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Several studies have examined individual mating behaviors of wild peromyscine rodents. Many of these studies were short term and were limited to a single population in a single breeding season, so it is not clear to what extent mating behaviors vary within these populations over time. Therefore, I assessed mating behavior over four years (2003-2006) in short season populations of deer mice (*Peromyscus maniculatus*) from the Kananaskis Valley in Alberta Canada. In addition, I examined variation in home range size, home range overlap, and frequency of multiple mating within populations over time with respect to population density. I found that spatial behaviors varied over time but patterns of genetic mates did not. Behavioral changes did not correlate with changes in population density. My results suggest that male and female spatial behaviors and patterns of genetic mates may be more influenced by resource availability and mate choice than mate availability.

**A GENETIC AND BEHAVIORAL ANALYSIS OF INTRASPECIFIC
VARIATION IN MATING BEHAVIOR OF DEER MICE
(*PEROMYSCUS MANICULATUS*)**

by
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CHAPTER I

INTRODUCTION

Variation in mating behaviors of individuals in a population and the intrinsic and extrinsic factors that influence them are important for understanding basic population dynamics and the evolution of social behaviors. Understanding the extent of variation in behavior affords insight for understanding the overall plasticity of social behavior. Behavioral variation of individuals is a potential adaptive attribute to promote reproductive success, especially in those species such as small rodents that naturally possess high reproductive potential and exist in unpredictable environments (Lott 1991). Variation in reproductive or mating behaviors could be mediated by mate choice (Gowaty et al. 2003, Rolland et al. 2003, Fitze et al. 2005, Spence et al. 2006) and/or related to demographic and ecological factors such as population density, resource distribution and habitat type (Wolff 1985, Ribble & Salvioni 1990, Reynolds 1996, Petrie & Kempenaers 1998, Spence et al. 2006).

Understanding how mate choice promotes or constrains changes in behavior helps to explain the evolution of behavioral characteristics in an organism (Fitze et al. 2005, Duckworth 2006, Spence et al. 2006). Female and male house mice (*Mus musculus* and *Mus domesticus*) have expressed mating preferences in laboratory studies. Female house

mice (*Mus musculus*) prefer to mate with socially dominant males (Rolland et al. 2003). Male house mice (*Mus domesticus*) that mate with females they choose have higher reproductive success and sire more litters in comparison to males who are not given a choice (Gowaty et al. 2003). A field study to investigate the effects of sex ratio on multiple-partner mating in common lizards (*Lacerta vivipara*) shows that the frequency of polyandry is more heavily influenced by mate choice rather than by changes in sex ratio of the population (Fitze et al. 2005). In promiscuous mating systems, whether or not a male or female is selective can influence extra-pair paternity and ultimately reproductive success.

In addition to mate choice, demographic and ecological factors can influence mating behaviors. Population density can influence home range size and overlap. The relationship between home range size and overlap and population density differs in small mammals; in some species there is a positive correlation, in some a negative correlation, while in others home range size and overlap are independent of population density (Taitt & Krebs 1981, Schoener & Schoener 1982, Erlinge et al. 1990, Ribble & Salvioni 1990, Batzli & Henttonen 1993, Travis et al. 1995, Priotto & Steinmann 1999, Priotto et al. 2002, Schradin & Pillay 2005). For example, male home range size decreases when population density increases in *Peromyscus californicus* (Ribble & Salvioni 1990), but in contrast, home range size of the singing vole (*Microtus miurus*) is independent of population density (Batzli & Henttonen 1993). Demographic and ecological factors can influence home range characteristics which could influence patterns of genetic mates by altering the number of accessible mates.

Population density is usually linked with ecological factors such as resource distribution and habitat type that influence intraspecific variation in behaviors. For example, a habitat with abundant food resources could lead to higher reproductive success among resident individuals and also could attract immigrants, resulting in an increase in population density and changes in home range characteristics (Taitt 1981, Taitt & Krebs 1981).

Resource distribution is associated with size, composition, and mating behavior of populations (Travis et al. 1995). For example, resource distribution (patchy vs uniform) determines the occurrence of monogamous vs polygynous mating behavior displayed by individuals within prairie dog (*Cynomys gunnisoni*) populations (Travis et al. 1995). Resource distribution influences home range size and immigration rates in deer mouse (*Peromyscus maniculatus*) and vole (*Microtus townsendii*) populations (Taitt 1981, Taitt & Krebs 1981) which can have an affect on the mating behavior of individuals in a population.

