Franklin’s ground squirrel (*Poliocitellus franklinii*) social distancing: home range size and overlap of a relatively asocial ground squirrel

by

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Abstract

Sociality among the ground-dwelling squirrels has been well researched via studies exploring life history traits, the formation of groups and how cooperation contributes to the success of these social species. The evaluation of socio-spatial organization, and in particular, kin-differential associations among individuals, can provide insight into the adaptive basis of coloniality and altruism among conspecifics. Relatively asocial Franklin's ground squirrels (*Poliocitellus franklinii*) discriminate kin from non-kin in the absence of any broader level of social discrimination, which, based on comparative analyses, may be ancestral to more advanced and inclusive expressions of sociality. In populations of Franklin's ground squirrels near Delta Marsh, Manitoba, Canada, spatial data were gathered to monitor home range and core area size and overlap across the annual reproductive cycle (gestation, lactation and post-weaning) of adult and yearling males and females both with close-kin (defined as known mother-offspring pairs or sibling pairs) and non-close-kin. Nest locations of lactating females were documented as well to test for differences in dispersion and relocation patterns among close- versus non-close-kin. Sex, age and kinship did not affect home range and core area size, which varied extensively across the different stages of the annual reproductive cycle. The degree of home range and core area overlap throughout the overall active season was not significantly affected by sex, age or kinship. Further, lactating females did not cluster nests with close-kin during lactation, and tended to move nests away from close-kin as lactation progressed. Taken together, the absence of preferential association with kin in above-ground space use and nest dispersion suggest that space use of Franklin's ground squirrels is not predicated on kinship. These findings also suggest that members of this Franklin's ground squirrel population are relatively asocial based on limited overlap within the 50% core area among conspecifics.

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Thesis Format

My thesis utilizes the manuscript (“sandwich”) style format with an introductory chapter and a concluding chapter flanking two chapters presenting original data. My introductory chapter provides background information related to my study, establishes general rationale for my thesis research, and outlines the research questions addressed. Chapter two (addressing how home range and core area size and overlap are affected by sex and age classes) and three (addressing how home range and core area size and overlap are affected by the relatedness of neighbouring conspecifics) are presented as draft manuscripts, each containing a title, abstract, introduction, methods, results, discussion and literature cited. The final chapter of my thesis concisely summarizes my findings, relates them to the overarching themes presented in the introductory chapter and discusses future research directions.

Chapter 1: General Introduction

The degree to which conspecifics reside, interact and cooperate with one another defines their level of sociality (Wilson, 1975). It is through these defining characteristics that researchers categorize species across a continuum of social complexity (Armitage, 1981; Michener, 1983), exploring contributions of both intrinsic (e.g. body size, life history) and extrinsic factors (e.g. physical factors, predation risk) to spatial organization (Michener, 1979; Rayor and Armitage, 1991), communal nesting associations (Lacey et al., 1997), and behavioural interactions (Hare and Murie, 1996; Mateo, 2002). Ground squirrels vary widely in their expression of sociality, from solitary species like the woodchuck (*Marmota monax*) (Maher, 2006) to highly social species like the Olympic marmot (*Marmota olympus*) (Barash, 1973). Group living is selected for and maintained by genetic (Hamilton, 1964), ecological (Emlen, 1982), phylogenetic (Sobrero, Inostroza-Michael, Hernándex, and Ebensperger, 2014), and/or sociobiological (Armitage, 1981; Thierry, 2008) factors. Species regarded as asocial (e.g. Franklin's (*Poliocitellus franklinii*: Hare, 2004), thirteen-lined (*Ictidomys tridecemlineatus*: McCarley, 1966; Vestal and McCarley, 1984), golden-mantled (*Callospermophilus lateralis*: Van Vuren, 2011) ground squirrels and woodchucks (Armitage, 1981; Michener, 1983; Maher, 2006)) are characterized by the absence of interactions among conspecifics, and reduced to no overlap in space outside the context of breeding and rearing young. These defining characteristics are typically quantified as an indirect measure of sociality through the documentation of home range overlap (Michener, 1983). In the broader sense, classification of a species level of sociality involves measures of social cooperation, spatial organization, frequency of behavioural encounters and relationships among conspecifics, that impose fitness costs and allow fitness benefits to accrue (Alexander, 1974; Wilson, 1975; Hare, 2004; Lacey and Sherman, 2007).

Cooperation

The sociality of ground-dwelling squirrels has been investigated via research documenting life history traits, the formation of groups and how cooperation contributes to the evolution and maintenance of advanced sociality (Alexander, 1974). The aggregation of individuals into a group results in fitness benefits and costs (Ebensperger, 2001; Krause and Ruxton, 2002). Benefits of group living include; enhanced anti-predator vigilance (Alexander, 1974; Hoogland, 1979; Hoogland, 1981; Macdonald, 1981; Ebensperger, 2001), social transmission of information (Wilson, 1975; Ebensperger, 2001), enhanced juvenile survival (Blumstein and Armitage, 1998; Hare and Murie, 2007), protection from environmental factors (Alexander, 1974), enhanced food gathering (Wilson, 1975), competitive advantages (Wilson, 1975), reproductive benefits, (Wilson, 1975; Emery and Thompson, 2017), division of labour (Ulrich et al., 2018), and inheritance of territories, often among female kin (Myles, 1988; Harris and Murie, 1984). In those contexts, fitness benefits accrue through social cooperation promoted via kin selection, reciprocal altruism, byproduct mutualism, and/or group selection (Goodnight, 2012; Wilson, 1975; Lacey and Sherman, 1997). The latter - group selection – can occur when group sizes are small, immigration is limited, and the probability of extinction is high (Wilson, 1975). While group living imparts fitness benefits, these benefits are offset by costs including: depletion of resources (Alexander, 1974; Wilson, 1975), habitat availability (Solomon, 2003), risk of parasite and disease transmission (Wilson, 1975), resource guarding (Alexander, 1974), predator attraction (Sherman, 1977), infanticide (Hoogland, 1985; 1995), reproductive competition (Blumstein and Armitage, 1998), and environmental degradation (Armitage, 1981; 2007).

Cooperation requires collective actions and reduced competition among individuals within a group (Hoogland, 1981; Dugatkin, 1997). Cooperative and antagonistic interactions between kin, familiars and strangers result in definitive patterns of spatial and temporal associations among conspecifics in nature (Alexander, 1974; Wilson, 1975), which can appear through the retention of relatives and/or familiar conspecifics in the natal area (Armitage, 1981; Rayor and Armitage, 1991; Michener, 1984). Cooperation among female Belding's ground squirrels (*Urocitellus beldingi*) appears to be limited to mother-daughter, and female sibling and half-sibling interactions; cooperative actions (nepotism - see below) were not recorded among grandparents, cousins or nieces, demonstrating that cooperation in some species is limited to close-kin (Sherman, 1980). By contrast, highly social Columbian ground squirrels (*Urocitellus columbianus*) show amicable behaviour toward all colony members, independent of kinship (Hare, 1992; 1994). Highly social rodents show greater cooperation and spatial overlap than rodents that are less social and extend amicable interactions beyond littermates and close-kin to include other conspecifics (Rayor and Armitage, 1991; Hare, 1996; Hare and Murie, 2007).

Rodents as a model for study

Ground squirrels have provided a convenient model to explore the evolution and maintenance of sociality, given pronounced variation in the structure of their societies (Armitage, 1981; Michener, 1983) ranging from relatively asocial to complex social groups approaching egalitarian societies (Armitage, 1981). Armitage (1981) and Michener (1983) proposed models to describe ground squirrel sociality based primarily on body size and discussed how spatial overlap contributes to different grades of sociality. Harsh social and environmental factors contribute to decision to remain philopatric, thus social ground squirrels tend to have larger body size, delayed sexual maturity, delayed dispersal and thus overlap in space use extensively. In contrast, relatively asocial ground squirrels tend to be small-bodied, attain sexual maturity and disperse early from their natal area, and have limited to no home range overlap with conspecifics (Armitage, 1981; Michener, 1983). The precise organization of individuals and nature of behavioural interactions between kin versus non-kin can provide insight into any possible role of kin discrimination and kin-differential association to the expression of selfishness and/or altruism leading to increased fitness among conspecifics (Hamilton, 1964; Maynard Smith, 1964; Alexander, 1974; Wilson, 1975; Lacey and Sherman, 2007). Most of the empirical evidence bearing on our understanding of the evolution of cooperation through kin-biased behaviour is derived from studies of highly social species (Hatchwell, 2009) that are typically larger in body size. However, the lack of information for relatively asocial ground squirrels, including the small-bodied, Franklin's ground squirrel's use of space during different periods of their reproductive cycle, represents a major knowledge gap in our understanding of the comparative sociality of ground squirrels and the analysis of ancestral forms that serve as the antecedents of advanced sociality (Hall, 1955; Michener, 1983; Rayor and Armitage, 1991; Hare and Murie, 2007; Duggan, 2011; Pero and Hare, 2017**.** Thus, Franklin's ground squirrels constitute an ideal species for study.

Non-kin aggregations

Individuals of many species aggregate together, discriminating among conspecifics at multiple levels. Documenting the level(s) at which social discrimination occurs can provide insight into the adaptive basis of social behaviour (Hare, 2004). Group selection (Goodnight and Stevens, 1997), reciprocal altruism (Axelrod and Hamilton, 1981) and/or byproduct mutualism

(Mesterton-Gibbons and Dugatkin, 1992) allow for fitness benefits to accrue through amicable interactions among non-kin (Hamilton, 1964; Goodnight, 2012). Both cooperative and antagonistic interactions beyond close-kin, such as between familiars and/or strangers, affect inclusive fitness and promote unique patterns of spatial and temporal associations among conspecifics in nature (Alexander, 1974; Wilson, 1975). Kin selection (see below) is not the only option among kin groups, as direct fitness benefits can reward helpers, who temporarily forestall the production of their own offspring (Balshine-Earn et al., 1998; Cockburn, 1998; Dierkes et al., 1999). Research involving more highly social species has revealed that kin-biased behaviour is not requisite to the evolution of advanced sociality as groups can form outside the confines of close kinship, and social benefits can accrue among non-kin (Jaisson, 1991; Hare and Murie, 2007; Hölldobler and Wilson, 2009). Richardson's ground squirrel (*Urocitellus richardsonii*) juveniles are able to distinguish littermates from non-littermates as well as familiar neighbours from strangers, suggesting that exclusive kin-biased behaviour may give way to broader social inclusion of less closely-related familiar individuals in more social species (Hare, 1998). Cooperative interactions impart fitness benefits at both the individual and group level, where investment in non-descendent conspecifics leads to inclusive fitness benefits (Hamilton, 1964). Highly social Columbian ground squirrels discriminate among juveniles at the level of the group, treating all group members, whether kin or non-kin, amicably (Hare, 1992; 1994). Cooperation among non-kin may also provide benefits via reciprocal altruism (Trivers, 1971), byproduct mutualism (West-Eberhard, 1975), and/or group selection (Dugatkin, 1998). Cooperation attributable to these mechanisms can result in nonrandom patterns of socio-spatial organization among adult females (Hare, 2004; Luna and Baird, 2004).

Territoriality occurs through defence and/or dominance within territories (Michener, 1979), which has the potential to reduce an individual's fitness (Jaeger, 1981; Luna and Baird, 2004), as encounters with strangers (outside the colony or kin cluster, in specific species) tend to involve antagonistic interactions in many ground squirrel species (Michener, 1983; Hare, 1994). However, social cooperation can be observed among familiar neighbouring conspecifics (Wilson, 1975; Sherman, 1980; Porter and Blaustein, 1989). The "Dear enemy" hypothesis predicts that an individual will avoid escalating aggressive encounters with frequently encountered distant-kin and/or non-kin neighbours, reducing energy expenditure and thus increasing the fitness of neighbouring individuals (Fisher, 1954; Wilson, 1975; Jaeger, 1981), though even with reduced agonism, individual distance is maintained (Wilson, 1975).

Kin selection

Kin selection can be understood within the context of genetic relatives and socio-spatial organization (Michener, 1983), and operates across a spectrum of sociality, from highly social to solitary or relatively asocial species (Hare and Murie, 2007). The expression of kin selection depends upon kin recognition, which in turn, enables the expression of kin-differential behaviour (Beecher, 1982; Holmes and Sherman, 1982). Kin recognition, and hence the prospect of kin selection has been reported for many ground squirrel species: Franklin's (Hare, 2004), thirteen-lined (Holmes, 1984), golden-mantled (Mateo, 2002), round-tailed (*Xerospermophilus tereticaudus*; Dunford, 1977), Richardson's (Michener, 1973; Hare, 1998), Columbian (King, 1989), as well as in marmots (*Marmota sp.;* Armitage, 1981) and prairie dogs (*Cynomys sp.*; Hoogland, 1995). Kin recognition, such as between siblings, may influence mate choice by changing mating behaviour to optimize the balance between inbreeding and outbreeding, rather than promoting nepotism (Bateson, 1983; Hare, 2004; Keane et al., 2015). In addition, kin selection promoted by kin recognition eliminates any cost that would otherwise be associated with directing beneficent behaviour toward non-relatives (King and Murie, 1985). Kin discrimination (as evidenced by the differential treatment of kin and non-kin) is evident in numerous social groups (Michener, 1983; Rayor and Armitage, 1991; Hare and Murie, 1996; Hare, 2004; Mateo, 2002), and may represent an ancestral state (Hare, 2004). This notion is supported by observations of expanded cooperation among non-kin or group members leading to more advanced and inclusive expressions of sociality (Hare and Murie, 1996; Hare, 2004). While, kin selection via kin recognition can promote mate selection ensuring the avoidance of close inbreeding, facilitate the protection of resources and vulnerable juveniles, and ensure nepotism (Mateo, 2002; Cross, Blumstein and Rosell, 2013), costs, including the risks associated with inbreeding and competition, have promoted the evolution of sex-biased dispersal and adaptive sex allocation (Gardner et al. 2007).

Kin selection can be expressed as cooperative breeding, alloparental care, alarm calling, group defense of territory, mate choice and inbreeding avoidance (Maynard Smith, 1964; Michener, 1983; Hare and Murie, 2007; Maher, 2009). Alarm calling to both direct and indirect descendent neighbours is expressed in Belding’s and round-tailed ground squirrels (Sherman, 1977; Dunford, 1977 respectively). Juvenile Franklin’s ground squirrels were amicable only toward siblings, suggesting that kin discrimination in this species may serve mate choice in optimizing the balance between inbreeding and outbreeding (Bateson, 1983; Hare, 2004). Group-living among Alpine marmots (*Marmota marmota*) including distant/non-kin associations provides alloparental care and group defence of territories (Arnold, 1990).

Kin selection, leading to natal philopatry allows for fitness costs and benefits to accrue (Hare and Murie, 2007). The fitness benefits of kin selection are widespread across taxa and appear in asocial to highly social species (Hare and Murie, 2007). Typically, kin-mediated behaviours are observed in species that delay dispersal, which leads to the retention of kin in the natal area (philopatry) (Hatchwell, 2009), which can promote the evolution of nepotism (Hare and Murie, 2007). Alpine marmots including distant/non-kin associations provides fitness benefits through shared hibernaculae and helpers that protect infants from the harsh winter (Arnold, 1990). A manipulation of Richardson's ground squirrel kin clusters found that closely-related females spent more time together feeding, shared core areas to a greater extent, were less vigilant, and had better breeding success than aggregations of non-close-kin (Davis, 1984). The availability of female kin allows societal benefits to accrue via kin selection, which may give way to more inclusive expressions of sociality within groups and promote the evolution and maintenance of broader cooperation (Hare, 1996; Hare and Murie, 2007).

On the other hand, fitness costs of kin selection do exist. Reproductive suppression, competition for mates/food/shelter (West, Pen and Griffin, 2002; West et al., 2001), and infanticide (Hoogland, 1985) have been documented across taxa. Lactating black-tailed prairie dog (*Cynomys ludovicianus*) females were the primary perpetrators of infanticide on the offspring of close-kin (Hoogland, 1985). Costs associated from competition among siblings for access to food occur in some bird species, promoting siblicidal behaviour (Fulmer and Hauber, 2016). Golden-mantled ground squirrel females that had littermate sisters living nearby were less likely to reproduce than females without a nearby female sibling, suggesting nearby kin can cause fitness costs through sibling competition (Wells and Van Vuren, 2018). Thus, the benefits of kin selection may be negated when competition occurs in a confined area (West et al., 2001).

Not only can kinship promote amicable behaviour among related conspecifics, it can also lead to differential association of individuals in time and space (Dunford, 1977; Michener, 1979; 1981, Sherman 1980; Murie and Harris, 1984). Environmental or physiological selective pressures can cause delayed dispersal, which can lead to philopatry (Barash, 1989; Michener, 1983; Solomon, 2003). This trend of delayed dispersal leading to philopatry has been documented repeatedly among female small mammals including prairie voles (*Microtus ochrogaster*; Keane et al., 2015), woodrats (*Neotoma sp.*; Winters and Waser, 2003), kangaroo rats (*Dipodomys ingens;* Meshriy et al., 2011), woodchucks (Keane et al., 2015), California ground squirrels (*Otospermophilus beecheyi*; Boellstorff and Owings, 1995), and gray mouse lemurs (*Microcebus murinus*; Wimmer et al., 2002). It has also been reported for some carnivore species (Jackson et al., 2017; Tirelli et al., 2018). Females tend to spatially aggregate in kin clusters, which are correlated with enhanced breeding success and survival (Silk, 2007). Arctic ground squirrels (*Urocitellus parryii*) have more extensive home range overlap with close-female-kin, while distant kin were treated more similarly to non-kin (Mclean, 1982). Thus, spatial organization is intimately linked with kin selection, and provides a way to study sociality in elusive species in which social interactions are more difficult to observe, such as in the Franklin's ground squirrel (Sowls, 1948).

Spatial organization among multiple levels of relatedness (e.g., close-kin, distant-kin and non-kin) in natural populations is crucial in understanding the role played by kin selection in animal societies (Hare and Murie, 2007). Comparative studies exploring these phenomena are valuable tools for answering questions pertaining to sociality and can identify the drivers of social evolution. Coincident with this method of inquiry, studies are increasingly shifting focus toward asocial or solitary species as a means of understanding more primitive forms of sociality

(Michener, 1983; Ferron, 1985). The inclusion of space use provides key insights into socio-spatial behavioural patterns (Kappeler, 2019).

Nesting behaviour

Nesting association with close-kin at different stages during the annual reproductive cycle can promote both fitness costs and benefits (Pero and Hare, 2017). In social species, communal nesting allows individuals to sleep and rear young together, which presumably reduces predation and infanticide, while aiding in thermoregulation, providing more nutrients for young to grow, and enhancing the probability that adoption will occur if one dam dies (Ebensperger, 2001; 2003, Hayes, 2000). Female Arctic ground squirrel relatives aggregate pups together in one burrow (McLean, 1982). In thirteen-lined ground squirrels, allogrooming and sharing of hibernaculae provide evidence of nepotism (Schwagmeyer, 1988). Contrary to Michener and Murie's (1983) findings for Columbian ground squirrels, Hoogland (1983) noted more amicable interactions among female adult and yearling black-tailed prairie dogs during the pre-breeding, early breeding and post-weaning periods, with more hostile interactions involving infanticide confined to the late breeding and lactation periods. In a seven-year study, the majority of infanticides were perpetrated by lactating female black-tailed prairie dogs who were found to be genetically related to the mothers whose litters they killed (Hoogland, 1985). However, following late lactation into post-weaning, black-tailed prairie dog dams were found to nurse juveniles other than their own (Hoogland, 1983). Young female Columbian ground squirrels tend to organize themselves spatially to promote proximity to more close-kin (Arnaud et al., 2012). Nest sites are a defended resource and young females have trouble establishing themselves among female competitors (Harris and Murie, 1984), leading Michener (1983) to suggest that mothers may bequeath nests to their daughters as a form of parental investment. Franklin's ground squirrels are known to relocate their nests and pups while lactating, sometimes more than once, which is energetically costly (Pero and Hare, 2017; Pero and Hare, unpublished data), but may lead to selective aggregation of kin. Among Franklin's ground squirrel dams, six incidents of adoption have been documented around the time of juvenile emergence when dams disappeared (Hare, unpublished data), suggesting that having kin nearby may prove beneficial in providing care for orphaned young. While it appears that nest relocations can reduce ectoparasite pressure and are associated with conspecific discovery of nest locations (Pero and Hare, unpublished data), whether female nest movements are directed with respect to kinship (i.e. toward kin versus away from kin) is, at present, undocumented.

Behaviour shifts over reproductive phases

Changing reproductive status can promote temporal changes in the socio-spatial organization of female ground squirrels (Mclean, 1984). Species such as Uinta (*Urocitellus armatus*) (Balph, 1984), Richardson's (Michener, 1979), Columbian (Betts, 1976), round-tailed (Dunford, 1977), and Arctic (Mclean, 1981) ground squirrels have been described as aggressive throughout the breeding season until the post-weaning period of the annual reproductive cycle, where the need to accrue mass to survive hibernation appears to preclude escalated aggression among conspecifics (Michener, 1979). Home range overlap (not including core areas) occurred only between Richardson's ground squirrel nearest neighbours (Michener, 1979; 1980). Dams preferred to spend most of their time within their core area during gestation and lactation, however, after juveniles emerged, female space use expanded, intruding into neighbouring territories (Michener, 1979). Richardson's and thirteen-lined ground squirrels reduced their rate of interactions among conspecifics shortly after copulating until young emerged (Michener, 1973; Holmes, 1984). The lactation period of the annual reproductive cycle tends to be when females are most aggressive (Armitage, 1965; Michener, 1979). Female Columbian ground squirrels, for example, reduce their home range size in order to defend their territory protecting young pups from non-related infanticidal females (Hare, 1991; Stevens, 1998). In the yellow-bellied marmot (*Marmota flaviventris*), Armitage (1965) noted the highest levels of aggression occurred toward the end of the lactation period. Hoogland (1981) reported amicable behaviour during the pre-breeding and post-weaning phases, but aggression during the late breeding through early lactation period for black-tailed prairie dogs. These results indicate that home range overlap is greatly reduced during pregnancy and lactation among most group-living rodents (Michener, 1979). There are always exceptions, however, as highly social Olympic marmots are characterized by extensive home range overlap and amicable interactions with conspecifics throughout their active season (Barash, 1973).

Male sociality

Because space use by males influences mating, my research also explored male space use. Mate choice may ultimately achieve an optimal balance between inbreeding and outbreeding in that there are benefits and costs associated with both (Bateson, 1983). Two mechanisms via which species can optimize the balance between inbreeding and outbreeding include sex-differential dispersal, wherein members of one sex preferentially disperse from their natal area and/or the ability of conspecifics to recognize close-kin (discussed above) (Bateson, 1983). The ability to recognize kin can also reduce the likelihood of inbreeding, ultimately limiting the match-up of deleterious alleles and promoting greater genetic diversity in the population (Bateson, 1983).

Although male and female interactions have been well documented in ground squirrels, few studies have investigated resident male spatial organization among female relatives throughout the breeding season. In Columbian ground squirrels, adult male core areas remained distant from their mother's centre of activity (Harris and Murie, 1983). Michener (1979), reported that three male Richardson's ground squirrels organized themselves in close proximity to one another, while avoiding entering female core areas; however, whether males were avoiding females in general or just female relatives was not documented. In thirteen-lined ground squirrels male territories overlapped with those of females, though interactions were rare and relatedness between the members of the two sexes were unknown (Schwagmeyer and Brown, 1983). Contradictory findings have been reported for Franklin's ground squirrel space use. Choromanski et al. (1989) reported extensive overlap of home ranges, while Armitage (1981) and Michener (1983) asserted that these squirrels have nonoverlapping home ranges. Adult male spatial organization among female conspecifics throughout the breeding season requires further investigation and can promote a better understanding of Franklin's ground squirrel sociality.

