KINSHIP AND USE OF UNDERGROUND SPACE BY ADULT FEMALE RICHARDSON'S GROUND SQUIRRELS (*UROCITELLUS RICHARDSONII*)

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Dedication

To all the strong, independent, and amazing women in my life who have influenced me in every way possible.

Thank you.

Abstract

Although female Richardson's ground squirrels (*Urocitellus richardsonii*) spend 80% of their lives sleeping and hibernating underground, studies on interactions and space-use have historically focused on the 20% of the time they spend aboveground. The type and frequency of aboveground interactions and degree of home-range overlap among female Richardson's ground squirrels depend on their reproductive status and degree of kinship. The purpose of my study was to determine whether reproductive status and kinship influence underground sharing of space as well. I radio-collared 54 adult female Richardson's ground squirrels (18 in 2008, 30 in 2009, and 6 in both years) of known maternal kinship in 5 spatially adjacent matrilines at a field site near Picture Butte, Alberta, Canada. Radio-collared females were located underground every evening after they retired and every morning before they emerged during both the 2008 and 2009 active seasons to determine sleep-site use and sleep-site sharing. The locations at which females were observed to retire in the evening (170 evenings) and emerge in the morning (141 mornings) in 2008 and 2009 were used to determine underground connections between surface entrances and underground sleep sites. Females commonly shared burrow systems, sleep sites, surface entrances, and underground connections after emergence from hibernation until mid-pregnancy and they shared again, though less frequently, after litters had been weaned, but they never shared underground features during lactation and hibernation. Close kin shared underground space more frequently than distant kin, and distant kin more frequently than non-kin. Variation in underground sharing of space over the active season and selective sharing with respect to kinship suggest that reproductive status and degree of kinship influence underground sharing.

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List of abbreviations

PMP Pre-mid-pregnancy

LPL Late-pregnancy/lactation

PW Post-weaning

S Sleep site shared simultaneously

CS Common sleep site

B Sleep site used both simultaneously and in common

AS Active season

Chapter I

1.1. Sociality and nepotism in ground-dwelling squirrels

Sociality or group living has evolved independently in many species of mammals when environmental constraints such as food resources force conspecifics to inhabit the same area and when benefits of group living (e.g. increase in predator detection) outweigh the costs (e.g. sharing environmental resources). Groups vary in size, structure, and cohesion, and degrees of sociality are often defined based on a species kin structure, including their spatial structure and social interactions, and reproductive strategy (Lacey & Sherman 2007); natural selection should favour different degrees of sociality depending on fitness gains and costs to individuals. Not only does sociality vary among species but within a species as well. Populations may differ in their degree of sociality due to varying ecological conditions and, depending on individual's reproductive state or age, may shift between degrees of sociality (Lacey & Sherman 2007).

Conspecifics (individuals of the same species) can either settle in their natal area (philopatry) or disperse to a new area or population (Michener 1983; Nunes 2007). Whether males, females, or both are philopatric or disperse, the age at which individuals disperse, and whether dispersal occurs before or after reproduction contribute to the spatial structure of individuals within a population which can influence the degree of sociality of a species (Nunes 2007).

Overlap of conspecifics in space and time is one consequence of group living that may lead to increased amicable and cooperative interactions and sharing of space over evolutionary time (Hare & Murie 2007). Cooperative interactions could evolve in the

form of reciprocity or mutualism; with the former, one individual helps another individual because the favour will eventually be returned, whereas with the latter, individuals help each other; in both forms, cooperation should only evolve through natural selection if both the individual performing the behaviour (the actor) and the individual receiving the behaviour (the recipient) increase their individual fitness (Sherman 1980).

Altruism, which is a form of cooperation in which one individual permanently loses reproductive fitness by helping another individual, violates the rule of natural selection (Hamilton 1964). Hamilton (1964) hypothesized that altruism could evolve through indirect fitness in which fitness is gained through an actor helping kin (the recipient) to survive and reproduce more successfully than the recipient could have achieved without help. Consequently, the actor indirectly passes genes onto the next generation. Kin-selection theory suggests that an animal may increase its inclusive fitness (the sum of both direct and indirect fitness) by exhibiting nepotism, the preferential treatment of kin (Mateo 2002).

Degree of kinship can be quantified by the coefficient of relatedness, which is the probability that an allele in one individual will be present in another individual as a result of shared ancestry. If Hamilton's (1964) rule, $r \times b > c$, in which r is the coefficient of relatedness between the individual who is performing the behaviour (the actor) and the individual who is receiving the behaviour (the recipient), b is the reproductive benefit to the actor, and c is the reproductive cost to the actor, is met, preferential treatment of kin may occur. Therefore, conspecifics can increase their inclusive fitness by exhibiting

nepotism towards conspecifics through reciprocity, mutualism, and altruism that varies

with the coefficient of genetic relatedness (Hamilton 1964).

Ground-dwelling squirrel, including prairie dogs (*Cynomys*), marmots (*Marmota*),

antelope squirrels (*Ammospermophilus*), and ground squirrels (*Urocitellus* and 7 other

genera that were previously classified in the single genus *Spermophilus*; Helgen et al.

2009) exhibit kin-biased behaviours. Although social structures among species of

ground-dwelling squirrels range from asocial to highly social polygynous harems

(Armitage 1981; Michener 1983), conspecifics are not geographically solitary and

individuals are typically found in clusters, even though individuals may be socially

solitary (Michener 1983). Species within these genera are usually obligate hibernators;

however, some do not hibernate (e.g. *Ammospermophilus leucurus*; Karasov 1983) and

some are facultative hibernators (e.g. *Otospermophilus beecheyi*; Dobson & Davis 1986).

Because North American ground-dwelling squirrels are medium sized (from 110 g

to 9000 g), diurnally active from 4 to 12 months of the year, and usually live in open

habitats, their social structures have been extensively studied. Females are usually

philopatric whereas males typically disperse from the natal area; therefore, matrilineal

kinship, fitness-neutral behaviours, and nepotism among females are basic components of

social organization in ground-dwelling squirrels (Dunford 1977; Armitage 1981;

Michener 1983; Mateo 2002). Male ground squirrels may disperse due to competition for

mates and environmental resources or to avoid inbreeding; dispersal by females usually

occurs because of competition for food or nest sites (Nunes 2007).

Even though the majority of ground-dwelling squirrels have a polygynous mating

system and a kin structure that is based on matrilineal kin groups, the extent of spatial

overlap, the type (amicable, neutral, and agonistic) and frequency of social interactions, and type of polygyny vary considerably among species leading to a continuum of social complexity from asocial to highly social (Armitage 1981; Michener 1983; Table 1.1). The degree of aboveground spatial overlap among females ranges from no overlap among neighbouring kin, to retaining individual core areas with outer edges overlapping with several adjacent close kin, to complete overlap of aboveground home ranges (Michener 1983; Table 1.1). Interactions among females vary from infrequent and mostly agonistic, to amicable within a kin group but agonistic to all other females, to amicable and frequent with conspecifics within their home range regardless of kinship (Michener 1983; Table 1.1). Polygyny ranges from promiscuous when both males and females mate with multiple partners and males do not defend territories, to males defending a territory of one or more female kin groups during the breeding season, to harems where the male and several females defend a common territory throughout the year (Michener 1983; Table 1.1).

North American ground squirrels have been placed into 5 distinct but continuous social categories independently by both Armitage (1981), who based social groups on body-size energetics, and Michener (1983), who based social groups on philopatry and cooperation among female kin (Table 1.1). Although species of ground squirrels have been placed in 1 of the 5 levels of sociality, species within each category may not have identical social systems, and within a species, the social system may differ slightly due to habitat differences.

North American species of ground squirrels most likely evolved from an ancestral asocial species (Michener 1983); thus, comparisons of social structures among closely-

Table 1.1. Classification of five social grades in ground squirrels summarized from Michener (1983). Grades 1 – 2 are considered less social, grade 3 is considered moderately social, and grades 4 – 5 are considered highly social.

Social Grade	RS*	HRE**	IT °	FI˟	Example species
1	P	High	Agonistic	Low	*Marmota monax* *Callospermophilus lateralis*
2	P	Medium	Amicable in kin group	Low	*Urocitellus richardsonii* *Urocitellus beldingi*
3	RD	Medium	Amicable in territory	Medium	*Urocitellus columbianus* *Urocitellus parryii*
4	H	Low	Amicable in harem	High	*Cynomys gunnisoni*
5	H	None	Amicable in harem	High	*Marmota olympus* *Cynomys ludovicianus*

* RS is the reproductive strategy, P = promiscuous, RD = resource defense, H = harem defense.

** HRE is home-range exclusivity among adult females.

° IT is interaction type between adult females.

˟ FI is frequency of interaction types between adult females.

related species of ground squirrels allow evolutionary biologists to formulate models for the evolution of sociality and nepotism. The 3 factors that influenced the evolution of group living in ground-dwelling squirrels are ecological factors (Hare & Murie 2007), life-history traits (Armitage 1981), and kinship and philopatry (Michener 1983).

A combination of ecological factors including: harsh winters; nutritionally poor environments; short growing-season length; clumped burrow systems; and predation pressure in an open habitat, and life-history factors including: overlap in time and space of sex and age cohorts; delayed dispersal; delayed reproductive maturity; and parental investment, contributed to the evolution and maintenance of group living in ground-dwelling squirrels (Hare & Murie 2007). Once group formation evolved, kin selection acted on groups when amicable social interactions, cooperation, relaxation of territorial boundaries, and broadened nepotism occurred (Michener 1983).

For nepotism to occur, conspecifics must have a mechanism to recognize genetic relatedness (Mateo 2002). Kin recognition is the process of conspecifics assessing genetic relatedness; if there is differential treatment of conspecifics based on relatedness, then kin discrimination is inferred by the observer (Mateo 2002). If the benefits to an individual performing an act are greater than the costs, and if the coefficient of relatedness between the individual performing the act and the recipient of the act is high enough, preferential treatment of kin may occur (Hamilton 1964). However, if costs outweigh benefits then there may not be preferential treatment of kin, no matter how closely related the participants (Mateo 2003). Kin discrimination occurs in all degrees of sociality in ground squirrels from asocial Franklin's ground squirrels (*Poliocitellus franklinii*; Hare 2004) to highly social black-tailed prairie dogs (*Cynomys ludovicianus*;

Hoogland 1995). Kin recognition can be either indirect, in which individuals consider conspecifics kin when in close spatial proximity, such as a natal nest or exclusive home range, or direct in which individuals use phenotypic traits of conspecifics to infer genetic relatedness (Mateo 2002).

Two forms of direct recognition are prior association and phenotype matching. In prior association individuals learn phenotypes of close kin, such as individuals in their natal nest, and can later discriminate familiar from unfamiliar individuals (Mateo 2002), whereas in phenotype matching, individuals learn their own phenotypes and those of close kin, and then match them with the phenotypes of unknown individuals to assess genetic relatedness, which requires a correlation between heritable genotypic and phenotypic kin labels (Mateo 2003). For species in which kin are philopatric, spatial proximity and prior association should be sufficient as kin-recognition mechanisms such that individuals in the natal nest and home range are inevitably kin, whereas phenotype matching would be favoured when non-kin are encountered (as a result of natal or breeding dispersal) and if close kin reside outside the natal area (if males mate with multiple females; Mateo 2003).

Kin-recognition mechanisms can be assessed from cross-fostering studies which are used to determine how rearing association (familiar or unfamiliar) and genetic relatedness (kin or non-kin) influence discrimination in both juvenile-juvenile and mother-juvenile relationships (Mateo & Holmes 2004). Cross-fostering is a technique in which infants from captive litters are transferred from their birth litter to an unrelated foster litter (Mateo & Holmes 2004). Whether individuals can recognize each other is usually assessed on the frequency of exploratory encounters, with individuals that exhibit

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a higher frequency of exploratory encounters considered unfamiliar with each other by the observer (Holmes 1984a). In arctic (*Urocitellus parryii*), Belding's (*Urocitellus beldingi*), golden-mantled (*Callospermophilus lateralis*), and thirteen-lined ground squirrels *(Ictidomys tridecemlineatus*), juveniles who were not fostered treated both fostered litter-mates who were transferred a few days after birth and genetic litter-mates (siblings) similarly, indicating that differential treatment of siblings is based on rearing association (familiar vs. unfamiliar) and not genetic relatedness (Hare & Sherman 1982; Holmes 1984a; Holmes 1995). In contrast, when juvenile Belding's ground squirrels are fostered at about the time of weaning, discrimination between nest-mates and transplanted foster juveniles occurs (Holmes 1994; Holmes 1997). Additionally, dams retrieve unfamiliar foster juveniles placed in their cage up to 15 days old but at 22 days old (about the time of weaning) mothers discriminate between familiar and unfamiliar juveniles (Holmes 1984b). Richardson's ground squirrel juveniles (*Urocitellus richardsonii*) and dams start discriminating between nest-mates and non-nest-mates after 20 days of age (Michener 1974). These studies indicate that in the less-social Belding's and Richardson's ground squirrels conspecifics start discriminating amongst individuals at the time of weaning.

In the more highly social Columbian ground squirrels (*Urocitellus columbianus*), captive juveniles also do not discriminate between foster juveniles transplanted before weaning and siblings (Hare & Murie 1996); furthermore in the field, even after weaning, nest-mates and non-nest-mates in the same territory do not discriminate against each other, unlike the less-social Belding's and Richardson's ground squirrels (Hare 1992). Juvenile Columbian ground squirrels do discriminate between individuals in different

colonies (Hare 1992). In black-tailed prairie dogs, discrimination between juveniles does not occur until a month after emerging from their natal burrow and when it does occur, it is only between coterie members (individuals in the same territory) and non-coterie members (Hoogland 1995).

Because female ground squirrels are usually philopatric, prior association should be sufficient to identify kin because individuals in the natal nest and home range are inevitably kin (Holmes & Mateo 2007). However, prior association does not explain how female Belding's ground squirrels distinguish between paternal half-siblings who are non-littermates and unrelated individuals (Holmes 1986a) or how Richardson's ground squirrel siblings can recognize siblings that have been reared apart from 24 h after birth until 37 days of age (Davis 1982), indicating that in the absence of familiarity, both Belding's and Richardson's ground squirrels can still recognize kin. Holmes (1986b) reported that female Belding's ground squirrels who are indirectly exposed to one another via rearing with each other's siblings were significantly less agonistic than females not indirectly exposed to one another.

Mateo (2002) supported Holmes' (1986b) study in phenotype matching by reporting that Belding's, and additionally, golden-mantled ground squirrels, have oral and dorsal apocrine glands which secrete odours that vary with genetic relatedness. These odours are heritable and vary linearly with relatedness, allowing for estimates of degrees of kinship (Mateo 2002). When juveniles are exposed to odours from unrelated adult females prior to litter emergence, they treat juveniles of the unrelated mother preferentially over other non-kin, indicating that the juveniles incorporate the unrelated mother's odours into their kin template and, through phenotype matching, consider the

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foreign mother's juveniles as kin (Mateo 2009). Phenotype matching, unlike prior association, allows conspecifics to direct nepotism toward previously unfamiliar kin and discriminate between familiar full and half siblings (Mateo 2002).

In aboveground interactions among female Belding's ground squirrels, nepotistic cooperation extends to close kin such as offspring and littermate siblings but not more distant female kin such as grandmothers and granddaughters, aunts and nieces, and first cousins or close and distant male kin (Sherman 1981). Male Belding's ground squirrels do not act nepotistically but they do produce kin labels and can recognize kin (Mateo 2002). Thus, Belding's ground squirrels can recognize both close and distant kin but choose not to act nepotistically towards them (Mateo 2002). Nepotism should only occur if Hamilton's (1964) rule, that the combined coefficient of relatedness and benefit to the actor is greater than the cost, is fulfilled; therefore, the lack of nepotism toward distant kin in Belding's ground squirrels may be due to the failure to satisfy this rule.

Golden-mantled ground squirrels also produce odours from their oral and dorsal apocrine glands that vary with genetic relatedness but do not act nepotistically toward any conspecifics (Mateo 2002), further supporting the observation that the ability to recognize kin is not a sufficient condition for nepotism to be expressed.

Kin-differential behaviours in ground-dwelling sciurids include: parental care (e.g. Hoogland 1995; McGuire & Bemis 2007); sharing of aboveground space (e.g. Michener 1979; McLean 1982; Maher 2009); thermoregulation (e.g. Karasov 1983; Arnold 1988, 1990); interaction rates (e.g. Armitage & Johns 1982; Hoogland 1986; Rayor 1988); alarm calling (e.g. Sherman 1977; Hoogland 1996; Blumstein et al. 1997; Hauber & Sherman 1998); cooperative defense against conspecifics (Sherman 1981);

defense against infanticide (McLean 1983; Dobson 1990; Hoogland 1995); and sharing of belowground space (Armitage & Johns 1982; Arnold 1990; Michener 2002). Depending on the level of sociality of a species and the degree of kinship among conspecifics performing the behaviour, kin-differential behaviours may or may not occur.

Parental care in mammals can be classified as either direct such as nursing, grooming, and huddling or indirect such as acquiring or defending resources, maintaining nests and burrows, and defending offspring against conspecifics; whether the mother, father, or both exhibit these behaviours depends on the species (McGuire & Bemis 2007). Within ground squirrels, males provide no direct paternal care and the only indirect paternal care they may provide is defense against conspecifics within a territory or coterie and this only occurs in highly social species (Michener 1983). Female ground squirrels exhibit both direct and indirect parental behaviours across all degrees of sociality. In addition to nursing altricial infants, other maternal behaviours include, but are not restricted to: retrieval of young; defense against infanticide; defense against predators; alarm calling; bequethal of burrow systems; and sharing of space (Michener 1971; Harris & Murie 1984; Hoogland 1995).

Sharing of aboveground home ranges by female ground squirrels has been documented in asocial species such as the woodchuck (*Marmota monax*; Maher 2009), moderately social species such as the arctic ground squirrel (McLean 1982), and highly social species such as the Gunnison's prairie dog (*Cynomys gunnisoni*; Rayor 1988). In all 3 species, home ranges overlap with close, distant, and non-kin but the degree of home range overlap is positively correlated with kinship.

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Alarm calls, which have been reported in most species of ground-dwelling squirrels (e.g. Sherman 1985; Hauber & Sherman 1998; Hare 1998; Mateo & Holmes 1997), are given in response to aerial and terrestrial predators, and Sherman (1977) reported that the most likely function of alarm calling in ground squirrels is to warn conspecifics of a predator. Giving alarm calls is potentially dangerous for the vocalizing individuals because it directs the predator's attention to them (Sherman 1977, 1985; Hoogland 1996). In Belding's, Richardson's, Columbian, California (*Otospermophilus beecheyi*), and round-tailed ground squirrels (*Xerospermophilus tereticaudus*) and in Gunnison's and Utah prairie dogs (*Cynomys parvidens*) and yellow-bellied and hoary marmots (*Marmota caligata*), females are more likely to produce an alarm call when their offspring are nearby than when only parents, full siblings, or distant kin are nearby (Owings & Leger 1980; Schwagmeyer 1980; Davis 1984; Sherman 1985; MacWhirter 1992; Hoogland 1996; Blumstein et al. 1997; Hoogland 2007). However, in black-tailed prairie dogs, females call as often when only close and distant kin are nearby as when offspring are nearby (Hoogland 1983). Therefore, for species with asocial and moderate social systems, nepotistic alarm calling appears to be directed toward offspring whereas in the highly social black-tailed prairie dog nepotism extends to non-offspring close and distant kin.

