that if communal nesting was occurring, it would be driven by kin selection (inclusive fitness benefits) and function as a thermoregulatory mechanism to reduce energy expenditure. Based on this overarching hypothesis, we predicted that individuals within a communal nest should be highly related and that communal nesting should occur more frequently when it was colder outside. We also expected the ability of squirrels to defend their hoard might be compromised by sharing an off-territory nest, and we, thus, predicted the propensity to nest communally would decrease with increasing distance to a neighbor's hoard. We used radio-telemetry to study female nesting behavior prior to and during the mating season in 3 years and monitored litters in nests during the first 20–30 days post-parturition for 22 years. We assessed the degree of relatedness among individuals sharing a nest based on a complete maternal pedigree that spanned multiple generations and/or by using microsatellite allele frequencies to calculate genetic relatedness.

## Materials and methods

### Study species

We studied a wild population of red squirrels in the southwest Yukon, near Kluane National Park. The landscape had a willow (*Salix* spp.) understory and a white spruce (*Picea glauca*) dominated canopy. White spruce seeds are the primary food source for red squirrels at our study site; squirrels clip new spruce cones containing the seeds each autumn and cache them in a larder hoard (middens; Smith 1968; Fletcher et al. 2010). These middens form the center of individual territories (0.2–0.5 ha; LaMontagne 2007), which are defended against members of both sexes year round (Smith 1968; Price et al. 1990). Breeding in this population is highly asynchronous (Descamps et al. 2006); mating of the earliest females commences in late January to mid-February, whereas late breeders first become pregnant 2 to 4 months later (Lane et al. 2007; SB, unpublished data). Females typically produce a single litter (mean litter size = 3.1 pups) each year following a 35-day gestation period but occasionally attempt a second litter after litter loss (McAdam et al. 2007) and, rarely, following a successful litter (Boutin et al. 2006).

### Nest use

Since 1989, we have used complete enumeration to track population density, survival, and reproductive output of red squirrels on two ~40-ha study grids (Kloo and Sulphur) located in the south-western Yukon, Canada (61°N, 138°W) (see details in Boutin et al. 2006; McAdam et al. 2007). All squirrels were marked with alphanumeric ear tags and given

a unique color combination of wires for visual identification. We monitored the reproductive status of every female each year and all offspring were sexed, weighed, and tagged in the nest; over the 22 years (1989–2010) of our study, we monitored 4,315 juveniles in 1,381 litters.

In 2003, we deployed radio-collars (model PD-2C, 4 g, Holohil Systems Limited, Carp, ON, Canada) on females from February to May to facilitate behavioral observations during the mating season and to aid in the location of nests (Lane et al. 2008). We observed nest use by tracking radio-collared females to nest sites and identified nest occupants that subsequently emerged based on their uniquely colored wires. We began tracking >1-year-old females on February 21 ( $n=42$ ) and yearling females (born the prior spring/summer) on March 21 ( $n=21$ ) and systematically disturbed the nesting tree every time a female was tracked to a nest site off of her territory. Females were flushed from the nest by kicking the nesting tree which allowed us to ensure that two individuals tracked to the same tree were, in fact, sharing a nest (rather than being in different nests within the same tree) and to ensure that a squirrel without a transmitter was not in the nest. Radio-collared females were radio-tracked up until the time they went into oestrus and mated.

In two additional years, 1995 and 2008, we also tracked radio-collared females (1995:  $n=29$ ; 2008:  $n=33$ ) from late February until mating and obtained opportunistic detections of communal nesting when radio-collared females were tracked to a nest and more than one female subsequently emerged. We employed the same methods and materials for radio-tracking in 1995 and 2008 as were employed in 2003; however, nests were not systematically disturbed in 1995 or 2008 and, given differences in tracking effort and nest disturbance between years, we do not make annual comparisons.