Study species and objectives

Franklin's ground squirrels have been portrayed in the literature as relatively asocial owing to their early sexual maturation, small size, early dispersal, agonistic nature, non-overlapping spatial organization, and the absence of burrow sharing (Armitage, 1981; Michener, 1983; Hare, 2004). Franklin's ground squirrels are diurnal, semifossorial species that range across the central United States following the Apsen Parkland ecotone through the Canadian prairie provinces including Manitoba, Saskatchewan and the central Alberta plains (Ostroff and Finck, 2003). While published information regarding socio-spatial organization is limited, contradictions exist as to the extent to which adult Franklin's ground squirrel home ranges overlap. Thus, further investigation is required. To my knowledge, there has not been a detailed study of Franklin's ground squirrel socio-spatial organization incorporating kinship, following any one population throughout its entire active season. Both Armitage (1981) and Michener (1983) suggested that Franklin's ground squirrels have nonoverlapping territories, conspecific interactions typified by aggression, and phenology consistent with relatively small-bodied ground squirrels, with relatively early sexual maturation and dispersal shortly after weaning, placing them among the relatively asocial ground squirrel species. Contrary to Armitage (1981) and Michener (1983), however, Choromanski et al. (1989) reported extensive overlap of home ranges between same sex and opposite sex Franklin's ground squirrels. Krohne et al. (1973), collected radio-telemetry data for adult Franklin's ground squirrels over a period of one week (in mid-summer, after parturition) to assess home range sizes. This short-term study had a small sample size composed of one male and two females and found that the male had a smaller home range than the females. They did, however, acknowledge that home range sizes can change throughout the active season (Krohne et al., 1973) and thus, the one-week period examined may not be representative of male versus female home range sizes in general.

There are only a few species of ground squirrel (Franklin's, thirteen-lined, golden-mantled, and woodchucks) that are considered to be relatively asocial, though in presenting her comparative sociality of the ground squirrels, Michener, (1983), conceded that patterns of socio-spatial organization have yet to be investigated throughout an entire active season for any of the asocial species. Thus, Franklin's ground squirrels provide an excellent opportunity to study and further understand sociality related to spatial dynamics in a relatively asocial species. Understanding the relationships between these individuals, their home ranges, and degree of philopatry will promote an understanding of whether Franklin’s ground squirrels associate differently with kin and non-kin as documented for many other ground squirrel species (Armitage, 1981; Michener, 1983), and ultimately promote a more robust understanding of the degree of sociality of this seldom-studied species.

I investigated the dynamics of spatial organization relative to kinship, sex, age and reproductive phase in Franklin’s ground squirrels. I examined and documented spatial proximity, extent of overlap and home range and core area size of a subset of males and females with varying ages within a population of Franklin’s ground squirrels occupying habitat near Delta Marsh, Manitoba, Canada, relative to relatedness among those individuals to better understand sociality in this species. I predicted that females would: 1) tolerate spatial overlap in the home range (innermost 95% kernel density area) and core (innermost 50% kernel density area) areas with close female kin only, 2) selectively cluster nests with close female kin toward the end of lactation, and 3) move their nests toward close female kin and away from non-kin during lactation. Further, by tracking above ground space use by males throughout their active season, I explored how male space use may be influenced by kinship and the spatial dispersion and seasonal activity of female conspecifics.

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Chapter 2: Movement patterns and home range analysis of a population Franklin's ground squirrels (*Poliocitellus franklinii*) throughout their active season

Abstract

Spatial associations within populations have pronounced effects on genetic structure and social dynamics. To contribute to our understanding of sociality, I monitored above ground space use of seldom-studied Franklin's ground squirrels (*Poliocitellus franklinii*) near Delta Marsh, MB, Canada, accruing data documenting home range size (innermost 95% of above-ground locations), core area size (innermost 50% of above-ground locations) and degree of overlap of those for male and female adults and yearlings across their annual reproductive cycle (gestation, lactation and post-weaning). While I failed to detect a statistically significant difference in home range and core area size between breeding female and male squirrels, average home range and core area sizes of females tended to be larger than those of males during the overall active season. Yearlings also showed a trend for larger overall home range and core area sizes than adults during the overall active season. Home range and core area size varied significantly across the different stages of the annual reproductive cycle, though the degree of home range and core area overlap was not significantly affected by sex or age. Further, there were no significant interactions between sex and age on home range and core area size, though a significant interaction between those factors was detected for home range and core area overlap. These data only weakly support the general trend evident among ground squirrels toward males having larger home ranges than females. However, consistent with findings for other ground squirrel species, home ranges of both sexes and age classes expanded the most during the post-weaning period. My findings are also consistent with earlier assertions that Franklin's ground squirrels are relatively asocial based on limited overlap within the 50% core area among conspecifics.

Key words: Franklin's ground squirrel, home range, overlap, sociality, space use, socio-spatial organization

Introduction

Socio-spatial distribution in relation to the sex, age class and relatedness of interacting individuals defines a population's social system (Lacey et al., 2019). Members of asocial species tend to avoid interactions and have nonoverlapping, or at most, limited home range overlaps, while members of highly social species have amicable interactions and share home ranges with overlap modulated by the sex, age class, and genetic relatedness of individuals (Armitage, 1981; Michener, 1983). Thus, establishment of home ranges and their overlap is indicative of sociality. Burt (1943) first described an animal's use of space to be its "home range," which meant it was the area that encompasses the necessary resources that individuals need to survive and where they spend the most amount of time, foraging and looking for mates (Wilson, 1975; Kubiak, 2017). The size of an animal's home range depends on a variety of ecological factors and life-history traits (Crook, 1970; 1976; Alexander, 1974; Michener, 1979; Rayor and Armitage, 199l) and through the influence of these factors, species arrange themselves spatially so that fitness benefits are maximized (Sandell, 1989).

Factors affecting space use

Spatial organization is a product of myriad influences, including population demography, social dynamics and genetic composition (Cheepko-Sade and Halpin, 1987; Stenseth and Lidicker, 1992). The size of a species plays a major part in the size of its home range: larger individuals tend to have larger home range sizes, presumably owing to their greater resource demands and reduced energetic costs in navigating their range (Pereira et al., 2006). Sex differences also contribute to differential patterns of space use among ground squirrels (Michener, 1983). Highly social Olympic marmot (*Marmota olympus*) societies are characterized by extensive home range overlap and amicable interactions with conspecifics throughout their active season for both sexes (Barash, 1973). Males tend to have larger home ranges than females (Armitage, 1974; Yeaton, 1972; Dunford, 1977; Priotto et al., 2002) and male-biased dispersal not only reduces the risk of inbreeding, but also enables females to maintain access to resources (Greenwood, 1980; Ostfeld, 1985), which increases reproductive success (Trivers, 1972). Vesper mouse (*Calomys musculinus)* males have home ranges larger than females during their breeding period, presumably facilitating the location of mates, while after the breeding season, males devote their attention to food, and limit their range accordingly (Priotto et al., 2002).

Population density can affect the degree of home range overlap, as has been documented for thirteen-lined ground squirrels (*Ictidomys tridecemlineatus*), where higher population density increased the amount of overlap between conspecifics thus, increasing the incidence of aggressive encounters (Luna and Baird, 2004). As population density decreases, home range sizes tend to increase, and individuals adjust themselves so as to reduce overlap, especially at the outset of the breeding period for various terrestrial mammals (Lambin and Krebs, 1991; Agrestis-Erlinge et al., 1990; Priotto et al., 2002). In some species, population density interacts with kinship, as has been documented among bat-eared foxes (*Otocyon megalotis*), where overlap was most pronounced between related females in high density populations (Kamler, 2013).

Territoriality occurs through defence and/or dominance within territories (Michener, 1979), which has the potential to reduce an individual's fitness (Jaeger, 1981; Luna and Baird, 2004), as encounters with strangers (outside the colony or kin cluster in specific species) tend to involve agonistic interactions in ground squirrel species (Michener, 1983; Davies and Houston, 1984; Hare, 1994). Intraspecific competition occurs within species for food, shelter and access to mates, thus affecting interactions between conspecifics (Davies, 1978; Sandell, 1989), which can limit home range size and movements of individuals (Kubiak et al., 2017). Costs associated with territoriality can be mitigated via benefits that accrue via inclusive fitness, where related individuals are present (Hamilton, 1964) (discussed below) or through dear enemy recognition, where familiarity of neighbours reduces the costs of actively defending a territory, and the risk of injury implicit in such defence (Jaeger, 1981). The "Dear enemy" hypothesis predicts that an individual will avoid escalating aggressive encounters with frequently encountered distant-kin and/or non-kin neighbours, reducing energy expenditure and thus increasing the fitness of neighbouring individuals (Fisher, 1954; Wilson, 1975; Jaeger, 1981), though even with cooperation, individual distance is maintained (Wilson, 1975).

Ecological factors ultimately limit the movement and home range size of animals (Kubiak, 2017). In studies of ungulates, males and females spatially segregate when foraging, thereby reducing the risk of predation experienced by females with offspring (Main el al., 1996). Food abundance has a larger effect on Arctic ground squirrel (*Urocitellus parryii*) home range sizes than the presence of predators, suggesting that the benefits of obtaining additional food outweigh the energetic costs and enhanced risk of predation when preparing for hibernation (Hubbs and Boonstra, 1998). Food resources also affect socio-spatial organization among solitary foragers of the female grey mouse lemur (*Microcebus murinus*), causing females to cluster, while food resource patchiness causes female Madame Berth's mouse lemurs (*Microcebus berthae*) to disperse widely and reduce associations between conspecifics (Dammhahn and Kappeler, 2009). According to Dammhahn and Kappeler (2009), if territories are not actively defended by solitary females then competition over food with nearest neighbours occurs. A study done on grey red-backed voles (*Clethrionomys rufocanus)* manipulated food availability and found that reproductively active females reduced the size of their home range, clustered around the food supply and had highly overlapping home ranges. Reproductive males also had substantial home range overlap, but it decreased as the breeding season wound down (Ims, 1987).

Home range size and how species associate spatially and interact can be affected by an adaptive response to highly seasonal environments, thus affecting foraging and shelter accessibility (Harris and Leitner, 2005; Hoset et al., 2007). Female root voles (*Microtus oeconomus*) tend to reduce their overall home range size in winter compared to summer, although this trend was not observed for the core area (Hoset et al., 2007). Home range size of desert-dwelling giant kangaroo rat (*Dipodomys ingens*) males is dependent upon the onset of the breeding period, which is dependent upon the seasonality of the environment, while, female home range sizes remained relatively constant throughout the entire active season (Cooper and Randall, 2007). Thus, the ability to be socially flexible to adapt to varying environments provides fitness benefits (Randall, 1993).

Space use and kinship

Close association of kin has been documented across taxa (Fletcher and Michener, 1987; Hepper, 1991). The evaluation of socio-spatial organization among kin can provide insight into sociality within cooperative groups (Hare and Murie, 2007). Selective pressures, either environmental or physiological, can give rise to delayed dispersal and could lead to the retention of related individuals, typically females, within the natal area (Barash, 1989; Michener, 1983; Solomon, 2003; Greenwood, 1980). A philopatric group of females can increase their reproductive success and survival of offspring (Lambin and Krebs, 1993) through enhanced social tolerance, amicable behavioural interactions, territorial defense, cooperative breeding and the sharing of space (Michener, 1983; Hare and Murie, 2007). Beyond direct fitness benefits, however, individuals cooperating with genetic relatives within groups may enhance their indirect fitness through effects on the reproductive effort of related individuals. While once regarded the sine qua non of advanced sociality among ground squirrels (Holmes and Sherman, 1982), kin-biased sociality may represent an ancestral social state, that is first augmented, and then ultimately replaced, by societal cooperation and benefits that accrue outside the limits of close-kin (Hare, 2004).

Kin clustering has been repeatedly implicated as a factor influencing an animal's home range size. Kin discrimination leads to relaxed territorial aggression (Walls and Kenwood, 2001) and amicable interactions resulting in spatial clustering of kin (Hamilton, 1964). This trend is commonly documented among female mammals, e.g. prairie voles (*Microtus ochrogaster;* Keane et al., 2015), big-eared woodrat (*Neotoma macrotis*; Matocq, 2004)*,* banner-tailed kangaroo rats (*Dipodomys spectabilis;* Winters and Waser, 2003), woodchucks (*Marmota monax*; Keane et al., 2015), and California ground squirrels (*Otospermophilus beecheyi*;

Boellstorff and Owings, 1995). Although territoriality is commonplace among ground squirrels, social cooperation can be observed among familiar neighbouring conspecifics (Wilson, 1975; Sherman, 1980; Porter and Blaustein, 1989). Arctic ground squirrel home ranges overlapped more among close female kin than among non-close kin, while distant kin were treated similar to non-kin (McLean, 1982). The greater incidence of amicable interactions among close-kin reveals nepotism (McLean, 1982).

Study species and objectives

Few studies have focused on asocial species as a means of understanding the evolution of sociality (Smuts et al., 1987). Franklin's ground squirrels (*Poliocitellus franklinii*) are one of four ground squirrels that are considered to be relatively asocial (Armitage, 1981; Michener, 1983). More social ground squirrels postpone dispersal, enhancing survival of young (Wells and Van Vuren, 2018), however, Franklin's ground squirrels disperse early (Martin and Heske, 2005), and do not appear to suffer a higher risk of offspring mortality than other more social, parapatric species like Richardson's ground squirrels (*Urocitellus richardsonii*; Hare, unpublished data). Few field studies have been conducted on Franklin's ground squirrels, presumably owing to their elusive nature, which precludes any direct behavioural observations in the field (Sowls, 1948). Both Armitage, 1981 and Michener, 1983 originally classified Franklin's ground squirrels as relatively asocial due to their early sexual maturation, small size, early dispersal, agonistic nature, non-overlapping spatial organization, and the absence of burrow sharing. Most or all juvenile males disperse from their natal area, while females tend to remain philopatric, although some females may also disperse (Martin and Heske, 2005). However, there are limited data on the socio-spatial organization of Franklin's ground squirrels and what little primary literature exists presents contradictory results regarding the extent of adult Franklin's ground squirrels home range overlap. In apparent exception to the patterns noted by Armitage (1981), Michener (1983), and Martin and Heske (2005), Choromanski et al. (1989), reported extensive overlap of home ranges between same sex and opposite sex Franklin's ground squirrels. The paucity of field work on space use in Franklin's ground squirrels precludes a definitive asocial classification, and yet provides a unique opportunity for further study contributing to our understanding of ground squirrel sociality. Understanding the relationships between free-living individuals, their home ranges, and degree of philopatry will resolve the degree to which Franklin's ground squirrels are social, and determine whether or not their expression of sociality is predicated on kinship, as has been suggested for other ground squirrel species (Armitage, 1981; Michener, 1983).

In the present study, I documented spatial proximity, extent of overlap and size of home range and core area of Franklin's ground squirrels residing within populations inhabiting sites near Delta Marsh, Manitoba, Canada. I specifically quantified home range and core area size as well as home range and core area overlap, comparing males versus females, and yearlings versus adults for the overall active season, as well as within discrete periods (gestation, lactation, and post-weaning) of the annual reproductive cycle. Knowledge of home range and core area size, overlap and the association of free-ranging individuals is critical to understanding sociality (Cooper, 2007), and will provide novel insight into the sociality of Franklin's ground squirrels.

Materials and Methods

Study animal

Franklin's ground squirrels (*Poliocitellus franklinii*) are diurnal, semifossorial squirrels that range across the central United States following the Apsen Parkland ecotone northwestward through the Canadian prairie provinces of Manitoba, Saskatchewan and Alberta (Ostroff and Finck, 2003). Franklin's ground squirrels prefer tall grass prairie habitat, avoid grazed land, and tend to prefer marsh and forest edge, but can also be found along road and railroad roadbed edges (Ostroff and Finck, 2003). Currently, Franklin's ground squirrels are listed as "Least Concern" according to the International Union for Conservation of Nature (IUCN), based on their high abundance in local populations (Pergams et al. 2008). However, in certain areas in the southeastern extent of their range (i.e. Illinois, Indiana, Missouri, Wisconsin), they are considered vulnerable, threatened or endangered (Iowa Department of Natural Resources 2012, Illinois Endangered Species Board 2015, Indiana Department of Natural Resources 2013, Missouri Department of Natural Resources 2015, Wisconsin Department of Natural Resources 2014).

Franklin's ground squirrels are considered diurnal (Sowls, 1983; Choromanski-Norris, 1989) and spring body mass ranges from 320-400 grams, while in fall before entering hibernation, mass ranges from 500-900 grams (males tending to be larger) (Ostroff and Finck, 2003; Pero and Hare, 2017). Males enter hibernation earlier than females and hibernation begins around late July for males and late August for females, while juveniles in Manitoba populations remain above ground until the beginning of October (Sowls, 1948; Iverson and Turner, 1972). Franklin's ground squirrels typically exist at relatively low densities across their range (Hall, 1955), and among breeding yearlings and adults, females tend to outnumber males 2:1 (Pero and Hare, 2017). Males emerge from hibernation earlier than females by about one to two weeks (end of April in Manitoba) to establish breeding territories (Iverson and Turner, 1972).

Study site and subjects

During the active season of 2019, Franklin’s ground squirrels were studied from 01 May through 31 July at two field sites, Inkster (50°9’N, 98° 19’W) and Beach Ridge (50°11.3’N, 98°18’W) near Delta Marsh, Manitoba, Canada. The Inkster site is described in detail in Löve and Löve (1954), and was characterized as a mix of rural roadside, marsh edge, hayfields and deciduous forest habitat by Hare (2004). The Beach Ridge site lines the southern-most end of Lake Manitoba and comprised of a wooded sand ridge and marsh-adapted vegetation (Sowls, 1948).

During the summer field season, my two field assistants, myself and my advisor, James Hare, trapped and marked 54 animals (24 females and 30 males) between the two study sites. Franklin’s ground squirrels occupying those sites were captured using National or Tomahawk (Tomahawk Live Trap, Tomahawk, Wisconsin, USA) live-traps, baited with No Name™ peanut butter and rolled oats (Loblaw Companies Ltd., Brampton, ON, Canada). Traps were checked hourly to reduce the risk of heat shock. Upon each capture, weight (using a Pesola™ spring scale; Bar, Switzerland) to the nearest 5 grams, was recorded. As per methods from Murie and Harris (1982), breeding conditions of males and females were collected throughout the breeding season during each capture. Trapping occurred daily to assess breeding conditions and to determine parturition dates. Franklin’s ground squirrels had a permanent fish fingerling tag (Monel #1, National Band and Tag Co., Newport, Kentucky, USA) for individual identification attached through their right pinna. Their dorsal pelage was marked with hair dye (Clairol Hydrience 52S Pearl Black, Clairol Corp., Stamford, Connecticut, USA) in unique individual patterns for individual identification. Squirrels were subsequently released at point of capture after measurements and identification marks were applied.

Radiotracking

The deployment of radio-telemetry collars on squirrels was optimized to ensure quantification of space use by as many closely-related (known mother-offspring, sibling pairs) individuals as possible. Maternal relatedness was established from data collected in 2018. Juveniles had been trapped within three days of their emergence from their natal burrows. Of the 63 known juveniles which emerged from nest burrows of nine lactating females in 2018 on the Inkster site, 12 closely-related individuals (from four discrete female kin groups) constituting three adult females, seven yearling females and two yearling males, emerged from hibernation on the Inkster site in spring 2019. Twenty-four Holohil Systems Ltd. (Carp, ON) PD-2C VHF telemetry collars were deployed on squirrels overall including: 11 females (F) (five adults (A) and six yearlings (Y)) and 13 males (M) (seven adults (A) and six yearlings (Y)). Of these, three adult males resided on the Beach Ridge site, while the rest resided on the Inkster site. All Franklin's ground squirrels and burrow locations were obtained by locating collar-bearing squirrels with Telonics (Mesa, AZ) TR-4 telemetry receivers and Telonics RA-14K 2-element Yagi antennae. Transmitter collars were affixed around the squirrel's necks via a custom-fitted 200 x 4 mm nylon ToolBench™ zip-tie collar (Burnaby, BC C.N. DTSC Imports) covered with a 4.8 mm custom-fitted Tygon™ tube (Saint-Gobain North America, Valley Forge, PA). Squirrels were trapped weekly to check collar tension, and if collars were deemed too loose, or were tight to the point of causing excessive hair loss or abrading the squirrel's skin, they were removed and refitted. Squirrel locations were recorded using Garmin GPS 72 WAAS-corrected handheld GPS receivers (Garmin Ltd. Olathe, KS), for subsequent mapping and analysis (see below). Fixes were gathered to determine above ground space use and burrow locations. To quantify space use, each collared squirrel within the two sites was located above ground twice each day during morning (0800-1100 hours CDT), and afternoon (1500-1800 hours CDT) tracking sessions, to promote the independence of GPS fixes obtained for the same individual in the same day. To further ensure independence, we randomized the order of squirrels by randomly selecting individuals from a hat (separately for both sites) each time before radio-tracking sessions began within sites. Juveniles were not included in the study because they had not established their own home ranges and there was the risk of dispersal, potentially precluding the recovery of their telemetry collar. Squirrels that were detected above ground and that could unambiguously be identified by the dye mark on their dorsal pelage within each tracking session had their GPS location recorded without resorting to telemetry. Franklin's ground squirrel locations were grouped by unique phases (gestation, lactation and post-weaning) of their annual reproductive cycle. Females were considered to be in the gestation phase once 51% of the females on each site were observed to have a copulatory plug and/or evidence of copulation. Once 51% of females drastically dropped their weight, they were considered to be in the lactation phase. When 51% of juveniles appeared above ground from their burrows, females were considered to be in the post-weaning period. Breeding phase was only obtained for males, because males emerge prior to females. Males were considered to be in the breeding phase until 51% of the females on the same site had evidence of copulation, then males shifted to the gestation phase. Once 51% of females were lactating males entered the lactation phase and subsequently once 51% of females had juveniles emerge above ground then males shifted to the post-weaning phase.

Home range analysis

I derived data from two sites (Beach Ridge and Inkster) in the Delta Marsh area. I collared three adult males of unknown relatedness at the Beach Ridge site. The paucity of females at the Beach Ridge site and the absence of known relatives among those, precluded telemetry collaring any females at the Beach Ridge site. Therefore, data from males inhabiting this site were used for calculation of home range and core area size and overlap averages between males only, and omitted from subsequent statistical analysis, as the inclusion of data from this site would inflate variation in male home range and core area sizes, as well as male home range and core area overlap, without the benefit of complementary data from Beach Ridge females with which to account for site-specific effects. The Inkster site did, however, have females with known close-kin and contained about an equal number of males and females (see above) and thus was selected as the primary focus of my analysis.

Home range and core area estimates were measured in R statistical software (version 3.5.1, R Core Team 2018) with the package adehabitatHR (version 0.4.15; Calenge, 2017) using least-biased fixed kernel density estimators with least squares cross-validation (LSCV) (Kenward and Hodder, 1996; Seaman and Powell, 1996; Worton, 1989). I obtained more than the minimum number of points required to use fixed kernel density estimators (n > 30 locations) (Seaman and Powell, 1996) for each reproductive period for each collared squirrel. I calculated the 95% and 50% isopleths similarly using the kernel density function. The 95% isopleth was chosen because it omits extreme outliers, providing a commonly used estimate of an animal's overall home range (Worton, 1987). The 50% isopleth represents the core area of an animal's home range (Worton, 1987). Kernel density estimators have been favoured over minimum convex polygon (MCP), since MCP tends to be less sensitive, causing overestimation of home range sizes, while kernel density uses utilization densities (frequency that an individual occupies a particular space in time) (Worton, 1989). Some individuals (n= 3) disappeared over the course of data collection and were presumed to have been depredated. Where such incidents occurred early (fewer than 5 locations in a given reproductive period), I omitted data for those individuals. I assessed the data for normality via the Shapiro-Wilk normality test on the home range and core area data and found that the data constituting home range and core areas were unlikely to have been derived from a normal underlying population of measurements (Shapiro-Wilk, w= 0.038, $P = < 0.001$; reject the null hypothesis of normality). I thus performed a $\log_{10}$ transformation, of the location data underlying home range and core areas of all individuals, which resulted in those transformed data satisfying the assumption of normality (Shapiro-Wilk, w= 0.99, $P = 0.72$; accept the null hypothesis of normality). For the remaining individuals, size and overlap of the home range (95%) and core area (50%) averages (mean ± SE) were computed and compared for individuals of both sexes (male versus female) and age classes (adult versus yearling), both for the overall active season and by unique periods within the annual reproductive cycle (gestation, lactation, and post-weaning).