Nepotistic defense to protect a territory or young occurs in many species of ground-dwelling squirrels. In black-tailed prairie dogs, mothers defend their young against small predators (Hoogland 1995). Infanticide has been documented in Belding's, Columbian, California, and thirteen-lined ground squirrels, yellow-bellied marmots, and black-tailed prairie dogs; females defend their young against infanticide by conspecifics

of either sex through territory exclusion (Balfour 1983; McLean 1983; Brody & Melcher 1985; Trulio et al. 1986; Dobson 1990; Vestal 1991; Hoogland 1995). In the highly social black-tailed prairie dog, infanticide occurs most often within the coterie and is directed towards infants that are close kin (Hoogland 1995).

Ground squirrels share underground space, and depending on the species, sex of individuals, and time of year, sharing occurs during hibernation in a communal hibernaculum (Arnold 1988) and during the active season in sleep sites (Michener 2002) and burrows systems (Armitage & Johns 1982; Hoogland 1995). In alpine marmots (*Marmota marmota*), hibernating in a kin group reduces winter mortality and enhances female fertility in the following spring (Arnold 1988). However, when first year juveniles are part of the hibernating group, joint hibernation increases the weight loss of all older group members (Arnold 1988). Adult female Richardson's ground squirrels share sleep sites with mothers, daughters, and littermate sisters but they do not share hibernacula (Michener 2002). Female black-tailed prairie dogs share burrows with close and distant kin in the coterie throughout the active season with the exception of the natal burrow during lactation (Hoogland 1995).

All ground squirrels are dependent on burrow systems for sleeping, hibernating, protection, and rearing young (Michener 1983). Burrow systems are composed of underground chambers used for sleep sites and latrines, both of which are connected to underground tunnels that reach aboveground to surface entrances (Verdolin et al. 2008). Although burrow systems are a vital resource to ground squirrels, studies on underground behavioural interactions among conspecifics and sharing of underground space are rare because individuals cannot be directly observed in naturally constructed burrow systems.

In contrast, interactions and sharing of aboveground space by female ground squirrels have been studied extensively (e.g. Michener 1979; McLean 1982; Dobson 1983; King 1989).

Some of the more-social species of ground squirrels are known to share burrow systems throughout the active season (e.g. black-tailed prairie dog, yellow-bellied marmot; Armitage & Johns 1982; Hoogland 1995); however, whether they share features (sleep sites, underground tunnels, and aboveground entrances) within burrow systems is unknown. Knowledge of burrow-system sharing in less-social species of ground squirrels throughout the entire active season is restricted to the round-tailed ground squirrel in which burrow sharing occurs from emergence from hibernation until the start of pregnancy (Dunford 1977). Additionally, most species of marmots hibernate communally (Arnold 1990), but in species of *Urocitellus* such as the Columbian ground squirrel (Young 1990), arctic ground squirrel (Buck & Barnes 1999), and Richardson's ground squirrel (Charge 2001), individuals hibernate alone in an isolated hibernaculum.

For Richardson's ground squirrels, one of the less-social species of ground squirrels, aboveground sharing of space has been extensively studied and females are known to share underground sleep sites (Michener 1979, 2002). The extent of spatial overlap between adult female Richardson's ground squirrels varies over an active season in accordance with their reproductive cycle (Michener 1979). On average, female Richardson's ground squirrels go into estrus 3 days after they emerge from hibernation and are pregnant for 23 days (Michener 1985). Between emergence and mid-pregnancy females share belowground sleep sites (Michener 2002) and their aboveground home ranges overlap (Michener 1979). Adult females then give birth underground to an

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average of 6 - 8 altricial young in an isolated natal burrow (Michener 1985); between mid-pregnancy and emergence of the litter, 29 - 30 days post-partum, females do not share belowground sleep sites (Michener 2002) and their aboveground home ranges constrict and home-range overlap decreases (Michener 1979). After the litters emerge aboveground the females home ranges expand (Michener 1979). Females do not share hibernacula (Michener 2002).

The purpose of my study was to determine whether sharing of underground space, including burrow systems, sleep sites, surface entrances, and connections, by female Richardson's ground squirrels varies over an active season in accordance to their reproductive status as their aboveground space does. From research done thus far in species of ground squirrels, nepotism extends to distant kin within territories or coteries in highly-social species, whereas nepotism does not seem to extend past close-kin groups in less-social species. Therefore, the second purpose of my study was to determine whether nepotistic sharing of underground space in adult female Richardson's ground squirrels is limited to close kin (mothers, daughters, and litter-mate sisters). By examining underground behaviours and the extent to which kin tolerate one another underground, another step can be made in unraveling the social complexities of ground-dwelling squirrels.

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Chapter II

Kinship and sharing of underground sleep sites in female Richardson's ground squirrels (*Urocitellus richardsonii*)

2.1. Abstract

Female Richardson's ground squirrels (*Urocitellus richardsonii*) are philopatric, live in female kin clusters, and share underground sleep sites. To assess when and which degrees of genetic kin tolerate each other's underground proximity and whether the extent, duration, and limits to tolerance are similar throughout the active season, 54 adult female Richardson's ground squirrels of known maternal kinship in 5 adjacent matrilines were radio-collared (18 in 2008, 30 in 2009, and 6 in both years). Each radio-collared female was located after retiring for the evening and again before emerging the next morning on each night throughout the active season; if radio-signals were within 20 cm of each other, the females were considered to be sharing a sleep site. Sleep-site sharing was most common (91% of all females shared) between emergence from hibernation until mid-pregnancy, less common (47% of all females shared) between litter emergence and emergence into hibernation, and absent during lactation and hibernation. Females shared more frequently and in larger groups before mid-pregnancy than after litter emergence, and close kin (mother-daughters and littermate sisters) shared more frequently than distant kin or non-kin. Distant-kin pairs and non-kin pairs shared more frequently after emergence from hibernation than after litter emergence. Thus, sleep-site

sharing by female Richardson's ground squirrels extends to close kin more often than distant kin or non-kin and the limits to sleep-site sharing vary throughout the year.

2.2. Introduction

Among North American ground-dwelling squirrels (antelope squirrels, ground squirrels, prairie dogs, and marmots), species exhibit a range of social systems from solitary to multi-harem colonies (Armitage 1981; Michener 1983). Both ecological factors (harsh winters, reduced growing season, clumped burrow systems, predation pressure, and open habitats) and life-history traits (female philopatry, temporal, spatial, and seasonal overlap of sex and age cohorts, age at dispersal, and delayed reproductive maturity) influence the evolution and maintenance of group living (reviewed in Hare & Murie 2007).

Within ground squirrels (*Urocitellus* and related genera; Helgen et al. 2009), females are usually philopatric and males typically disperse; this results in female kin clusters in both space and time. Philopatry can promote cooperation between individuals in the form of mutualism and reciprocity, which in turn can promote kin selection and nepotism (Hare & Murie 2007). Kin-selection theory suggests that an animal may increase its inclusive fitness by exhibiting nepotism towards conspecifics that varies with the coefficient of genetic relatedness (Hoogland 1986).

The extent of nepotism in ground squirrels varies from species to species (Sherman 1981; McLean 1982; Maher 2009); however, in most species nepotism only extends to close female kin that share a natal nest (i.e. mothers, daughters, and littermate

sisters). In some of the moderate and highly-social species of ground squirrels, including

the Olympic marmot (*Marmota olympus*), black-tailed prairie dog (*Cynomys*

ludovicianus), and Columbian ground squirrel (*Urocitellus columbianus*), females do not

discriminate between close and distant kin (e.g. Barash 1973; Hoogland 1986; Hare &

Murie 1996). Richardson's ground squirrels (*Urocitellus richardsonii*) are one of the

less-social species of ground squirrels and can recognize kin in the absence of familiarity

(Davis 1982).

Adult female ground squirrels spend approximately 80% of their lives

underground sleeping in sleep sites and hibernating in hibernacula within burrow systems

(Michener 2002). Burrow systems are composed of numerous sleep sites, tunnels, tunnel

branches, surface entrances, and latrines (Verdolin et al. 2008). Burrow systems are used

for sleeping (Michener 2002), hibernation (Dobson & Davis 1986; Michener 1992;

Charge 2001), copulation (Michener & McLean 1996; Manno et al. 2008; Magyara

2009), parturition and litter rearing (Michener 1985), thermoregulation (Long et al. 2005;

Váczi et al. 2006), and protection against weather (Long et al. 2005) and predators

(Karels & Boonstra 1999; Swaisgood et al. 1999). Sleep sites and hibernacula are

supplied with grass and other vegetation for insulation (Gedeon et al. 2010).

Ground-dwelling sciurids cannot be observed underground and, therefore, most

ecological and behavioural research on ground-dwelling squirrels focuses on above-

ground sharing of space and social interactions in which both differential treatment of kin

and nepotism are known to occur among females. In highly social species of ground

squirrels, underground nepotistic behaviours have been found, including joint hibernation

in marmots (Arnold 1990) and burrow-system sharing in black-tailed prairie dogs

(Hoogland 1995). Whether less-social species share belowground space is limited to the round-tailed (*Xerospermophilus tereticaudus*) and Richardson's ground squirrels. In round-tailed ground squirrels, burrow-system sharing, usually with kin, occurs after emergence from hibernation until early pregnancy but not during any other time of the year (Dunford 1977). Among species of ground squirrels, patterns of underground sleep-site and hibernaculum use have been studied only in Richardson's ground squirrels (Michener 2002).

Richardson's ground squirrels are medium-sized, diurnal rodents native to the short and mixed grass prairies of North America (Armitage 1981; Michener 1983). The extent of aboveground spatial overlap and type of interactions between adult female Richardson's ground squirrels vary over an active season in accordance with their reproductive cycle (Michener 1979). On average, female Richardson's ground squirrels in southern Alberta emerge from hibernation in early March and go into estrus 3 days later (Michener 1985). Between emergence from hibernation and mid-pregnancy, females' aboveground home ranges overlap and interactions are commonly amicable (Michener 1979). Females are pregnant for 23 days and then give birth underground to an average of 6 - 8 altricial young in an isolated natal nest (Michener 1985). Between mid-pregnancy and emergence of the litter, 29-30 days post-partum, females' aboveground home ranges contract and interactions are more antagonistic; after the litters are weaned home ranges expand and interactions become more amicable (Michener 1979). The patterns of aboveground sharing of space in adult female Richardson's ground squirrels indicate that the costs and benefits of sharing space vary seasonally.

Adult female Richardson's ground squirrels use numerous underground chambers within a season (typically 8), of which some are dedicated to a single function and others have multiple functions (Michener 2002). Although females re-use sleep sites throughout the active season and use their parturition site before parturition, they do not use their hibernaculum site before hibernation (Michener 2002). Females usually stay in the same sleep site overnight during nights from emergence from hibernation until litter emergence, whereas within-night switches between sleep sites are most common in the 20 days after the litter first emerges aboveground (Michener 2002). Females use 1 sleep site for many consecutive nights until 5 to 6 weeks before entry into hibernation after which females start moving back and forth between sleep sites every few nights (Michener 2002). Females share sleep sites after they emerge from hibernation in the spring but stop sharing pre-partum (Michener 2002).

The goals of this study were to assess when and which degrees of genetic kin tolerate each other's underground proximity and whether the extent, duration, and limits to tolerance were similar throughout the active season. Because littermate sisters and their mother are the closest kin available, if alive, and Richardson's ground squirrels are classified in the same social category as Belding's ground squirrels (*Urocitellus beldingi*) but are less social than arctic ground squirrels (*Urocitellus parryii*; Michener 1983), species in which females are only nepotistic toward close kin (McLean 1982; Sherman 1981), I predicted that nepotistic sharing of sleep sites by female Richardson's ground squirrels is limited to mothers and daughters and to littermate sisters.

2.3. Methods

2.3.1. Subject species and study site

Free-living adult female Richardson's ground squirrels were studied in a population within a 3-ha site 5 km east and 1 km south of Picture Butte, Alberta, Canada (49º52'N 112º43'W, elevation 870 m) that has been investigated continuously since 1987 (Risch et al. 2007). The study area, which reverted to exotic grassland when agricultural activities ceased in the 1970s, is bordered on 3 sides by cultivated fields and on the fourth side by a road with cultivated fields beyond.

As part of long-term studies (e.g. Michener 2002; Risch et al. 2007), ground squirrels on the site are live trapped (Tomahawk Live Trap Co.; single-door squirrel traps) and then handled in conical cloth bags and tagged on first capture, usually as newly emerged juveniles, with numbered ear tags (National Band and Tag Co.) for permanent identification. Focal animals are uniquely dye-marked with hair dye (Clairol Hydrience) for observational purposes. Juveniles are trapped, ear-tagged, and assigned maternity within 3 days of first emergence from their underground natal burrow. Maternity is assigned from the location of litter emergence relative to the known area of residence of the mother combined with expected date of litter emergence based on known parturition date of the mother.

For females in my study, maternal kinship is known for 2 - 14 generations. Females that shared natal nests, i.e., mother-daughters and littermate sisters, were considered close kin; all other maternal kin were considered distant kin. Paternity cannot be assigned from mating observations alone as copulation usually occurs underground

(Michener & McLean 1996) and some females mate with multiple males (van Staaden et al. 1994; Hare et al. 2004; Magyara 2009). Kinship in this study is described only in terms of maternal associations. Thus, animals that share a common father but unrelated mothers are classified as non-kin, whereas littermates born in the same year to the same mother are treated as close kin, though some might be full-sibs and others half-sibs if the mother mated with multiple males.

Because Richardson's ground squirrels typically wean a litter each year, and subject females were 1 - 4 years old and had reared 0 - 3 litters, some kin relationships involved a variety of age combinations. Whereas daughters and grand-daughters must always be at least 1 or 2 years younger than their mother and grandmother, respectively, and non-littermate sisters must always differ in age, other classes of distant kin can be either of similar age or different ages (e.g. aunts can be either older, the same age, or younger than their nieces; Figure 2.1).

2.3.2. Radiotelemetry

Adult female Richardson's ground squirrels were live trapped and transported 30 - 70 m to an indoor lab where I used a cloth bag to restrain the female while I attached a radiocollar; females were released at the capture site within 15 minutes of capture. Females were radio-collared with either a Holohil PD-2C (Holohil Systems Ltd, Carp, Ontario; 5 g) or AVM G3 radiocollar (AVM Instrument Company, Livermore, California; 10 g). Individuals were then re-trapped every 10 - 14 days to check the fit of the collar and to readjust the sizing as necessary due to growth (yearlings) and weight