#### Relatedness

Because of the low dispersal distance of red squirrels (Larsen and Boutin 1994), a large majority of females present on our study site were born within the site, enabling us to identify their mother and siblings (litter-mates). Using maternal ancestry data for all squirrels born within our study area, we constructed a complete maternal pedigree spanning multiple generations. Assuming Mendelian inheritance, we used this maternal pedigree to estimate relatedness between communal nesters; we consider this a minimum estimate of relatedness as individuals related through paternal lineages were not identified within this pedigree. However, following previously established protocols for this population (Lane et al. 2007), beginning in 2003, we also used microsatellite allele frequencies to calculate the pairwise genetic relatedness value,  $r$  (Wang 2002), in the program SPAGeDi 1.3 (Hardy and Vekemans 2002). This relatedness coefficient estimates the degree of genetic similarity of two individuals

by using the proportion of shared alleles between the individuals weighted by the allele frequencies in the whole population. Details of the molecular methods for microsatellite loci isolation from tissue samples are provided in Gunn et al. (2005) and Lane et al. (2008).

#### Statistical analyses

For 2003, the year we employed systematic searching for detecting communal nesting, we used a Student's  $t$  test with unequal variance to assess whether mean distance to neighbor (the distance from a female's midden to her nearest female neighbor's midden) differed between squirrels that occasionally shared a nest ( $n=12$ ) and squirrels that were never observed to nest communally ( $n=51$ ). We also investigated the effects of ambient temperature on the probability of communal nesting in 2003 using a generalized linear mixed-effects model (GLMM) with a logit link and communal group included as a random effect using version 9.3 of the SAS software package (SAS Institute Inc., Cary, NC, USA). Because we were interested in how temperature affected an individual's decision to nest communally, only individuals that were found in a communal nest at least once were included in this analysis as individuals that never nested communally would not inform the model. Groups (individuals found within the same nest at least once during the study) were considered to be communal when all individuals emerged from the same nest following disturbance and non-communal when group members were radio-tracked to separate nests; cases in which one individual from a group was alone in a nest and other members of that group were outside of a nest or not located were not included in the analysis. Ambient temperature data were obtained from Environment Canada's Haines Junction weather station ([www.climate.weatheroffice.gc.ca](http://www.climate.weatheroffice.gc.ca)), located ~40 km SE of our study site. Because nests were not systematically disturbed in 1995 or 2008, we do not include these data in any statistical analyses; these data are only used in our assessment of relatedness of individuals within a communal nest.

## Results

### Summer nests

Of the 1,381 litters we tracked over 22 years, we recorded a single case of nest sharing in which two females pooled their litters into a single nest that was located on the edge of one of our study areas. Both females were immigrants to the study area and had not been captured prior to the breeding season. One of these females was first caught before giving birth, and her three offspring were individually marked a week after parturition by removing a small tissue biopsy

from the ear for later identification and paternity analysis. We radio-tracked this female to a nest 19 days later where we witnessed a second unmarked female emerge from the same nest containing six juveniles, three of which had been previously marked (ears biopsied). We obtained tissue samples from all six offspring and the first female but were unable to capture the second female thereafter. The first female was highly related with her own litter as expected ( $r=0.495\pm 0.009$  sem), while this same female was also related to the other offspring in the nest ( $r=0.260\pm 0.034$ ) despite having 1–2 mismatching loci with each offspring. Average pairwise relatedness between juveniles from the two litters ( $r=0.126\pm 0.049$ ; excluding within-litter comparisons) provided further support that these two adult females were related at  $r=0.5$ .