Statistical comparisons of home range size and overlap

I tested for effects of sex, age and period (gestation, lactation and post-weaning) within the annual reproductive cycle on home range and core area sizes, home range and core area overlap, and also tested for effects of sex or age class pooling all data for individuals across the 3 separate periods within the annual reproductive cycle. I first averaged the area overlap for each unique individual with other individuals by sex class and age class both overall and for individual periods. Averaging both reduced and smoothed the pseudoreplicated data in each model. I fit predictive models using linear mixed effects (LME) models from the nlme package (Bates, 2009; Pinheiro, 2020), from R software (version 1.2.5019, R Development Core 2019) to assess the relationship among sex or age and period within the annual reproductive cycle with squirrel individuals as a random factor to account for multiple measurements across periods. I also fit predictive models using linear models from R software (version 1.2.5019, R Development Core 2019) to assess the relationship among sex or age and overall home range size and overlap calculated across the whole summer. LME models paired with function VIF in package car were used to assess multicollinearity. I then presented the results in a two-way ANOVA table using Satterthwaite's degrees of freedom. All models were considered statistically significant where $p < 0.05$. Lastly, Tukey's Honest Significant Difference (HSD) post-hoc tests were employed to test all pairwise comparisons between multiple groups (reproductive periods: gestation, lactation, and post-weaning) where an overall effect of an independent variable was detected (Tukey, 1949). The Tukey's HSD post-hoc tests utilized the single step method based on the t-distribution of the model and adjusted p-values sequentially (Hothorn, 2020).

Overlap of home ranges and core areas were examined for all possible sex pair combinations (F-F, F-M, M-M) and separately for all possible age pair combinations (A-A, A-Y, Y-Y). Total overlap was calculated in square meters as the intersection between a pair of individual's home ranges or their core areas. I fit predictive models using linear models from R software (version 1.2.5019, R Development Core 2019) to assess the relationship among sex or age pairs and overall home range and core area overlap calculated across the entire active season. To test for any effect of sex or age class on the likelihood of overlap within each period of the annual reproductive cycle, I fit predictive models using linear mixed effects (LME) models using the nlme package and function, lme (Pinheiro et al. 2020) from R software (version 1.2.5019, R

Development Core 2019). LME models were used to control for psuedoreplicated data paired with function VIF in package car were used to assess for multicollinearity. I then presented the results in a two-way ANOVA table using the Satterthwaite's degrees of freedom method (method used for estimating the degrees of freedom if using LME models). Lastly, Tukey's HSD post-hoc tests were employed to test all pairwise comparisons between multiple groups (reproductive periods: gestation, lactation, and post-weaning, and all possible sex and age pair combinations) where an overall effect of an independent variable was detected (Tukey, 1949). The Tukey's HSD post-hoc tests utilized the single step method based on the t-distribution of the model and adjusted p-values sequentially (Hothorn, 2020).

Results

Male-Female differences in home range and core area sizes and overlap

Home range (innermost 95% kernel density area) and core area (innermost 50% kernel density area) sizes of males (n = 10) and females (n = 11) throughout the overall active season did not differ at the Inkster site (Table 2.1; home range size, two-way ANOVA, $F_{1,19} = 0.35$, p = 0.56 and core area size, $F_{1,19} = 0.34$, p = 0.57). The absence of data for females at the Beach Ridge site precluded an assessment of inter-site variability in female space use. Average core area sizes of males on both sites, remained similar throughout the overall active season (Table 2.1). Home range and core areas of most individuals at the Inkster and Beach Ridge site were associated with roadways (Figure 2.1).

The interaction between sex and phase did not affect home range (two-way ANOVA, $F_{2,37} = 2.68$, p = 0.1) and core area sizes (two-way ANOVA, $F_{2,37} = 0.08$, p = 0.5) and therefore it was removed from the model. The absence of any difference between male and female home range and core area size at the Inkster site persisted when home range and core area sizes were considered by period within the annual reproductive cycle (Figure 2.2: home range size, two-way ANOVA, $F_{1,19} = 1.37$, $p = 0.26$ and core area size, $F_{1,22} = 0.88$, $p = 0.36$). Seasonal phase had significant effects on home range (two-way ANOVA, $F_{2,86} = 13.61$, $p = < 0.001$) and core area size (two-way ANOVA, $F_{2,66} = 6.55$, $p = 0.002$), however, post-hoc comparisons using Tukey's HSD tests revealed that among all reproductive periods, only the post-weaning period differed from the other phases of the annual reproductive cycle at the Inkster site for the home range (post-weaning-gestation, $z = 3.87$, $p = 0.0003$, post-weaning-lactation, $z = 5.1$, $p = <0.001$) and the core area (post-weaning-gestation, $z = 3.45$, $p = 0.002$, post-weaning-lactation, $z = 2.92$, $p = 0.01$). While, home range and core area size were not significantly different between the gestation and lactation period (home range, $z = -1.57$, $p = 0.26$ and core area, $z = 0.09$, $p = 0.99$), mean home range and core area sizes were largest in the post-weaning period and smallest during the gestation period for squirrels on the Inkster site (Table 2.2). However, among Franklin's ground squirrels on the Beach Ridge site, both home range and core area sizes were at their maximum during the breeding period and smallest during the post-weaning period (Table 2.2).

Home range overlap between males and females did not differ throughout the overall active season at the Inkster site (home range, two-way ANOVA, $F_{2,21} = 0.71$, $p = 0.50$), while core area overlap did differ throughout the overall active season (core area, two-way ANOVA, $F_{2,18} = 6.12$, $p = 0.009$). However, mean home range and core area overlap was largest for male-female pairs and smallest for female-female pairs at the Inkster site (Table 2.3).

When distinct periods within the annual reproductive cycle are accounted for in the analysis, a significant difference was detected in home range overlap between males and females overall at the Inkster site (Figure 2.3: two-way ANOVA, $F_{2,45} = 6.01$, $p = 0.005$). However, core area overlap did not differ among the three possible sex pairs (two-way ANOVA, $F_{2,44} = 0.99$, $p = 0.38$). Mean home range and core area overlap between males at the Beach Ridge site was largest during the breeding period and smallest during the post-weaning period, while at the Inkster site male-male overlap was largest during the post-weaning period (Table 2.4). Female-female home range and core area overlap at the Inkster site was smallest during the post-weaning period (Table 2.4).

When controlling for sex pairs, seasonal period had a significant effect on both home range (two-way ANOVA, $F_{2,86} = 13.61$, $p = < 0.001$) and core area overlap (two-way ANOVA, $F_{2,66} = 6.55$, $p = 0.002$), however, post-hoc comparisons using Tukey's HSD tests revealed that among all reproductive periods, only the post-weaning period differed from the other phases of the annual reproductive cycle at the Inkster site for the home range (post-weaning-gestation, $z = 3.87$, $p = 0.0003$, post-weaning-lactation, $z = 5.1$, $p = <0.001$) and the core area (post-weaning-gestation, $z = 3.45$, $p = 0.002$, post-weaning-lactation, $z = 2.92$, $p = 0.01$) overlaps (Figure 2.4). Home range and core area overlap did not differ between the gestation and lactation period (home range, $z =-1.57$, $p = 0.26$ and core area, $z = 0.09$, $p = 0.99$).

Age differences in home range and core area sizes and overlap

Home range and core area sizes did not differ between adults (n = 9) and yearlings (n = 12) throughout the overall active season at the Inkster site (Table 2.5; home range size, two-way ANOVA, $F_{1,19} = 0.32$, $p = 0.58$ and core area size, $F_{1,19} = 0.365$, $p = 0.56$). Adults at the Beach Ridge site had mean home range and core area sizes larger than adult males on the Inkster site (Table 2.5; two-tailed t-test, $t_{25} = 3.73$, $p = < 0.001$). The absence of data for yearlings at the Beach Ridge site precluded an assessment of inter-site variability in yearling space use.

The absence of any significant difference in home range and core area size between adults and yearlings on the Inkster site persisted when periods within the annual reproductive cycle were accounted for in the analysis (Table 2.6; Figure 2.6: home range size, two-way ANOVA, $F_{1,19} = 4.81$, $p = 0.19$ and core area size, $F_{1,19} = 4.5$, $p = 0.19$). Among adult Franklin's ground squirrel males on the Beach Ridge site, mean home range and core area sizes were largest during the breeding period and smallest during the post-weaning period (Table 2.6).

When controlling for age, home range and core area sizes differed significantly among the different periods of the reproductive cycle (home range size, two-way ANOVA, $F_{2,31} = 5.37$, $p = 0.01$ and core area size, $F_{2,31} = 5.55$, $p = 0.008$), however, post-hoc comparisons using Tukey's HSD tests revealed that among all reproductive periods, only the post-weaning period differed from the other phases of the annual reproductive cycle at the Inkster site for home range (post-weaning-gestation, $z = 2.9$, $p = 0.01$, post-weaning-lactation, $z = 2.88$, $p = 0.01$) and core area sizes (post-weaning-gestation, $z = 2.96$, $p = 0.009$, post-weaning-lactation, $z = 2.9$, $p = 0.01$). Home range and core area size did not differ between the gestation and lactation period (home range, $z = -0.04$, $p = 0.99$ and core area, $z = -0.11$, $p = 0.99$).

Mean home range and core area overlap was greatest for adult-yearling pairs and lowest for adult-adult pairs (Table 2.7), although the differences were not significant among any pair (adult-adult, adult-yearling or yearling-yearling) over the active season at the Inkster site (home range, two-way ANOVA, $F_{2,24} = 1.72$, $p = 0.20$, core area, $F_{2,22} = 2.18$, $p = 0.14$).

Consideration of age class overlap by period within the annual reproductive cycle also revealed no significant difference in home range or core area overlap among all possible age class pairs at the Inkster site (Figure 2.7: home range, two-way ANOVA, $F_{2,79} = 2.06$, $p = 0.08$; core area, $F_{2,68} = 1.16$, $p = 0.32$). Despite those differences not achieving statistical significance, trends suggest that mean home range and core area overlap between adult-adult pairs was maximal during the breeding period and smallest during the post-weaning period at the Beach Ridge site. Similarly, adult-adult, adult-yearling and yearling-yearling home range and core area overlap were greatest during the breeding period at the Inkster site (Table 2.8).

While controlling for age class, seasonal phase had significant effects on home range (Figure 2.8: two-way ANOVA, $F_{2,88} = 7.74$, $p = < 0.001$) and core area overlap (Figure 2.8: two-way ANOVA, $F_{2,66} = 5.17$, $p = 0.008$). However, post-hoc comparisons revealed that only overlap during the post-weaning period differed from the other phases of the annual reproductive cycle at the Inkster site for home range (post-weaning-gestation, $z = 2.83$, $p = 0.01$, post-weaning-lactation, $z = 3.86$, $p = < 0.001$) and core area (post-weaning-gestation, $z = 3.05$, $p = 0.006$, post-weaning-lactation, $z = 2.71$, $p = 0.02$). Home range and core area overlap did not differ between the gestation and lactation period (home range, $z = -1.28$, $p = 0.4$ and core area, gestation-lactation, $z = -0.045$, $p = 0.99$).

Interactions

No interactions between sex and age were detected for either home range (two-way ANOVA, $F_{4,16} = 0.48$, $p = 0.75$) or core area size (two-way ANOVA, $F_{4,16} = 0.70$, $p = 0.70$). There were, however, statistically significant interactions between sex and age class on overlaps of home ranges (two-way ANOVA, $F_{5,79} = 5.31$, $p = 0.02$) and core areas (two-way ANOVA, $F_{5,50} = 3.05$, < 0.001; Table 2.9).

Discussion

Among Franklin's ground squirrels inhabiting the Inkster site, sex did not significantly influence either home range or core area size either during the overall active season or within distinct periods within the annual reproductive cycle (gestation, lactation and post-weaning). While the sample size was small, trends suggest that average overall home range and core area size for females were, however, consistently larger than those of males at the Inkster site, which is not consistent with sex-differences documented in other rodent species (Ostfeld et al., 1985, Ribble and Stanley, 1998; Steinmann et al., 2005; Cooper and Randall, 2007). This difference may by attributable to the fact that the vast majority of location data was recorded after the breeding period had ended, coincident with reduced male home range size during the gestation and lactation periods as the quest for estrus females declines (Ostfeld and Heske, 1993; Harris and Leitner, 2005; Nunes, 2014). Average home range sizes were larger for males at the Beach Ridge site than males at the Inkster site, while average core area sizes remained relatively similar. This may represent a result of increases in overall home range size with decreasing population density, reducing interference competition in the face of prospective mate scarcity, or with more widely dispersed resources (Slade and Balph, 1974; Boag and Murie, 1981; Nunes, 1997). It may also be a product of the relative paucity of estrus females on the Beach Ridge site in the spring of 2019, causing males to expand their ranges in searching for reproductively active females. It remains possible, however, that the documented inter-site difference in home range size may be an artefact of small sample size. Further research documenting inter-site variation in home range size and the factors controlling it, is warranted. Age class had no effect on home range and core area size either during the overall active season or within the distinct periods defining the annual reproductive cycle, though there was limited sample size, trends suggest that yearlings often appeared to maintain larger mean home range and core area sizes than adults.

Home range and core area size by reproductive phase

Home range and core area size was largest during the post-weaning period and smallest during the gestation period at the Inkster site. Males at the Beach Ridge site had their largest average home range and core areas occur during the breeding period and smallest during the post-weaning period. For both age classes, home ranges and core areas during the post-weaning period were significantly larger than those during the gestation and lactation periods. Sex and age class differences in the size of home range and core areas are attributable to reproductive strategies and mating systems of a species (Swihart and Slade, 1989), therefore, it is important to interpret male and female home ranges across age classes separately to account for these differential strategies (Priotto et al., 2002, Bleske-Rechek and Buss, 2001). Yearling female Franklin’s ground squirrels typically breed later than adults, consistent with age class differences in female reproductive phenology for other ground squirrel species (Murie and Harris, 1982). Home range and core areas increasing during the post-weaning period may reflect the need for individuals to search for higher quality food before entering hibernation and/or searching for suitable hibernacula (Ostfeld et al., 1985). Comparative data suggest that males of other ground squirrel species maintain their largest home range size during the breeding period so as to enhance the probability of locating mates and increasing territory size to encompass more breeding females (Michener, 1983; Harris and Leitner, 2005; Cooper and Randall, 2007). For females, range expansion during the post-weaning phase may be attributable to the need for females to recoup the high energy demands associated with reproduction (Harris and Leitner, 2005, Rubach et al., 2016; Pero and Hare, 2017). Female Mojave ground squirrels (*Xerospermophilus mohavensis*), like many other ground squirrel species (Dunford, 1977; Michener. 1979; Hoogland 1981; Balph, 1984; Ostfeld et al., 1985), maximize their home range sizes during the post-weaning phase, as reported here for female Franklin's ground squirrels. Empirical studies of Uinta (Slade and Balph, 1974), Columbian ground squirrels (Festa-Bianchet, 1982; Betts, 1991) and Richardson's ground squirrels (Michener, 1979) have revealed that female behaviour changes most drastically during lactation, prompting changes, such as the reduction of home range size during those periods. Female Franklin's ground squirrels reduced their home range and core area sizes during gestation and lactation consistent with range reductions during these periods documented for other rodent species (Festa-Bianchet, 1982; Michener, 1983). Female Richardson's ground squirrel overall home range size decreased the most during gestation and lactation presumably to protect their young from infanticidal conspecifics (Michener, 1979). Among Columbian ground squirrels, females tended to stay near their burrow and maintain reciprocal avoidance instead of aggression from the breeding period to the beginning of the post-weaning period (Boag and Murie, 1981; Festa-Bianchet and Boag, 1982)

Home range and core area overlap

Male-Male home range overlapped to a greater extent than any other sex pair throughout the overall active season, suggesting that no individual male had exclusive access to any one female. This is consistent with results for home range overlap among Richardson's ground squirrels reported by Michener (1979). Home range and core area overlap were reduced among male Franklin's ground squirrels during female gestation and lactation relative to those measures of space use during the breeding and post-weaning phases on the Inkster site. Such results may reflect a shift in male focus to optimizing the accrual of food resources rather than actively searching for mates as opportunities for reproduction disappear (Ims, 1987; 1988; Priotto et al., 2002). This is characteristic of polygynous rodent societies in which females maintain exclusive core areas and male home ranges encompass broad overlapping territories of many females (Ostfeld and Heske, 1993), resulting in extensive male-male spatial overlap. Female golden-mantled ground squirrel home ranges overlapped, but overlap did not occur in core areas, suggesting the expression of female territoriality (Jesmer et al., 2011). My data similarly suggest that female Franklin's ground squirrels limited overlap within the 50% core area among conspecifics. Female-female overlap was less pronounced among females than for other sex pairs both during the overall active season and by distinct periods within the annual reproductive cycle. This indicates that any element of sociality in Franklin's ground squirrels does not involve selective association among females, as is commonly reported for other asocial ground squirrel species (Armitage, 1981, Michener, 1983). Home range and core area overlap between adults and yearlings were not significant, though average home range and core area overlap was greatest between adults and yearlings during the overall active season. Adult female Columbian ground squirrels chased other adult females the most when those females intruded into a female's core area, suggesting that adult females are likely to be infanticidal (Betts, 1991). Here, home range and core area overlap was most reduced during the lactation and gestation period across both age classes. Female Franklin's ground squirrels' limited sharing of core areas may reflect the need to protect juveniles from other infanticidal females, though there is no evidence of infanticide for Franklin's ground squirrels.

Factors affecting home range size

Selective pressures, such as ecological and life-history factors affect the socio-spatial organization of a species, leading to group cooperation in which fitness benefits are maximized (Sandell, 1989; Kubiak et al., 2017). Human modified environments can have major effects on home range size and degree of overlap. Habitat fragmentation attributable to agriculture, roads and railways, leave behind remnants of suitable habitat affecting food distribution, which in turn restricts movement, reduces the colonization of habitat, changes home range size, shape, and degree of overlap (Kozakiewicz, 1993). Franklin's ground squirrel home ranges and core areas depicted in the kernel density maps are associated with roads, which can cause increased risk of predation and higher energetic costs. This trend was also evident in drylands vesper mice (*Calomys musculinus*) where home ranges were narrowed due to limiting space, extending foraging trips linearly to ensure adequate food intake (Sommaro, 2010). Long foraging trips may increase the risk of predation as well as increasing energetic costs (Banks et al., 2000). These factors are major considerations when analyzing social organization among species and are crucial in designing conservation management plans.

Limitations

While my results represent the most comprehensive documentation of Franklin’s ground squirrel home range and core area size and overlap complied to date, certain limitations remain. First, limited sample size may have affected these results. Second, home ranges vary annually, and thus ideally require documentation over multiple years. Third, the general trend toward females maintaining larger home ranges and core areas than males may be dependent on the fact that I was not able to include location data for females during the breeding season. Among the squirrels at the Beach Ridge site, females emerged from hibernation later than in past seasons (Hare, unpublished data). This may explain why male home range sizes were largest during the breeding and through the gestation period as they continued to search for estrus females.

Asocial species

These data support the assertion that Franklin’s ground squirrels are, in fact, relatively asocial by maintaining territoriality through intolerance of intrusions into the core area by conspecifics. This suggests that Franklin’s ground squirrels do not conform to the pattern of female philopatry, thus do not form female kin clusters that are commonly observed among other ground squirrel species (Michener, 1983).

Conclusions

Sex and age class did not affect home range and core area sizes. Male-male overlap was greatest, while female-female overlap was smallest. For both male and female yearlings and adults, home range and core area sizes, as well as overlap of those, were maximal during the post-weaning period. Limited core area overlap among this species reveals intolerant behaviour toward conspecifics. These results, along with those of Armitage (1981) and Michener (1983), provide further evidence that Franklin's ground squirrels are relatively asocial.

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Table 2.1. Summary of home range and core area sizes (mean ± SE m^2) for male ($\mathrm{n}_{\mathrm{male}}$= 10) and female ($\mathrm{n}_{\mathrm{female}}$ = 11) Franklin's ground squirrels at the Inkster and Beach Ridge ($\mathrm{n}_{\mathrm{male}}$= 3) sites over their entire active season.

	Inkster		**Beach Ridge**	
	Home range	Core Area	Home range	Core Area
Sex	$\bar{X} \pm SE$	$\bar{X} \pm SE$	$\bar{X} \pm SE$	$\bar{X} \pm SE$
Females	25494 ± 16062.5	3272 ± 2028.3	NA ± NA	NA ± NA
Males	15813 ± 3401.3	2064 ± 486.3	44377 ± 20412.8	3152 ± 797.6

Note: There were no comparable females on the Beach Ridge site.

Table 2.2. Summary of home range and core area sizes (mean ± SE m^2) for male (n_{male}= 10) and female (n_{female} = 11) Franklin's ground squirrels at the Inkster site and Beach Ridge (n_{male}= 3) sites throughout each phase of their annual reproductive cycle.

			Home Range	Core Area
Site	**Group**	**Phase**	$\bar{X} \pm SE$	$\bar{X} \pm SE$
Beach Ridge	Males	Breeding	29636 ± 6516.0	4396 ± 619.4
		Gestation	33756 ± 16505.3	3806 ± 1480.7
		Lactation	15937 ± 1773.4	1649 ± 420.0
		Post-weaning	9092 ± 6007.6	1547 ± 1031.0
Inkster	Males	Breeding	34554 ± 26520.0	7315 ± 5448.5
		Gestation	8320 ± 1625.3	1375 ± 254.3
		Lactation	10461 ± 3585.0	1643 ± 541.2
		Post-weaning	72082 ± 31714.9	15537 ± 6859.0
Inkster	Females	Gestation	7369 ± 3295.1	1305 ± 698.9
		Lactation	10539 ± 2888.1	1463 ± 351.3
		Post-weaning	24865 ± 20504.0	5606 ± 4850.4

Notes: There were no comparable females on the Beach Ridge site. There were no comparable data for breeding home range size for females. Breeding phase of males was used for mean comparisons only and not for statistical analysis.

Table 2.3. Summary of home range and core area overlaps (mean ± SE m^2) for male (n_{male}= 10) and female (n_{female} = 11) Franklin's ground squirrels at the Inkster and Beach Ridge (n_{male}= 3) sites over their entire active season.

		Home Range			Core Area		
Group		$\bar{X} \pm SE$			$\bar{X} \pm SE$		
Beach Ridge	Male - Male	6043	±	1533.0	118	±	< 0.001
			±				
Inkster	Male - Male	2740	±	293.3	344	±	73.0
	Male - Female	2785	±	349.5	357	±	50.0
	Female - Female	2362	±	422.0	210	±	38.7

Note: There were no comparable females on the Beach Ridge site.

Table 2.4. Summary of home range and core area overlaps (mean ± SE m^2) for male (n_{male}= 10) and female (n_{female} = 11) Franklin's ground squirrels at the Inkster and Beach Ridge (n_{males}= 3) sites throughout each phase of their annual reproductive cycle.

Site	Group	Phase	Home Range $\bar{X} \pm SE$			Core Area $\bar{X} \pm SE$		
Beach Ridge	Male-Male	Breeding	4968	±	268.3	107	±	19.1
		Gestation	3488	±	1694.9	711	±	< 0.001
		Lactation	1052	±	537.6	0	±	0.0
		Post-weaning	72.0	±	< 0.001	0	±	0.0
Inkster	Male-Male	Breeding	9123	±	1009.2	1626	±	299.1
		Gestation	2330	±	215.7	277	±	35.4
		Lactation	1516	±	257.3	521	±	337.7
		Post-weaning	11183	±	3043.1	1137	±	540.6
Inkster	Male-Female	Gestation	12123	±	157.5	246	±	22.6
		Lactation	1220	±	201.3	168	±	32.7
		Post-weaning	3991	±	613.8	1137	±	540.6
Inkster	Female-Female	Gestation	1285	±	186.7	145	±	22.5
		Lactation	504	±	66.0	168	±	32.7
		Post-weaning	294	±	46.8	6.5	±	< 0.001

Notes: There were no comparable females on the Beach Ridge site. There was no breeding phase recorded for females.

Table 2.5. Summary of home range and core area sizes (mean ± SE m^2) for adult (n_{adult}= 9) and yearling ($n_{yearling}$ = 12) Franklin's ground squirrels at the Inkster and Beach Ridge (n_{adult}= 3) sites over their entire active season.

	Inkster		**Beach Ridge**	
	Home Range $\bar{X} \pm SE$	Core Area $\bar{X} \pm SE$	Home Range $\bar{X} \pm SE$	Core Area $\bar{X} \pm S E$
Age				
Adult	13224 ± 4397.2	1738 ± 672.4	44377 ± 20412.8	3152 ± 797.6
Yearling	34646 ± 25921.7	4455 ± 3268.8	NA	NA

Note: There were no comparable yearlings on the Beach Ridge site.

Table 2.6. Summary of home range and core area sizes (mean ± SE m^2) for adult (n_{adult}= 9) and yearling ($n_{yearling}$ = 12) Franklin's ground squirrels at the Inkster site and Beach Ridge (n_{adult}= 3) sites throughout each phase of their annual reproductive cycle.