Matriline1

2005

2006

2007

2008

Matriline2

2005

2006

2007

2008

Matriline3
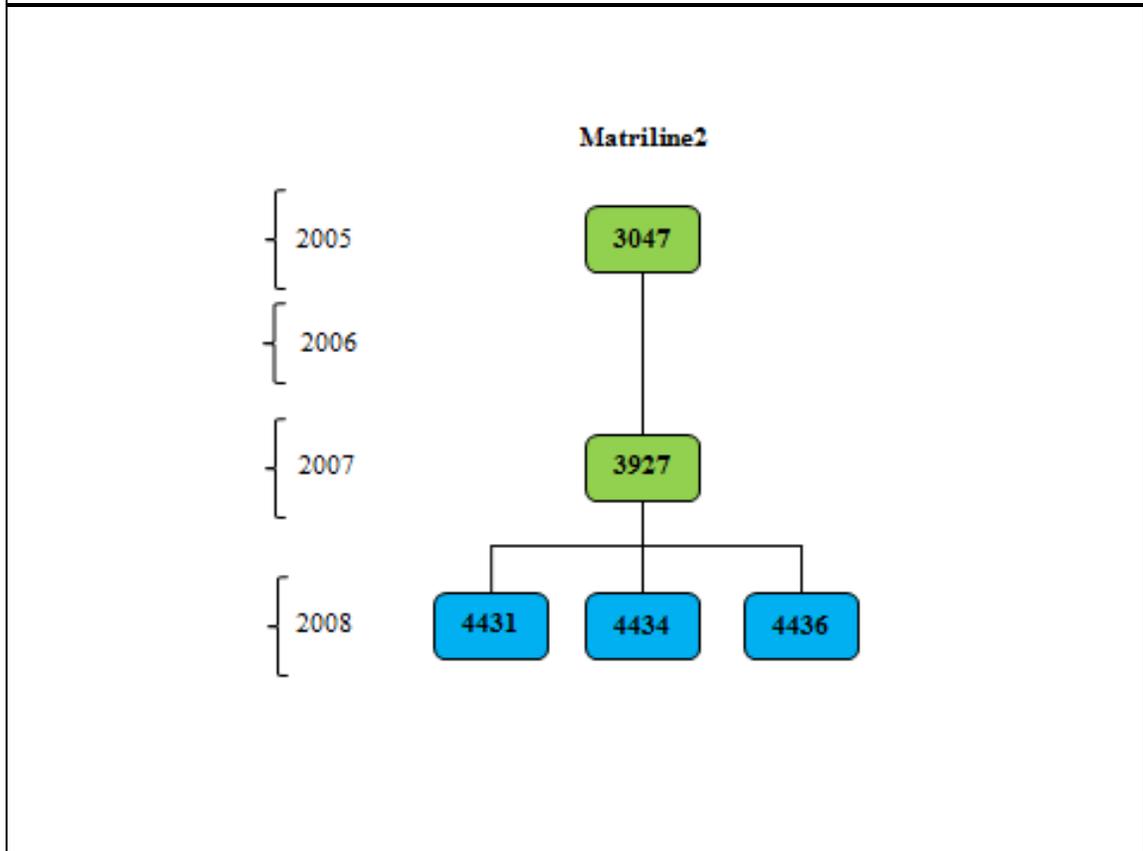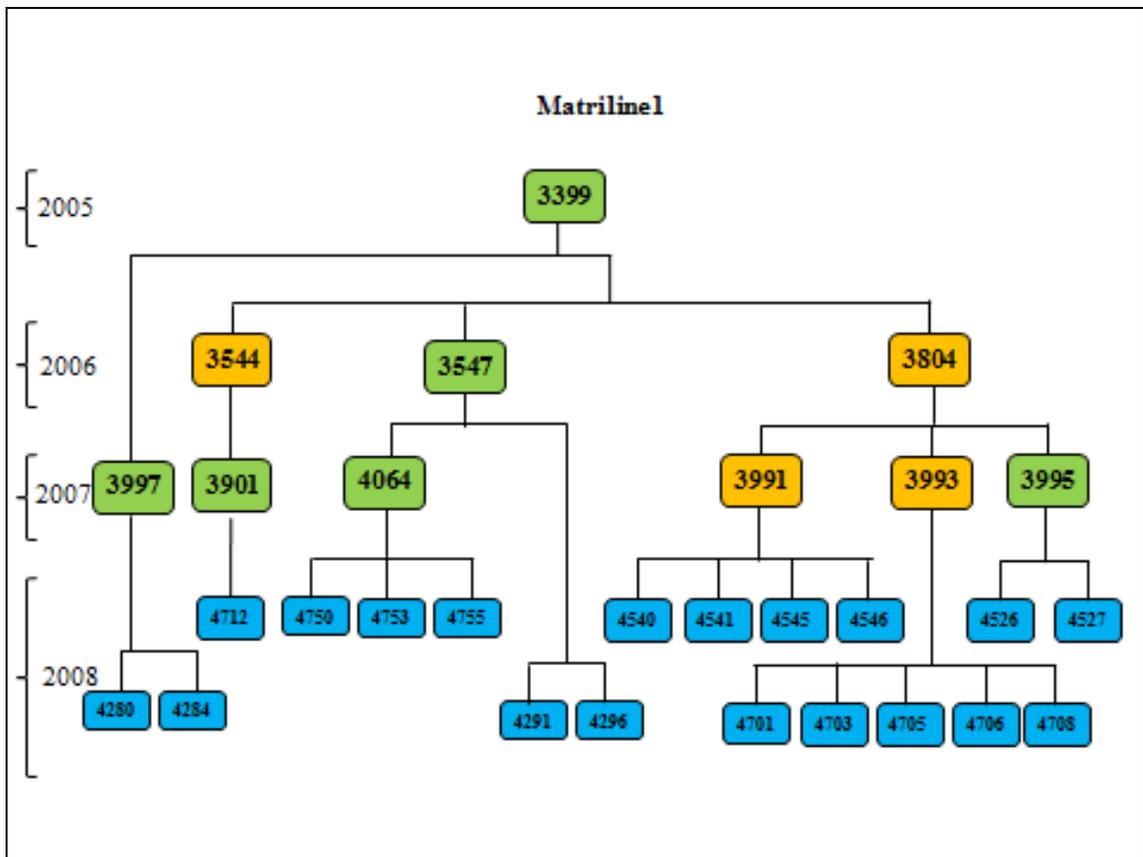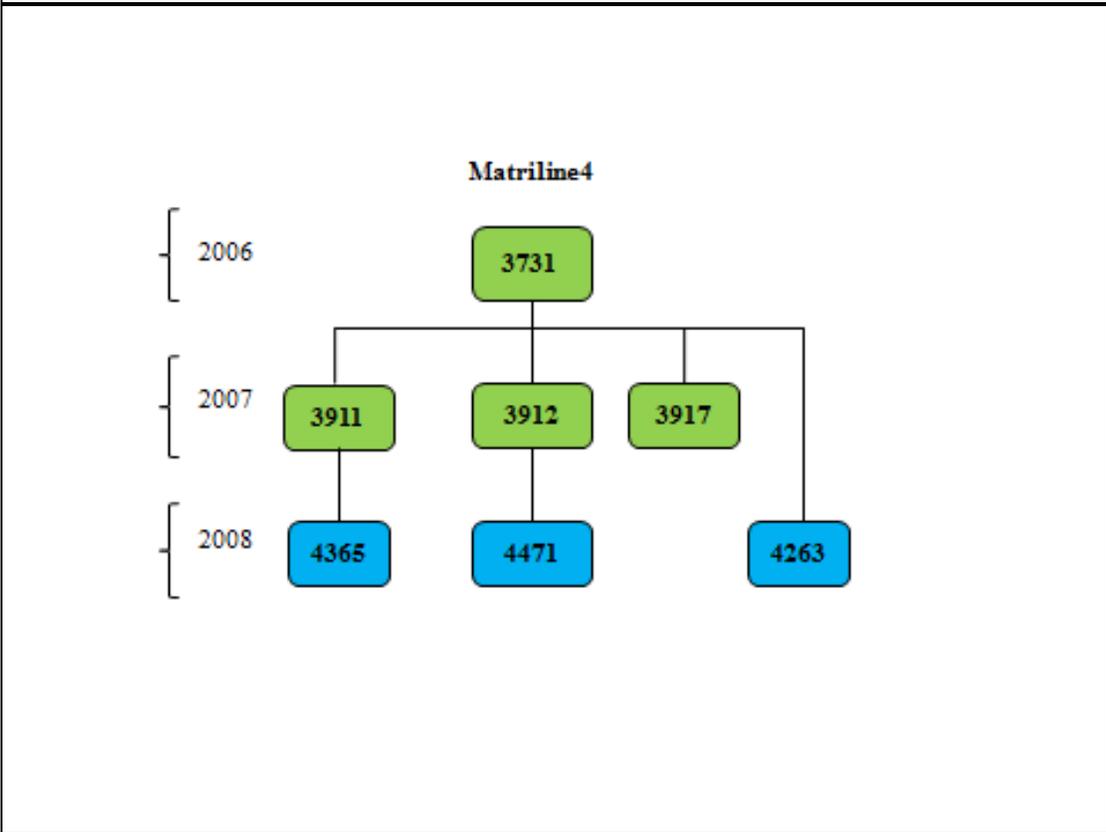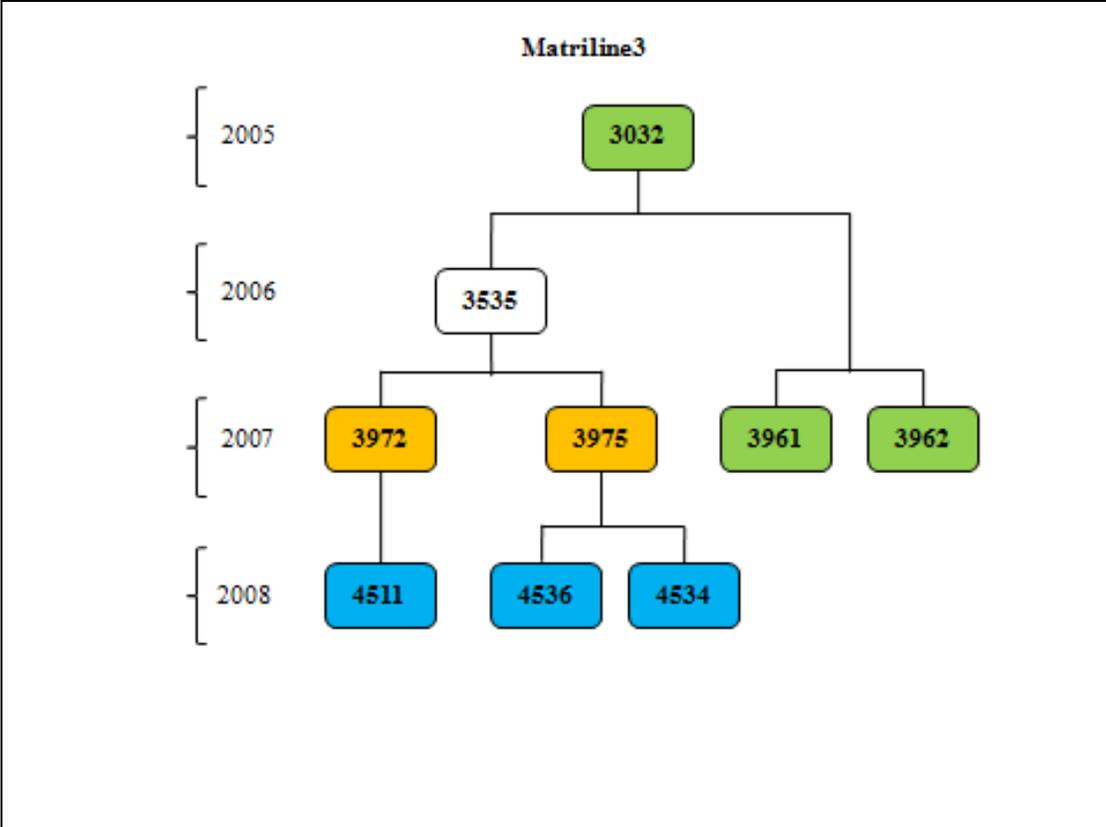
Matriline4

Figure 2.1. Four of the 5 matrilines of radio-collared female Richardson's ground squirrels; the fifth matriline consisted of a single female. Colours indicate the year a female was radio-collared (green = 2008, blue = 2009, orange = both 2008 and 2009, and white = not radio-collared). The year on the left side of each matriline indicates the year of birth of females within that row. Numerals inside the small boxes are the ear-tag number of the female.

fluctuations (all females) throughout the active season in association with reproductive status and prehibernation fattening.

Before hibernation, subjects were re-collared with either a PD-2CT (Holohil Systems Ltd, Carp, Ontario; 5 g) or AVM G3 (AVM Instrument Company, Livermore, California; 10 g) temperature-transmitting collar to detect where they sequestered themselves for hibernation and when they entered torpor. A LA12-Q receiver with a 3-element Yagi antenna (AVM Instrument Company, Livermore, California) and a TR-4 receiver with a 2-element antenna (Telonics, Telemetry-Electronics Consultants, Mesa, Arizona) were used to locate radio-transmitter signals. When females dispersed, disappeared, or died underground they could be located up to distances of 20 m from their radio signals and were considered missing only if searches extending 250 m away from the study site did not detect the radio signal.

2.3.3. Focal animals

When adult ($\geq$1-year-old) female Richardson's ground squirrels emerged from hibernation in late February - March 2008 and 2009, I selected 54 females aged 1 - 3 years and of known maternal kinship in 5 spatially adjacent matrilines occupying an area of 0.05-ha for radio-collaring. Matrilines that were adjacent to each other were chosen to determine whether, and the extent to which, spatially neighbouring non-kin shared underground space. Females in different matrilines had no known common maternal ancestor for at least 2 generations and females within a matriline encompassed a range of kinship relationships: mother-daughter; grandmother-granddaughter; littermate sisters;

non-littermate sisters; aunt-niece; grand aunt-niece; first and second cousins; and first cousins once removed (Figure 2.1).

Of 24 adult female Richardson's ground squirrels radio-collared from 0 to 7 (*mean* = 1 ± 1) days after emergence from hibernation in 2008, 16 were radio-collared on the first day out of hibernation and the other 8 were radio-collared 2 – 7 days after emergence. Most females (*n* = 21) were radio-collared for the entire active season, but 2 had their radio-collars removed when they relocated to the periphery of the field site during pregnancy and another female, who had already weaned a litter, was euthanized when she was confirmed to have myiasis attributable to the sarcophagid fly *Neobellieria citellivora* (Michener 1993). Once the 21 females that hibernated in the focal area ceased aboveground activity and their radio signals remained at a constant strength at the same location for 2 days, they were considered to be sequestered for hibernation; each female was located and her temperature recorded daily throughout the hibernation period to track torpor patterns.

During the 2008 - 2009 hibernation season, 10 radio-collared females were killed by a resident badger (*Taxidea taxus*), 4 died underground of unknown causes, and the earliest emerging female (29 January 2009) was killed by a conspecific male 5 days later. The 6 remaining subjects from 2008 and 28 yearlings, comprising all the surviving daughters of both the surviving and deceased radio-collared females from 4 of the 5 matrilines in 2008, were radio-collared 0 – 2 (*mean* = 0 ± 0) days after emergence in 2009; most females (*n* = 29) were radio-collared on the first day out of hibernation. I did not radio-collar the only survivor of the fifth matriline, a yearling who resided outside the focal area.

In 2009, 7 females relocated to the periphery of the field site and their radiocollars were removed 5 - 17 days after emergence. Two additional females that were not part of the 5 original matrilines were radio-collared when they were suspected to be sharing sleep sites with the focal radio-collared females; their radiocollars were removed 6 and 8 days after they ceased sharing with the radio-collared females. One female disappeared 12 days after emergence and 1 female died underground of an unknown cause 31 days after emergence. The remaining 25 females were radio-collared throughout the 2009 active season and into hibernation, after which they were monitored daily by radio-telemetry until they emerged from hibernation in spring 2010 when their radio-collars were removed.

2.3.4. Reproductive periods

Dates of each female's active season (emergence from and immergence into hibernation) and reproductive events (estrus, parturition, and litter emergence) were determined through both behavioural and physical observations. Each day a census was completed for each radio-collared female to determine whether she was active aboveground and, if so, her location on the study site. Emergence from hibernation was the first day the female was seen aboveground in the spring. Estrus usually occurred 3 days later, but the exact date was determined through observation of mating behaviour and by live-trapping each female to examine external genitalia. To determine parturition dates, females were live-trapped for at least 2 sequential days around their predicted date of parturition to detect weight loss and changes in external genitalia and mammae characteristic of parturition and initiation of lactation (Michener 1985). Litter emergence,

the first day the litter was observed aboveground, was determined through daily censusing of each mother's area of residence.

Data from the 2008 and 2009 active seasons for the radio-collared adult female Richardson's ground squirrels were separated into 3 time periods to compare sharing of underground space by reproductive status within the active season; time periods were determined from the female's reproductive status and information regarding sleep-site use from Michener (2002). The first period (pre-mid-pregnancy, PMP) was between emergence from hibernation to day 11 of pregnancy, around the time that females are reported to start using their future parturition site. The second period (late-pregnancy/lactation, LPL) was from mid-pregnancy to the day before litter emergence. The final period (post-weaning, PW) was from litter emergence until immergence into hibernation. The 3 reproductive periods were determined for each female based on the dates of her reproductive events, independent of calendar date.

One female in 2009 that mated but did not get pregnant was removed from data analyses involving reproductive periods. Additionally, 3 females from 2008 and 7 females from 2009 were not included in between-period or entire active season analyses because their radio-collars were removed during the active season ($n = 8$) or they died/went missing ($n = 2$).

2.3.5. Sleep-site locations

Each radio-collared female was located underground twice daily during the active season, after the last female retired for the night and before the first female emerged in the morning. Radio-telemetry commenced 29 ± 3 min ($n = 196$ evenings when retirement

times were known) after the last female retired underground for the night and 67 ± 4 min

($n = 176$ mornings when emergence times were known) before the first female emerged

in the morning. A sleep site was defined as the location where the radio signal was at the

greatest constant strength when the antenna was rotated through 180º. Michener (2002)

established that sleep sites can be pinpointed by radio-telemetry to a horizontal accuracy

of 20 cm, a distance that is slightly less than the diameter of a chamber. The ground

immediately above the sleep-site location was spray painted and identified with a

sequentially numbered wooden block for each user to indicate which animal used that site

(Figure 2.2).

The sleep site each female was in every evening and morning was recorded and

the total number of sleep sites used by the 54 radio-collared females (60 squirrel seasons

as 6 females were radio-collared in both years) as well as how many sleep sites each

individual female used during the active season and within each reproductive period were

extracted from the data. Additionally, the number of hibernacula used over-winter was

calculated for each female who survived the entire hibernation period.

A sleep-site bout was a period during which a female used the same sleep site on

consecutive nights. For analyses of between night changes in sleep-site location, 1 sleep

site was assigned for each night. If a female switched sleep sites during the night, the

sleep site that was used more consistently on consecutive nights before and after the night

she switched overnight was assigned as the sleep site for that night. The number of sleep-

site bouts and the number of times a female switched sleep sites during the night were

calculated for the entire active season and for each reproductive period. The number of

sleep sites used is usually fewer than the number of bouts per female because females

Figure 2.2. Wooden sleep-site markers at a sleep site that was used by 5 adult female Richardson's ground squirrels. Each female was assigned a unique colour for all her sleep-site markers; information written on each marker indicated the identity of the female (ear-tag number and dye mark) and the sequential order of use of sleep sites. For example, the red and blue block identifies that this sleep site was the third location used for sleeping by adult female 3541, who had the dye mark parallel lines.

return to previously used sites (Michener 2002). To adjust for differences in the duration of each of the 3 reproductive periods, the number of sleep sites used, the number of sleep-site bouts, and the number of overnight and between night sleep-site switches were calculated as proportions of nights in the reproductive period for between period comparisons.

2.3.6. Sleep-site sharing

When the radio signal of more than one animal remained constant and stationary at the same site, those females were considered to be sharing a sleep site. Sleep-site sharing was considered simultaneous when 2 or more females were in the same sleep site during the same night. Whether or not a female shared a sleep site with another female within an active season was extracted from the data. For females who did share, the reproductive period and duration of sharing were determined. Additionally, the number of cumulative individuals with whom each female shared a sleep site simultaneously, the number of females that shared a single sleep site, and the number of different sleep sites that were shared simultaneously by each female were calculated. Use of a common sleep site occurred when 2 or more females used the same sleep site but on different nights.

In 2009, 7 females were removed from data analyses involving sleep-site sharing because they either died ($n = 1$) while still sharing sleep sites or moved ($n = 6$) to a location where they were not observable but might have shared with non-collared females. For 2 females in 2008 that dispersed but were still observable, I determined that they had ceased sharing and included them in data analyses. All radio-collared females were included in the total number of females that shared sleep sites during pre-mid-

pregnancy as the 7 females that died or dispersed were known to share at least 1 sleep site. For data analyses on sleep-site sharing during post-weaning, all females still radio-collared were included.

2.3.7. Kinship

Maternal kin relationships (close kin, distant kin, and non-kin) between all radio-collared females that shared sleep sites simultaneously or used a common sleep site were analyzed. When 3 or more females shared a sleep site, each possible pairwise combination was included in analyses. Data analyses were separated into 2 categories, unique pairs and cumulative pairs. Unique pairs were composed of 2 individuals that shared at least once during the active season; each pair that shared was only counted once, regardless of the number of nights sharing. Number of sleep sites used and number of nights sharing were compared by kin relationship using unique pairs. Cumulative pairs were pairs of females that shared independent of the number of times they shared (i.e. if the same pair of close kin shared for 5 nights then 5 pairs of close kin shared). The maternal kinship relationships of all of the cumulative pairs that shared a sleep site were totalled and the proportion of close kin, distant kin, and non-kin that shared were compared.

2.3.8. Retirement and emergence observations

Female Richardson's ground squirrels were observed by 1 to 3 people from 1 to 3 observation sites for 71 mornings and 92 evenings (190 hours) in 2008 and for 70 mornings and 78 evenings (178 hours) in 2009. Observations were used to determine

entry or exit time (all times were recorded in Mountain Standard Time) and whether non-radio-collared females were also using the same surface entrances as the radio-collared females. I attached radio-collars to 2 females that used the same surface entrances as collared females to determine whether they were also sharing sleep sites with radio-collared females. All radio-collared and adjacent non-radio-collared females could be identified from their individual dye-marks and could be viewed clearly from each observation site. Additionally, 2 camcorders (Sony DCR-TRV19, Canon ZR100) were positioned to record 1 to 5 different holes during periods when females were sharing sleep sites. Video-recordings were then viewed to see when females retired and emerged.

Exact time (to the nearest second) of retirement or emergence was obtained on 74% of 6767 female-observations. Because each female's presence or absence was noted at 5-minute intervals during the evening retirement observations and 2-minute intervals during morning emergence observations, an approximate time was available for the remaining observations. The average time spent sleeping underground overnight for the entire active season and for each reproductive period was calculated for each female on nights with both retirement and emergence observations, then those averages were averaged. For time spent underground sleeping, both exact and estimated times were used as it was only the average time spent underground that was calculated.

2.3.9. Statistics and sample sizes

Values are reported as the mean ± standard deviation and statistical significance is set at $P < 0.05$. The sample size for combined years was described as squirrel seasons as

there were 6 females radio-collared in both years and had 2 squirrel seasons; therefore there were 54 females radio-collared over 2008 and 2009 and 60 squirrel seasons.