### Winter nests

During 2003, the year we systematically disturbed nests when radio-collared females were tracked to off-territory nests, we observed communal nesting among five groups comprised of 12 females (three dyads and two triads) on a total of 19 occasions (Table 1); 51 females (81%) were not observed nesting communally. No individuals were observed to engage in communal nesting with more than one group. Two of the dyads comprised a mother and one yearling daughter, and the third dyad comprised two individuals that were not *closely* related based on our maternal pedigree ( $r=0.008$ ), although

this is a minimum estimate because no paternity data were available. One of the triads comprised a mother and two daughters; one daughter was a yearling and the other was 2 years old. The second triad comprised three individuals that immigrated to the study area 4 to 5 years earlier and were, thus, not included in our maternal pedigree; pairwise analysis of genetic relatedness indicated two of these individuals were closely related ( $r=0.47$ ); the third individual was weakly to moderately related to the other two ( $r=0.05$  and  $0.20$ ). On average, the primary middens of nest sharing females were  $43.4\pm 18.0$  m (SD) apart (range, 20–69 m). The distance between a female's midden and the next nearest midden was significantly shorter for females that occasionally shared nests compared to females that were never observed to nest communally (Student's *t* test with unequal variance;  $t=-3.85$ ,  $P<0.001$ ; Fig. 1). For females that sometimes shared a nest, the mean daily temperature negatively affected the probability that they would be found in a communal nest on a given night (GLMM;  $Z=-3.42$ ,  $P=0.0006$ ), although there was substantial overlap in temperature ranges at which individuals were found to be nesting alone vs. nesting communally (Fig. 2).

In late winter/early spring of 1995, we observed eight instances of communal nesting involving two dyads of radio-marked females (Table 1). Both of these dyads comprised an adult female and her 1-year-old daughter (born the previous spring). In one case, the mother and daughter occupied adjacent territories, while in the other, the two occupied territories were separated by two intervening

**Table 1** Relatedness of nest sharers based on pedigree data and microsatellite allele frequencies. Relatedness from maternal pedigree represents a minimum estimate because they only consider relatedness through the maternal lineage

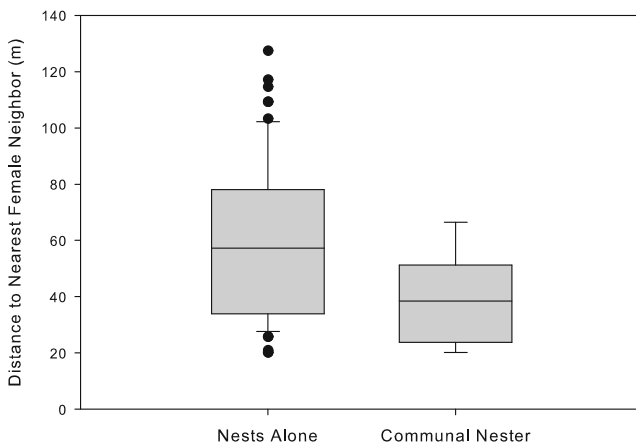
Case	Year	Number of communal nesters	Individuals in group	Relatedness from maternal pedigree <sup>a</sup>	Relatedness from genetic similarity	Distance between primary middens (m)
WN1	1995	2		0.5 md	–	–
WN2	1995	2		0.5 md	–	–
WN3	2003	2		0.5 md	0.52	66.4
WN4	2003	2		0.5 md	–	51.3
WN5	2003	2		0.008	–	69.1
WN6	2003	3	a-b	0.5 md	0.62	47.4
			a-c	0.5 md	–	30.2
			b-c	0.25 hs	–	50.3
WN7	2003	3	d-e	–	0.47	20.1
			d-f	–	0.20	35.0
			e-f	–	0.05	21.0
WN8	2008	2		0.25 hs	0.26	64.7
LN1	2010	2		–	~0.5 <sup>b</sup>	–

Cases WN1–WN8 are winter nests found using radio-telemetry. Case LN1 is a nest containing two litters of young; *En dash* (–) indicates no data. See results for details.