			Home Range			**Core Area**		
			$\bar{X} \pm SE$			$\bar{X} \pm SE$		
Site	**Group**	**Phase**						
Beach Ridge	Adults	Breeding	29636	±	6516.0	4396	±	619.4
		Gestation	33756	±	16505.3	3806	±	1480.7
		Lactation	15937	±	1773.4	1649	±	420.0
		Post-weaning	9092	±	6007.6	1547	±	1031.0
Inkster	Adults	Breeding	56445	±	66314	11924	±	13488
		Gestation	4751	±	1129.0	905	±	237.7
		Lactation	5212	±	2016.0	1018	±	439.6
		Post-weaning	16049	±	10394.1	3516	±	2377.4
Inkster	Yearlings	Breeding	12663	±	3932.0	2706	±	492.0
		Gestation	6958	±	2216.4	1503	±	523.7
		Lactation	7782	±	1513.5	1418	±	276.6
		Post-weaning	61540	±	26612.0	14008	±	6056.7

Notes: There were no comparable yearlings on the Beach Ridge site.

Table 2.7. Summary of home range and core area overlaps (mean ± SE m^2) for adult (n_{adult}= 9) and yearling ($n_{yearling}$ = 12) Franklin's ground squirrels at the Inkster and Beach Ridge (n_{adult}= 3) sites over their entire active season.

Site	Group	Home Range $\bar{X} \pm SE$			Core Area $\bar{X} \pm SE$		
Beach Ridge	Adult - Adult	3694	±	1048.0	160	±	22.2
Inkster	Adult - Adult	2312	±	393.5	290	±	60.9
	Yearling - Yearling	2461	±	321.0	244	±	48.2
	Adult - Yearling	2946	±	356.0	377	±	68.8

Note: There were no comparable yearlings on the Beach Ridge site.

Table 2.8. Summary of home range and core area overlaps (mean ± SE m^2) for adult (n_{adult}= 9) and yearling ($n_{yearling}$ = 12) Franklin's ground squirrels at the Inkster and Beach Ridge (n_{adult}= 3) sites throughout each phase of their annual reproductive cycle. The breeding phase was only included for males.

			Home Range	Core Area
			$\bar{X} \pm SE$	$\bar{X} \pm SE$
Site	**Group**	**Phase**		
Beach Ridge	Adult- Adult	Breeding	4968 ± 268.3	107 ± 19.1
		Gestation	3488 ± 1694.9	711 ± < 0.001
		Lactation	1052 ± 537.6	0 ± 0.0
		Post-weaning	72.0 ± < 0.001	0 ± 0.0
Inkster	Adult - Adult	Breeding	8581 ± 648.9	1379 ± 672.0
		Gestation	1746 ± 126.3	198 ± 21.8
		Lactation	834 ± 103.3	103 ± 40.1
		Post-weaning	6496 ± 1632.0	928 ± 314.2
Inkster	Adult - Yearling	Breeding	8581 ± 648.9	1474 ± 341.3
		Gestation	1909 ± 118.0	218 ± 17.5
		Lactation	1202 ± 136.0	212 ± 56.8
		Post-weaning	6120 ± 1242	928 ± 247.7

Notes: There were no comparable yearlings on the Beach Ridge site.

Table 2.9. Table depicts VIF numbers that determine whether collinearity is occurring within the model.

Model	**Interaction**	**Tolerance**	**VIF**
Home range size	Sex	1.1	1.3
	Age	1.0	1.3
Core area size	Sex	1.1	1.3
	Age	1.0	1.3
Home range overlap	Pair-sex	2.1	20.2
	Pair-age	1.8	11.3
Core area overlap	Pair-sex	1.0	1.0
	Pair-age	1.0	1.0

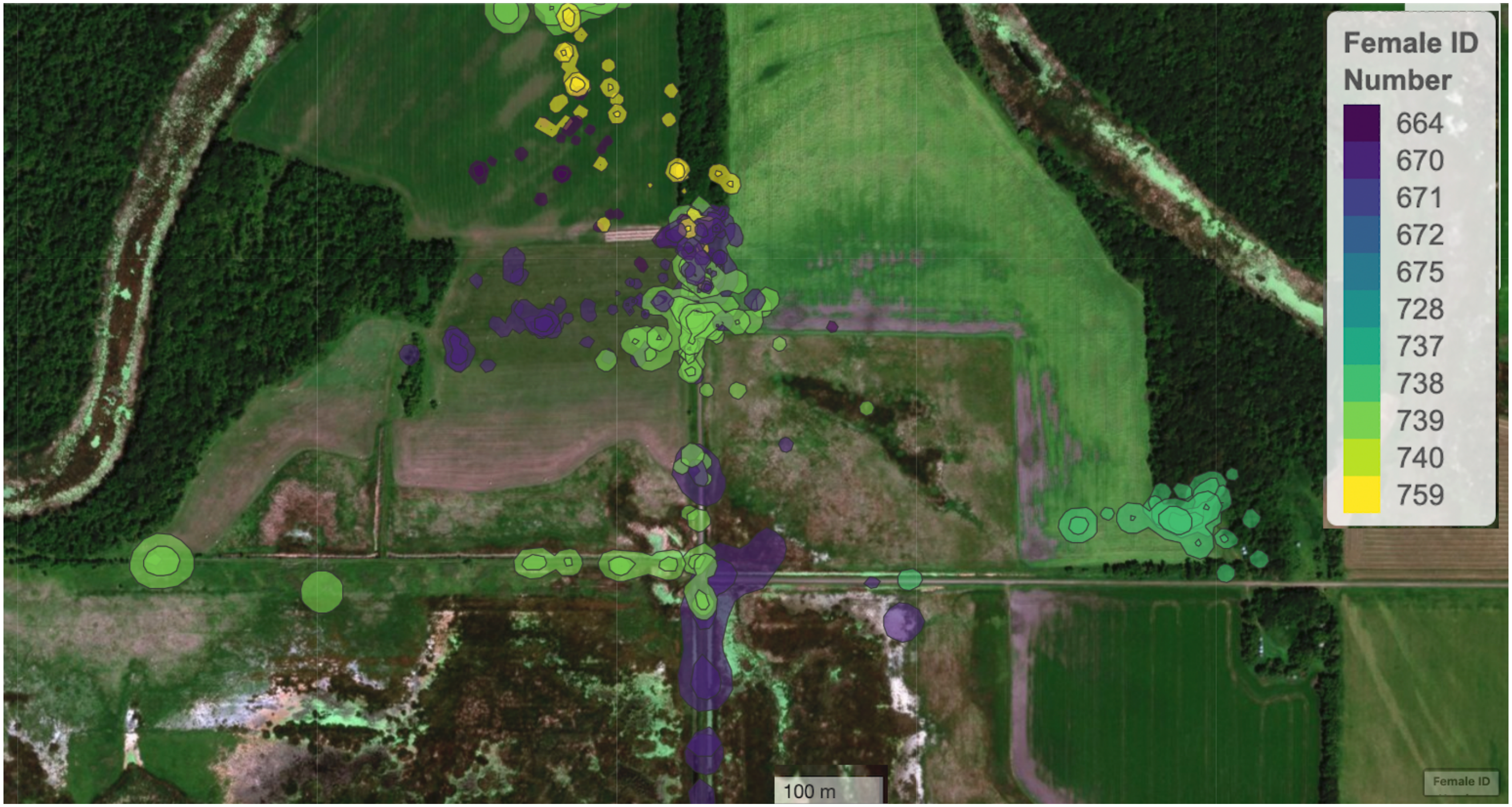

Figure 2.1.A. Map representing home range (innermost 95% kernel density area) and core (innermost 50% kernel density area) areas calculated with kernel density estimators for females (n = 11) on the Inkster site organized by female ID number.

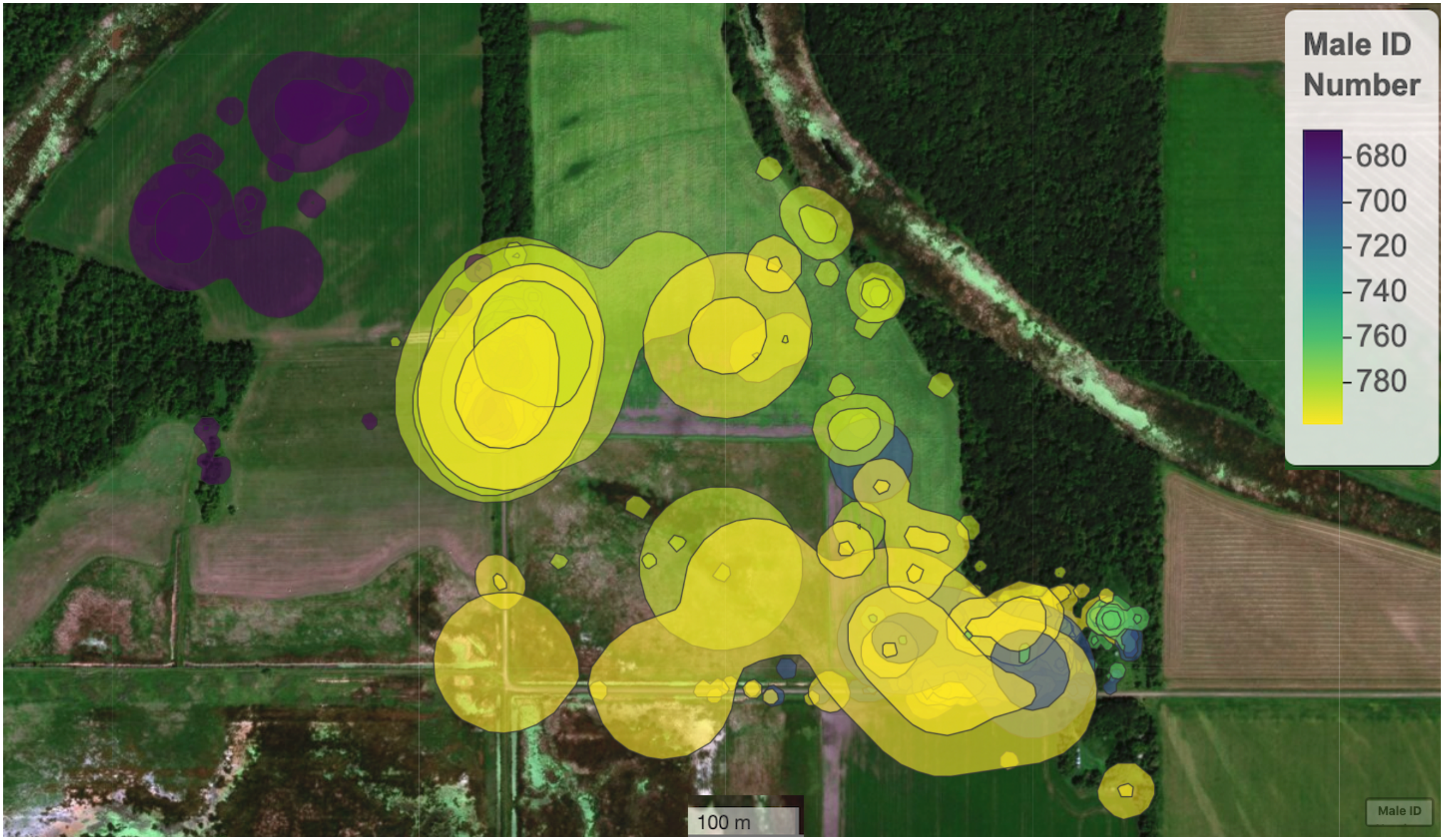

Figure 2.1.B. Map representing home range (innermost 95% kernel density area) and core (innermost 50% kernel density area) areas calculated with kernel density estimators for males (n = 10) on the Inkster site, organized by male ID number.

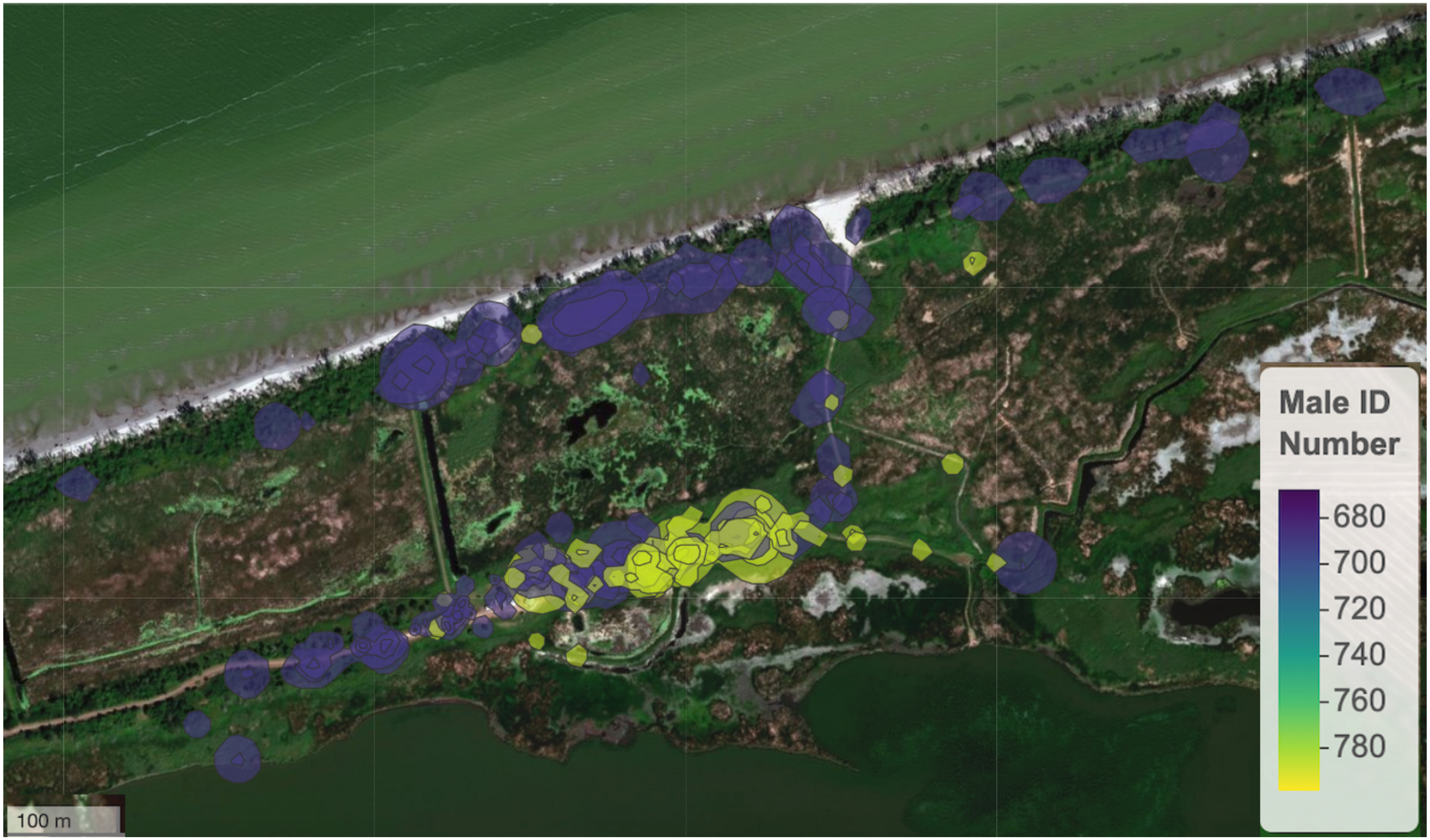

Figure 2.1.C. Map representing home range (innermost 95% kernel density area) and core (innermost 50% kernel density area) areas calculated with kernel density estimators for males (n = 3) on the Inkster site, organized by male ID number.

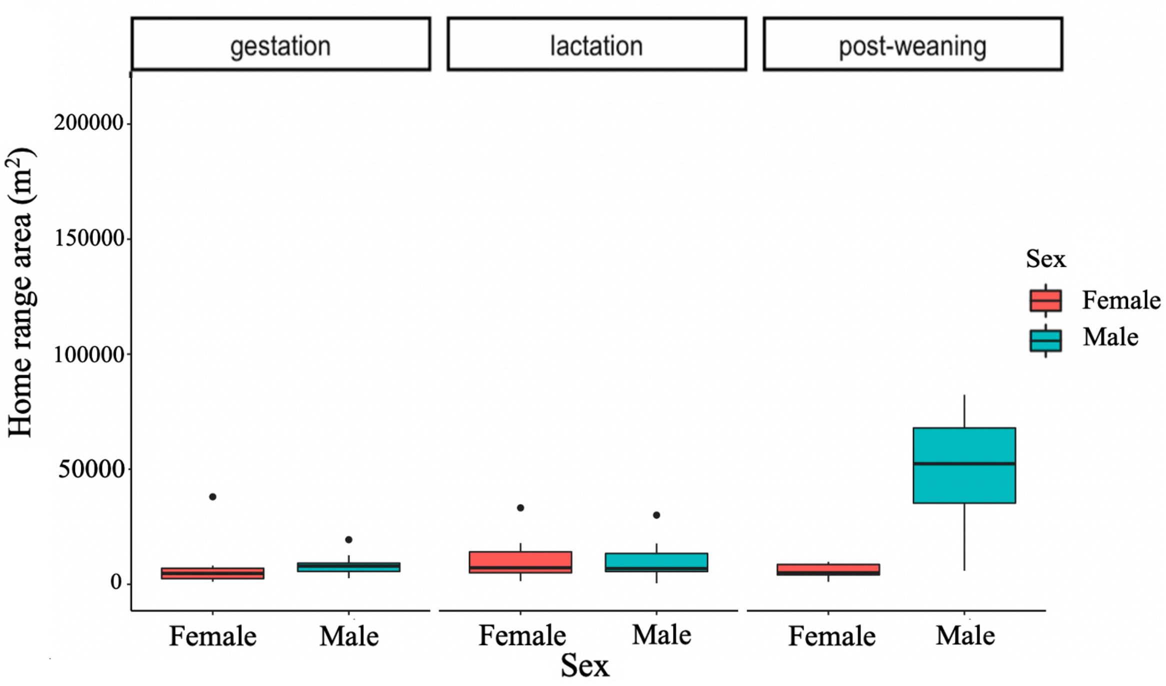

Figure 2.2.A. Comparison of the spatial distribution of home range size between sex classes ($n_{male} = 10$, $n_{female} = 11$) in m^2 for the 95% areas distributed by reproductive phase on the Inkster site. ANOVA tests reveal that the effect of sex did not significantly impact the size of home ranges (two-way ANOVA, $F_{1,19} = 1.37$, $p = 0.26$). The bold middle line is the median, the edges of the boxes represent the upper and lower quartiles, while the whiskers represent the minimum and maximum area points. Outliers are represented as individual data points.

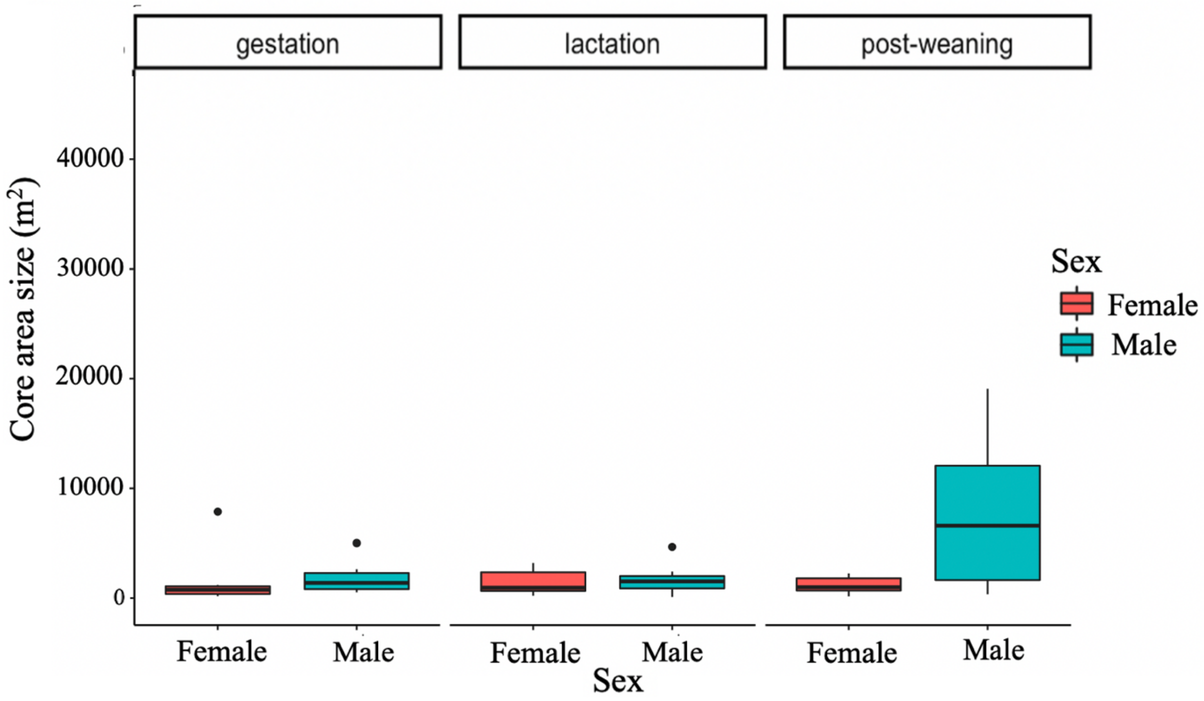

Figure 2.2.B. Comparison of the spatial distribution of home range size between sex classes ($n_{male} = 10$, $n_{female} = 11$) in m^2 for the 50% areas distributed by reproductive phase on the Inkster site. ANOVA tests reveal that the effect of sex did not significantly impact the size of home ranges (two-way ANOVA, $F_{1,22} = 0.88$, $p = 0.36$). The bold middle line is the median, the edges of the boxes represent the upper and lower quartiles, while the whiskers represent the minimum and maximum area points. Outliers are represented as individual data points.

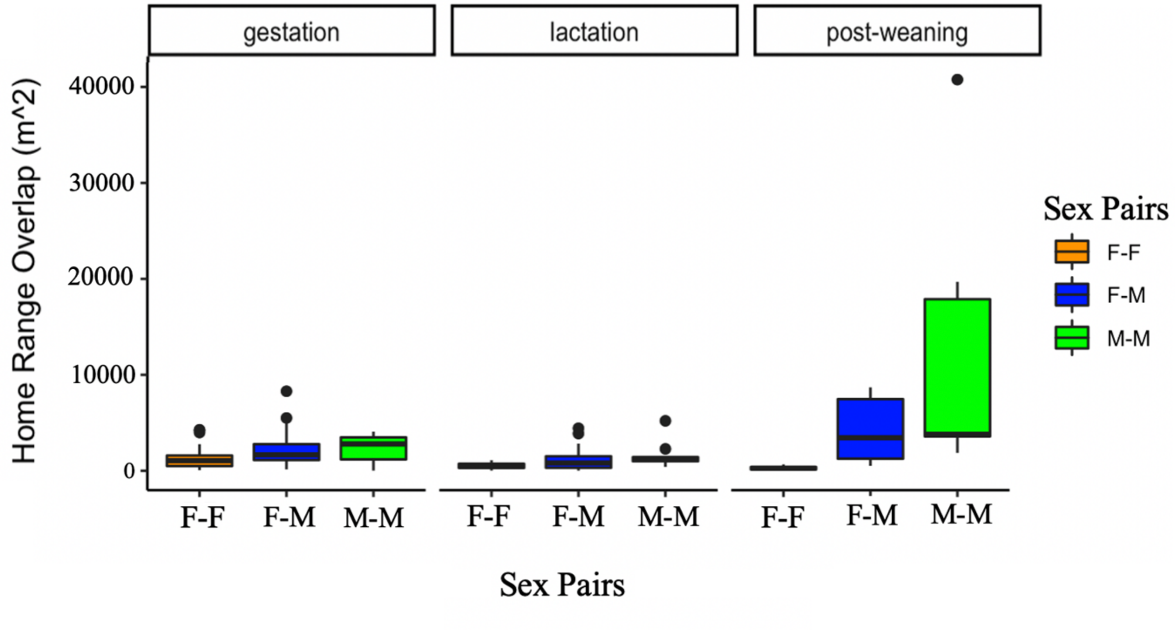

Figure 2.3.A. Comparison of the spatial distribution of home range overlap between sex classes (n_{male} = 10, n_{female} = 11) in m^2 for the 95% areas during each phase of the annual reproductive cycle on the Inkster site. ANOVA tests reveal that the effect of sex did significantly impact the overlap of home ranges in the 95% (two-way ANOVA, $F_{2,45} = 6.01$, $p = 0.005$).The bold middle line is the median, the edges of the boxes represent the upper and lower quartiles, while the whiskers represent the minimum and maximum overlap points. Outliers are represented as individual data points. F = female and M = male.