2.4. Results

2.4.1. Time periods

Female Richardson's ground squirrels were active for approximately 4 months. Radio-collared adult females emerged from hibernation significantly earlier in 2008 (*mean* = 1 March ± 6 days, *range* = 19 February – 12 March, n = 24 females) than 2009 (*mean* = 16 March ± 8 days, *range* = 21 February - 31 March, n = 36 females; unpaired Student's t-Test, t = -7.5, $P < 0.001$, n = 60 squirrel seasons, 54 females), but immergence dates did not differ significantly between years (*mean* = 25 June ± 7 days, *range* = 10 June - 10 July, n = 21 females; *mean* = 2 July ± 11 days, *range* = 13 June - 11 August, n = 25 females, in 2008 and 2009 respectively; unpaired Student's t-Test; t = -1.9, $P = 0.07$, n = 46 squirrel seasons, 41 females). Thus, the active season was 10 days longer (unpaired Student's t-Test; t = 3.5, $P = 0.001$, n = 46 squirrel seasons, 41 females) in 2008 than 2009 (Table 2.1). Durations of pre-mid-pregnancy and late-pregnancy/lactation did not differ between years (unpaired Student's t-Test; t = 0.9, $P > 0.20$, n = 45 squirrel periods, 40 females; t = -0.1, $P > 0.20$, n = 45 squirrel periods, 40 females, respectively; Table 2.1), but post-weaning was significantly longer in 2008 than 2009 (unpaired Student's t-Test; t = -5.5, $P < 0.001$, n = 45 squirrel periods, 40 females; Table 2.1).

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With increasing day length, females retired later, emerged earlier, and thus spent fewer hours underground overnight. Time sleeping underground declined from 14.2 ± 1.0 hours during pre-mid-pregnancy in March ($n = 55$ squirrel periods, 49 females with an average of 10 ± 4 nights on which evening retirement and morning emergence times were known), to 12.9 ± 0.6 hours during late pregnancy/lactation in April and early May ($n = 47$ squirrel periods, 41females with an average of 24 ± 5 nights on which evening retirement and morning emergence times were known), to 10.1 ± 0.8 h during post-weaning in May through early July ($n = 46$ squirrel periods, 41 females with an average of 20 ± 4 nights on which evening retirement and morning emergence times were known). Insufficient observations were available on both evening retirement and morning emergence in the week preceding immergence (*mean* = 2.0 ± 1.5 observations per female; $n = 46$ squirrel seasons, 41 females) to determine if time underground sleeping increased in the week preceding immergence into hibernation as reported by Michener (2002).

Duration of hibernation was significantly longer in the 2008 – 2009 hibernation season (*mean* = 265 ± 10 days; $n = 6$ surviving radio-collared females) than the 2009 - 2010 hibernation season (*mean* = 249 ± 10 days; $n = 23$ surviving radio-collared females; unpaired Student's t-Test, $t = -3.4$, $P < 0.05$, $n = 29$ squirrel seasons, 25 females).

2.4.2. Sleep-site use

Of 354 sleep sites used by the 54 radio-collared adult female Richardson's ground squirrels in 2008 and 2009 ($n = 60$ squirrel seasons), 131 were used in 2008, 178 were used in 2009, and 45 were used in both years. Radio-collared females used between 6

and 16 sleep sites within a single active season (*mean* = 10 ± 2.0, n = 46 squirrel seasons, 41 females; Table 2.1) and females radio-collared for both active seasons (n = 5) used 12 – 25 sleep sites over the 2 active seasons (*mean* = 18 ± 4). Although females used more sleep sites during post-weaning than during pre-mid-pregnancy or late-pregnancy/lactation, in proportion to duration of the reproductive period, females used more sleep sites during pre-mid-pregnancy ($24 \pm 10\%$ of nights in the period used a different sleep site; n = 45 squirrel periods, 40 females) than during late-pregnancy/lactation ($7 \pm 3\%$ of nights in the period used a different sleep site; n = 45 squirrel periods, 40 females), or post-weaning ($12 \pm 4\%$ of nights in the period used a different sleep site; n = 45 squirrel seasons, 40 females; Table 2.1).

All females used an underground site for hibernation that they had not used during the previous active season. Females rarely used the hibernaculum as a sleep site after hibernation. Of 6 radio-collared females who survived the 2008 - 2009 hibernation season, 5 switched to a sleep site for the first night after emergence from hibernation in spring 2009 and the other female used her hibernaculum site for sleeping for 1 night immediately after emergence. Of 5 females radio-collared for both 2008 - 2009 and 2009 - 2010 hibernation seasons, none re-used their 2008 - 2009 hibernaculum for hibernation in 2009 - 2010.

Females used sleep sites for an average of 3.5 ± 1.0 consecutive nights (n = 46 squirrel-seasons, 41 females) before re-locating to another site, and they switched to another site 34 ± 8.9 times within an active season (n = 46 squirrel seasons, 41 females). The female with the shortest active season (84 nights) had 28 sleep-site bouts with an average length of 3.0 ± 3.1 consecutive nights (*range* = $1 - 12$) and the female with the

Table 2.1. Descriptive statistics for sleep-site use by radio-collared adult female Richardson's ground squirrels ($n = 21$ in 2008, $n = 25$ in 2009) for the active season and for each reproductive period within the active season (PMP – pre-mid-pregnancy, LPL – late-pregnancy/lactation, PW – post-weaning; $n = 21$ in 2008, $n = 24$ in 2009). Sleep-site bouts are periods in which a female stayed in the same site on consecutive nights and overnight sleep-site switches are the number of nights a female switched sleep sites at some point during the night.

		Active season		Reproductive periods					
				PMP		LPL		PW	
	Year	$\overline{X} \pm SD$	Range	$\overline{X} \pm SD$	Range	$\overline{X} \pm SD$	Range	$\overline{X} \pm SD$	Range
Duration of period (days)	2008	117±6	107-127	15±2	13-19	39±1	38-43	60±6	46-72
	2009	107±10	93-144	14±4	13-29	39±1	38-42	51±9	37-88
Number of sleep sites used *	2008	9±3	6-15	3±1	1-6	3±1	1-6	7±3	3-13
	2009	10±3	6-16	4±2	1-7	3±1	1-5	7±2	4-12
Number of sleep-site bouts	2008	34±9	15-46	4±2	1-8	5±4	1-15	27±8	10-42
	2009	34±10	20-58	5±2	1-10	5±3	1-16	26±9	13-46
Number of overnight sleep-site switches	2008	10±5	1-22	0±1	0-2	1±1	0-5	9±5	1-21
	2009	11±6	1-21	1±1	0-4	1±2	0-7	9±6	1-21

* Because females sometimes re-used sleep sites, the total number of sleep sites is less than the sum of sleep sites used over the 3 reproductive periods.

longest active season (144 nights) had 58 sleep-site bouts lasting on average 2.5 ± 3.2 consecutive nights (*range* $= 1 - 20$). The shortest and longest bouts were 1 and 63 nights ($n = 46$ squirrel seasons, 41 females).

Proportionally, females switched sleep sites between nights more often during post-weaning ($49 \pm 13\%$ of nights, $n = 45$ squirrel seasons, 40 females) than during pre-mid-pregnancy or late-pregnancy/lactation ($33 \pm 13\%$ and $13 \pm 9\%$ of nights respectively; $n = 45$ squirrel seasons, 40 females; Table 2.1). Many sleep sites were re-used for subsequent sleeping bouts by every female, both within and between each reproductive period; therefore the additive number of sleep sites used in each period is greater than the total number of sleep sites used throughout the active season (Table 2.1).

Females usually stayed in the same sleep site overnight (92% of nights, $n = 46$ squirrel seasons, 41 females; Table 2.1); the rare occasions when females moved between sleep sites overnight were proportionally more common in post-weaning ($16 \pm 10\%$ of nights, $n = 45$ squirrel seasons, 40 females) than in pre-mid-pregnancy or late-pregnancy/lactation ($5 \pm 7\%$ and $2 \pm 4\%$ of nights, respectively, $n = 45$ squirrel seasons, 40 females; Table 2.1).

Of 176 and 223 sleep sites used by the 54 radio-collared adult female Richardson's ground squirrels ($n = 60$ squirrel seasons) in 2008 and 2009, respectively, 143 and 172 were used by only one adult female. About a fifth (84 of 399) were not the exclusive property of a single female but were used by 2 - 10 females within the same active season, sometimes simultaneously but more often at different times (Table 2.2). Females only shared sleep sites simultaneously during pre-mid-pregnancy and post-weaning. They also used a common sleep site during different nights within pre-mid-

Table 2.2. Number of sleep sites shared simultaneously (S), used in common (CS; i.e., not simultaneously), or both simultaneously and in common (B), by radio-collared adult female Richardson's ground squirrels within an active season. When 3 or more females used a sleep site, each possible pairwise combination was included in analyses. Thus, the sum of S + CS + B equals the product of pairwise combinations by sites.

n females that used a sleep site	*n* pairwise combinations	2008				2009			
		n sleep sites used	S	CS	B	*n* sleep sites used	S	CS	B
2	1	22	1	12	9	23	1	13	9
3	3	3	0	5	4	17	14	16	21
4	6	2	1	3	8	4	3	17	4
5	10	3	5	16	9	4	4	26	10
6	15	1	0	8	7	1	0	9	6
7	21	0	0	0	0	1	7	9	5
10	45	0	0	0	0	1	9	19	17

pregnancy and post-weaning, and between all 3 reproductive periods but during late-pregnancy/lactation, only a few females used a common sleep site and none shared a sleep site simultaneously.

2.4.3. Sleep-site sharing

Of 48 females that were radio-collared for only 1 active season, 41 shared a sleep site simultaneously with at least one other radio-collared female for at least 1 night during the active season. The 6 females radio-collared in both years shared a sleep site with at least one other another radio-collared female for at least 1 night in both years. No females shared during lactation ($n = 46$ squirrel seasons, 41 females) and all females hibernated alone ($n = 29$ squirrel seasons, 25 females).

In 2008, 20 of the 24 radio-collared females shared a sleep site during pre-mid-pregnancy and 9 of the 22 females still radio-collared during post-weaning shared, 1 of which had not shared during pre-mid-pregnancy. In 2009, 32 of the 36 females shared a sleep site for at least 1 night during pre-mid-pregnancy and 13 of the 25 females still radio-collared during post-weaning shared, all of whom had already shared during pre-mid-pregnancy. Two of the 5 females radio-collared in both years did not share during post-weaning in 2008 but did in 2009, whereas the other 3 females only shared during pre-mid-pregnancy in both years; no females that shared during post-weaning in 2008 survived to 2009.

Of the adult female Richardson's ground squirrels that shared a sleep site during pre-mid-pregnancy, sharing commenced, on average, 2 – 3 nights after emergence (Table 2.3). Females shared for an average of 7 nights, but sharing did occur for up to 16 nights

Table 2.3. Descriptive statistics describing when female Richardson's ground squirrels shared sleep sites simultaneously during pre-mid-pregnancy (PMP; $n = 20$ in 2008, $n = 24$ in 2009) and post-weaning (PW; $n = 8$ in 2008, $n = 12$ in 2009) for 2008 and 2009. For PMP, females were described to start sharing in reference to the number of nights after they had emerged from hibernation and for PW in reference to the number of nights after their litter had emerged aboveground. The duration of sharing is the number of nights a given female shared a sleep site during a given reproductive period. Females ceased sharing in PMP in reference to the number of nights before mid-pregnancy and ceased sharing in PW in reference to the number of nights before immergence into hibernation. A negative value indicates the number of nights past mid-pregnancy a female ceased sharing sleep sites.

		Started sharing		Duration of sharing		Ceased sharing	
		$\overline{X} \pm SD$	Range	$\overline{X} \pm SD$	Range	$\overline{X} \pm SD$	Range
PMP	2008	2.8±3.6	0-13	7.4±2.5	1-14	6.4±2.9	1-13
	2009	1.7±3.2	0-16	8.8±3.8	2-15	3.8±5.7	12-(-6)
PW	2008	29.0±8.9	19-41	8.0±4.0	1-12	16.0±10.2	3-25
	2009	20.0±7.8	9-29	8.3±4.7	1-16	15.0±19.0	2-70

(Table 2.3). No females shared after mid-pregnancy in 2008, whereas 7 females shared

for $1 - 6$ (*mean* $= 2.4 \pm 1.9$) nights past mid-pregnancy in 2009, but none shared

simultaneously when lactating. Sleep-site sharing during post-weaning was more

variable; females started sharing from 9 to 41 nights after the litters had been weaned and

ceased sharing from 2 to 70 nights before immergence into hibernation (Table 2.3).

During post-weaning, sharing lasted for an average of 8 nights (Table 2.3).

Simultaneous sleep-site sharing by the 38 radio-collared female Richardson's

ground squirrels monitored in both periods (44 squirrel seasons) occurred in significantly

larger groups during pre-mid-pregnancy than during post-weaning (unpaired Student's t-

Test; $t = 5.5$, $P < 0.001$, $n = 168$ groups in PMP, $n = 86$ groups in PW; Table 2.4). In

both years, females shared with significantly more collective individuals within pre-mid-

pregnancy than during post-weaning (unpaired Student's t-Test; $t = 2.6$, $P < 0.05$, $n = 50$

squirrel periods in PMP, $n = 21$ squirrel periods in PW; Table 2.4). The number of nights

females shared was similar for both time periods, but because post-weaning lasted about

3 times longer than pre-mid-pregnancy, females shared for proportionally more nights

during pre-mid-pregnancy than during post-weaning ($44 \pm 3.4\%$ and $19 \pm 0.1\%$ of the

nights respectively, $n = 43$ squirrel periods, 38 females and $n = 20$ squirrel periods, 20

females, respectively, that were monitored in both periods; Table 2.4).

2.4.4. Kinship of individuals sharing

Of 41 females radio-collared throughout the entire active season in either 2008 or

2009 (46 squirrel seasons), 6 had no close kin available. Of these 6 females, 2 did not

Table 2.4. Descriptive statistics for adult female Richardson's ground squirrels that shared a sleep site at least once simultaneously during each reproductive period in the 2008 and 2009 active seasons (PMP – pre-mid-pregnancy, LPL – late-pregnancy/lactation, PW – post-weaning). Nights shared is the number of nights each female shared a sleep site simultaneously, group size is the number of females that used the same sleep site simultaneously, and collective individuals is the number of different females each female shared with. Sample sizes for number of nights shared and number of collective individuals each female shared with include females radio-collared throughout entire respective reproductive period. Sample size for number of females in group is the number of groups that shared a sleep site.

			PMP			LPL			PW	
		n	$\overline{X} \pm SD$	Range	n	$\overline{X} \pm SD$	Range	n	$\overline{X} \pm SD$	Range
***n* nights**	2008	20	7.4±2.5	1-14	0	0±0	0	8	8.0±4.0	1-12
shared	2009	30	8.8±3.8	2-15	0	0±0	0	13	8.3±4.7	1-16
***n* females**	2008	60	2.4±0.7	2-4	0	0±0	0	32	2.0±0.0	2-2
in group	2009	108	2.5±0.8	2-7	0	0±0	0	54	2.1±0.3	2-3
***n* collective**	2008	20	2.5±1.2	1-5	0	0±0	0	8	1.1±0.4	1-2
individuals	2009	30	3.6±2.8	1-9	0	0±0	0	13	2.1±0.9	1-4

share a sleep site simultaneously with any other female and 4 shared a sleep site at least

once with distant kin. The 35 females (40 squirrel seasons) with close kin available had

an average of 2.5 ± 1.5 close kin. Of these, almost all (36 of 40 squirrel seasons) shared a

sleep site at least once with close kin, whereas sharing with distant kin when close kin

were available occurred rarely (3 of 40 squirrel seasons), and only 1 did not share a sleep

site with any other female. Many females (21 of 36 squirrel seasons) shared a sleep site

at least once with every close kin available to them and 15 shared a sleep site with some

but not all close kin available (*mean* = 57.3 ± 19.1% of available close kin).

Of all the close-kin pairs available in 2008 and 2009, 65% and 70% shared a sleep

site at least once during the active season, whereas only 6% and 9% of all the distant-kin

pairs available shared; in both years, only 2% of non-kin pairs shared (Table 2.5). Of 50

unique groups of 3 or more females that shared a sleep site simultaneously during both

pre-mid-pregnancy and post-weaning in both years (*n* = 50), 49 included kin, of which

the most common grouping (*n* = 22) involved only close kin with less-frequent groups

composed of: distant kin only (*n* = 5); both close and distant kin (*n* = 12); close, distant,

and non-kin (*n* = 3); close and non-kin (*n* = 4); distant and non-kin (*n* = 3); and non-kin

only (*n* = 1).

Of 169 groupings of females that shared a sleep site, the most common group

sizes were 2 (*n* = 101) and 3 (*n* = 56), with groups of 4, 5, 6, and 7 occurring rarely (*n* =

9, 1, 1, and 1, respectively). When 3 or more females shared a sleep site simultaneously

and each possible pairwise combination was analyzed (*n* = 362 cumulative pairs), pairs of

close kin were the most common (72% of 362), distant kin sometimes slept together

(20% of 362), and non-kin rarely did so (8% of 362). During post-weaning, 87

cumulative groups shared a sleep site. The most common group size was 2 (83 of 87 groups) with only 4 of 87 groups comprising 3 individuals. When 3 or more females shared a sleep site and each possible pairwise combination was analyzed ($n = 95$ cumulative pairs), pairs of close kin were the most common (80% of 95), pairs of distant kin rarely slept together (20% of 95), and non-kin never slept together.

The earliest emerging female in any matriline initially had no kin with whom to share, whereas later emerging females had the option of sharing with kin on their first night out of activity. Indeed, 19 of 36 females with close kin available on emergence immediately slept with kin on their first night, a further 14 females began sharing $2 - 6$ nights after emergence, and only 3 did not share. When close kin were available, females started sharing on average 1.9 ± 1.3 nights (*range* $= 1 - 6$, $n = 33$ squirrel seasons, 17 females) after emergence from hibernation which is significantly sooner than females that had no close kin available at emergence (*mean* $= 4.8 \pm 4.6$ nights after emergence, *range* $= 1 - 16$, $n = 18$ squirrel seasons, 17 females; unpaired Student's t-Test, $t = 3.4$, P $=$ 0.001, $n = 51$ squirrel seasons, 45 females).

Of the 18 females that did not have close kin available at emergence and shared a sleep site during pre-mid-pregnancy, 6 started sharing with distant kin before close kin emerged, 4 had no close kin alive but shared with distant kin, and the remaining 5, 2, and 1 females started sharing with kin on the first, second, and third nights, respectively, that kin became available.

Sharing by distant kin typically occurred either in groups that also included close kin or at times when no closer degree of kin was available. Of 23 pairs of distant kin that shared a sleep site simultaneously during pre-mid-pregnancy in 2008 or 2009 (Table 2.5),

all females in 9 pairs also had close kin present in the group, 1 female in each of 6 other pairs had close kin present but the other female did not, whereas none of the females in a further 5 pairs had any close kin available for sharing, and the remaining 3 pairs were in groups that did not include any of their available close kin. In the post-weaning period, no distant kin shared sleep sites simultaneously in 2008, but 3 pairs shared in 2009, all of whom had close kin available to them.

Sharing by non-kin typically occurred when females had no kin available. In 2008, 3 non-kin pairs shared a sleep site simultaneously during pre-mid-pregnancy; both females from 1 of these pairs had no kin available, whereas 1 female in the other 2 pairs had one close kin within the sleep site but the other female had no kin available. In 2009, 7 non-kin pairs shared a sleep site simultaneously during pre-mid-pregnancy; both females from 1 pair had distant kin but no close kin available, in the other 6 pairs, greater than 3 individuals were in the sleep site and one female had either close or distant kin in the sleep site whereas the other female was one of the 2 females that were not part of the original five matrilines. The only information I have on where the kin of the 2 additional females were sleeping is that some of their kin used the same surface entrances as the radio-collared females but whether both families were all sharing a sleep site could not be assessed. In both cases, 2 family groups were sharing surface entrances for $1 - 3$ nights and therefore may have been sharing a sleep site. No non-kin pairs shared a sleep site simultaneously during post-weaning in either 2008 or 2009.