*md* mother–daughter, *hs* half-sisters

<sup>a</sup> Relatedness from maternal pedigree represents a minimum estimate because they only consider relatedness through the maternal lineage

<sup>b</sup> Relatedness determined based on tissue biopsies from one dam and both litters

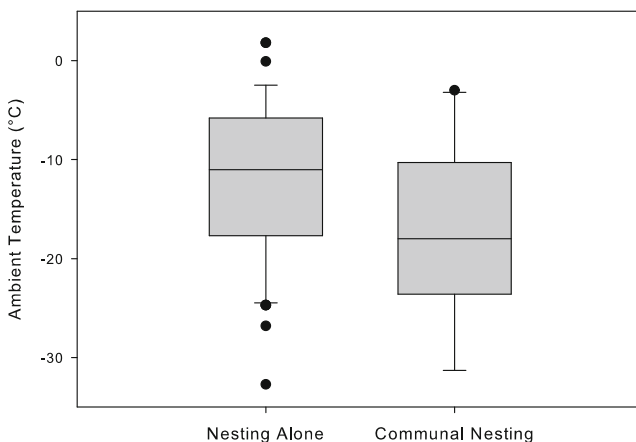


**Fig. 1** Box plot showing variation in distance to nearest female neighbor for squirrels that were only found to be nesting alone ( $n=51$ ) and squirrels that were occasionally found in a communal nest ( $n=12$ ). Medians (horizontal line within the box), quartiles (top and bottom of box), and the 90th and 10th percentiles (lines extending from the top and bottom of each box) are shown

territories. Communal nesting was never observed among the other 25 (of 29) females that were followed closely in 1995. In 2008, we opportunistically detected a single instance of communal nesting involving one dyad comprised of half-sisters (same dam, different sires) reared in the same litter the prior summer (Table 1).

## Discussion

We found that communal nesting in female red squirrels, which are spatially dispersed due to their year-round



**Fig. 2** Box plot showing variation in average daily ambient temperature when squirrels were found to be nesting alone ( $n=19$  observations for five groups comprising 12 squirrels) and nesting communally ( $n=50$  observations). Medians (horizontal line within the box), quartiles (top and bottom of box), and the 90th and 10th percentiles (lines extending from the top and bottom of each box) are shown. Data for squirrels that were never observed to nest communally are not included

territorial defense of food resources, is relatively common during late spring and early winter but is exceptionally rare during lactation. Females that nested communally were more likely to do so when ambient temperatures were lower, supporting the hypothesis that communal nesting is a means of reducing thermoregulatory costs. Although communal nesting was most common between mothers and yearling daughters, this cooperative behavior also occurred between half-sisters and among individuals that were not closely related, at least through the maternal lineage.

Social thermoregulation is a taxonomically widespread phenomenon that allows individuals to reduce energy expenditure by decreasing their cold-exposed body surface area and through warming of ambient temperatures surrounding the group (reviewed in Gilbert et al. 2010). For example, Scantlebury et al. (2006) demonstrated that reducing group size in free-living African four-striped grass mice (*Rhabdomys pumilio*) resulted in increases in daily energy expenditure (DEE) and water turnover by 19 and 37 %, respectively. Similarly, Merritt et al. (2001) found that captive southern flying squirrels forced to nest singly up-regulate their capacity for non-shivering thermogenesis by 28 % relative to individuals permitted to nest communally. Social thermoregulation is not restricted to mammals; communally roosting during the nonbreeding season reduces energy expenditure in birds (e.g., Du Plessis et al. 1994; McKechnie and Lovegrove 2001), and incubating emperor penguins (*Aptenodytes forsteri*) will huddle to conserve energy during the Antarctic winter (Ancel et al. 1997).

Despite the cold temperatures that characterize northern boreal regions, red squirrels at our study site have unexpectedly low energy expenditure during winter, and DEE actually decreases as it gets colder (Humphries et al. 2005). This low cost of living is likely achieved by reducing activity and relying on stored food hoards when thermoregulatory costs outside the nest are high. Social thermoregulation, however, may be an important additional mechanism for reducing energy expenditure, particularly in individuals that have not yet achieved adult body mass; female red squirrels do not obtain peak body mass until 3 years of age (Descamps et al. 2007). Smaller size will result in a higher surface area to volume ratio resulting in increased heat loss in addition to higher mass-specific metabolic rates, and mothers may be extending parental care to help offset these elevated costs.