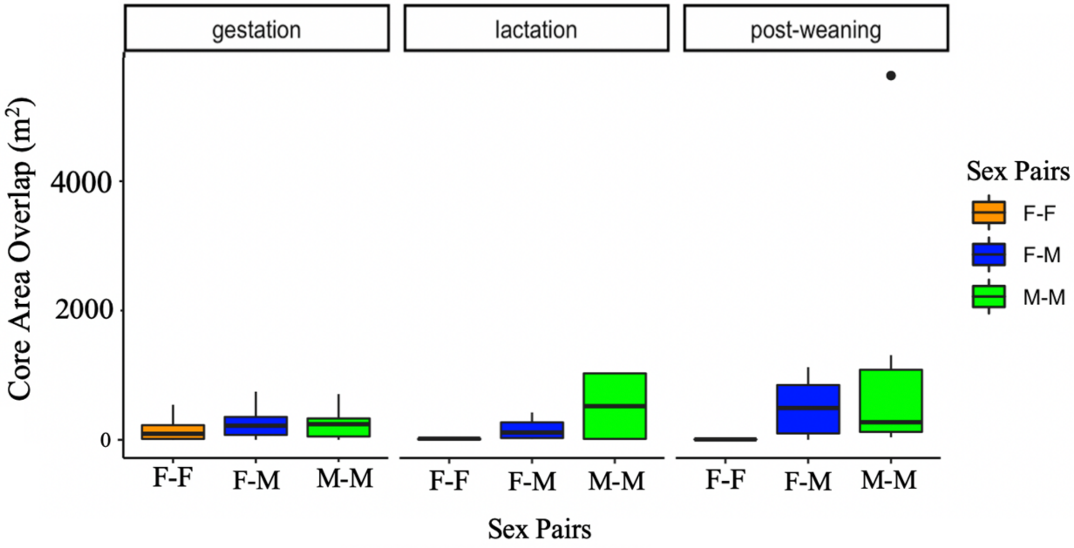

Figure 2.3.B. Comparison of the spatial distribution of home range overlap between sex classes ($n_{male} = 10$, $n_{female} = 11$) in m^2 for the 50% areas during each phase of the annual reproductive cycle on the Inkster site. ANOVA tests reveal that the effect of sex did not significantly impact the overlap of home ranges in the 50% overlap only (two-way ANOVA, $F_{2,44} = 0.99$, $p = 0.38$).The bold middle line is the median, the edges of the boxes represent the upper and lower quartiles, while the whiskers represent the minimum and maximum overlap points. Outliers are represented as individual data points. F = female and M = male.

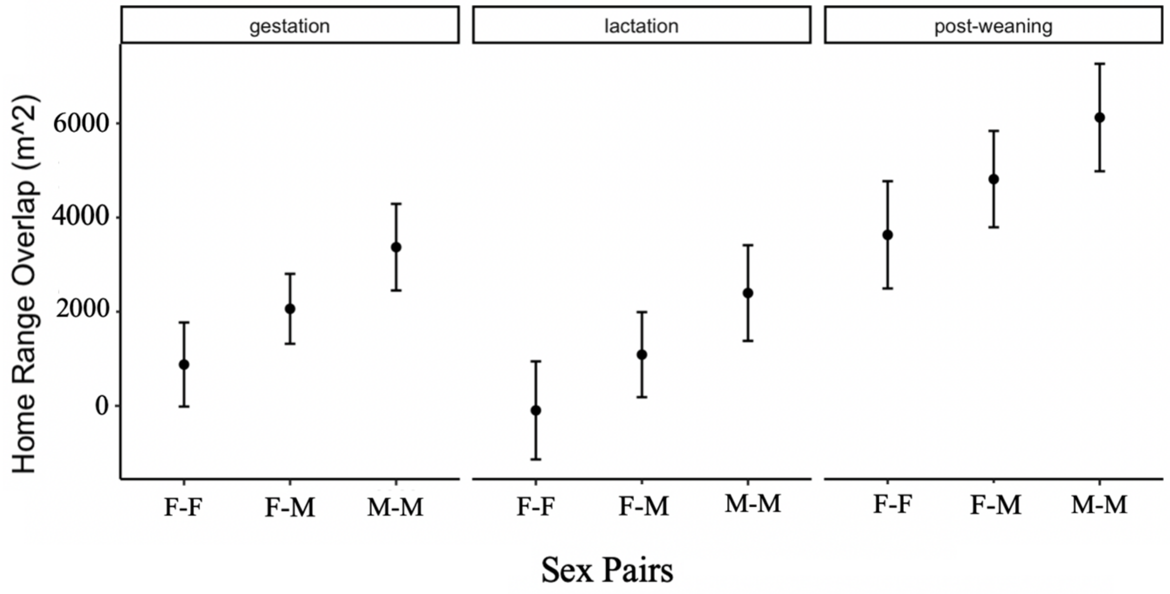

Figure 2.4.A. Home range overlap (mean ± SE m^2) for all possible sex pairs ($n_{male} = 10$, $n_{female} = 11$) over each phase of the annual reproductive cycle. Points represent means while error bars represent ± SE. F = female and M = male.

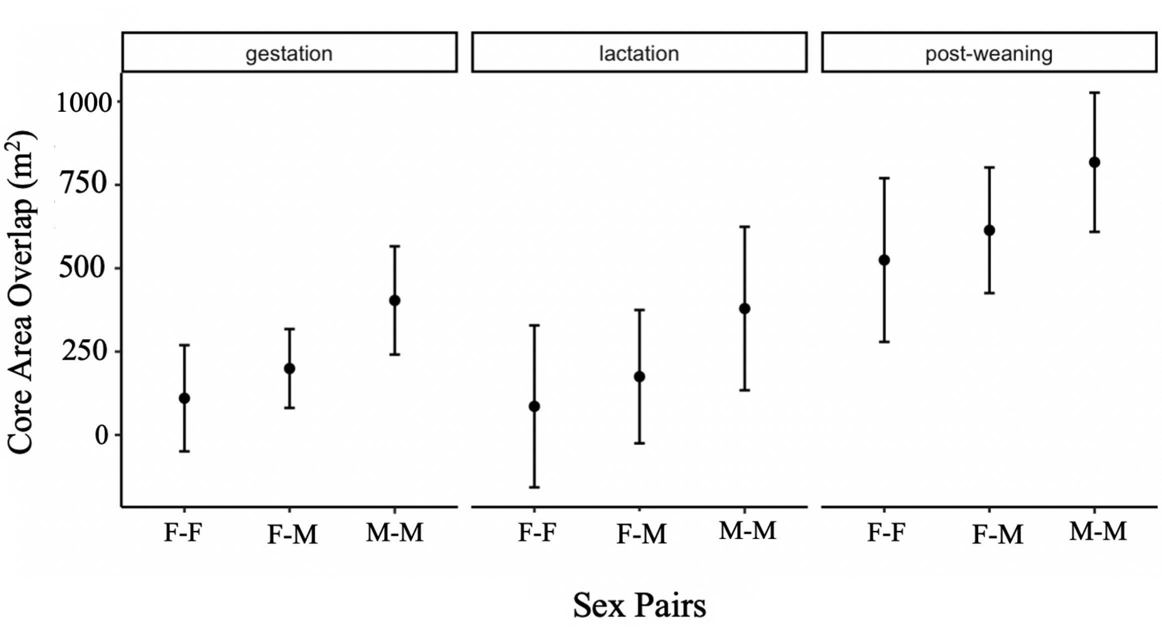

Figure 2.4.B. Core area overlap (mean ± SE m^2) for all possible sex pairs ($n_{male} = 10$, $n_{female} = 11$) over each phase of the annual reproductive cycle. Points represent means while error bars represent ± SE. F = female and M = male.

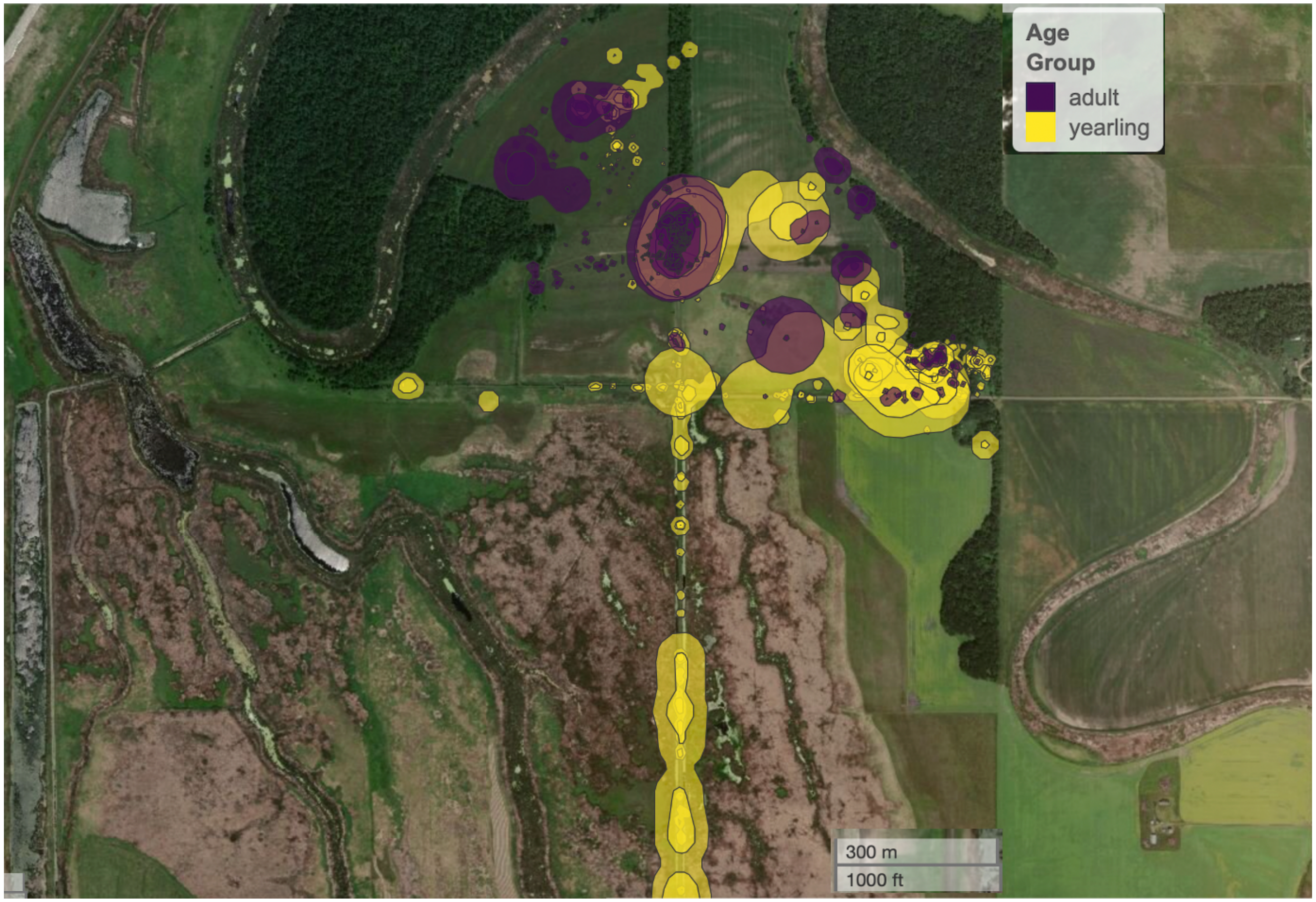

Figure 2.5.A. Map representing home range (innermost 95% kernel density area) and core (innermost 50% kernel density area) areas calculated with kernel density estimators for age groups (n_{adult} = 9, $n_{yearling}$ = 12) on the Inkster site, organized by age group.

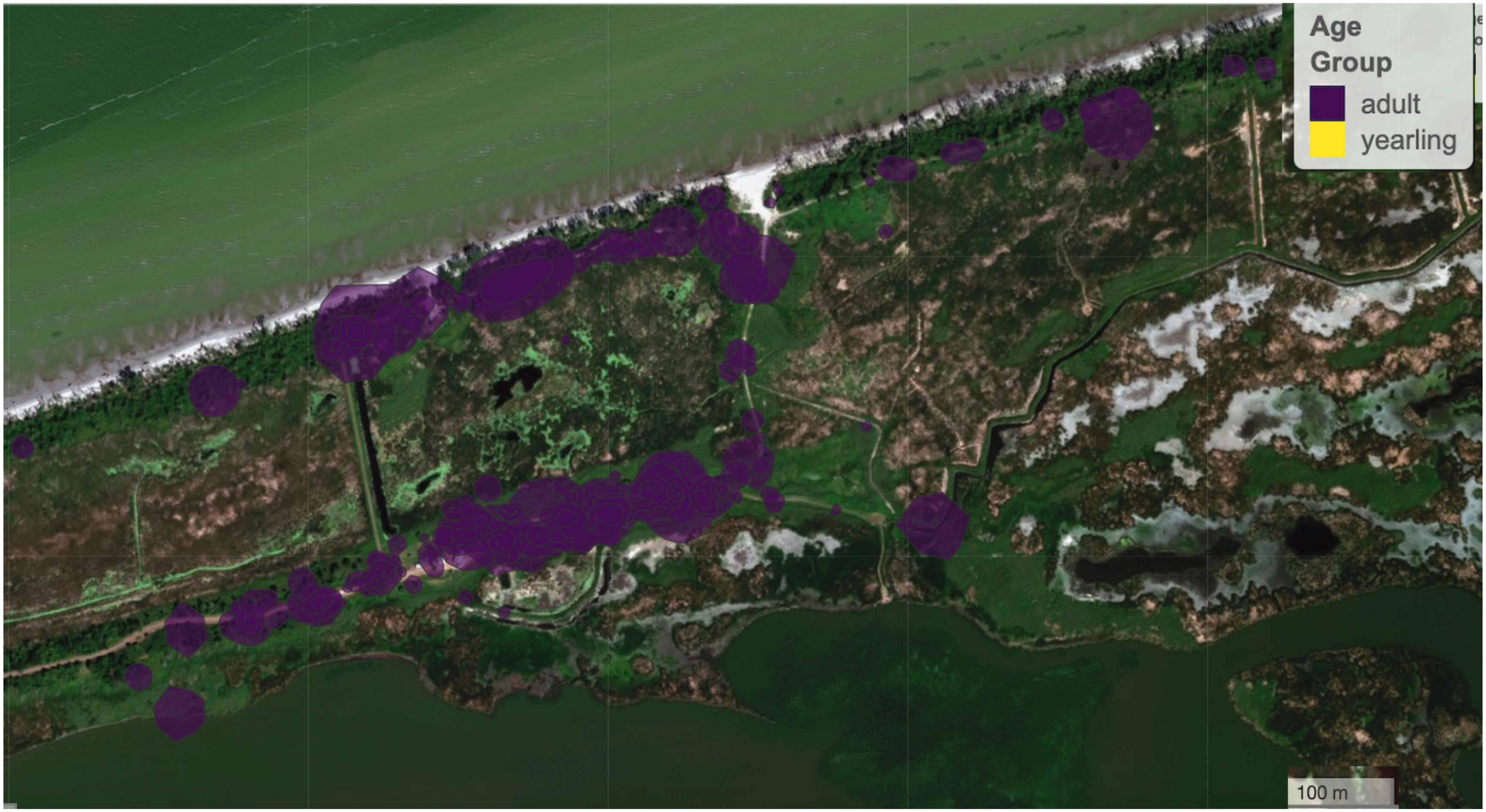

Figure 2.5.B. Map representing home range (innermost 95% kernel density area) and core (innermost 50% kernel density area) areas calculated with kernel density estimators for age groups (n_{adult} = 3) on the Beach Ridge site, organized by age group.

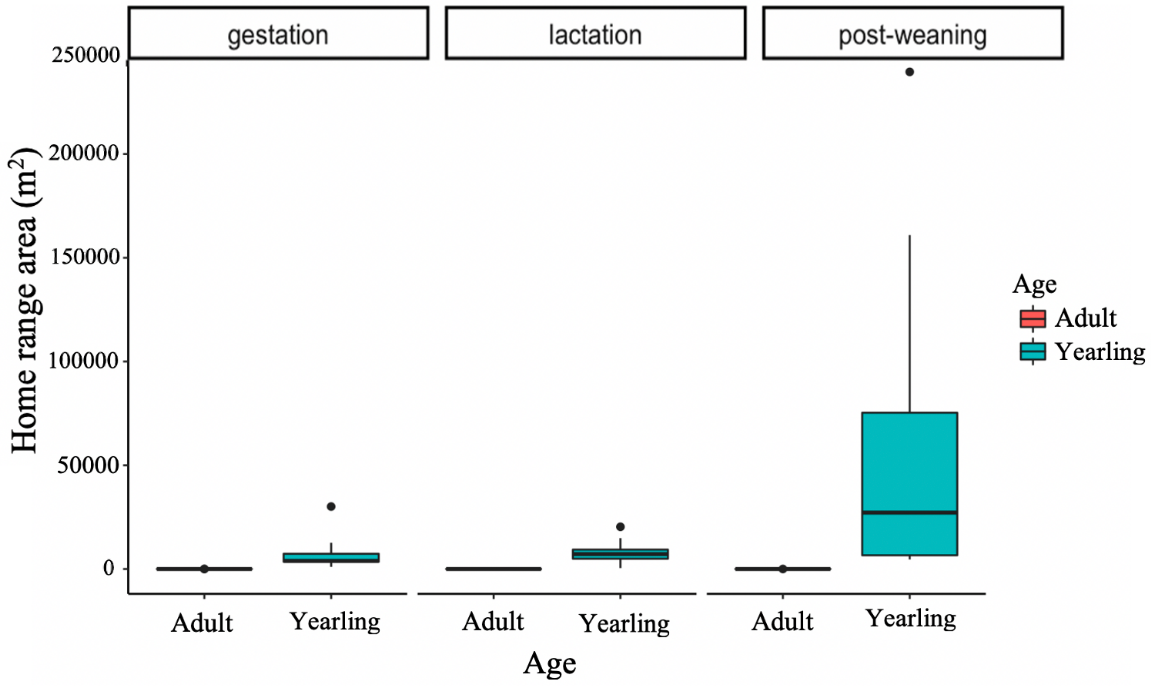

Figure 2.6.A. Comparison of the spatial distribution of home range size between age classes ($n_{adult} = 9$, $n_{yearling} = 12$) in m^2 for the 95% areas during each reproductive phase on the Inkster site. ANOVA tests reveal that the effect of age did not significantly impact the size of home ranges (two-way ANOVA, $F_{1,19} = 4.81$, $p = 0.19$). The bold middle line is the median, the edges of the boxes represent the upper and lower quartiles, while the whiskers represent the minimum and maximum area points. Outliers are represented as individual data points.

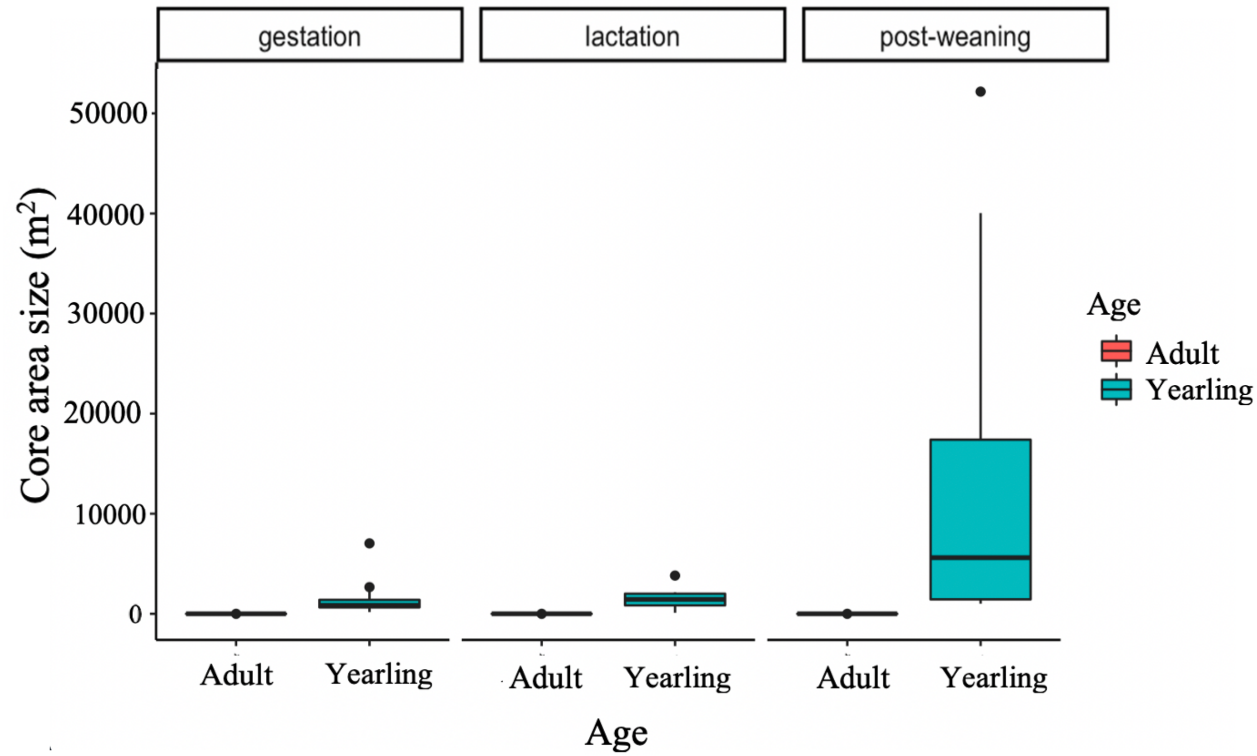

Figure 2.6.B. Comparison of the spatial distribution of home range size between age classes (n_{adult} = 9, $n_{yearling}$ = 12) in m^2 for the 50% areas during each reproductive phase on the Inkster site. ANOVA tests reveal that the effect of age did not significantly impact the size of home ranges (two-way ANOVA, $F_{1,19} = 4.5$, $p = 0.19$).The bold middle line is the median, the edges of the boxes represent the upper and lower quartiles, while the whiskers represent the minimum and maximum area points. Outliers are represented as individual data points.

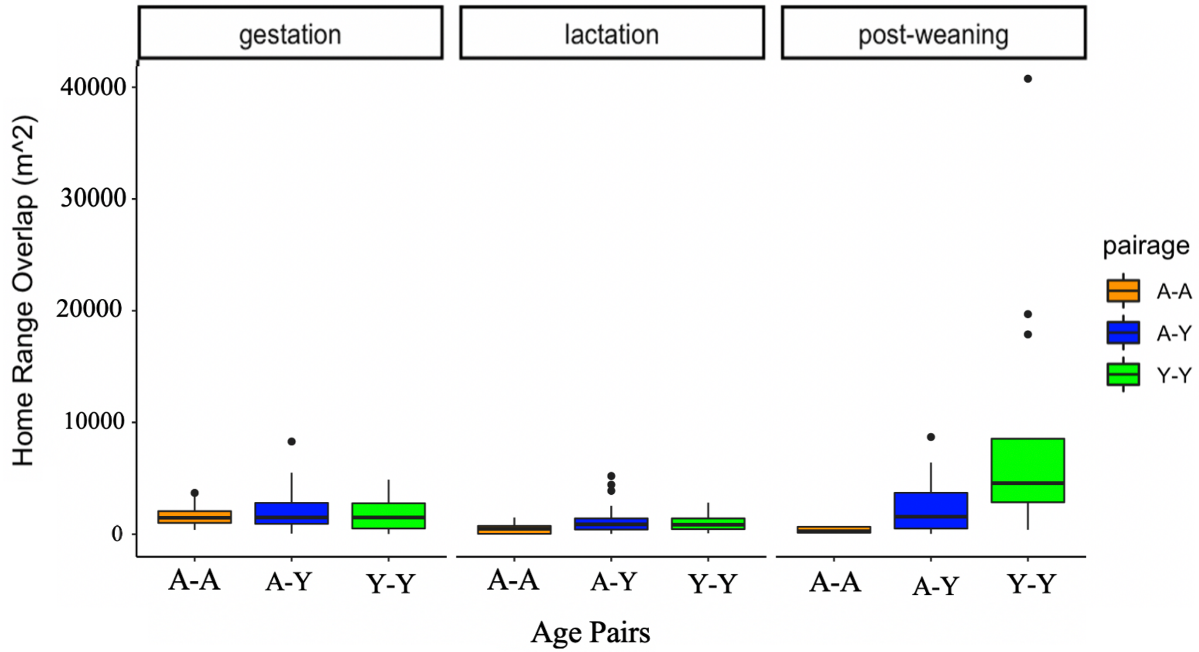

Figure 2.7.A. Comparison of the spatial distribution of home range overlap between age classes ($n_{adult} = 9$, $n_{yearling} = 12$) in m^2 for the 95% areas during each phase of the annual reproductive cycle on the Inkster site. ANOVA tests reveal that the effect of age did not significantly impact the overlap of home ranges in the 95% (two-way ANOVA, $F_{2,79} = 2.06$, $p = 0.08$).The bold middle line is the median, the edges of the boxes represent the upper and lower quartiles, while the whiskers represent the minimum and maximum overlap points. Outliers are represented as individual data points. A = adult and Y = yearling.