Too few unique pairs of distant kin shared sleep sites during pre-mid-pregnancy in 2008 to compare duration of sharing by close versus distant kin, but such comparisons were made for 2009. Unique close kin pairs that shared sleep sites simultaneously during

Table 2.5. Kin relationships of 54 radio-collared adult female Richardson's ground squirrels in 2008 and 2009, and the number of unique kin relationship pairs that shared a sleep site at least once during the active season; 6 females were present in both years. Females either shared a sleep site simultaneously when 2 or more females were in the same sleep site at the same time (S) or they used a common sleep site (CS). When 3 or more females shared a sleep site, each possible pairwise combination was included in analyses. Non-kin includes all possible non-kin relationships between the radio-collared females; for 2009, 2 females not part of the original 5 matrilines are also included.

	2008			2009		
	Sample	n pairs sharing		Sample	n pairs sharing	
Kin relationships	size	S	CS	size	S	CS
Close Kin						
Mother-Daughter	17	10	11	14	12	13
Littermates Sisters	14	10	12	29	18	21
Distant Kin						
Aunt-Niece	25	2	9	28	4	11
1st Cousins	15	1	2	53	4	24
Grandmother-Granddaughter	9	0	1	12	7	7
Great Aunt/Great Niece	0	0	0	18	4	7
1st Cousins once removed	0	0	0	68	1	4
2nd Cousins	0	0	0	47	0	3
Non-littermate Sisters	3	0	0	0	0	0
Non-Kin	193	3	7	361	7	17

pre-mid-pregnancy in 2009 slept together for significantly more nights (*mean* = 5.8 ± 3.1, *range* = 1 - 11, *n* = 30 pairs) than unique pairs of distant kin (*mean* = 2.8 ± 2.7, *range* = 1 - 10, *n* = 20 pairs; unpaired Student's t-Test, *t* = 3.5, *P* < 0.001). Unique pairs of close kin also shared significantly more sleep sites (*mean* = 2.0 ± 0.1, *range* = 1 - 2, *n* = 30 pairs) than unique pairs of distant kin (*mean* = 1.2 ± 0.4, *range* = 1 - 2, *n* = 20 pairs; unpaired Student's t-Test, *t* = 3.4, *P* < 0.05) during pre-mid-pregnancy. No pairs shared during late-pregnancy/lactation.

During post-weaning in 2008, no distant kin pairs shared a sleep site, whereas close-kin pairs that shared, did so for an average of 3.8 ± 3.0 nights (*range* = 1 - 10, *n* = 11 pairs) and used 1.6 ± 0.6 (*range* = 1 - 2, *n* = 5 pairs) sleep sites. During post-weaning in 2009, unique close-kin pairs shared a sleep site for about the same number of nights as distant-kin pairs (*mean* = 6.6 ± 4.5, *range* = 1 - 12, *n* = 5 pairs and *mean* = 6.7 ± 7.2, *range* = 2 - 15, *n* = 3, respectively). Additionally, unique close-kin pairs and distant-kin pairs used about the same number of sleep sites while sharing during post-weaning (*mean* = 1.6 ± 0.8, *range* = 1 - 3, *n* = 11 and *mean* = 1.3 ± 0.6, *range* = 1 - 2, *n* = 3 pairs, respectively).

The probability of aunts and nieces sharing a sleep site was similar whether the aunt was older than the niece (5 of 53 pairs) or the same age as the niece (1 of 13 pairs; Fisher's exact test, *P* = 1.0). The probability of cousins sharing a sleep site was similar whether the cousins were the same age (5 of 60 pairs) or different ages (0 of 8 pairs; Fisher's exact test, *P* = 1.0).

2.4.5. Sleep sites used at different times

In addition to using the same sleep site at the same time, females often used each other's sleep sites when sleeping alone such that a given sleep site was used by many females throughout the active season. All radio-collared adult female Richardson's ground squirrels ($n = 60$ squirrel seasons, 54 females) used at least one common sleep site that had already been used or was subsequently used by another adult female. Common sleep sites were used by as many as 6 and 10 radio-collared females in 2008 and 2009, respectively (Table 2.2).

Of the 9.6 ± 2.9 sleep sites each female used during the active season (*range* = 6 − 16; $n = 46$ squirrel seasons, 41 females), 4.8 ± 2.7 were never used by another radio-collared female (*range* = 1 − 11; $n = 46$ squirrel seasons, 41 females), whereas 0.1 ± 0.3, 1.6 ± 1.5, and 3.1 ± 2.2 were used simultaneously, at another time, or both, respectively (*range* = 0 − 1, 0 − 5, 0 − 9, respectively; $n = 46$ squirrel seasons, 41 females). Sleep sites were used by more than 1 female on various nights throughout the entire active season except for within late-pregnancy/lactation. Close kin pairs were almost as likely to use a given site simultaneously as non-simultaneously (68% and 77% of 74 pairs), whereas distant kin were less likely to use a given site simultaneously than non-simultaneously (8% and 24% of 278 pairs; Table 2.5).

2.5. Discussion

Adult female Richardson's ground squirrels were more likely to share sleep sites with close kin (mothers and littermate sisters) than distant kin and with distant kin more

than non-kin, and therefore, are nepotistic towards close kin. For all degrees of kinship, sharing was more common before mid-pregnancy than post-weaning and was almost absent during late pregnancy, lactation, and hibernation. Collectively, these patterns indicate that season and kinship strongly influence sharing of sleep sites. The degree of home-range overlap and type and frequency of aboveground interactions among female Richardson's ground squirrels are also dependent on reproductive status and degree of kinship (Michener 1979). Females have greater home-range overlap and interactions are more frequent and amicable before mid-pregnancy and post-weaning than during lactation, and interactions are more frequent and amicable among close kin (Michener 1979). Therefore, spatial patterns, interaction rates, and selective interactions with respect to kinship among female Richardson's ground squirrels are similar both aboveground and underground.

About a fifth of sleep sites were not the exclusive property of a single female but were used by multiple females at the same and/or different times. The majority of radio-collared females (91%) shared a sleep site simultaneously with a conspecific female at least once in the active season. Additionally, every female used at least 1 sleep site that was also used by another radio-collared female at some point within the active season. Although females moved their offspring during lactation, typically twice, they never moved their young into a site that had been vacated by another female and her young. Sharing and using a common sleep site indicate considerable overlap of underground space among female Richardson's ground squirrels, the extent of which varies throughout the active season.

Only 34% of sleep sites that were used during 2008 were re-used in 2009; the sleep sites that were not re-used may have no longer existed because of underground destruction/closure by ground squirrels, destruction by the badger that hunted in the winter of 2008 - 2009, or because sleep sites became unsuitable for sleeping. The large number of sites and the low proportion of re-use indicates that underground sleep sites are not permanent entities or a limiting resource but are used and then abandoned or renovated, and new sleep sites are excavated or old ones are re-established and provisioned.

Mateo (2002) suggested that kin discrimination can be inferred when differential treatment of conspecifics is based on relatedness. In female Richardson's ground squirrels, close kin shared sleep sites for significantly more nights than they did with distant kin, shared more sleep sites with close kin than with distant kin, and shared with more individuals who were close kin than individuals who were distant kin, all of which suggests that females recognize close kin. However, females may share underground sites more frequently with close kin because they just happen to be in closer spatial proximity when aboveground. For nepotism to occur, conspecifics must have a mechanism to recognize kin; for Richardson's ground squirrels this mechanism is not known although in species with similar social structures, such as the Belding's ground squirrel, individuals can recognize varying degrees of kinship through phenotype matching (Mateo 2002). Therefore, female Richardson's ground squirrels may also have a mechanism to identify different degrees of kin and because female Richardson's ground squirrels preferentially share underground space with close kin, nepotism most likely occurs.

Regardless of the mechanism for kin recognition in Richardson's ground squirrels, females frequently sleep with conspecifics but only at certain times of the active season suggesting that benefits and costs of underground sharing of space vary throughout an active season. Benefits that have been proposed for sleeping aggregations in other species of rodents and primates are thermoregulation (Karasov 1983; Edelman & Koprowski 2007) and social territoriality, characterized by mutual defence of shared territories (Génin 2010). Alternatively, individuals may share sleep sites due to a lack of available sleep sites (Génin 2010). Costs associated with sharing sleep sites are transmission of parasites and disease, sharing of a valuable resource, and, if sharing occurred during lactation, misdirected parental care. Reasons why female Richardson's ground squirrels share sleep sites may influence whether, when, and with whom they share.

Two potential reasons why female Richardson's ground squirrels share sleep sites are to decrease thermoregulatory costs through huddling and because there is a lack of adequate sleep sites available. Huddling, defined as a close and active aggregation of individuals who are involved in social thermoregulation to conserve heat, occurs in 67 mammal species from 20 families (Gilbert et al. 2010) including the white-tailed antelope ground squirrel (*Ammospermophilus leucurus*; Karasov 1983) and Olympic marmot (Arnold 1990).

When adult female Richardson's ground squirrels share sleep sites there is no direct evidence that they are huddled underground; however, because the average diameter of a sleep site is 20 cm (Michener 2002) and yearling and older female Richardson's ground squirrel weigh, on average, 210 and 275 g at emergence from

hibernation and immediately increase in mass (Michener 1989), individuals within a sleep site are unlikely to sleep separately.

When adult female Richardson's ground squirrels emerge during spring in southern Alberta, ambient air temperatures are still usually below freezing and soil temperatures at 50 cm, which is the typical depth for a hibernation site, are 0 – 10 ºC (Michener 1992). At emergence from hibernation, females have been underground for approximately 8 months, have lost 44% of their pre-hibernation body mass (Michener & Locklear 1990), and are at their lowest mass for the year. Low body mass combined with the 10 – 14 hours that females spend fasting underground at night (females do not store food belowground; Michener 1992) may make it difficult for adult females to produce or conserve heat; therefore, females may share underground sleep sites to decrease thermoregulatory costs. Free-living white-tailed antelope squirrels do not hibernate and share underground natural nest sites overnight during the winter (Karasov 1983). In the laboratory, white-tailed antelope squirrels can decrease daily energy expenditure by 40% through huddling in artificial nests during cold ambient temperatures (Karasov 1983).

Thermoregulatory advantage increases with the number in group, but is independent of kinship. Female Richardson's ground squirrels shared in significantly larger groups in pre-mid-pregnancy during the coldest months of the active season than during post-weaning which are the hottest. Additionally, females shared with more distant and non-kin during pre-mid-pregnancy than during post-weaning. Therefore, huddling may be a contributing factor to explain why females share sleep sites for 2 - 3 weeks during pre-mid-pregnancy regardless of kinship. Sharing during post-weaning occurs during the hottest months when females are at their heaviest weight and therefore

huddling is less likely to be beneficial during this period and may explain why females are more biased with whom they share sleep sites.

Gray squirrels (*Sciurus carolinensis*) are the most social tree squirrel, they do not hibernate, females are philopatric resulting in kin clusters, and sharing of nests is common, especially among close kin (82% of nesting pairs were close kin; Koprowski 1996). Although the reasons for nest sharing in gray squirrels is unclear, sharing is more common during the winter months than in other months, which may suggest a thermoregulatory benefit in a non-hibernator (Koprowski 1996).

Female Richardson's ground squirrels may share sleep sites because insufficient adequate sleep sites are available for each female to sleep alone. Of 6 female Richardson's ground squirrels for which I had post-emergence data, only 1 used its hibernaculum as a sleep site after emergence from hibernation, whereas Michener (2002) reported that in 50% of 28 squirrel seasons (18 females), females used their hibernaculum as a sleep site for an average of 2 nights immediately after emergence. Post-hibernation use of hibernacula for sleeping indicates that hibernaculum sites are adequate for sleeping after hibernation. Additionally, within the first 2 - 3 weeks out of hibernation females used at least 2 different sleep sites indicating sufficient sleep sites for each female to have her own. Therefore, sharing sleep sites by adult female Richardson's ground squirrels during pre-mid-pregnancy is not attributable to a shortage of adequate underground sleep sites.

Female Richardson's ground squirrels do not share sleep sites during lactation; additionally, no species of ground squirrel is known to share a burrow during lactation. Females most likely do not share during this time period because producing milk is

physiologically costly and under most circumstances mothers should avoid suckling offspring who are not their own (König et al. 1988). In the laboratory, lactating Richardson's ground squirrels provide milk to non-offspring infants up to 20 days old when placed in their cage (Michener 1974), suggesting that lactating females cannot identify their own offspring, or do, but do not discriminate between, their own and alien young prior to weaning. Therefore, female Richardson's ground squirrels may not share sleep sites between mid-pregnancy and litter weaning because to do so could result in misdirected parental care.

Because each female used at least 3 sleep sites during post-weaning, sharing sleep sites during post-weaning was also not due to a lack of adequate sleep sites. Additionally, this period encompasses the hottest months during the adult female active season, and females during this time are at their heaviest weight in preparation for hibernation, therefore females do not share underground sleep sites for thermoregulation. From this study it is unclear why adult female Richardson's ground squirrels share sleep sites during post-weaning.

Adult female Richardson's ground squirrels do not share hibernacula, unlike most species of marmots (Arnold 1990). Female Richardson's ground squirrels warm up on average every 17 days during hibernation (Michener 1992); if individuals were to share hibernacula, synchrony of inter-torpor arousal periods would result because if they did not, the warm individual may disturb the cold individual and cause the cold individual to warm up unnecessarily causing them to expend more energy. Female Richardson's ground squirrels hibernating in separate hibernacula do not have synchronized warming

bouts (Michener, unpublished data) and therefore, hibernating together may have more energetic costs associated with it than hibernating alone.

Female Richardson's ground squirrels preferentially share sleep sites with close kin indicating that nepotism occurs among females; additionally, sharing occurs only during certain times of the year dependent on their reproductive status. Because females share in larger groups and with more distant and non-kin during pre-mid-pregnancy than during post-weaning, and because benefits of thermoregulation increase with numbers in a group, independent of kinship, sharing of sleep-sites before pre-mid-pregnancy may be attributable to huddling. However, why females share after weaning is still unclear.

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Chapter III

Underground space use by adult female Richardson's ground squirrels

(*Urocitellus richardsonii*)

3.1. Abstract

Most female Richardson's ground squirrels (*Urocitellus richardsonii*) are

philopatric whereas most males disperse as juveniles, resulting in female kin clusters in

space and time. Female Richardson's ground squirrels have overlapping aboveground

home ranges, and close kin frequently share underground sleep sites from emergence

from hibernation until mid-pregnancy and sometimes resume sharing after litters have

been weaned; they do not share sleep sites during lactation or hibernation. To assess how

females co-use their underground space, which is composed of burrow systems and their

components, surface entrances, sleep sites, and underground connections, adult female

Richardson's ground squirrels of known maternal kinship (18 in 2008, 30 in 2009, and 6

in both years) in 5 spatially adjacent matrilines were radio-collared throughout the active

season. Underground sleep sites used by each female were located by radio-telemetry

each evening after retirement and each morning before emergence throughout the active

season, and the surface entrances used for retirement and emergence were monitored on

92 evenings and 71 mornings in 2008 and 78 nights and 70 mornings in 2009.

Underground connections from entrance hole to evening sleep site and from morning

sleep site to exit hole were mapped to generate a 2-dimensional version of burrow-system

architecture. Co-use of burrow-systems among adult female Richardson's ground

squirrels occurred throughout the entire active season but co-use of specific sleep sites, surface entrances, and underground connections within those burrow systems varied with reproductive status. Females that co-used burrow systems before mid-pregnancy and after the litters had been weaned also co-used sleep sites, surface entrances, and underground connections, whereas females that co-used burrow systems during late-pregnancy and lactation separated burrow systems such that sleep sites, surface entrances, and connections were only used by a single female. Females co-used underground space more frequently with close kin (mothers, daughters, and littermate sisters) than with distant kin or non-kin. Seasonal variation in the co-use of burrow systems by adult female Richardson's ground squirrels is most likely associated with the costs and benefits of sharing underground space during different stages of reproduction.

3.2. Introduction

Individuals can either settle in their natal area (philopatry) or disperse to a new area or population (Michener 1983; Nunes 2007). Whether males, females, or both are philopatric or disperse, the age at which individuals disperse, and whether dispersal occurs before or after reproduction contribute to the distribution of individuals and the demographic structure of a population (Nunes 2007). Within species of ground squirrels (*Urocitellus* and related genera; Helgen et al. 2009), males are typically the dispersing sex, whereas females tend to be philopatric resulting in female kin clusters in space and time (Armitage 1981; Michener 1983).

Although sex-biased dispersal is characteristic of all species of ground squirrels, social structures range from asocial to multi-harem colonies (Armitage 1981; Michener 1983); the degree of sociality is correlated with the tolerance of spatial proximity between conspecifics and degree of cooperative and competitive interactions (Lacey & Sherman 2007). Female ground squirrels may remain in the natal area because of access to familiar environmental resources, proximity to kin, or a combination of both (Hare & Murie 2007); dispersal by females is primarily due to competition for familiar environmental resources (Nunes 2007).

Subterranean burrow systems are an environmental resource for ground squirrels which are composed of surface openings connected to underground tunnels which lead to underground chambers that are used for sleeping or hibernation or as latrines (Burns 1989; Verdolin et al. 2008). Burrow systems provide a relatively safe and stable habitat that is used for sleeping (Michener 2002), hibernation (Dobson & Davis 1986; Michener 1992; Charge 2001), copulation (Michener & McLean 1996; Manno et al. 2008), parturition and litter rearing (Michener 1985), thermoregulation (Long et al. 2005; Váczi et al. 2006), and protection against weather (Long et al. 2005) and most predators (Karels & Boonstra 1999; Swaisgood et al. 1999).

Burrow architecture in various species of ground squirrels (e.g. Scheck & Fleharty 1980; Burns 1989; Yensen et al. 1991;Verdolin et al. 2008) has been documented by excavation, which reveals geometrical structure of burrow systems, but destroys the system and does not ascertain how conspecifics utilize sleep sites, surface entrances, and underground connections within burrow systems nor the extent to which conspecifics co-use underground space. Depending on the degree of sociality of a species, with more-

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social species having a greater degree of overlapping aboveground space, Michener (1979) predicted a positive correlation between aboveground home-range overlap and common underground burrow-system use.

Although burrow systems can be used over multiple generations, burrow systems are not static features but are created, altered, and eliminated by individual ground squirrels (Harris & Murie 1984). Creating and altering burrow systems is energetically costly and time consuming; therefore, burrow systems already in existence are valuable resources. Agonistic interactions among female ground squirrels increase during pregnancy (Michener 1983), and Sherman (1980) hypothesized that such interactions peaked in early pregnancy as a result of competition for adequate burrow systems. Natal burrows are a critical resource for female ground squirrels because reproductive success can be affected by females' choice of a natal burrow (Pfeifer 1982). Because burrow systems are clumped in space and are a valuable environmental resource that can be used between multiple generations, burrow systems have been proposed as one of the ecological factors that has promoted and maintained sociality in ground-dwelling squirrels (Alexander et al. 1991; Hare & Murie 2007; Lacey & Sherman 2007).