Habitat type can influence social organization and mating behavior of individuals. For example, in African striped mice (*Rhabdomys pumilio*) habitat type is known to influence the occurrence of polygynous vs promiscuous mating behavior (Schradin & Pillay 2005). For African striped mice, home range sizes are larger and reproductive activity occurs earlier for both males and females in the grassland habitat (which has lower population density) than in the succulent karoo habitat (which has higher population density). Habitat type can influence home range size, home range overlap,

dispersal, and duration of breeding seasons of small mammals, as seen in African striped mice (Schradin & Pillay 2005).

The purpose of my study is to examine variation in mating behavior that occurs within three wild populations of deer mice (*Peromyscus maniculatus*), that exist in the same habitat type, to investigate 1) variation in mating behavior (in terms of home range size, home range overlap, frequency of polyandry, and frequency of polygyny) between breeding seasons, and 2) the effects of population density on mating behaviors. Home range size and home range overlap are treated as mating behaviors with respect to interactions between individuals. The frequency of polyandry and the frequency of polygyny refer to patterns of genetic mates. Deer mouse mating behavior is promiscuous and females and males display social and genetic polyandry and polygyny.

I hypothesize that there will be differences in behaviors within a population over time and that these differences will correlate with population density. I predict that population density will be negatively correlated with home range size, and positively correlated with frequency of polyandry and polygyny.

CHAPTER II

METHODS

Study organism

The genus *Peromyscus* has played a major role as a model organism in mammalian evolution, reproductive physiology, and behavioral ecology (Kirkland & Layne 1989). *Peromyscus* is found in a large variety of terrestrial habitats (Kirkland & Layne 1989), and display a wide range of genetic, morphological, physiological, and behavioral variation (Kirkland & Layne 1989).

Deer mice (*Peromyscus maniculatus*) are one of the most abundant species of the genus *Peromyscus*, and the species is one of the most well studied mammals in North America (Kirkland & Layne 1989). Deer mouse mating behaviors are typical of those displayed in promiscuous mating systems. Deer mice are considered to be the least likely *Peromyscus* species to display monogamous mating behavior (Birdsall & Nash 1973, Millar et al. 1985, Wolff 1989, Wolff 1993, Ribble & Millar 1996, Ribble et al. 2002, Avise 2004, Kalcounis-Rüppell & Ribble in press). Despite the large numbers of studies that that investigate rodent mating behavior, little is understood about the natural variation in mating behavior that occurs in wild deer mouse populations or the effect of population density on deer mouse mating behavior.

Field methods

Study site

The mice were studied in the Kananaskis Valley (51°N, 115°W) located in the front range of Rocky Mountains in Alberta, Canada; the area consists of three main habitat types: subalpine meadow, alpine meadow and talus rock fields. Deer mice in the study area are most abundant in the talus rock fields. The talus rock field habitat is located along the tree line, and the main feature is the dominance of rock over plant cover (Millar et al. 1985).

Study grids

Three long-term trapping grids, Grizzly (Figure 1a), Fortress (Figure 1b), and Lorette (Figure 1c), have been established in the study site since 1979. The grids were geo-referenced and mapped in ArcView GIS. All three grids are located in the same valley of the Kananaskis River drainage system. The distance between Grizzly and Lorette is approximately 25 km, the distance between Lorette and Fortress is approximately 20 km, and the distance between Fortress and Grizzly is approximately 5 km. The traps on each of the grids were spaced approximately 20 m apart. Each grid area included the area covered by the traps plus a buffer surrounding the entire grid that is equal to half of the inter-trap distance (approximately 10 m). The grid sizes, including the 10m buffer, ranged from 1.42-1.77 hectares (ha).

Live trapping methods

During the study period, mice were captured using Longworth live traps baited with rolled oats from early May through mid August (the summer breeding season) in the years 2003-2006. Upon first capture, individuals were ear-tagged and two (2 mm) ear punches were collected and stored in 95% ethanol. Trapped individuals were examined and the following data recorded: ear-tag number, sex, weight, age, and reproductive condition. The grids Grizzly and Lorette were live trapped for three consecutive days each week alternating between the grids in 2003. The grids Grizzly and Fortress were live trapped two days each week alternating between the grids each day in 2004 and 2005. All three grids were trapped two days each week alternating between the grids each day in 2006: Lorette and Fortress were trapped on the same days, and Grizzly was trapped on the alternate days in 2006. All field methods were conducted in accordance with the regulations set forth by the Canadian Council for Animal Care.