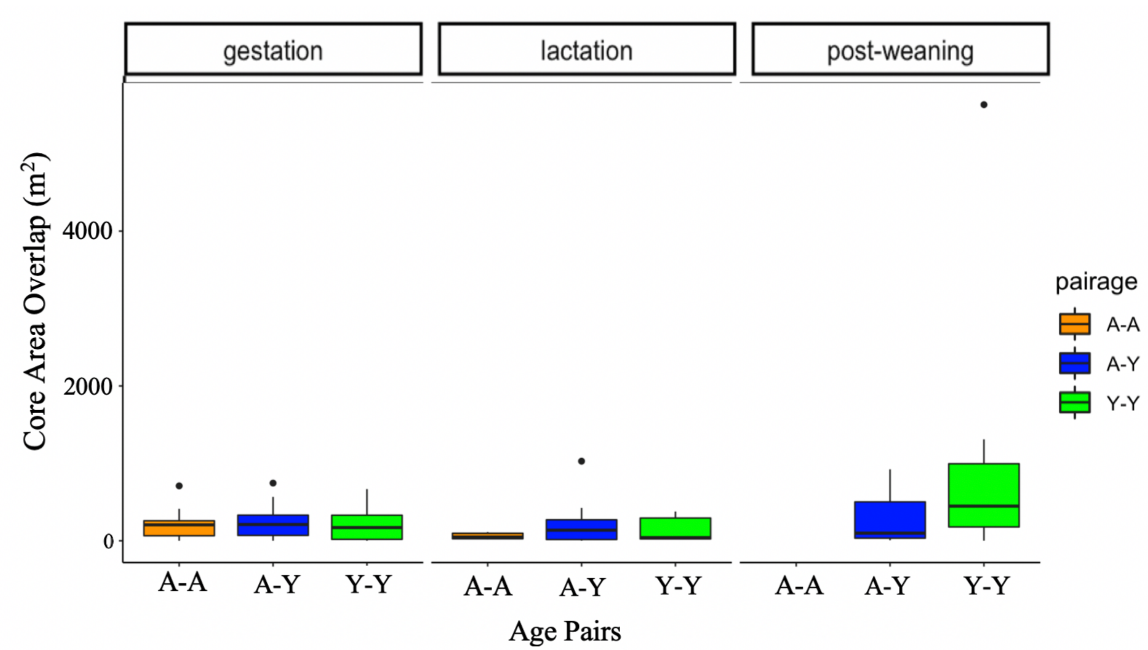

Figure 2.7.B. Comparison of the spatial distribution of home range overlap between age classes ($n_{adult} = 9$, $n_{yearling} = 12$) in m^2 for the 50% areas during each phase of the annual reproductive cycle on the Inkster site. ANOVA tests reveal that the effect of age did not significantly impact the overlap of home ranges in the 50% (two-way ANOVA, $F_{2,68} = 1.16$, $p = 0.32$).The bold middle line is the median, the edges of the boxes represent the upper and lower quartiles, while the whiskers represent the minimum and maximum overlap points. Outliers are represented as individual data points. A = adult and Y = yearling.

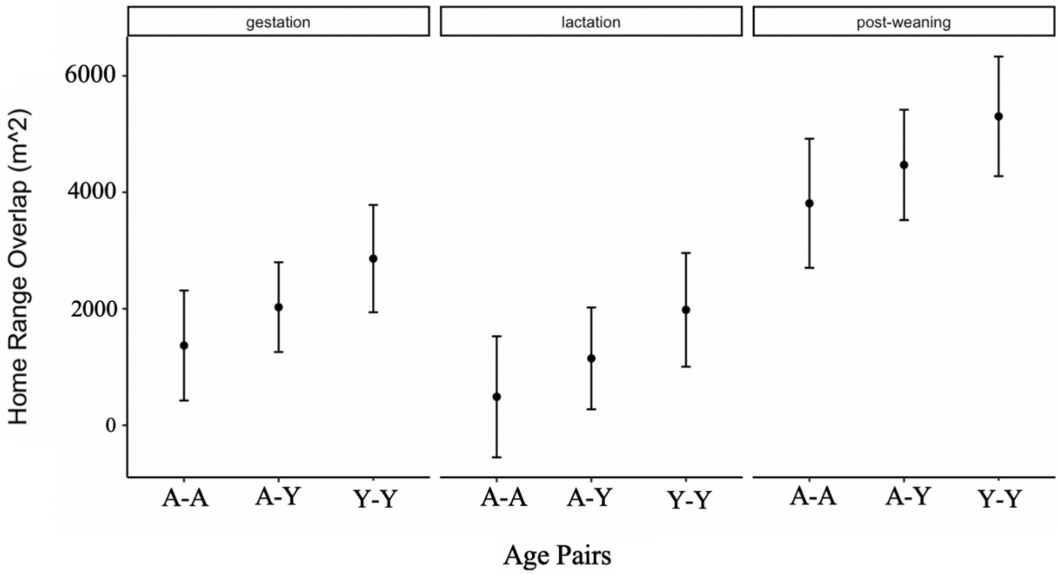

Figure 2.8.A. Home range overlap (mean ± SE m^2) for all possible age pairs (n_{adult} = 9, $n_{yearling}$ = 12) over each phase of the annual reproductive cycle. Points represent means while error bars represent ± SE. A = adult and Y = yearling.

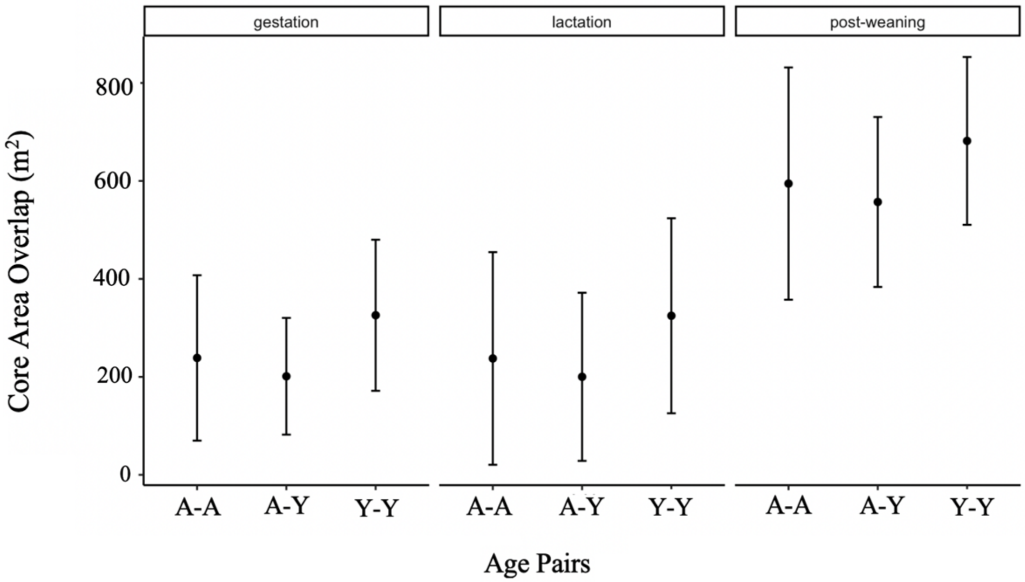

Figure 2.8.B. Core area overlap (mean ± SE m^2) for all possible age pairs ($n_{adult} = 9$, $n_{yearling} = 12$) over each phase of the annual reproductive cycle. Points represent means while error bars represent ± SE. A = adult and Y = yearling.

Chapter 3: Does home range overlap and nest distance correlate with relatedness among Franklin's ground squirrels (*Poliocitellus franklinii*)?

Abstract

Kin differential association and kin-biased behaviour can modulate the expression of selfishness and apparent altruism so as to enhance the fitness of individuals living in groups. Amicable interactions among neighbouring individuals are often attributable to natal philopatry, which has been documented across taxa. One key component in understanding sociality is the evaluation of socio-spatial organization relative to kinship among group members. Highly social species often cluster with close-kin, allowing the accrual of indirect fitness benefits. While female kin clustering is typical of the most social ground squirrel species, little is known about how kinship may structure populations of relatively asocial species, though it has been proposed that kin-biased sociality may represent an ancestral state, setting the stage for the evolution of more egalitarian societies. Relatively asocial Franklin's ground squirrels (*Poliocitellus franklinii*) thus provide an excellent opportunity to investigate sociality related to spatial dynamics, and the role kinship may play in structuring populations of asocial species. I used radio-telemetry to locate Franklin's ground squirrels in a population near Delta Marsh, MB, Canada, quantifying home range and core area spatial overlap among those by close kin versus more distant/non-kin across the squirrels' annual reproductive cycle. I also documented nest locations of individuals during the lactation period to test for any effect of kinship on the dispersion of nest burrows or orientation of nest movements relative to close-kin. Kinship did not affect overlap of home ranges and core areas throughout the overall active season. Further, lactating females did not cluster nests during the lactation period with close-kin, nor did they selectively move nests toward close-kin during the end of the lactation period. However, there was a tendency to move nests away from close-kin as lactation progressed. Taken together, my findings reveal that sociality in this population of Franklin's ground squirrels is not predicated on kinship.

Key words: Franklin's ground squirrel, natal philopatry, home range, nest dispersion, sociality, kin discrimination, kin cluster, spatial overlap

Introduction

Hamilton's (1964) inclusive fitness theory suggests that the preferential treatment of genetic relatives enhances fitness, and may serve as the evolutionary basis of advanced sociality (Wilson, 1975). Accruing indirect fitness benefits requires that genetic relatives can be discriminated, which implies that kin recognition occurs (Holmes and Sherman, 1982; Porter and Blaustein, 1989). Kin selection may give way to more inclusive expressions of sociality (e.g. social tolerance, amicable behavioural interactions and the sharing of space) within groups, extending cooperation to non-kin, which would allow societal benefits to accrue (Hamilton, 1964; Maynard Smith, 1964; Hare, 2004; Hare and Murie, 2007). Hare (2004) reported that juvenile Franklin's ground squirrels (*Poliocitellus franklinii*) are amicable only toward siblings, suggesting that kin discrimination in this species may serve mate choice in optimizing the balance between inbreeding and outbreeding rather than promoting nepotism (Bateson, 1983). One key component in understanding sociality is the evaluation of socio-spatial organization relative to kinship among group members (Hare and Murie, 2007). Highly social species like Belding's ground squirrels (*Urocitellus beldingii*; Sherman, 1981), Columbian ground squirrels (*Urocitellus columbianus;* Festa-Bianchet and Boag, 1982) and Olympic marmots (*Marmota* *olympus;* Barash, 1973) show extensive spatiotemporal overlap with female kin, while relatively asocial species like woodchucks (*Marmota monax*; Maher, 2009) are socially intolerant of each other.

Kin recognition

As kin associate, the risk of inbreeding increases. This risk can be diminished, however, by sex-differential dispersal from the natal area (Pusey and Wolf, 1996), or via the ability to recognize kin (Holmes and Sherman, 1983). For kin-mediated behaviour to occur, kin must possess the ability to recognize genetic relatives (Fletcher and Michener, 1987; Hepper and Cleland, 1998). Both direct and indirect mechanisms have been proposed for kin recognition (Hepper and Cleland, 1998). Four mechanisms have been advanced to explain the proximate basis of kin recognition: spatial distribution, association, phenotype matching and allelic recognition (Holmes and Sherman, 1982; 1983). Spatial affiliation is described as conspecifics recognizing a location rather than the individual, treating all individuals found in a particular place over a given time period as kin (Holmes and Sherman, 1983). Association is described as time spent with particular conspecifics in close proximity and therefore becoming associated with those individuals that are ultimately treated as kin (does not require actual kinship) (Holmes and Sherman, 1983). Phenotype matching requires that individuals form a template of what constitutes kin, based on discriminator substances emanating from itself or familiar relatives, and then applying that template in discriminating among both familiar and previously unencountered individuals with respect to their match to that template (Holmes and Sherman, 1983). Finally, allelic recognition requires recognition of genetically-based cues shared with related conspecifics (Dawkins,1976; Holmes and Sherman, 1982; 1983). Direct mechanisms of recognition are supported by the correlation between genes and recognition (fire ants: *Solenopsis invicta*; Obin and Meer Vander, 1989, mice; Willse et al., 2006; *Botryllus schlosseri*; Grosberg and Quinn, 1989), and phenotypic matching cues detected olfactorily (spiny mice: *Acomys cahirinus*; Porter et al., 1983). Indirect mechanisms of recognition are described in the context of association or familiarity (Holmes and Sherman, 1983; Waldman, 1988) and occur in various taxa including mammals (Hilborn, 1975; Porter and Wyrick, 1979; Bekoff, 1981; Holmes and Sherman, 1983; Holmes, 1995; Michener, 1983; Waldman, 1987; Hare, 2004), birds (Burtt, 1977; Greenwood et al., 1979; 1983; Keppie, 1980; Beecher et al., 1981; Davies et al., 1992; McRae, 1996), and reptiles (Davis, 2012). The ability to recognize kin can aid in the decision to either disperse from a natal area or remain philopatric, both of which impose fitness costs and benefits (Nunes, 2007).

Natal philopatry versus dispersal

The decision to undertake natal dispersal (moving from the natal area to a new site) or remain philopatric (remaining in the natal area), leads to the wide range of socio-spatial organization among conspecifics (Nunes, 2007). Both males and females can disperse from their natal area, although mammalian species are typified by male-biased dispersal (Greenwood, 1980). Male dispersal is thought to be more common because of high reproductive competition among males (Greenwood, 1980), and high costs associated with dispersal for reproductively active females (Sherman, 1977). Typically, females remain in their natal area and tend to aggregate together, forming kin clusters, which promote the accrual of inclusive fitness benefits (Hare and Murie, 2007). Differing degrees of kin associations have important consequences for the evolution of sociality ranging from relatively asocial or solitary species to highly social species (Clutton-Brock and Lukas, 2012).

Dispersal reduces risks of inbreeding (Greenwood, 1980), competition between relatives for food and shelter (Wilson, 1975) and/or to enhance access to resources (Alexander, 1974; Wilson, 1975; Hoogland, 1979) or mates (Wilson, 1975; Griffin and West, 2002; West et al., 2002; Emery and Thompson, 2017). Dispersal can either occur before reproduction (natal dispersal), prior to breeding (breeding dispersal) or after breeding has occurred (post-breeding dispersal) (Nunes, 2007). In group living species where fathers and brothers are present, females have been documented to either avoid mating, delay breeding, or disperse entirely from the natal area prior to breeding (Hoogland, 1982). Female white-footed mice (*Peromyscus leucopus*) delay going into estrus until they have had a chance to disperse from closely-related males (Wolff, 1992). Natal dispersal can also occur in adults if habitat, food and shelter become limiting factors (Lurz et al., 1997). On the other hand, post-breeding dispersal occurs after individuals have bred and relocated to new breeding sites, which may prove adaptive in avoiding mating with one's own offspring in subsequent breeding seasons (Nunes, 2007). This is seen in male Belding's ground squirrels, where once successful breeding occurs in a given area, males relocate to other breeding sites, thus avoiding inbreeding, while increasing their reproductive fitness by gaining access to additional mates (Sherman, 1976). Another hypothesis states that post-breeding dispersal occurs in order for territories to be ceded to offspring (Harris and Murie, 1984), which may be seen as a form of parental investment (Berteaux and Boutin, 2000).

Costs associated with dispersal include; energy loss, lower breeding success, heightened predation risk and risks of not finding food and shelter (Clutton-Brock and Lukas, 2012). Studies of Alpine marmots (*Marmota marmota*) revealed that the presence of unrelated females promoted greater female reproductive suppression than did the presence of close female kin (Hacklander et al., 2003). Individual white-footed mice that dispersed were more likely to be depredated by local owl populations (Metzgar, 1967). Food availability reduced the propensity of female golden-mantled ground squirrels (*Callospermophilus lateralis*) to disperse and delayed reproductive maturity among those philopatric individuals (Wells and van Vuren, 2018). Therefore, at least for females, the benefits of philopatry (see below) leading to the formation of kin clusters can outweigh the benefits of dispersal (Hare and Murie, 2007).

Females endure costs associated with the growth and care of their offspring, therefore the tendency to remain philopatric imparts fitness benefits (Nunes, 2007). As outlined above, females tend to aggregate to form kin clusters, which are correlated with enhanced breeding success and survival (Silk, 2007). Home ranges in proximity to close-kin among voles (*Microtis sp.*) result in earlier breeding dates (Lambin, 1977), greater fecundity, and increased juvenile survival rates over time (Pusenius et al., 1998; König, 1994; Lambin and Yoccox, 1998; Lambin and Krebs, 1993). Offspring survival over winter in Alpine marmots increased when hibernating with close-kin and lowered fitness costs to individual dams (Arnold, 1990). The presence of yellow-bellied marmot (*Marmota flaviventris*) mothers reduced the chance of daughters dispersing (Armitage et al, 2011), which increased their daughter's likelihood of establishing a home range among other females (Bekoff, 1977). The benefits of female philopatry accrue through female tolerance, cooperation and reduced aggression between genetically-related individuals (Lambin and Yoccoz, 1998; Silk, 2007).

Study species and objectives

Many studies of mammals have explored the role kinship plays in group-living species, however, few studies utilize asocial species to understand the evolution of sociality (Smuts et al., 1987). Franklin's ground squirrels are one of four ground squirrels (golden-mantled

(*Callospermophilus lateralis*), thirteen-lined (*Ictidomys tridecemlineatus*) and woodchucks) that are considered relatively asocial (Armitage, 1981; Michener, 1983). More social ground squirrels delay dispersal enhancing survival (Michener, 1983), however, Franklin's ground squirrels disperse early in life (Martin and Heske, 2005).

Field studies documenting Franklin's ground squirrel space use and movement patterns are few and limited in scope. This is likely owing to the elusive nature of members of this species (Sowls, 1948) along with its challenging marsh-edge/forest-edge habitat, which precludes direct behavioural observations in the field. Both, Armitage (1981) and Michener (1983) originally classified Franklin's ground squirrels as relatively asocial due to their early sexual maturation, small body size, early dispersal, agonistic nature toward conspecifics, non-overlapping spatial organization, and the apparent absence of burrow sharing. Choromanski et al. (1989), however, reported extensive overlap of home ranges between same sex and opposite sex individuals from the end of April through mid-August. Most or all juvenile males disperse from their natal area, while females tend to remain philopatric, although some females may also disperse (Martin and Heske, 2005). There are limited data on the socio-spatial organization of Franklin's ground squirrels and what data are there, provide contradictory results as to the extent to which adult Franklin's ground squirrels home range distributions overlap. Thus, further investigation is required. Lack of field data on Franklin's ground squirrels space use relative to kinship has precluded the definitive classification of Franklin's ground squirrel sociality and thus hampered efforts to achieve a robust understanding of the factors that play a role in the evolution of ground squirrel sociality. Understanding the relationships between Franklin's ground squirrel individuals, their home range and core areas, and degree of philopatry will shed light on how kin associate socio-spatially, enhancing our understanding of the comparative sociality of ground squirrels and social evolution in general.

In the present study, I investigated the dynamics of spatial organization in relation to relatedness and reproductive phase in a population of Franklin's ground squirrels near Delta Marsh, Manitoba, Canada. I documented spatial proximity, extent of home range and core area size and overlap relative to kinship during the overall active season to determine whether any element of sociality in Franklin's ground squirrels is predicated on kinship. I predicted that 1) female close-kin would tolerate spatial overlap in their home range (95%) and core area (50%) with close female kin more so than with more distant relatives, and 2) lactating females will selectively cluster nests with close female kin, and 3) nest movements by lactating females will be directed toward close female kin and away from more distantly-related conspecifics toward the end of the lactation period. Lastly, I quantified home range and core area size and spatial overlap among those by close versus more distant/non-kin across the squirrels' annual reproductive cycle (gestation, lactation, and post-weaning) to examine how space use among relatives may change over the course of the annual reproductive cycle. Knowledge of how genetic relatives organize themselves spatially and the degree to which their home ranges and core areas overlap can allow assessment of the degree of sociality (Cooper, 2007) of free-ranging Franklin's ground squirrels.

Materials and Methods

Study species

Franklin's ground squirrels are listed as a species of "Least Concern" according to the International Union for Conservation of Nature (IUCN), in that densities are purported to remain high in local populations (Pergams et al., 2008). However, in certain states in the southeastern extent of their range, they are either considered vulnerable, threatened or endangered (Iowa Department of Natural Resources, 2012; Illinois Endangered Species Board, 2015; Indiana Department of Natural Resources, 2013; Missouri Department of Natural Resources, 2015; Wisconsin Department of Natural Resources, 2014). Franklin's ground squirrels are diurnal, semifossorial species that prefer tall grass prairie habitat, avoid grazed land, and tend to prefer marsh and forest edge, but can also be found along road and railway edges (Ostroff and Finck, 2003). They range across the central United States following the Apsen Parkland ecotone through the Canadian prairie provinces including Manitoba, Saskatchewan and the central Alberta plains (Ostroff and Finck, 2003), while spending the majority of their lives below ground (Sowls,1983).

Males emerge from hibernation earlier than females by about one to two weeks (end of April) to establish breeding territories (Iverson and Turner, 1972). Hibernation occurs around late July for males and late females, while juveniles stay above ground until the beginning of October (Sowls, 1948; Iverson and Turner, 1972). Sexual dimorphism occurs in Franklin's ground squirrels with males tending to be larger in size (Ostroff and Finck, 2003; Pero and Hare, 2017). Spring body mass ranges from 320-400 grams, while in fall before entering hibernation, mass ranges from 500-900 grams (Ostroff and Finck, 2003; Pero and Hare, 2017). Franklin's ground squirrels typically exist at relatively low densities over most of their range (Hall, 1955), and females tend to outnumber males 2:1 (Pero and Hare, 2017).

Study site and subjects

During the active season of 2019, Franklin's ground squirrels occupying the Inkster field site near Delta Marsh, Manitoba, Canada (50°9'N, 98° 19'W) were studied from 01 May through

31 July. The Inkster site consisted of about a 1 km^2 area and is described in detail in Löve and Löve (1954), but can be described generally as a mix of rural roadside, marsh edge, hayfields and deciduous forest habitat (Hare, 2004).

A total of 37 squirrels (19 females and 18 males) were trapped and marked on the Inkster site with the help of my advisor, James Hare, and two field assistants during the summer of 2019. Franklin's ground squirrels occupying the Inkster site were captured using National or Tomahawk (Tomahawk Live Trap, Tomahawk, Wisconsin, USA) live-traps, baited with No Name™ peanut butter and rolled oats (Loblaw Companies Ltd., Brampton, ON, Canada). Traps were checked hourly to reduce the risk of heat shock. Upon each capture, weight (using a Pesola™ spring scale; Baar, Switzerland) to the nearest 5 grams, was recorded. As per methods from Murie and Harris (1982), breeding condition of males and females was recorded throughout the breeding season during each capture. Trapping occurred everyday, between location gathering, during the breeding period to assess parturition dates for females. Franklin's ground squirrels had a permanent fish fingerling tag (Monel #1, National Band and Tag Co., Newport, Kentucky, USA) for individual identification attached through their right pinna. Their dorsal pelage was marked with hair dye (Clairol Hydrience 52S Pearl Black, Clairol Corp., Stamford, Connecticut, USA) in unique individual patterns for individual identification. Squirrels were subsequently released at the point of capture after identification marks were applied or after data was recorded.