In contrast to late winter and early spring, however, we found that communal nesting was exceptionally rare during lactation. This behavioral shift might reflect energetic costs of transferring milk to unrelated (or less related) individuals, particularly if some mothers cheat by reducing their own maternal investment (Hayes 2000). Additionally, competitive asymmetries resulting from different aged litters in a nest can affect the distribution of resources (Mennella et al. 1990). The costs associated with misdirected care toward unrelated or less related offspring may partially explain why

communal oviposition is relatively common in reptiles, which lack parental care, although the benefits associated with this behavior appear to vary widely among species (reviewed in Doody et al. 2009). For squirrels, thermoregulatory benefits decrease during lactation as ambient temperatures increase, offspring commence generating their own heat, and milk production increases maternal heat load. In red squirrels, mothers supporting large litter masses of furred offspring select nests of lower insulative value (Guillemette et al. 2008), presumably to increase their ability to dissipate heat. Thus, communal nesting during late lactation might often be detrimental from a thermoregulatory standpoint.

Although the propensity for communal nesting in tree squirrels increases during the winter months as temperatures drop (Layne and Raymond 1994; Edelman and Koprowski 2007; this study), there is substantial variation among species in the size and sex structure of the aggregations within nests. This variation is likely due to species-level differences in the proximal spacing among individuals and in spatial kin structure, which is determined by patterns of natal and post-breeding dispersal. In flying squirrels, for example, large aggregations of individuals (mean 7–9 individuals, depending on age) will nest communally in mixed-sex and mixed-age groups following the seasonal dissolution of territorial structure (Layne and Raymond 1994), and the acceptance of new individuals into groups depends upon relatedness (Thorington and Weigl 2011). Among sympatric breeding populations of fox (*Sciurus niger*) and gray squirrels (*Sciurus carolinensis*), the propensity for communal nesting and the number of individuals in a communal nest are higher for female gray squirrels, which presumably relates to their much higher degree of natal philopatry (Koprowski 1996).

Based on the high degree of relatedness among most communally nesting red squirrels, we propose that the frequency of this behavior is also affected by kin selection. However, as Griffin and West (2002) point out, high relatedness alone is insufficient to establish whether kin selection is responsible for promoting an observed behavior as fitness benefits may be direct. This is particularly true for communal nesting which provides direct thermoregulatory benefits to all individuals in the nest. Nevertheless, we expect that inclusive fitness benefits are likely to be important in red squirrels, particularly given the large number of communal nests that involved mother–daughter dyads, which might more appropriately be regarded as extended parental care.

Although communal nesting is relatively common among tree squirrels, red squirrels in the boreal forest were not previously thought to engage in this behavior due to the persistent defense of food-based territories (reviewed in Koprowski 1998); Layne (1954) previously reported instances of communal nesting in a non-territorial population of red squirrels found in a mixed hardwood forest. Red squirrel territories in our study area are maintained throughout the year using territorial

vocalizations (Price et al. 1990) and, with the exception of matings and dam–offspring and sibling–sibling interactions prior to dispersal, observations of direct social interactions among individuals are rare and involve exclusively agonistic behaviors (Gorrell et al. 2010; Dantzer et al. 2012). Nevertheless, we found that neighboring territory holders will share nests during cold winter conditions, although this behavior was typically restricted to kin. Interestingly, Rhind (2003) also observed communal nesting in a ‘solitary’ territorial marsupial, but only among females along territory margins during a period of nutritional stress driven by prolonged drought conditions. Thus, individual food-based territoriality does not preclude the use of social thermoregulation, although such aggregations appear to be relatively small (2–3 females) and are likely favored when short natal dispersal distances maintain connectivity among kin. Our findings, along with those of Gorrell et al. (2010) who report that female red squirrels will adopt orphaned kin, indicate a previously underappreciated social dimension to behavior in persistently territorial red squirrels.

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**Ethical standards** Data collection methods and experiments complied with the current laws of Canada and were authorized under provincial and federal permits.

**Conflict of interest** The authors declare that they have no conflict of interest.

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