Population density

The live trapping data were transcribed into a capture-history record format which consists of a contiguous series of ones and zeros that represent trapping events. The data were then entered into the program JOLLY (Jolly 1965) which uses the Jolly-Seber model to compute an estimate of population size and probability of capture in open populations for one age class. To estimate population density, the mean estimate of population size for each trapping period was divided by the area of each grid. All reproductive individuals that were trapped during at least three trapping periods were included in the density estimates.

Parentage analysis

Laboratory methods

Genomic DNA was extracted from one ear punch of each individual tissue sample using a DNeasy[®] Tissue Kit (QIAGEN). Seven microsatellite loci (Chirhart et al. 2000, Table 1) were amplified in 25 μ L polymerase chain reactions (PCRs) using an Eppendorf Mastercycler Gradient Thermocycler. Cycling conditions for PCRs were one three-minute denaturation cycle at 95°C, 30 one-minute denaturation cycles at 95°C, 30 one-minute cycles at annealing temperature, 30 two-minute extension cycles at 72°C, and one eight-minute final extension cycle at 72°C. The PCRs consisted of approximately 6 ng of template DNA, 1X Taq buffer with Mg²⁺ (Eppendorf; 500mM KCl, 100mM Tris-HCl pH 8.3 at 25°C, 15mM Mg(OAc)₂), 1.25 units Taq DNA Polymerase (Eppendorf), 0.4 μ M primer (0.2 μ M forward and 0.2 μ M reverse), and 0.1 mM dNTP. To ensure that amplification of the target fragment of DNA occurred, 5 μ L of PCR product and a 100 base pair DNA step ladder (Promega) were run on a 1% agarose gel in 1X TBE buffer. The agarose gel was then stained using SYBR[®] Gold nucleic acid gel stain (Invitrogen[™] Molecular probes[™]) and viewed on an illuminator. This procedure was carried out on a subset of samples for all loci.

Samples were desalted using Milipore MultiScreen[™] dialysis plates (pore size 0.05 μ m) in 0.1X TE buffer for approximately 20 minutes, and an in-lane size standard (ET 400-ROX; GE Healthcare) was added to each sample prior to loading in a MegaBACE[®] 500 Automated DNA Sequencer. Fragment sizes were determined using Fragment Profiler[®] software based on electropherograms produced by the sequencer.

Determination of parentage

Each microsatellite locus was tested for Hardy-Weinberg equilibrium using GENEPOP (Pollock et al. 1990). GENEPOP performs an exact test of Hardy-Weinberg proportion for multiple alleles by utilizing a Markov Chain method.

The parentage analysis program CERVUS 2.0 (Marshall et al. 1998), was used to determine frequency of multiple mating and observed and expected heterozygosity. CERVUS 2.0 calculates the maximum probability of progeny assignments to potential parents based on allele frequencies and accounts for potential non-amplifying alleles and missing data. The parent-offspring assignments are estimated using randomization to assess the statistical significance of each match.

Parent-offspring matches were generated using CERVUS 2.0 and were supported by the trapping records. The offspring assigned to each dam, based on the CERVUS 2.0 data and the trapping records, were grouped into litters after taking into account the date and location of first capture for the offspring relative to the date of parturition and home range location of the assigned dam. After the dams were assigned to the offspring CERVUS 2.0 was used to assign sires to the offspring using a data file that included the respective dam as a known parent to the offspring. For the parentage analysis the simulation cycle was conducted using 10,000 cycles at a 1% frequency of typing error. The average percentage of loci typed was 90%. The proportion of candidate parents sampled was 85% due to the possibility that there were some parents that DNA samples were not collected for or that were not trapped during the study period.

Parentage analysis was conducted for individuals trapped in the years 2003 and 2006. The years 2004 and 2005 were not included in the parentage analysis due to insufficient DNA sampling.