One consequence of multiple female kin remaining in their natal area is that females have to partition a limited amount of environmental resources. Additionally, depending on the population density, females may be constrained in space by neighbouring kin groups. If the population density increases in a natal area, adult female Richardson's ground squirrels could increase the overlap of aboveground home ranges and underground burrow systems, sub-divide home ranges and burrow systems such that they use a smaller portion which they may have to compete for, or disperse to a less-

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dense area. Costs of dispersal are high; females may have to by-pass aggressive non-kin to find a suitable area or compete with a conspecific for already occupied areas, both of which are time consuming and energetically costly and may not result in acquisition of an adequate area.

Aboveground spatial proximity among conspecifics is well understood in many species of ground squirrels (e.g. Michener 1979; McLean 1982; King & Murie 1984; Maher 2009). Typically, the degree of spatial overlap among conspecifics' home ranges is dependent on the degree of sociality of the species, kinship of individuals within the group, reproductive status, age, sex, and density of the population (Nunes 2007). Underground spatial proximity among conspecifics is not as well understood because individuals cannot be observed in naturally constructed burrow systems.

Burrow-system co-use can be detected by aboveground observations of surface-entrance use, which is known to occur among females in some of the more-social species of ground squirrel such as the golden marmot (*Marmota caudata*; Blumstein & Arnold 1988) and black-tailed prairie dog (*Cynomys ludovicianus*; Hoogland 1995). In these species, burrow systems are co-used throughout the active season except during lactation, when each female has her own natal burrow which is determined by observations on surface-entrance use. In less-social species of ground squirrels such as the round-tailed ground squirrel (*Xerospermophilus tereticaudus*), burrow-system co-use, usually with kin, occurs after emergence from hibernation until early pregnancy but not during any other time of the year (Dunford 1977). However, whether conspecifics co-use underground features within shared burrow systems cannot be directly observed. By using indirect methods, such as radio-telemetry, highly-social marmot species are known

to share hibernacula with kin (Arnold 1990) but ground squirrels hibernate alone in an isolated hibernaculum (Young 1990; Charge 2001). This variation in underground co-use of space in different species of ground squirrels suggests that social complexity, kinship, and reproductive status influence underground co-use of space.

Richardson's ground squirrels are one of the less-social species of ground squirrels (Armitage 1981; Michener 1983), and are the only species of ground squirrel in which underground sharing of sleep sites has been studied (Michener 2002; Chapter 2). Use of both aboveground home ranges and underground sleep sites among adult female Richardson's ground squirrels varies over the active season in accordance with their reproductive status. From emergence from hibernation until mid-pregnancy, females have overlapping home ranges and most females share underground sleep sites (Michener 1979; Michener 2002; Chapter 2). From mid-pregnancy until the litters are weaned, home ranges decrease with less overlap among neighbours and females do not share underground sleep sites (Michener 1979; Michener 2002; Chapter 2). After the litters are weaned, home ranges expand and overlap with more females, and some females resume sharing sleep sites (Michener 1979; Chapter 2). Before immergence into hibernation, home ranges decrease and females are found in different feeding areas and burrow systems than they used previously in the active season (Michener 1979). Female Richardson's ground squirrels do not share hibernacula (Michener 2002; Chapter 2), and hibernaculum systems are isolated both from adjacent burrow systems and the surface (Charge 2001).

When adult female Richardson's ground squirrels share sleep sites, they are implicitly sharing burrow systems; however, whether natal nests, which are unshared

sites that might or might not be within a burrow system used by other females, are a part of a larger burrow system is unknown. Females can either use a discrete burrow system for lactation that had not been connected to a larger burrow system or subdivide larger burrow systems by either social or physical barriers. The first purpose of my study was to determine whether adult female Richardson's ground squirrels co-use underground burrow systems for sleeping at night during the active season and if so, how females partition burrow-system features among conspecifics. The second purpose was to determine whether the degree of underground spatial co-use is influenced by reproductive status and kinship by obtaining information on behavioural use of underground space.

Because sleep-site sharing is dependent on reproductive status and kinship (see Chapter 2), I predicted that underground co-use of burrow systems, surface entrances, and underground connections is also dependent on reproductive status and kinship. Additionally, because no species of ground squirrel share natal nests, I predicted that female Richardson's ground squirrels use discrete burrow systems, surface entrances, and connections for lactation regardless of their degree of kinship.

3.3. Methods

3.3.1. Subject species, study site, and focal animals

I studied free-living adult female Richardson's ground squirrels in a population within a 3-ha site 5 km East and 1 km South of Picture Butte, Alberta, Canada (49º52'N 112º43'W, elevation 870 m; Risch et al. 2007). When adult (≥1-year-old) female Richardson's ground squirrels emerged from hibernation in late February - March 2008

and 2009, I selected 54 females for radio-collaring (refer to Chapter 2 for information regarding focal females and radio-collaring). Maternal kinship for females in my study, is known for 2 - 14 generations, and females within a matriline encompassed a range of kin relationships: mother-daughter; grandmother-granddaughter; littermate sisters; non-littermate sisters; aunt-niece; grand aunt-niece; first and second cousins; and first cousins once removed (see Figure 2.1 in Chapter 2). I considered mother-daughters and littermate sisters as close kin, and all other maternal kin I considered distant kin; paternal kinship was not included in this study (see Chapter 2 for relatedness criteria).

As part of long-term studies (e.g. Michener 2002; Risch et al. 2007), ground squirrels on the site are live trapped (Tomahawk Live Trap Co.; single-door squirrel traps), weighed, and their reproductive status assessed at frequent intervals during the active season (see Chapter 2 for trapping techniques). Dates of each female's active season (emergence from and immergence into hibernation) and reproductive events (estrus, parturition, and litter emergence) are determined through both behavioural and physical observations (see Chapter 2).

3.3.2. Reproductive periods

Data from the 2008 and 2009 active seasons for the radio-collared adult female Richardson's ground squirrels were separated into 3 time periods (pre-mid-pregnancy, late-pregnancy/lactation, and post-weaning) to compare sharing of underground space by reproductive status within the active season (see Chapter 2 for descriptions and criteria of reproductive periods). One female in 2009 that mated but did not get pregnant was removed from data analyses involving reproductive periods. Additionally, 3 females

from 2008 and 7 females from 2009 were not included in between-period or entire active season analyses because either their radio-collars were removed during the active season ($n = 8$) or they died/went missing ($n = 2$).

3.3.3. Female dispersal

Females in this study were considered to have dispersed if they were in their natal area one day and were in a different area the next day and did not return to their natal area. The distance that females dispersed was calculated from a straight line between where they were first seen as juveniles emerging from their natal nest to where either their litter emerged during the year they dispersed ($n = 4$) or, if their litter weaning location was unknown, the location where they were last trapped during late pregnancy ($n = 5$).

3.3.4. Sleep-site locations

Each radio-collared female was located twice daily during the active season, after the last female retired for the night and before the first female emerged in the morning (refer to Chapter 2 for radiotelemetry times and definitions of sleep sites, sleep-site locations, sleep-site sharing, and statistical tests).

3.3.5. Locations of surface openings

Female Richardson's ground squirrels were observed by 1 to 3 people from 1 to 3 observation sites for 71 mornings and 92 evenings (190 hours) in 2008 and for 70 mornings and 78 evenings (178 hours) in 2009. Observations were used to determine:

entry or exit time (all times were recorded in Mountain Standard Time); the surface entrance each radio-collared female used to enter her sleep site during the evening and exit her sleep site in the morning; whether females that shared sleep sites also shared surface entrances; and whether non-radio-collared females were also using the same entrances as the radio-collared females.

Additionally, 2 camcorders (Sony DCR-TRV19, Canon ZR100) were positioned to record 1 - 5 surface entrances during periods when females were sharing sleep sites. Video-recordings were then viewed to see when and where females retired and emerged. Surface entrances used by females to access underground chambers were marked with a uniquely labeled flag after a female was observed to use a surface entrance during either retirement or emergence observations.

Each female's presence or absence was noted at 5-minute intervals during the evening retirement observations and 2-minute intervals during morning emergence observations; therefore, if a retirement or emergence event was not observed, an approximate time was known. The surface entrance used and exact entry or exit time during retirement or emergence were obtained on 74% of 6767 female-observations; for the other 26% of observations, an approximate time of entry or exit was calculated as the midpoint between the times the animal was present then absent. The number of known retirement and emergence events for each female for the entire active season and in each reproductive period were averaged among all radio-collared females as a measure of intensity of observation effort.

The interval between the first and last females to retire and emerge each night was averaged over the entire active season to determine the degree of synchrony of retirement

and emergence among radio-collared females. To determine whether specific females retired or emerged more synchronously when sharing a sleep site simultaneously than when not sharing, the differences in retirement times and in emergence times for each member of a sharing pair were averaged for 3 – 5 consecutive nights when sharing and for the subsequent 3 – 5 nights when not sharing times of retirement. Because some females started sharing sleep sites immediately after emergence from hibernation, and therefore did not have 3 – 5 pre-adjacent nights when they did not share, only post-sharing nights were used for comparisons. Only events for which time of entry or exit was known to the nearest second were used so that the exact time difference between female retirement or emergence could be calculated.

3.3.6. Underground connections and burrow systems

The surface entrance each adult female Richardson's ground squirrel used to retire at night and the sleep site she was in during evening radio-telemetry was considered as an underground connection; likewise, the sleep site she was in during morning radio-telemetry and the surface entrance she used to emerge was considered as an underground connection. A total of 2359 and 2665 connection observations (74% of 6767 observations when sleep site and surface entrance the female used were known) were made during the 2008 and 2009 active seasons, respectively.

Locations of sleep sites and surface entrances were surveyed using a Sokkia SET4110R Electronic Total Station, then entered to ArcGIS to construct 2-dimensional maps of underground connections in which all sleep sites, surface entrances used to enter and exit sleep sites, and underground connections were individually numbered. Burrow

systems were constructed independently for the 2008 and 2009 active seasons. Because juveniles were still aboveground after adult females had immerged into hibernation in 2008 and adult males emerged from hibernation before adult females in 2009, either may have altered underground space between immergence of adult females and their re-emergence the next year. Additionally, badger predation may have destroyed portions of burrow systems and surface entrances.

Because burrow systems are not static, and features used later in the active season may not have been present earlier and therefore may not have been connected underground, the definition of a burrow system depended on what was being analysed. Analysis of burrow-system architecture and the number of burrow systems and burrow system features each female used were based on burrow systems constructed from features used at any time in the active season (i.e. observations revealed connections between sleep sites and surface entrances at some point in the active season). For data analysis of burrow-system co-use (defined as more than 1 female either using the burrow system simultaneously or using the same burrow system at different times within an indicated period), features were only considered to be co-used during a certain reproductive period if the feature in the burrow system that had been co-used was known to exist previously in the active season.

Every sleep site, surface entrance, and underground connection used by the 54 radio-collared female Richardson's ground squirrels was assigned to a burrow system. Because adjacent burrow systems did not overlap in space (unpublished data), if a sleep site, surface entrance, or connection was not observed to be connected with a burrow system, and if the location fell within the boundaries connecting the outermost points of a

Figure 3.1. Photograph of aboveground surface entrances (blue flags) and aboveground sleep-site markers (wooden blocks) in the field. Burrow-system architecture was constructed by maps of sleep sites and surface entrances with straight lines drawn from surface openings to sleep sites (black lines) to represent underground connections. This technique created a simplified 2-dimensional version of each burrow system. Within the burrow system in this photograph, 6 females used 3 sleep sites and accessed those sites using 5 surface entrances.

burrow system, the feature at that location was assumed to be part of the system. If a feature did not meet these criteria it was assigned as an individual burrow system.

Because I do not know depths or tunnel routes, my technique creates a simplified 2-dimensional version of the burrow systems with straight lines from surface openings to sleep sites which is sufficient for this study, as questions only address how females behaviourally utilize underground space (Figure 3.1).

Because every sleep site was assigned to a burrow system and sleep sites were known for every night during the active season, the burrow system each radio-collared female was in every night was known. Because more sleep sites, surface entrances, and connections may have been available in the burrow systems, but not used or not observed to be used by the radio-collared females, underground architecture of burrow systems may not be complete; therefore for this study, underground architecture was termed behavioural architecture of underground burrow systems.

To analyse the behavioural architecture of burrow systems, the sleep sites, surface entrances, and connections that were used at any time within the active season by any of the 54 radio-collared females were used to construct burrow systems even though some features may not have existed earlier in the active season and some features may have been eliminated later in the active season. To describe how many sleep sites, surface entrances, and connections were in each burrow system, only burrow systems with at least 1 retirement or emergence observation were used for analyses because I needed to know at least 1 aboveground entrance in order to attach a sleep site. For all burrow systems with at least 1 retirement or emergence observation, the ratio of sleep sites to surface entrances was calculated for each burrow system. To describe the variation of

features in the larger burrow systems, they were separated into complex (at least 2 sleep sites and 2 aboveground entrances) and simple (fewer than 2 sleep sites and 2 aboveground entrances).

To describe how each radio-collared adult female Richardson's ground squirrel used underground space, the numbers of burrow systems, sleep sites, aboveground entrances, and connections each female used in the entire active season and each reproductive period were calculated. To compare feature use in each reproductive period, data were only analysed for females radio-collared for the entire active season; additionally, only burrow systems that were used by these females were included. The number of burrow systems each female used was based on burrow systems constructed from features used throughout entire active season. To adjust for differences in the duration of each of the 3 reproductive periods, the numbers of burrow systems, sleep sites, surface entrances, and underground connections used were calculated as proportions of nights in the reproductive period for between period comparisons.

To determine the amount of co-use in underground space by the radio-collared females, the proportion of burrow systems, sleep sites, surface entrances, and connections that were used by more than 1 female was calculated. Additionally, the number of radio-collared adult female Richardson's ground squirrels that co-used a given burrow system, and when they co-used the burrow systems were calculated. Kinship of individuals that co-used were compared and the proportions of all close kin, distant kin, and non-kin that were available and that co-used burrow systems were calculated.

3.4. Results

3.4.1. Philopatry and dispersal

Although adult female Richardson's ground squirrels are the philopatric sex, some females do disperse. In 2008, 2 radio-collared females dispersed (65.6 m and 87.6 m) and in 2009, 7 dispersed (*mean* = 72.9 ± 58.0 m, *range* = 30.1 – 207.9 m). Nine of 37 yearling radio-collared females dispersed and none of 8 older adults dispersed. Of these 9 dispersing females, 2 dispersed on the first day out of hibernation, whereas the other 5 females relocated 4 – 10 days after emergence. All 9 females were present in their natal area the day before dispersal; none of them returned to either sleep or forage in their natal area in either active season.

3.4.2. Behavioural architecture of burrow systems

In 2008 and 2009, 46 and 55 burrow systems, respectively, with varying numbers of sleep sites, aboveground entrances, and connections within each burrow system, were used by 24 and 36 radio-collared females, respectively (Table 3.1). Within these burrow systems, 348 sleep sites, 336 aboveground entrances, and 680 connections were used (*n* = 60 squirrel seasons, 54 females). Females used 1 – 10 surface entrances to access a single sleep site (*mean* = 2.7 ± 1.7, *n* = 328 sleep sites), and used a single surface entrance to access 1 – 6 sleep sites (*mean* = 1.9 ± 1.0, *n* = 257 surface entrances).

Most sleep sites (86% of 348), surface entrances (98% of 336), and connections (98% of 680) could be assigned to a burrow system by underground connections. For 10 of 46 and 12 of 55 burrow systems in 2008 and 2009, respectively, no observational data

Table 3.1. Descriptive statistics for the number of sleep sites, surface entrances, and connections within 36 burrow systems used by 24 radio-collared adult female Richardson's ground squirrels in 2008 and in 43 burrow systems used by 36 radio-collared females in 2009. Burrow systems with information only on sleep sites and with no emergence or retirement observations ($n = 10$ in 2008 and $n = 12$ in 2009) are not included.

	2008		2009	
	$\overline{X} \pm SD$	Range	$\overline{X} \pm SD$	Range
Sleep sites	4.0±2.7	1-13	3.9±4.0	1-17
Surface entrances	5.3±4.2	1-21	4.3±4.6	1-19
Connections	9.4±9.2	1-47	8.1±10.8	1–46

were obtained and the sleep site did not fall within the boundaries of a larger burrow system, so the known behavioural architecture was limited to 1 sleep site. For the remaining 36 and 43 burrow systems, 56% and 40%, respectively, had more surface entrances than sleep sites, 33% and 37% had the same number of surface entrances as sleep sites, and 11% and 23% had fewer surface entrances than sleep sites.

Of 36 burrow systems in 2008 and 43 burrow systems in 2009 with at least 1 retirement and emergence observation, 27 and 22, respectively, were complex with at least 2 sleep sites and 2 aboveground entrances. The number of sleep sites, surface entrances, and connections that adult female Richardson's ground squirrels used within the complex burrow systems varied considerably. Females used 2 – 17 sleep sites (*mean* = 5.6 ± 3.4), 2 – 21 surface entrances (*mean* = 7.0 ± 4.3), and 2 – 47 connections (*mean* = 13.2 ± 10.5) within a given complex burrow system (*n* = 49).

3.4.3. Underground-space use

Individual radio-collared adult females used 1 - 8 burrow systems and 6 - 16 sleep sites within an active season (*n* = 45 squirrel seasons, 40 females; Table 3.2); 4 females used a single burrow system throughout an active season, whereas 2 females used 8 burrow systems in an active season. During an average of 106.3 ± 14.0 retirement and emergence observations per female per year (*range* = 71 – 134; *n* = 45 squirrel seasons, 40 females), females used 6 – 16 surface entrances and 7 – 28 connections within an active season (Table 3.2).

Although females used the least number of burrow systems and sleep sites during late-pregnancy/lactation and used about the same number of burrow systems and sleep

Table 3.2. Descriptive statistics for the number of burrow systems, sleep sites, surface entrances, and underground connections each radio-collared female in 2008 (n = 21) and 2009 (n = 24) used in an active season (AS) and each reproductive period (PMP – pre-mid-pregnancy, LPL – late-pregnancy/lactation, PW – post-weaning). Burrow systems and sleep sites were known for each female on every night in each active season. Surface entrances and connections were known for an average of 106 ± 14 retirement and emergence observations per female per year (*range* = 71 − 134), 26 ± 5 during PMP (*range* = 17 − 48), 59 ± 6 during LPL (*range* = 43 − 70), and 62 ± 10 during PW (*range* = 44 − 84; n = 45 squirrel seasons, 40 females).

| | Burrow systems | | | | Sleep sites | | | |
| | 2008 | | 2009 | | 2008 | | 2009 | |
Period*	$\overline{X}$ ±SD	Range	$\overline{X}$ ±SD	Range	$\overline{X}$ ±SD	Range	$\overline{X}$ ±SD	Range
AS	3.6±1.4	1-6	4.1±1.9	1-8	8.9±2.6	6-15	10.0±3.1	6-16
PMP	2.4±0.8	1-4	2.9±1.3	1-5	3.4±1.1	1-6	4.0±1.5	1-7
LPL	1.4±0.7	1-4	1.5±0.7	1-3	2.6±1.3	1-6	3.3±1.1	1-5
PW	2.3±1.3	1-6	2.3±1.2	1-5	6.7±2.6	3-13	6.5±2.2	4-12

| | Surface entrances | | | | Connections | | | |
| | 2008 | | 2009 | | 2008 | | 2009 | |
Period*	$\overline{X}$ ±SD	Range	$\overline{X}$ ±SD	Range	$\overline{X}$ ±SD	Range	$\overline{X}$ ±SD	Range
AS	11.1±2.5	6-16	11.2±2.7	7-16	17.8±3.8	7-28	17.3±3.4	11-23
PMP	4.3±1.2	1-6	5.2±1.8	1-9	4.7±1.5	1-7	5.5±2.0	1-11
LPL	5.1±1.9	2-9	4.7±1.5	2-8	6.3±2.4	2-11	6.5±1.8	3-10
PW	7.6±1.9	4-11	6.3±2.4	2-10	12.3±3.4	5-19	9.8±2.7	5-14

* For 2008 (n = 21 females) and 2009 (n = 24 females), the average durations of periods were: 117 and 107 days for the active season, respectively; 15 and 14 days for PMP; 39 and 39 days for LPL; and 60 and 51 days for PW. See Table 2.1 for SD and range.