Radiotracking

My team and I deployed radio-telemetry collars to quantify space use by as many closely-related (defined as known mother-offspring pairs or sibling pairs) individuals as possible.

Maternal relatedness was established from data collected in 2018. Juveniles had been trapped within three days of their emergence from their natal burrows (Hare, unpublished data). Of the 63 known juveniles which emerged from nest burrows of nine lactating females in 2018 on the Inkster site, 12 related individuals (from four discrete female kin groups) constituting three adult females, seven yearling females and two yearling males, emerged from hibernation on the Inkster site in spring 2019. Twenty-one Holohil Systems Ltd. (Carp, ON) PD-2C VHF telemetry collars were deployed on squirrels on the Inkster site, including; 11 females (5 adults and 6 yearlings) and 10 males (4 adults and 6 yearlings). Of the 21 collared squirrels on the Inkster site, 12 were considered close-kin and nine were considered non-close-kin. All Franklin's ground squirrels and burrow locations were obtained by locating collar-bearing squirrels with Telonics (Mesa, AZ) TR-4 telemetry receivers and Telonics RA-14K 2-element Yagi antennae. Transmitter collars were affixed around the squirrel's neck via a custom-fitted 200 x 4 mm nylon ToolBench™ zip-tie forming a collar (Burnaby, BC C.N. DTSC Imports.) covered with custom-fitted Tygon™ tube (4.8 mm diameter) (Saint-Gobain North America, Valley Forge, PA). Squirrels were trapped weekly to check collar tension, and if collars were deemed too loose, or were tight to the point of causing excessive hair loss or abrading the squirrel's skin, were removed and refitted. Squirrel locations were recorded using Garmin GPS 72 WAAS-corrected handheld GPS receivers (Garmin Ltd. Olathe, KS). My team and I gathered above ground fixes on each collared squirrel twice each day during morning (0800-1100 hours CDT), and afternoon (1500-1800 hours CDT) tracking sessions, which increased the likelihood of independence of GPS fixes obtained for the same individual in the same day. To further ensure independence, we randomized the order of squirrels by randomly selecting individuals from a hat (separately for both sites) each time before radio-tracking sessions began within sites. Juveniles were not included in the study because they had not established their own home ranges and there was the risk of dispersal, which would leave their telemetry collar attached, and increasingly too tight around the growing juvenile's neck. Squirrels that were detected above ground and that could unambiguously be identified based on the dye mark on their dorsal pelage within each tracking session had their GPS location recorded without recourse to telemetry. Franklin's ground squirrel locations were grouped by unique phases (gestation, lactation and post-weaning) of the annual reproductive cycle. Females were considered to be in the gestation phase once 51% of the females on the Inkster site were observed to have a copulatory plug and/or evidence of copulation where we could count backwards to the day it first occurred. Once 51% of females drastically dropped their weight, they were considered to be in the lactation phase. When 51% of juveniles appeared above ground from their burrows, females were considered to be in the post-weaning period. Breeding phase was gathered for males, because males emerge prior to females. Males were considered to be in breeding phase until 51% of the females on the Inkster site had evidence of copulation, then males shifted to the gestation phase. Once 51% of females were lactating males entered the lactation phase and subsequently once 51% of females had juveniles emerge above ground then males shifted to the post-weaning phase.

Nests were located on average, once per week, weather permitting, after sunset (which varied throughout the season), presumably when squirrels had retired for the night (Sowls, 1948). Nest locations were gathered more frequently toward the end of the lactation period (three-four days in a row) before juvenile emergence began so as not to lose track of any lactating dam's location just prior to juvenile emergence. Nest analysis focused on the lactation phase in order to answer my questions regarding nest movements. If a female's nest was unable to be located on a given night, location attempts occurred each additional night until her nest was located.

Relatedness of individuals

The relatedness of all individuals born and marked on the Inkster site in 2018 and overwintering to emerge on that site in the spring of 2019 served as the history of maternal relatedness for the present study. No genetic analysis occurred, however juveniles were trapped and ear tags were attached on the days following juvenile emergence to ensure they came from their presumptive dam. During the 2019 field season, eight yearlings emerged from the litters of four of the dams who brought juveniles above ground in 2018, giving us adult-yearling, mother-daughter (six pairs), mother-son (two pairs), and yearling-yearling, sibling (seven pairs: four female-female, and three female-male) to work with and were considered close-kin in that the coefficient of relatedness within those pairs of uterine kin (sensu King, 1984), barring any maternal half-siblings, was 0.5. All other individuals were considered to be non-close kin, which may have included more distant relatives, including grandparents and grandchildren, aunts, uncles nieces and nephews, paternal-half siblings, more distant kin and non-kin ($r < 0.5$).

Home range analysis

Home range and core area estimates were measured in R statistical software (version 3.5.1, R Core Team 2018) using the package adehabitatHR (version 0.4.15; Calenge, 2017) using least-biased fixed kernel density estimators with least squares cross-validation (LSCV) (Kenward and Hodder, 1996; Seaman and Powell, 1996; Worton, 1989). I obtained more than the minimum number of points required to use fixed kernel density estimators ($n > 30$ locations) (Seaman and Powell, 1996) for each reproductive phase for each collared squirrel. Next, I calculated the home range (innermost 95% kernel density area) and core area (innermost 50% kernel density area) similarly using the kernel density function. The 95% isopleth was chosen because it omits extreme outliers, providing a commonly used estimate of an animal's overall home range (Worton, 1987). The 50% isopleth represents the core area of an animal's home range (Worton, 1987). Kernel density estimators have been favoured over minimum convex polygon (MCP), since MCP tends to be less sensitive, causing overestimation of home range sizes, while kernel density uses utilization densities (frequency that an individual occupies a particular space in time) (Worton, 1989). Some individuals disappeared (n= 3) over the course of data collection and were presumed to have been depredated. Where such incidents occurred early (fewer than five locations in a given reproductive period) in my study, I omitted data for those individuals. For the remaining individuals, size and overlap of the home range and core area averages (mean ± SE) were computed and compared for individuals of differing relatedness (close-kin versus non-close-kin), both for the overall active season pooled across time and by unique periods within the annual reproductive cycle (gestation, lactation, and post-weaning). I assessed the data for normality via the Shapiro-Wilk normality test on the home range and core area data and found that the data constituting home range and core areas were unlikely to have been derived from a normal underlying population of measurements (Shapiro-Wilk, w= 0.038, p = < 0.001; reject the null hypothesis of normality). I thus performed a $\log_{10}$ transformation, of the location data underlying home range and core areas of all individuals, which satisfied the assumption of normality (Shapiro-Wilk, w= 0.99, p = 0.72; accept the null hypothesis of normality).

Statistical comparisons of home range and core area overlap

I tested for effects of relatedness and period within the annual reproductive cycle on home range and core area overlap, and also tested for effects of relatedness pooling all data for individuals across the three separate periods within the annual reproductive cycle. Overlap of home ranges and core areas were examined for close-kin versus non-close-kin pairs within the Inkster site. Average overlap was calculated as the intersection between a pair of individual's home ranges or their core areas for both the overall active season and by distinct phases of the annual reproductive cycle. Only area overlaps (m^2) greater than zero were included in the models. I first averaged the area overlap for each unique individual between kin and non-close-kin. Averaging both reduced and smoothed the pseudoreplicated data in each model. I fit predictive models using linear mixed effects (LME) models from the nlme package and function, lme (Bates, 2009; Pinheiro, 2020), for R software (version 1.2.5019, R Development Core 2019) to assess the relationship described above accounting for period within the annual cycle with squirrel individual as a random factor to account for multiple measurements across periods. I also fit predictive models using linear models from R software (version 1.2.5019, R Development Core 2019) to assess the relationship between relatedness and overall home range and core area overlap calculated across the whole summer. I then presented the results in a three-way ANOVA table using the Satterthwaite's degrees of freedom method (method used for estimating the degrees of freedom using LME models). Models were considered statistically significant when significance of $p < 0.05$. Lastly, Tukey's Honest Significant Difference (HSD) post-hoc tests were employed to test all pairwise comparisons between multiple groups (reproductive periods: gestation, lactation, and post-weaning) where an overall effect of an independent variable was detected (Tukey, 1949). The Tukey's HSD post-hoc tests utilized the single step method based on the t-distribution and adjust p-values sequentially (Hothorn, 2020).

Analysis of nest distances

Nest burrow GPS locations were obtained (see above) for all collared squirrels during the lactation period of the annual reproductive cycle on the Inkster site. I calculated the average distance in meters between close-kin and all neighbouring distant/non-kin surrounding the focal individual to determine whether close-kin cluster nests together during the lactation phase. Conspecifics are considered neighbours if nests are adjacent with no other conspecific's nest in between (Clark and Evans, 1954). Bar graphs were used to visually compare these averages. QQ plots were used to test normality of the distribution of differences, and once normality was confirmed, two-tailed paired-sample t-tests were used to test whether trends were statistically significant at $p < 0.05$. Next, I calculated the average nest distances in meters between close-kin groups during early versus late lactation to determine whether close-kin move their nests closer together during the end of the lactation period. Early lactation was considered to be the first half of points during the lactation phase, while late lactation was considered to be the second half kernel density area. One location point was chosen during the middle of early lactation and one location point was chosen during the middle of late lactation for each close-kin individual, avoiding the pooling fallacy that would otherwise occur where individuals contribute multiple observations to the data set (Machlis et al., 1985). A 2x2 contingency table was created to determine the frequency of moves toward versus away from close-kin of each focal individual in early versus late lactation. Fisher's exact test was then employed to test whether the tendency to move toward versus away from close-kin was independent of the time period within lactation. Lastly, I checked mapped points of nests to determine whether nest burrows were shared both in space and time between individuals.

Results

Close-kin versus non-close-kin differences in home range and core area overlap

Home range and core area overlap of close-kin and non-close-kin did not differ throughout the overall active season on the Inkster site (Figure 3.1: home range, two-way ANOVA, $F_{1,10} = 5.06$, $p = 0.05$, core area, two-way ANOVA, $F_{1,7} = 4.39$, $p = 0.07$) among the possible relatedness pairs (close-kin-close-kin, close-kin - non-close-kin or non-close-kin - non-close-kin). Trends suggest that mean home range and core area overlaps were larger among non-close-kin than among close-kin (Table 3.1).

Home range overlap did not differ between kin and non-kin pairs across the distinct periods of the annual reproductive cycle (two-way ANOVA, $F_{1,55} = 0.03$, $p = 0.87$). There was also no difference detected for core area overlap (two-way ANOVA, $F_{1,49} = 1.52$, $p = 0.22$; Figure 3.2). Mean overlaps for each of the relatedness pairs during the lactation period were smallest, while mean overlaps during the post-weaning period were largest (Table 3.2).

Seasonal phase had an overall effect on home range (two-way ANOVA, $F_{2,43} = 11.17$, $p = < 0.001$) and core area overlap (two-way ANOVA, $F_{2,37} = 6.58$, $p = 0.004$). Tukey's HSD tests revealed that among all reproductive periods, only the post-weaning period differed from the other phases of the annual reproductive cycle for both home range (post-weaning-gestation, $z = 3.8$, $p = < 0.001$, post-weaning-lactation, $z = 4.56$, $p = < 0.001$) and core areas (post-weaning-gestation, $z = 3.38$, $p = 0.002$, post-weaning-lactation, $z = 3.04$, $p = 0.007$). Home range and core area overlap did not differ between the gestation and lactation period (home range, $z = -1.1$, $p = 0.54$; core area, $z = 0.087.21$, $p = 0.99$; Figure 3.3).

Average nest distances between close-kin and non-close-/distantly related kin

Average distances between nest burrows of neighbouring close-kin during lactation did not differ from those of neighbouring non-close-kin (Figure 3.4; two-tailed t-test, $t_{49} = -0.22$, $p = 0.83$). Average distances between nest burrows of neighbouring close-kin during the overall active season did not differ from those of neighbouring non-close-kin (two-tailed t-test, $t_{392} = 0.64$, $p = 0.52$; Figure A.1). Male close-kin maintained distance from their mothers on opposite sides of the Inkster site for the entire active season (Figure 3.5). In the field, I also observed that one marked female, bearing the mark "Tie fighter" progressively moved away from her male offspring during the post-weaning period.

I used a Fisher's exact test to determine whether the tendency to move toward or away from close-kin varied between early versus late lactation. The tendency to move toward versus away from close-kin did not differ significantly between early versus late lactation (Table 3.3: Fisher's exact test, $p = 0.057$), although there is a strong trend toward nest movements being preferentially oriented toward close-kin early in lactation, but away from close-kin during late lactation.

Home range and core area sizes as estimated by kernel density were used to gather nighttime nest locations. I plotted the collared squirrel's nest locations and found that there were no shared sleeping burrows during nighttime nest surveys (Figure 3.6).

Discussion

Relatedness affected neither home range size nor core area overlap, suggesting that close-kin are not selectively sharing space with one another. Similar to Franklin's ground squirrels, female Richardson's (*Urocitellus richardsonii*) and Columbian ground squirrels were intolerant of intrusions into their core areas (Beets, 1973; Michener, 1979; Festa-Bianchet and

Boag, 1982). Although Franklin's ground squirrel non-close-kin overlapped more than close-kin throughout the single overall active season studied, all individuals had limited overlap in core areas, suggesting that female Franklin’s ground squirrels are territorial. Female Richardson’s ground squirrels maintained separate core areas that remained similar in size throughout multiple active seasons (Michener, 1979). Unlike Franklin’s ground squirrels, however, Richardson ground squirrel kin tended to cluster more than non-kin throughout the overall active season (Michener. 1979). Richardson’s ground squirrels exhibit behaviour consistent with social tolerance, where territoriality is relaxed in the broader home range among familiar neighbouring conspecifics, but access to the core area remains limited (Wilson, 1975; Sherman, 1980; Porter and Blaustein, 1989). Dear enemy recognition ensures social tolerance among neighbours, which avoid escalating aggressive encounters, reducing energy expenditure and thus increasing the fitness of neighbouring individuals (Fisher, 1954; Wilson, 1975; Jaeger, 1981). Even in that context, however, individual distance is maintained (Wilson, 1975).

Among Franklin’s ground squirrels in the present study, home range size and overlap among close-kin and non-close-kin varied significantly across the different stages of the annual reproductive cycle. The greatest home range and core area sizes and overlap occurred during the post-weaning period when compared to the gestation and lactation period. Home range size and overlap increasing during the post-weaning period may reflect a need for individuals to search for higher quality food before entering hibernation and/or search for suitable hibernacula, while during gestation and lactation, females remained closer to their burrows, investing in their offspring and/or protecting young from potentially infanticidal conspecifics (Ostfeld et al., 1985). That said, there is currently no evidence of infanticide occurring among Franklin’s ground squirrels.

Nest distances

While in most species, close-kin cluster nests, lactating female Franklin's ground squirrels in the present study did not cluster nests with close female kin during the lactation period. Nests of close-kin were not relocated so as to be closer to each other during late lactation and burrow sharing was not evident in this population. Lactating females did show a propensity to aggregate with close-kin early in lactation, but apparently avoided close-kin during late lactation. This pronounced trend merits further investigation not only to independently verify the trend documented in the present study, but to identify that adaptive basis of any kin-biased nest movements. It is conceivable that offspring are especially vulnerable at the beginning of lactation so dams may be more inclined to aggregate near close-kin for added offspring protection. Nest clustering in other ground squirrel species protects emerging young from predation, infanticidal conspecifics, and/or increases collective vigilance while foraging (Stevens, 1998; Hayes, 2000). The general absence of evidence of nest clustering by Franklin's ground squirrels is consistent with the categorization of the species as asocial (Armitage, 1981; Michener, 1983). Nevertheless, six incidences of adoption by neighbouring female Franklin's ground squirrels occurred over six previous years of field study (Hare, unpublished data). Nepotism may thus exist even in an asocial species, contrary to Michener's (1983) characterization of asocial species.

Inbreeding avoidance

Movement of close-kin during the post-weaning period may reflect reproductive strategies increasing the actor's fitness (Swihart and Slade, 1989). Wombat (*Vombatus ursinus*) mothers with male offspring dispersed shortly after weaning, likely to reduce the chance of inbreeding during the subsequent breeding season (Banks et al. 2002). This same pattern of behaviour was observed during the post-weaning period in one family group of Franklin's ground squirrels (dam and five male offspring), where the dam dispersed over a great distance from her nest burrow away from her offspring. In addition, yearling male Franklin's ground squirrels spaced their nests far from their mothers' home ranges, on opposite sides of the study site, and did not overlap with their mother's home range. Yearling male nest dispersion thus suggests that dispersal of male kin serves to promote inbreeding avoidance.

Limitations

Empirical studies of multiple populations of Franklin's ground squirrels are required to address the generality of my findings, and to document the extent of intraspecific variation in home range and core area size and overlap. Additionally, only a total of twelve (later ten due to presumptive losses to predators) individuals that were considered close-kin and nine non-close-kin individuals were used in this study. Thus, cautious interpretation is warranted. The addition of multiple populations and larger sample sizes will further contribute to our understanding of sociality, and provide potentially useful insights into the factors critical to the conservation of Franklin's ground squirrels.

Conclusions

The present data fail to support the hypothesis that female Franklin's ground squirrel home ranges overlap more with close-kin than with other conspecifics, that females are more tolerant of close female kin in their core areas, or that nests of close female kin are clustered spatially over the course of the lactation period. These results suggest that female Franklin's ground squirrels maintain distinct breeding territories, reducing access to their core area by other conspecifics, regardless of relatedness. These data also support the assertion that Franklin's ground squirrels are relatively asocial in maintaining social distancing, and do not conform to the pattern of female philopatry common to other ground squirrel species.

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Table 3.1. Summary of home range and core area overlaps (mean ± SE m^2) for close-kin (n = 12) and non-close-kin (n = 9) Franklin's ground squirrels over their entire active season on the Inkster site.

	Overlap	
	Home Range $\bar{X} \pm SE$	Core Area $\bar{X} \pm SE$
Level of Relatedness		
Close-kin	2398 ± 374.2	249 ± 47.0
Non-close-kin	3432 ± 597.9	265 ± 71.5
Non-close-kin-Close-kin	2771 ± 301.2	347 ± 48.1

Table 3.2. Summary of home range and core area overlap (mean ± SE m^2) for close-kin (n = 12) and non-close-kin (n = 9) Franklin's ground squirrels at the Inkster site throughout each phase of their annual reproductive cycle.

Group	Phase	Home Range	Core Area
		$\bar{X} \pm SE$	$\bar{X} \pm SE$
Close-kin-Close-kin	Gestation	1303 ± 152.5	187 ± 29.3
	Lactation	717 ± 91.3	9.6 ± 5.9
	Post-weaning	1677 ± 599.9	238 ± 96.8
Close-kin-Non-close-kin	Gestation	1992 ± 148.0	225 ± 21.1
	Lactation	1201 ± 160.5	166 ± 33.4
	Post-weaning	6433 ± 1692.4	970 ± 313.0
Non-close-kin-Non-close-kin	Gestation	2507 ± 175.3	206 ± 32.9
	Lactation	1329 ± 469.3	363 ± 230.3
	Post-weaning	7257 ± 3015.0	137 ± 48.7

Notes: There were no comparable data on the Beach Ridge site.

Table 3.3. Frequency of average nest movements during early versus late lactation by lactating females. Fisher's exact test (p = 0.057) reveals that the tendency to move nests toward versus away from close-kin does not differ between early and late lactation.

	Lactation Period	
Direction	Early	Late
Toward	7	2
Away	2	7

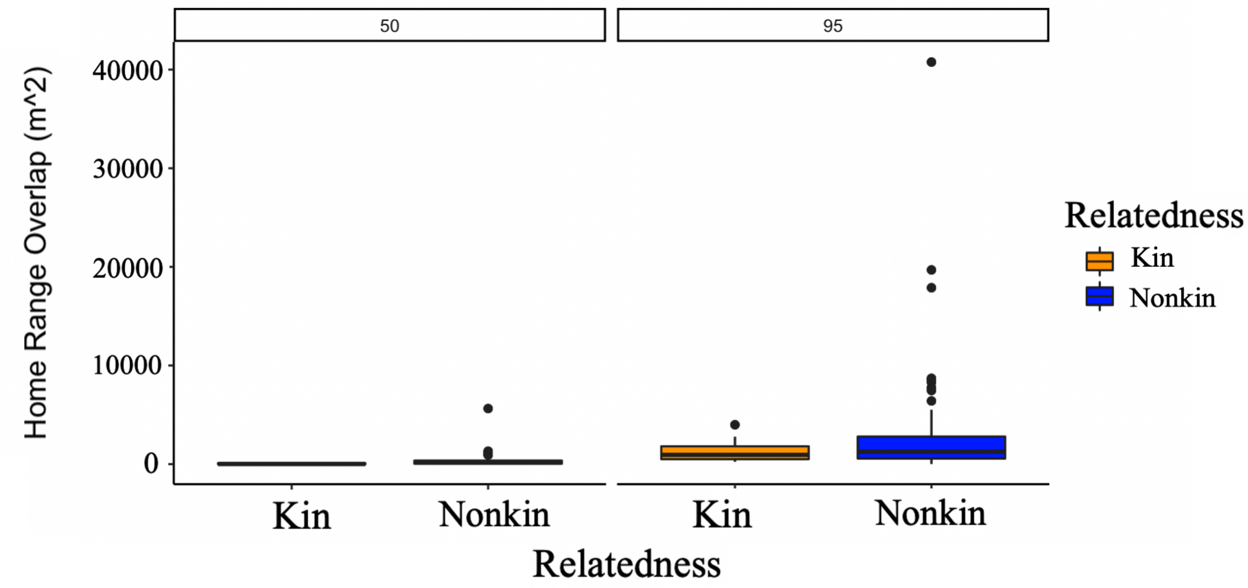

Figure 3.1. Comparison of the spatial distribution of home range overlap between relatedness close-kin groups (n_{groups}=4) and non-close-kin neighbours (n_{nonkin}= 9) in m^2 throughout the overall active season on the Inkster site. ANOVA tests reveal that the effect of relatedness did not significantly impact the overlap of home ranges in the 95% area (two-way ANOVA, $F_{1,10}$ = 5.06, p = 0.05) or the core area (50%) (two-way ANOVA, $F_{1,7}$ = 4.39, p = 0.07). The bold middle line is the median, the edges of the boxes represent the upper and lower quartiles, while the whiskers represent the minimum and maximum overlap points. Outliers are represented as individual data points. K = close-kin and N = non-close-kin.

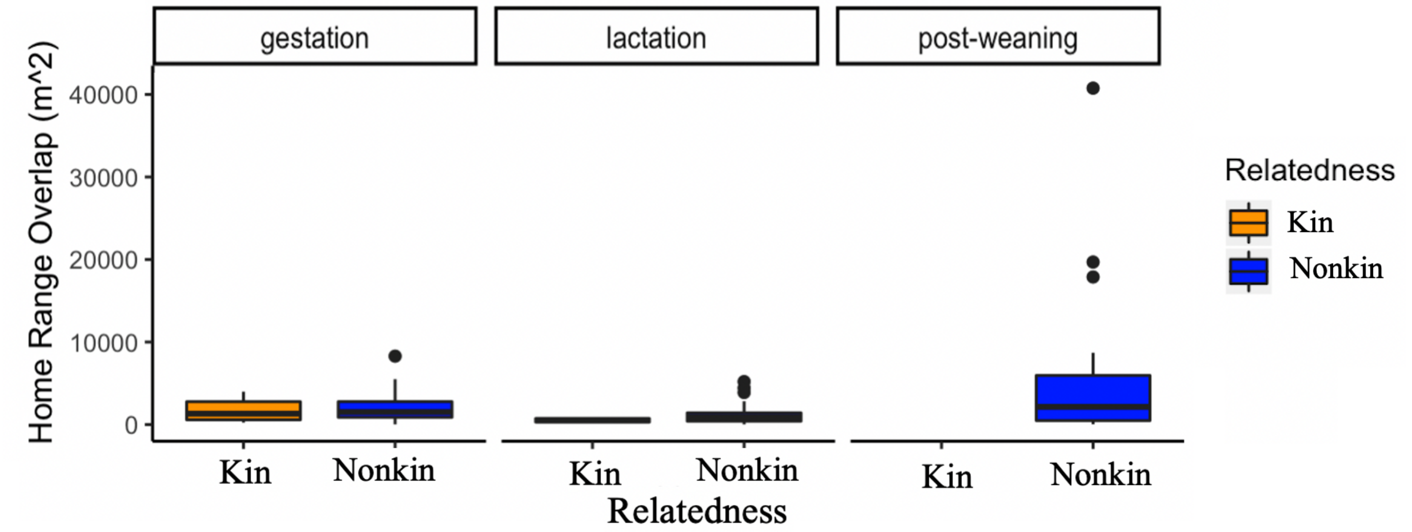

Figure 3.2.A. Comparison of the spatial distribution of home range overlap between relatedness close-kin groups (n_{groups}=4) and non-close-kin neighbours (n_{nonkin}= 9) in m^2 for the 95% areas during each period of the reproductive cycle on the Inkster site. ANOVA tests reveal that the effect of relatedness did not significantly impact the overlap of home ranges in the 95% area (two-way ANOVA, $F_{1,55}$ = 0.03, p = 0.87). The bold middle line is the median, the edges of the boxes represent the upper and lower quartiles, while the whiskers represent the minimum and maximum overlap points. Outliers are represented as individual data points. K = close-kin and N = non-close-kin.