Table 3.3. Average percentage of burrow systems, sleep sites, surface entrances, and connections used by radio-collared females in 2008 ($n = 21$) and 2009 ($n = 24$). Percentage is the number of each feature used by each female divided by the number of days within each period; AS – active season, PMP – pre-mid-pregnancy, LPL – late-pregnancy/lactation, PW – post-weaning. See Table 3.2 for the number of retirement and emergence features that were known.

Period	Burrow systems 2008 $\overline{X} \pm SD$	Burrow systems 2009 $\overline{X} \pm SD$	Sleep sites 2008 $\overline{X} \pm SD$	Sleep sites 2009 $\overline{X} \pm SD$	Surface entrances 2008 $\overline{X} \pm SD$	Surface entrances 2009 $\overline{X} \pm SD$	Connections 2008 $\overline{X} \pm SD$	Connections 2009 $\overline{X} \pm SD$
AS	4±1	4±2	8±2	9±3	6±1	6±1	8±2	8±2
PMP	15±5	19±9	22±7	27±9	14±4	18±7	15±5	19±7
LPL	3±2	4±2	6±3	8±3	6±2	6±2	8±3	8±2
PW	4±2	5±2	11±3	13±4	6±2	6±2	10±3	10±3

sites during pre-mid-pregnancy and post-weaning (Table 3.2), in proportion to duration of the reproductive period, females used more burrow systems and sleep sites during pre-mid-pregnancy than late-pregnancy/lactation or post-weaning (Table 3.3). Likewise, in proportion to duration of the reproductive period, more surface entrances and connections were used in pre-mid-pregnancy than in late-pregnancy/lactation or post-weaning (Table 3.3).

3.4.4. Co-use of underground space

Nineteen of 101 burrow systems (46 in 2008 and 55 in 2009) used by 54 radio-collared females were used by females without complete-season data (9 dispersers, 2 temporarily radio-collared, and 2 deaths), and 82 burrow systems (38 in 2008 and 44 in 2009) were used by 41 females with complete season data. Of these 38 and 44 burrow systems, 53% and 48%, respectively, were used by more than 1 female (Table 3.4). The greatest proportion of burrow systems were co-used during pre-mid-pregnancy (50% and 47% of 26 and 30 burrow systems) and during post-weaning weaning (37% and 34% of 37 and 34 burrow systems), whereas the least proportion of burrow systems were co-used during late-pregnancy/lactation (4% and 32% of 25 and 22 burrow systems; Table 3.4).

Co-use of burrow systems does not necessarily mean that females co-use specific sleep sites, surface entrances, or underground connections within the burrow system (Figure 3.2 as an example); conversely, if females share sleep sites, surface entrances, and underground connections, they are evidently sharing burrow systems. Although some females co-used burrow systems throughout the entire active season, how females co-used sleep sites, surface entrances, and connections within burrow systems varied

among reproductive periods (Figure 3.2). During pre-mid-pregnancy, between 28% and 52% of all sleep sites, surface entrances, and underground connections, were co-used by more than 1 radio-collared female (Table 3.4), whereas during late-pregnancy/lactation, burrow systems were partitioned such that females rarely or never co-used the same sleep sites, surface entrances, or underground connections within the shared burrow systems (Table 3.4). The rare occurrences of co-use in underground space during late-pregnancy/lactation in 2009 were restricted to the beginning of late-pregnancy/lactation when females were still pregnant; during lactation, no co-use occurred.

Although many of the same sleep sites, surface entrances, and underground connections that had been co-used by females in pre-mid-pregnancy were available in late-pregnancy/lactation (see Fig. 3.2), their use was now restricted to a single female. I cannot determine if females altered the underground architecture by blocking underground connections to form physical barriers or whether a social barrier was formed. Once litters had been weaned, use of underground space changed abruptly and between 5% and 21% of sleep sites, surface entrances, and underground connections were used by more than 1 radio-collared adult female (Table 3.4).

3.4.5. Burrow-system co-use among adult females

The 7 radio-collared females that dispersed outside the focal area were not followed thereafter; therefore, I do not have information on whether they shared burrow systems with each other or other unrelated females after dispersal. Of the remaining radio-collared females, up to 5 females in 2008 and 7 females in 2009 shared a burrow system simultaneously and up to 7 females in 2008 and 10 in 2009 shared a single burrow

Pre-mid-pregnancy

B
1, 2

C
3

EE
2

AA
1,2

D
1,2

E
1,2,3

F
1,2

H
1,2,4

BB
1,2

FF
1,2,3

A
3,4,5

G
3,4,5

CC
1,2,3

DD
3,4,5

1 m

Late-pregnancy/lactation

O
1

B
1

C
2

J
2

HH
1

N
1

D
2

E
1

P
1

H
1

BB
1

A
3

CC
1

GG
2

L
2

M
2

II
3

K
3

I
3

JJ
3

1 m

94

Post-weaning

1 m
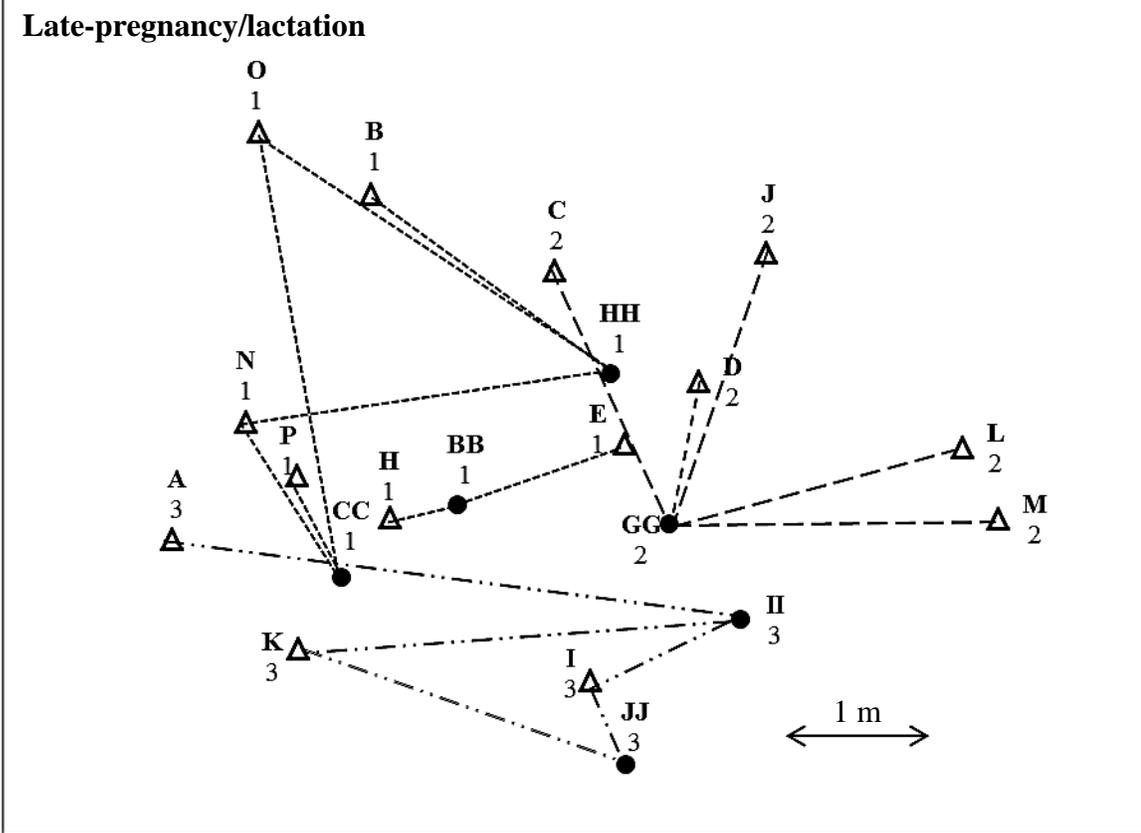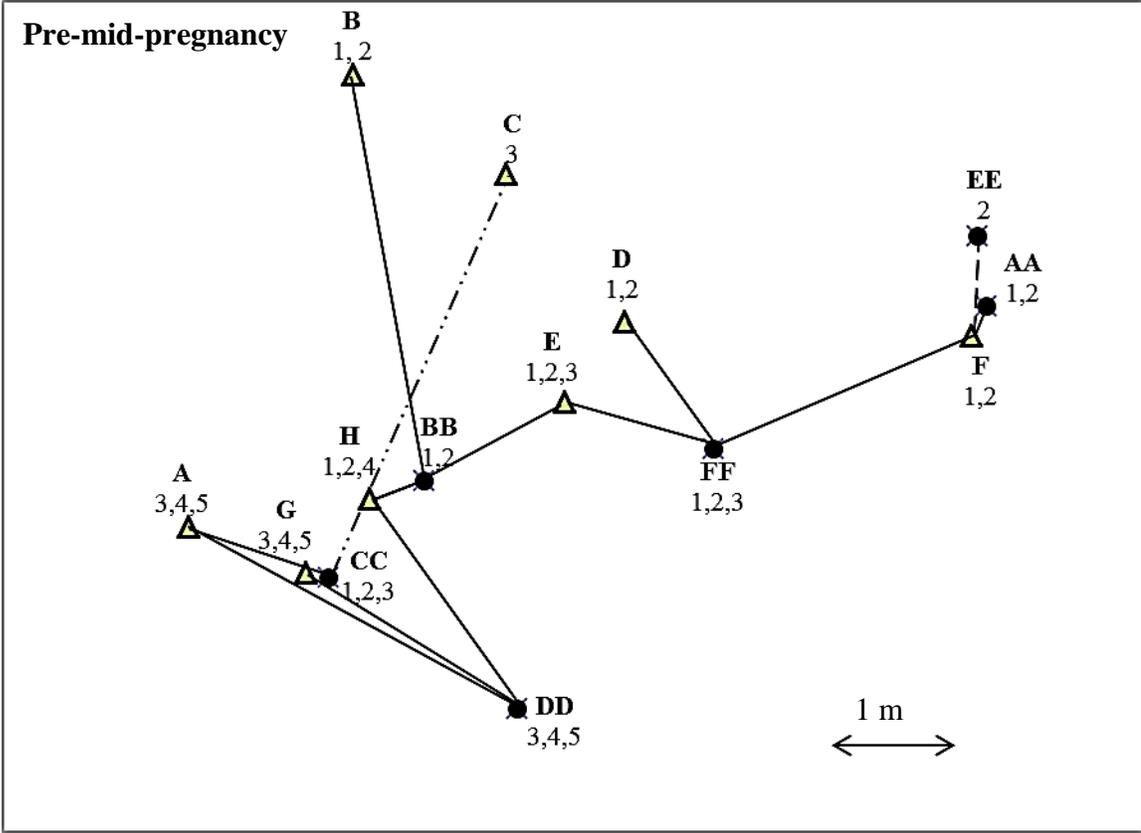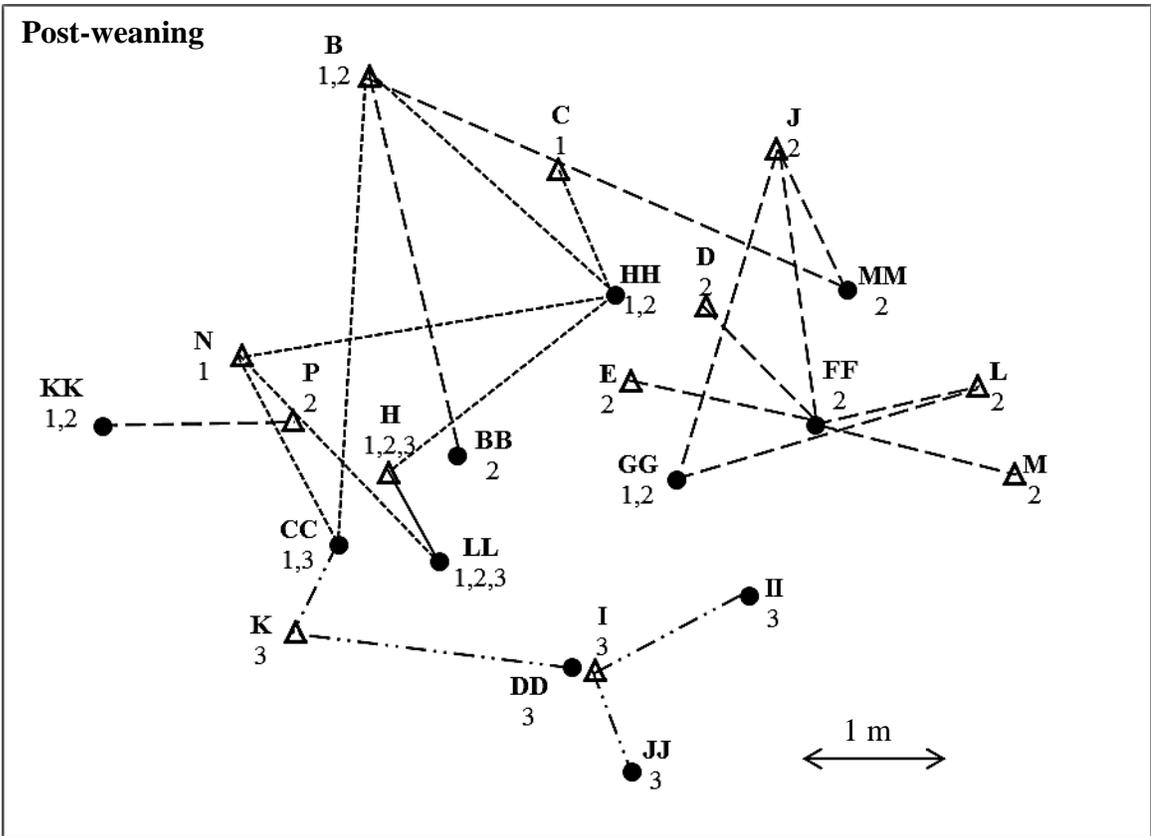
Figure 3.2. Two-dimensional maps of seasonal changes in co-usage of a single burrow system occupied in 2008 by 5 radio-collared adult female Richardson's ground squirrels. The 5 females, here numbered 1 through 5, include 3 littermate sisters (numbered 1, 2, and 4), their 1st cousin once removed (3), and a female that was a great aunt to the 3 littermate sisters and an aunt to their 1st cousin once removed (5). Solid circles with 2 letters indicate sleep sites (n = 6, 6, and 11 in PMP, LPL, and PW, respectively), unfilled triangles with a single letter indicate surface entrances (n = 8, 14, and 12 in PMP, LPL, and PW, respectively), and the 3 styles of dashed lines indicate connections used only by a particular female. Connections were frequently co-used in pre-mid-pregnancy but never in late-pregnancy/lactation and rarely in post-weaning. Some sleep sites (e.g. BB) were used in all periods, whereas others were used only in a single period (e.g. LL). Sleep sites and surface entrances used in more than 1 reproductive period retain the same letter codes.

Table 3.4. Descriptive statistics for usage and co-usage of underground space among radio-collared adult female Richardson's ground squirrels ($n = 21$ in 2008, $n = 25$ in 2009) for each active season (AS) and each reproductive period within the active season (PMP – pre-mid-pregnancy, LPL – late-pregnancy/lactation, PW – post-weaning). The total numbers of burrow systems, sleep sites, surface entrances, and connections used within each time period and the number of females that used each space were calculated. Co-usage is defined as more than 1 female using the same burrow system, sleep site, surface entrance, or underground connection at any time in the period and was calculated as the percent of the total number of each used by more than 1 female.

	2008				2009			
			n females that used each space				*n* females that used each space	
	Total used	% co-used	$\overline{X}$ ±SD	Range	Total used	% co-used	$\overline{X}$ ±SD	Range
AS								
Burrow systems	38	53	2.0±1.3	1-6	44	48	2.2±1.9	1-10
Sleep Sites	140	21	1.3±0.8	1-5	153	29	1.6±1.2	1-10
Surface entrances	177	21	1.3±0.7	1-5	173	29	1.5±1.1	1-9
Connections	327	10	1.1±0.5	1-5	324	16	1.3±0.8	1-8
PMP								
Burrow systems	26	50	2.0±1.4	1-5	30	47	2.3±2.0	1-9
Sleep Sites	47	28	1.6±1.2	1-5	50	44	1.9±1.6	1-10
Surface entrances	60	32	1.6±1.0	1-5	62	52	2.0±1.5	1-9
Connections	68	28	1.5±1.0	1-5	66	37	1.7±1.3	1-8
LPL*								
Burrow systems	25	4	1.2±0.5	1-3	22	32	1.5±0.9	1-4
Sleep Sites	56	0	1.0±0.0	1	72	7	1.1±0.3	1-3
Surface entrances	111	0	1.0±0.0	1	104	7	1.1±0.3	1-3
Connections	137	0	1.0±0.0	1	152	3	1.0±0.2	1-2
PW								
Burrow systems	37	37	1.4±0.5	1-3	34	32	1.6±1.0	1-5
Sleep Sites	129	13	1.1±0.4	1-3	118	21	1.3±0.7	1-4
Surface entrances	151	10	1.1±0.3	1-2	126	15	1.2±0.5	1-3
Connections	257	5	1.0±0.2	1-2	207	10	1.1±0.4	1-3

* All co-usage in LPL was limited to late pregnancy

system at different times throughout the entire active season.

When 3 or more females shared a burrow system simultaneously and each possible pairwise combination was included, 105 unique pairs of females shared ($n = 60$ squirrel seasons, 54 females); 102 during pre-mid-pregnancy ($n = 60$ squirrel seasons, 54 females), 17 during late-pregnancy/lactation ($n = 46$ squirrel seasons, 41 females), and 34 during post-weaning ($n = 46$ squirrel seasons, 41 females). Only 2 of 17 pairs that simultaneously shared a burrow system during late-pregnancy/lactation and post-weaning had not simultaneously shared a burrow system during pre-mid-pregnancy.

Of 21 and 25 (including 1 female who did not get pregnant) females radio-collared in 2008 and 2009, respectively, 20 and 24 co-used a burrow system within pre-mid-pregnancy with 1 – 10 other females, whereas only 4 and 15 continued to co-use a burrow system during late-pregnancy/lactation and they did so with fewer (1 or 2) other females; the remaining 10 and 17 females used a discrete burrow system throughout the entire late-pregnancy/lactation period. Co-use increased again during post-weaning; 18 and 20 females co-used with 1 – 3 different individuals.

3.4.6. Kinship and co-use of underground space

Of all close-kin pairs available in 2008 and 2009, 65% and 67% co-used a burrow system at least once during the active season ($n = 31$ and 43 close kin pairs, respectively); in contrast, only 12% and 16% of all distant-kin pairs ($n = 52$ and 226, respectively) and 2% and 3% of all non-kin pairs ($n = 193$ and 361, respectively) co-used a burrow system (Table 3.5). In 2008, the proportion of all pairs that co-used a burrow system that were close kin was about the same during pre-mid-pregnancy, late-pregnancy/lactation, and

Table 3.5. Kin relationships of 54 radio-collared adult female Richardson's ground squirrels in 2008 and 2009 and the number of kin relationship pairs that co-used a burrow system during the active season (AS) and in each reproductive period (PMP – pre-mid-pregnancy, LPL – late-pregnancy/lactation, PW – post-weaning); 6 females were present in both years. When 3 or more females co-used a burrow system, each possible pairwise combination was included in analyses.

	2008					2009				
	Sample	*n* pairs sharing				Sample	*n* pairs sharing			
Kin Relationships	size	AS	PMP	LPL	PW	size	AS	PMP	LPL	PW
Close Kin										
Mother-Daughter	17	10	9	2	4	14	11	11	2	5
Littermates Sisters	14	10	10	2	2	29	18	18	6	16
Distant Kin										
Aunt-Niece	25	5	4	1	2	28	6	5	1	1
1st Cousins	15	1	1	0	0	53	9	9	0	0
Grandmother-Granddaughter	9	0	0	0	0	12	7	7	0	0
Great Aunt/Great Niece	0	0	0	0	0	18	7	7	0	1
1st Cousins once removed	0	0	0	0	0	68	4	4	2	2
2nd Cousins	0	0	0	0	0	47	3	3	0	0
Non-littermate Sisters	3	0	0	0	0	0	0	0	0	0
Non-Kin	193	3	3	0	0	361	11	11	0	0

post-weaning (70%, 80%, and 75% in each period, respectively; Table 3.5); however, in 2009, only 37% of all pairs that shared during pre-mid-pregnancy were close kin, whereas 73% and 84% were close kin during late-pregnancy/lactation and post-weaning, respectively (Table 3.5). Distant kin accounted for the most common relationship of sharing pairs in pre-mid-pregnancy in 2009 (49%) and very few of those pairs returned to sharing during post-weaning (11%; Table 3.5).

3.4.7. Synchrony of retirement and emergence

Because sleep-site sharing can only be inferred by radio-telemetry, if females that share sleep sites retire and emerge more synchronously than females that are not sharing, observers may be able to predict whether non-telemetered individuals are sharing sleep sites from aboveground observations. During the active season, all radio-collared females retired, on average, within a 64-minute period (*range* = 17 – 152 min, *n* = 171 nights) and emerged within a 59-minute period (*range* = 13 – 155 min; *n* = 168 mornings). When females shared sleep sites, they did not retire or emerge more synchronously (*mean* = 14 ± 5 minutes, *n* = 17 female pairs and *mean* = 11 ± 9 minutes, *n* = 32, respectively) than when they stopped sharing (*mean* = 12 ± 5 minutes, *n* = 17 and *mean* = 11 ± 7 minutes, *n* = 32, respectively; paired Student's t-Test; *t* = 0.8, *P* > 0.10 and *t* = -0.2, *P* > 0.10, respectively).

Whereas latency between retirement and emergence times cannot be used as an indicator of sharing a sleep site, sharing a surface entrance to retire at night or emerge in the morning is a good predictor that females are sharing a sleep site simultaneously. Females that shared sleep sites simultaneously during pre-mid-pregnancy used the same

surface entrance to either enter or exit the sleep site on 65% ($n = 260$ pairwise observations) and 63% ($n = 48$ pairwise observations) of the observed nights and mornings, respectively. During post-weaning, females used the same surface entrance to enter and exit the shared sleep site on 66% ($n = 189$ pairwise observations) and 69% ($n = 49$ pairwise observations) of the observed nights and mornings, respectively. On only 7 of 16,992 pairwise observations did 2 females enter or exit the same surface entrance and not share a sleep site that night. Therefore using the same surface entrance is a good predictor of sleep-site sharing but not using same entrance is a weak predictor because a third of sharers used different entrances.

3.5. Discussion

Although adult female Richardson's ground squirrels co-use underground space including burrow systems and their components, sleep sites, surface entrances, and underground connections, the extent of underground co-use varies throughout the active season in accordance to their reproductive state. Between emergence from hibernation and mid-pregnancy, co-use of underground space among adult females is extensive and burrow systems and their components are not the exclusive property of a single female. Throughout late-pregnancy and lactation the extent of co-use decreases, and although some gravid and lactating females use the same burrow systems, the surface entrances, sleep sites, and connections within the burrow system become the exclusive property of a single female. After litters are weaned, the co-use of underground space increases but to a lesser extent than before mid-pregnancy.

Not only does the degree of sharing vary with reproductive status, it also varies with the degree of kinship. Female Richardson's ground squirrels co-use underground space more frequently with close kin than with distant kin or non-kin indicating that sharing of underground space in Richardson's ground squirrels is nepotistic behaviour. Underground sharing of space is a nepotistic behaviour exhibited by many species of ground squirrels including the less social round-tailed ground squirrel in which burrow-system sharing occurs most frequently with close kin (Dunford 1977) and the highly social alpine marmot and black-tailed prairie dog in which burrow-system sharing occurs with both close and distant kin (Arnold 1990; Hoogland 1995). Therefore, the extent of nepotism in underground sharing of space is correlated with degree of sociality with sharing extending to distant kin in more-social species but not in less-social species.

The greater degree of burrow-system sharing before mid-pregnancy and after litter weaning by female Richardson's ground squirrels may be a consequence or cause of sharing sleep sites. Because females that share sleep sites and surface entrances are sharing burrow systems, and females that share sleep sites most often use the same surface entrance to enter and exit the sleep site, whether sharing one feature causes females to share other features is unclear.

Female Richardson's ground squirrels are usually philopatric which leads to female kin clusters and may promote cooperative interactions and sharing of space (Michener 1983). Only 8% and 19% of radio-collared females in 2008 and 2009, respectively, dispersed from their natal area as yearlings and settled in a new area away from kin which resulted in a missed opportunity for nepotism to occur in the dispersing females. Available underground space in which to establish a home range is a critical

resource for survival and reproduction in females, and competition for available underground space may be an important cause of dispersal in female ground squirrels (Nunes 2007). Proximate causes for dispersal, such as a change in population density in a natal area, may make it advantageous for females to relocate to an area with more available space. A high population density in 2008 and 2009 may have constrained females that remained in their natal area to either share already available underground space or construct a new burrow system, which is time consuming and energetically costly. Unused burrow systems were available during late-pregnancy/lactation in both years suggesting that females did have the option of using separate burrow systems; however, the choice of natal burrow systems can affect reproductive success (Pfeifer 1982) and the unused burrow systems may have been somehow inadequate for a natal burrow.

All radio-collared female Richardson's ground squirrels co-used underground space at some point during the active season in both years, but a greater proportion of females co-used a given burrow system, surface entrance, sleep site, and underground connection in 2009 than in 2008. Additionally, the extent of underground overlap was greater in 2009 than in 2008; fewer burrow systems, sleep sites, surface entrances, and underground connections in 2009 were the exclusive property of a single female. Richardson's ground squirrels are one of the less-social species of ground squirrels, characterized by extensive overlapping of aboveground space among close female kin but not distant female kin (Michener 1983); therefore, the extent of sharing should be dependent on the number of available close kin. Because close female kin (mothers, daughters, and litter-mate sisters) shared underground space more often than distant kin

or non-kin and there was a greater number of close kin pairs available in 2009 than 2008 the greater extent of underground sharing of space in 2009 may have been due to the increased number of close kin pairs.

For female Richardson's ground squirrels, the only time during the active season when overlap of underground space is rare is during late-pregnancy and lactation. Female ground-dwelling squirrels give birth underground in isolated natal nests to altricial young who are dependent on the mother for 29 days until they emerge aboveground. During this time, young do not come into contact with any conspecifics other than their mother and litter-mate siblings. Female ground squirrels do not nest communally during lactation, presumably to avoid sharing milk with non-offspring which is energetically costly (König et al. 1988). Additionally, female Richardson's ground squirrels cannot identify, or do but do not discriminate, between their own and alien young up to 20 days of age (Michener 1974); therefore, females may separate their natal burrows to prevent misdirected parental care.

Exclusivity of underground space during lactation may reduce the likelihood of infanticide, which occurs in most species of ground-dwelling squirrels (Dobson 1990; Vestal 1991; Hoogland 1995; Trulio 1996; Blumstein 1997; Stevens 1998). However, infanticide has not been reported in Richardson's ground squirrels despite extensive long-term field studies (e.g. Michener 2002; Risch et al. 2007), and I had no evidence for infanticide from 149 hours of observations during lactation and all my lactating females weaned litters. Furthermore, litter loss, except due to weasel or badger predation, is extremely rare in Richardson's ground squirrels (Michener 1989, 2004). Female Columbian (*Urocitellus columbianus*) and arctic ground squirrels (*Urocitellus parryii*)

isolate their natal nests and make the location inconspicuous by plugging the entrance to the natal burrow with soil and not foraging around the area (McLean 1978, 1982; Balfour 1983). Infanticide occurs in both Columbian and arctic ground squirrels, and females may plug their holes to prevent conspecifics from finding their young. Female Richardson's ground squirrels do not use inconspicuous surface entrances during lactation; they use multiple surface entrances, sleep sites, and connections which suggests females are not trying to hide where their litters is located.

Even though adult female Richardson's ground squirrels hibernated alone, most immediately shared a sleep site with close kin on emergence from hibernation. The majority of females that shared sleep sites simultaneously at night used the same surface entrance to retire to the shared sleep site and the same surface entrance to emerge from the shared sleep site in the morning, whether or not that happened to be the same location as the retirement surface entrance. Blumstein et al. (2004) concluded that sharing of a surface entrance by yellow-bellied marmots (*Marmota flaviventris*) on the mornings following emergence from hibernation indicated that they had shared a hibernaculum during the previous hibernation period. Female Richardson's ground squirrels hibernated alone, but shared sleep sites and surface entrances following emergence from hibernation, which indicates that sharing surface entrances in the mornings following emergence from hibernation may not be a good indicator of hibernacula sharing in ground squirrels.

The degree of sociality of a species is partly defined by their kin structure which incorporates type and frequency of interactions and space use (Lacey & Sherman 2007). Species of ground squirrels have been placed in 1 of 5 different social categories depending on their type and frequency of aboveground interactions and amount of

aboveground sharing of space (Michener 1983), but studies have largely ignored underground interactions and space use because they are difficult to study. However, to correctly define the social structure of a ground squirrel species, underground sharing of space should be included because female ground squirrels spend up to 80% of their lives underground.

Studies on underground behaviour in ground squirrels have been limited to surface-entrance use in which females were only considered to be sharing a burrow system if they shared a surface entrance, and burrow system excavations, which establishes geometrical relationships within a burrow system but does not ascertain how individuals utilize the burrow systems. The combined use of surface entrance observations, radiotelemetry, and combining the two to infer underground connections in this study allowed burrow system architecture to be inferred without the destruction of burrow systems that occurs during excavations. Additionally, once burrow-system architecture was inferred, burrow-system sharing of space could be determined even when females did not use the same surface entrances. Future studies on other species of ground squirrels using this method could determine whether individuals do in fact share underground space and the extent of sharing which should be incorporated in defining their degree of sociality.

This study revealed that adult female Richardson's ground squirrels co-use underground space including burrow systems, sleep sites, surface entrances, and connections extensively and the degree of co-use varies with reproductive status and kinship. Female Richardson's ground squirrels co-use burrow systems during late-pregnancy and lactation but do not co-use sleep sites, aboveground entrances, and

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connections within burrow systems. Whether the belowground architecture is physically

modified during this period is unknown.

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Chapter IV

4.1. Kinship and underground space use in ground-dwelling squirrels

Degrees of sociality are often defined based on a species' kin structure including its spatial structure, social interactions, and reproductive strategy (Lacey & Sherman 2007). Because North American species of ground squirrels most likely evolved from an ancestral asocial species (Michener 1983), and species today exhibit a wide range of social structures in varying geographical habitats, they provide an excellent model for hypotheses on adaptive radiation and evolution. Ground squirrels spend the majority of their lives underground sleeping and hibernating, behaviours that cannot be observed in naturally constructed burrow systems, and therefore, their degrees of sociality have previously been based on aboveground behaviours alone.

Based on extensive research on aboveground behaviours (Michener 1983), species of ground-dwelling squirrels are classified on an increasingly complex social spectrum that ranges from 1 (least social) to 5 (most social). Richardson's ground squirrels (*Urocitellus richardsonii*) are one of the less-social species of ground squirrels and are classified as 2 on the social spectrum (Michener 1983). Species with a social class of 2 have a promiscuous mating system, adult females have medium aboveground home-range overlap, and frequency of aboveground interactions is low, but when interactions do occur, they are usually amicable between kin and agonistic towards all other conspecifics (Michener 1983). For adult female Richardson's ground squirrels, aboveground behaviours such as sharing of aboveground space and amicable aboveground interactions occur preferentially with kin (Michener 1979) and alarm calling is more prevalent if kin

are present (Davis 1984). Therefore, female Richardson's ground squirrels are an excellent study subject to determine whether, and the degree to which, nepotism occurs in sharing of underground space.

To infer underground behaviour in burrow systems, my study combined aboveground observations of surface-entrance use, radiotelemetry to determine sleep-site use, and a combination of the two to infer underground connections. Using these methods, I inferred underground burrow architecture and I determined whether adult female Richardson's ground squirrels share underground space and also the extent and tolerance of sharing. Female Richardson's ground squirrels do share underground space including sleep sites, surface entrances, connections, and burrow systems, but such underground sharing is not random and instead occurs most frequently with mothers, daughters, and littermate sisters, rarely with distant kin, and almost never with non-kin. These patterns of underground sharing of space and limits of nepotism in female Richardson's ground squirrels are consistent with their aboveground sharing of space and limits of nepotism. Therefore, spatial patterns and the extent of nepotism among female Richardson's ground squirrels are similar both aboveground and underground. Based on the similarity of aboveground and underground behaviour in female Richardson's ground squirrels, I do not expect knowledge of underground behaviour to significantly change categorization of sociality in ground-dwelling squirrels; however future studies on underground behaviour in other species with various social systems need to be completed for this conclusion to be verified.

To formulate models for the evolution of sociality and nepotism in North American species of ground squirrels, comparative studies need to include information on

the social structures of less social, moderately social, and highly social species including information on both aboveground and underground behaviours. Future studies can infer underground behaviour using radiotelemetry and aboveground observation of surface entrance use to determine whether, and the extent to which, other species of ground squirrels share underground space and whether aboveground and underground behaviours are similar with respect to sharing of space and nepotism.

Belding's ground squirrels (*Urocitellus beldingi*) have the same social-system grade (2) as Richardson's ground squirrels and have been extensively studied with regard to the limits of nepotism in aboveground behaviours, but not underground behaviours (Sherman 1980). In Belding's ground squirrels, close female kin seldom fight aboveground, are permitted access to defended aboveground territories, cooperate to defend young, and use alarm calls to warn of predators whereas distant kin are typically antagonistic towards each other (Sherman 1980); therefore, Belding's ground squirrels are nepotistic towards close kin but not distant kin in aboveground behaviours. Because Belding's ground squirrels are in the same social grade as Richardson's ground squirrels and exhibit similar aboveground nepotistic behaviours, I predict that Belding's ground squirrels also share underground sleep sites before mid-pregnancy and after the litters are weaned and they do so with close kin but not distant or non-kin.

Aboveground behaviour has also been extensively studied in the moderately social Columbian ground squirrels (*Urocitellus columbianus*) in which aboveground nepotism extends to both close and distant kin within a territory (Hare & Murie 1996) and in the highly social black-tailed prairie dogs (*Cynomys ludovicianus*) in which nepotism extends to both close and distant kin within the coterie (Hoogland 1995). Because

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underground sharing of space and nepotism in Richardson's ground squirrels is similar to aboveground sharing of space and nepotism, I predict that in both Columbian ground squirrels and black-tailed prairie dogs, underground sharing of space also occurs before mid-pregnancy and after litters are weaned but does not extend to rearing litters communally, and that the extent of nepotism in underground sharing extends to both close and distant kin in their territory and coterie, respectively.

Additionally, because North American species of ground squirrels are wide-spread, and species in the same social category live in different habitats, comparison of sleep-site sharing in species with the same social system that live in colder versus warmer climates may provide insights on the role of thermoregulation in sleep-site sharing. Female Richardson's ground squirrels share sleep sites in significantly larger groups during the coldest months of the active season than during the hottest. Additionally, females shared with more distant and non-kin during the coldest months than during the hottest. Because huddling may be a contributing factor to explain why female Richardson's ground squirrels share sleep sites for 2 - 3 weeks during the coldest months, I predict that other species of ground squirrels will share sleep sites most frequently during the coldest months.

Some highly social marmot species including the alpine marmot (*Marmota marmota*) and Olympic marmot (*Marmota olympus*) that live in colder climates than Richardson's ground squirrels, share hibernacula and it is hypothesized they do so for thermoregulation purposes (Arnold 1988; Arnold 1990). Because some marmot species are already known to share hibernacula, and most likely do so for thermoregulatory

purposes, I predict that species such as the alpine and Olympic marmot that live in colder climates also share sleep sites.

One limitation of my study, as well as other studies on ground-squirrel nepotism, is that paternity cannot be assigned from observations alone because females may mate with multiple males and copulation usually occurs underground (van Staaden et al. 1994; Hare et al. 2004; Magyara 2009); therefore, usually only maternal kin are included in kinship analyses. Lack of information on paternal kinship might lead to potential misinterpretations of the role of kinship in nepotism because, for example, paternal half-siblings are as closely related as maternal half-siblings, but only the latter kinship category is included in analyses. Possibly distant kin and non-kin that shared sleep sites and other underground space in my study were related paternally, and might even have been as closely related as paternal half-siblings given that males mate with multiple females (Magyara 2009). However, even if those maternal non-kin who shared were indeed related paternally, sharing by maternal non-kin is so rare that paternal kinship alone is an insignificant determinant of underground sharing of space in Richardson's ground squirrels. Paternal kinship combined with distant maternal kinship might be a factor in determining which distant kin do and do not occasionally share sleep sites simultaneously. In species in which parental care is provided exclusively by the mother, fewer mechanisms are available for paternal-kin recognition than maternal-kin recognition, and studies have not yet been conducted with Richardson's ground squirrels to assess whether or which degrees of paternal kin can be recognized. Regardless, my study reveals that paternal kinship alone has very weak explanatory power for sharing whereas close maternal kinship is a strong predictor of which types of kin share sleep

sites as adults. If degree of paternal kinship among distant maternal kin accounts for which distant kin do share, that would strengthen my position that sharing occurs preferentially among kin but would still leave maternal kinship as the primary determinant of sharing. Because paternity can often be assigned unambiguously from a combination of behavioural exclusion through observation and DNA analysis (Magyara 2009), future studies could establish the extent to which paternal kinship contributes to nepotism.

My study on underground space use by female Richardson's ground squirrels is one of the first in unraveling the somewhat mysterious underground behaviours of ground squirrels. Future studies on the underground behaviour of other species of ground squirrels will add to an already vast knowledge of ground-squirrel sociality that will strengthen evolutionary models from comparative studies in ground-dwelling squirrels.

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