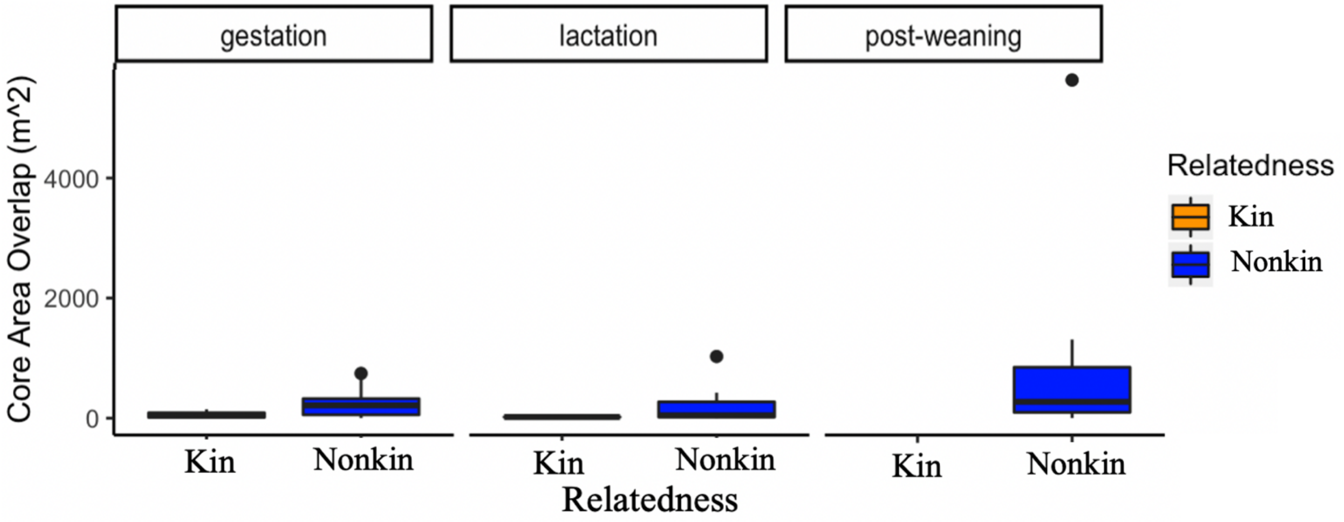

Figure 3.2.B. Comparison of the spatial distribution of home range overlap between relatedness close-kin groups (n_{groups}=4) and non-close-kin neighbours (n_{nonkin}= 9) in m^2 for the 50% areas during each period of the reproductive cycle on the Inkster site. ANOVA tests reveal that the effect of relatedness did not significantly impact the overlap of home ranges in the 50% (two-way ANOVA, $F_{1,49}$ = 1.52, p = 0.22). The bold middle line is the median, the edges of the boxes represent the upper and lower quartiles, while the whiskers represent the minimum and maximum overlap points. Outliers are represented as individual data points. K = close-kin and N = non-close-kin.

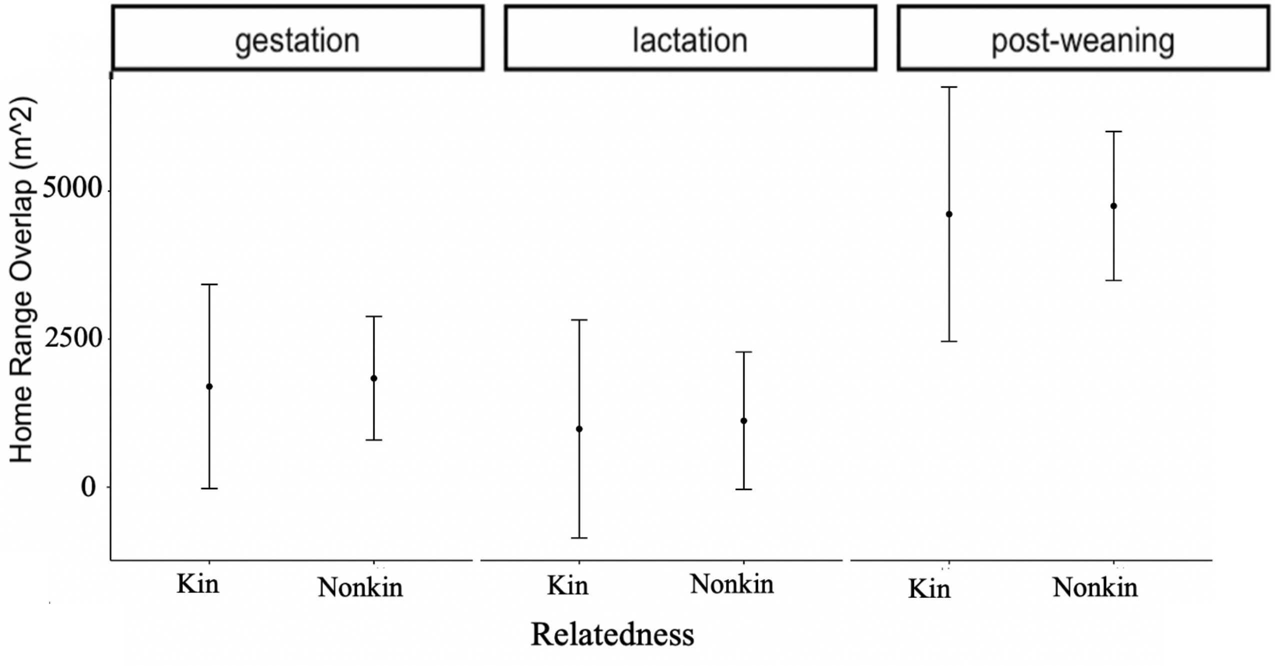

Figure 3.3.A. Home range overlap (mean ± SE m^2) for all possible relatedness pairs ($n_{closekin}$ = 12, n_{nonkin} = 9) over each phase of the annual reproductive cycle. Points represent means while error bars represent ± SE. Kin = close-kin and Nonkin = non-close-kin.

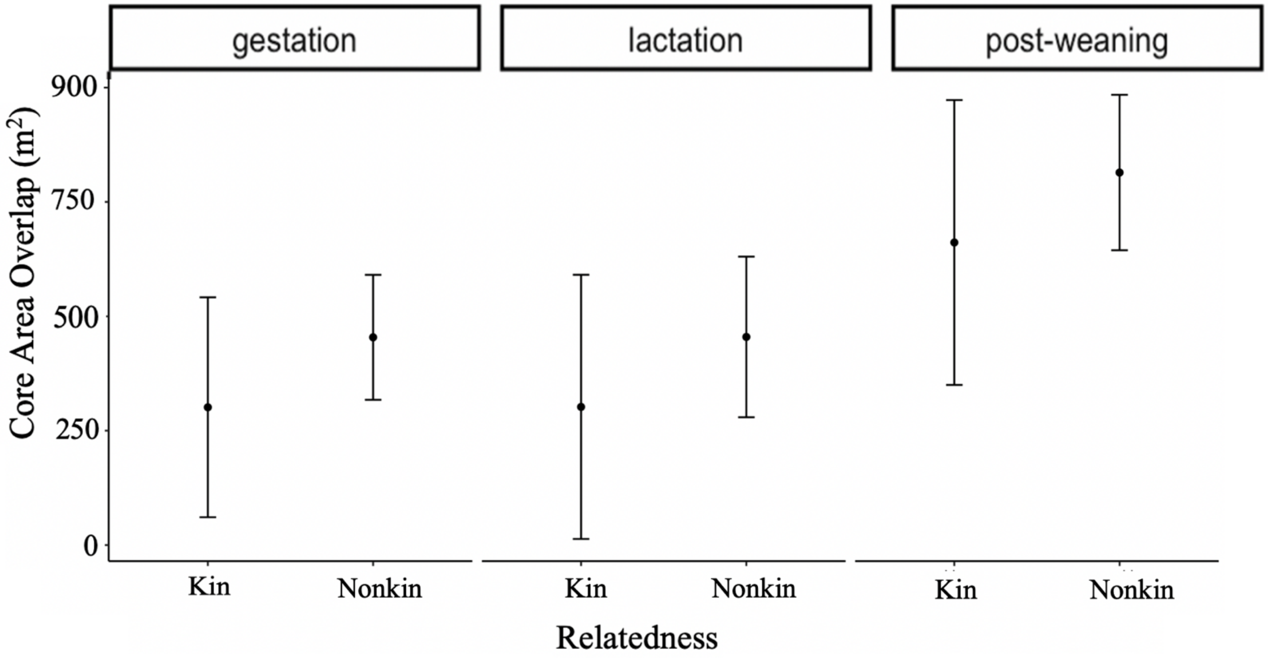

Figure 3.3.B. Core area overlap (mean ± SE m^2) for all possible relatedness pairs ($n_{closekin}$ = 12, n_{nonkin} = 9) over each phase of the annual reproductive cycle. Points represent means while error bars represent ± SE. Kin = close-kin and Nonkin = non-close-kin.

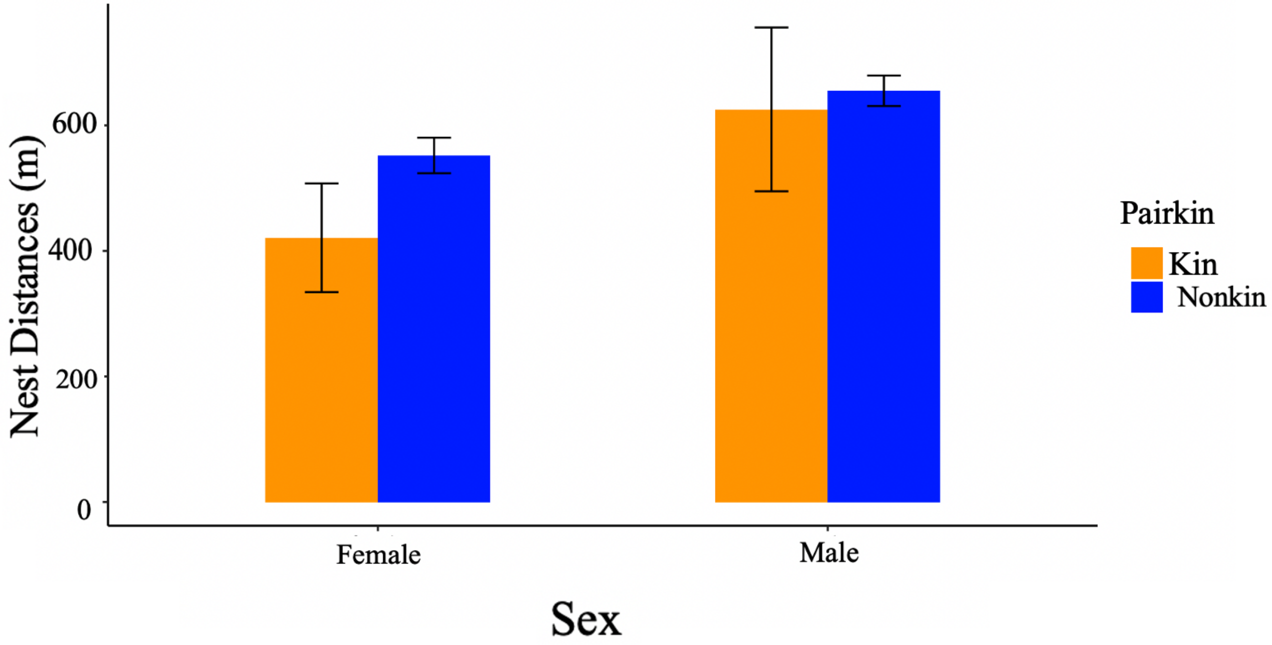

Figure 3.4. Spatial distribution of average nest distances (mean ± *SE* m) between close-kin ($n_{\text{kin groups}} = 4$) neighbours and non-close-kin neighbours ($n_{\text{nonkin}} = 9$) on the Inkster site during the lactation phase. Nest distances are not closer together between close-kin (paired-sample t-test: $t_{49} = -0.22$, $p = 0.83$).

Figure 3.5. Map of nest moves from dams (n = 2) and their male offspring (n = 2). Upon observation, males maintain distance from their mothers on opposite sides of the Inkster site for the entire active season.

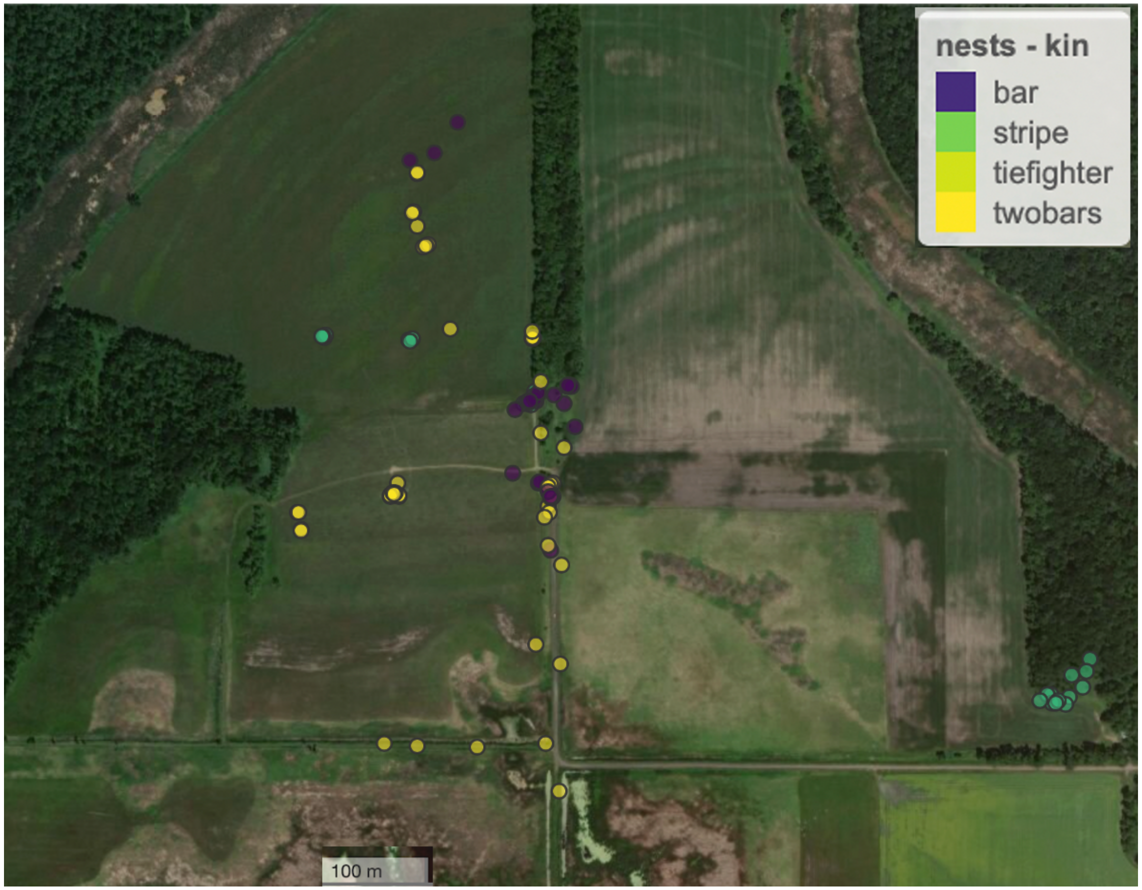

Figure 3.6. Map of four distinct groups of close-kin nest locations throughout the overall active season. No evidence of burrow sharing was detected in this population of Franklin's ground squirrels.

Chapter 4: Conclusions

The preceding thesis chapters explored socio-spatial organization among Franklin's ground squirrels. In Chapter 2, the effects of sex and age class on home range and core area size and overlap were examined over the course of the overall active season and by distinct periods of the annual reproductive cycle for a population of Franklin's ground squirrels near Delta Marsh, Manitoba, Canada. Sex and age class did not affect home range and core area size. Average female home range and core area sizes were consistently larger than those of males at the Inkster site, while average male home range size was largest at the Beach Ridge site overall. Yearlings maintained larger average home range and core area sizes than adults at the Inkster site, while average adult male home range size at the Beach Ridge site was largest overall. Sex differences in average home range and core area size are not consistent with sex differences documented among other rodent species. Among the periods studied in the annual reproductive cycle, home range and core area size were smallest during the gestation and lactation periods. Average male home ranges were larger at the Beach Ridge than the Inkster site, however, average core area size was similar between both sites. Inter-site variability among males requires further study long-term population monitoring to elucidate the factors driving home range and core area sizes.

Male-male pairs overlapped the most, while female-female pairs had the least overlap. Sex-related differences in the degree of overlap were statistically significant only for home ranges, with no differences in core area size detected among the three possible sex pairs either when pooled over the entire active season, or across the distinct periods of the annual reproductive cycle. Mean home range and core area overlap was most pronounced between adults and yearlings, though differences among these and interactants within other age classes (yearling-yearling or adult-adult) were not significant, contributing novel information on how age classes differ in terms of home range and core area overlap. Home range and core area size and overlap were significantly greater during the post-weaning period of the annual reproductive cycle for both sexes and age classes. This increase in size and overlap may reflect the need to recoup energy lost to reproduction and to ensure the accrual of mass by optimizing foraging strategies prior to hibernation. Increases in both home range and core area sizes in the post-weaning period may also reflect individuals searching further afield for potential hibernaculae, or to post-breeding dispersal, minimizing the risk of breeding with close relatives in the subsequent breeding season.

Taken together, data presented in Chapter 2 support the assertion that Franklin's ground squirrels are relatively asocial, with females maintaining territories and showing intolerance toward intrusions into their core area by conspecifics. Further, because females do not selectively cluster together, these data reveal that Franklin's ground squirrels do not conform to the pattern of female philopatry common to other ground squirrel species.

In Chapter 3, I investigated the effect of relatedness both during the overall active season and by distinct periods within the annual reproductive cycle on home range and core area size and home range and core area overlap. Relatedness, at least at the relatively coarse level employed in the present study, had no apparent effect on home range or core area size. Limited home range size of close female kin during the lactation period among many ground squirrel species suggest that dams may be staying close to their burrows to maintain growth and development of young and/or to lower the risk of infanticide. However, there is no evidence of infanticide among Franklin's ground squirrels. The reduction in home range size during the gestation and lactation period may be a product of direct maternal investment, where females focus their attention on their developing young. Home range and core area overlap were not affected by relatedness when data were pooled across the overall active season, though there were statistically significant differences in home range overlap during the post-weaning period of the annual reproductive cycle. Limited core area overlap among Franklin's ground squirrel close female kin reduces access of conspecifics to their core areas regardless of relatedness, which suggests strict female territoriality within female core areas during each distinct period of their annual reproductive cycle. Female close-kin Franklin's ground squirrels did not, however form matrilineal kin clusters, though they may maintain some degree of social tolerance within their home range, consistent with the notion that Franklin's ground squirrel sociality may not be restricted to amicable interactions with close-kin.

Finally, I investigated whether females selectively cluster nests with close female kin both during the overall lactation period or selectively toward the end of the lactation period. Close female kin did not cluster nests with close female kin during the lactation period or toward the end of the lactation period of the annual reproductive cycle. There was a strong trend toward aggregation of close female kin during early lactation and avoidance of close female kin during late lactation in this population. Unlike females, male close-kin maintained nest burrows that were spatially remote to the nest of their mothers, suggesting that the dispersal of male kin at least in part functions to promote inbreeding avoidance. Additionally, a dam (with all male offspring) moved extraordinary distances (several km) during the post-weaning period. This suggests that dispersal resulting in inbreeding avoidance in the subsequent breeding season may not be limited to males. In most species, close-kin tend to cluster nests as a means to protect emerging young from infanticidal conspecifics. This was not evident between closely-related

Franklin’s ground squirrels, suggesting limited sociality, consistent with their designation as an asocial species.

Taken together, my findings support the assertion that Franklin’s ground squirrels are relatively asocial, maintain social distancing, and defy the general rule of female philopatry among ground squirrels. Empirical studies of additional populations of Franklin’s ground squirrels are required to address the generality of my findings, and to document the extent of intraspecific variation in home range and core area size and overlap. Studies of multiple populations may also allow the identification of ecological factors contributing to intraspecific variation in space use by members of this species, further contributing to our understanding of sociality, and providing potentially useful insights into the factors critical to the conservation of Franklin’s ground squirrels.

Appendices

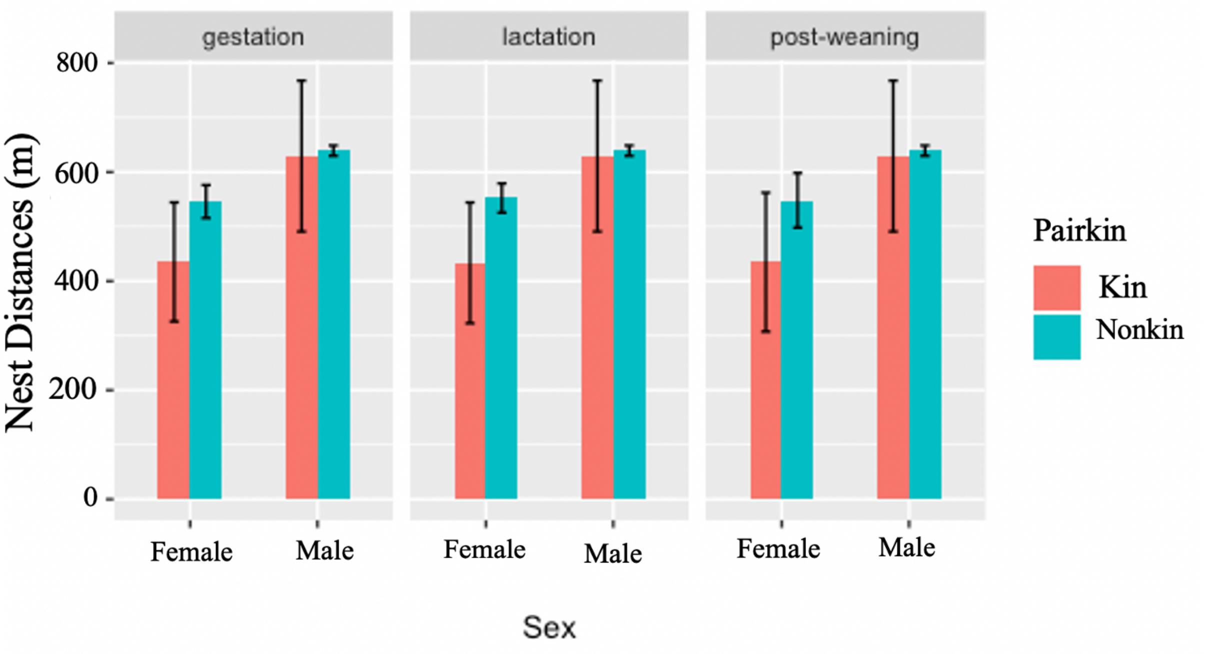

Figure A.1. Spatial distribution of average nest distances (mean ± SE) between close-kin ($n_{\text{kin groups}} = 4$) neighbours and non-close-kin neighbours ($n_{\text{nonkin}} = 9$) on the Inkster site during the overall active season (two-tailed t-test, $t_{392} = 0.64$, $p = 0.52$). Mean distance between close-kin pairs was 480 ± 353.5 m, while mean distance between close-kin and non-close-kin was 555 ± 271.5 m.