Study variables

Seven dependent variables and three independent variables were used in the statistical analyses. The dependent variables used in the statistical analysis were 1) *home range size*, 2) *number of overlapping females*, 3) *number of overlapping males*, 4) *percentage of home range overlapped by the home range of females*, 5) *percentage of home range overlapped by the home range of males*, 6) *frequency of polyandry* and 7) *frequency of polygyny*. The independent variables used in the statistical analyses were 1) *grid*, 2) *year*, and 3) *population density*.

Home range size (HRS) refers to a measure of the area (in hectares) within which an individual was trapped. *HRS* was determined by mapping the live trapping data on the three geo-referenced trapping grids Grizzly, Lorette, and Fortress in Arc View GIS. Animal Movement software (SA v2.04beta) was used to calculate kernel home range estimates for each resident individual. An individual was considered to be a resident if that individual was sexually reproductive and resident on the grid for at least three trapping periods (≈ 14 days) during the breeding season (as in Millar & McAdam 2001).

Number of overlapping females and *number of overlapping males* refers to the number of individuals that overlapped with the home range of a particular individual and accounts for female-female, male-male, female-male, and male-female overlapping individuals (Figure 2a). Kernel home range estimates were used to determine the *number*

of overlapping females and the *number of overlapping males* by intersecting a pair of kernel home range estimates using the X Tools extension in ArcView GIS.

Percentage of home range overlapped by the home range of females and *percentage of home range overlapped by the home range of males* refers the percentage of an individual's home range that was overlapped by other individuals, and accounts for female-female, male- male, female-male and male-female overlapping individuals (Figure 2b). The *percentage of home range overlapped by the home range of females* and the *percentage of home range overlapped by the home range of males* was determined by intersecting the Kernel home range estimates using the X Tools extension in ArcView GIS. The average percentage of an individual's home range that was overlapped by males and females was determined by building a matrix that consisted of all individuals and the area of their home ranges that were overlapped by other individuals. The average percentage of each individual's home range that was overlapped by males and by females was used in the statistical analyses. Figure 3 shows examples of male and female home range size and overlap on the grids Grizzly and Lorette in the year 2003 and the grid Fortress in the year 2004.

Frequency of polyandry refers to the percentage of resident adult females on a grid that produced offspring with more than one male during the breeding season. Those females that weaned more than one litter in a breeding season were considered polyandrous if at least one of the litters was sired by multiple males. *Frequency of polygyny* refers to the percentage of resident adult males on a grid that produced offspring

with more than one female on the grid during the breeding season. The variables *Frequency of polyandry* and *Frequency of polygyny* refer to patterns of genetic mates.

The independent variables used in the statistical analysis were *grid*, *year* and *population density*. *Grid* refers to the trapping grids Grizzly, Fortress, and Lorette. *Year* refers to the years 2003-2006. *Population density* refers to the number of resident individuals per hectare that were present on the trapping grids in each year.

Statistical analyses

Home range and parentage statistics were completed using the statistical analysis program SPSS v.14. A simple linear regression analysis (stepwise) of individual behaviors in all grids and years for resident males and females was used to determine if variation in spatial behaviors relate to grid, year, and population density. A binary logistic regression analysis was conducted to determine if variation in the frequency of multiple mating was related to grid, year and population density. A power analysis was conducted on the binary logistic regression associated with the frequency of polyandry and the frequency of polygyny to determine if sample sizes were too low to detect significant *grid* and *year* effect.

CHAPTER II

RESULTS

Sampling

Resident adults were each present for only one of the years of the study, so each mouse is accounted for only once. On average there were eight resident females, and nine resident males present on the grids during the study period (Table 2). In 2003 and 2006 a total of 81 offspring were assigned parentage (Table 3). All 81 offspring were assigned to dams, however genetic information was not available for the sires of 14 offspring (Table 3). On average there were 3.6 females per site that successfully weaned litters, 5.4 males that successfully sired offspring (Table 4) on the grids during the study period. The number of loci scored for each parent offspring match can be seen in Table 5. Not every locus was in Hardy-Weinberg equilibrium for each year and grid combination, therefore the number of loci used to determine parentage differed among grids and years (Table 6).

There were a total of 22 litters (Table 4) that were assigned to parents in 2003 and 2006. Twelve (55%) of 22 litters were sired by multiple males and 10 (45%) of 22 litters were sired by a single male (Table 4). The frequency of polyandry ranged from 40% to 100% and the frequency of polygyny ranged from 0% to 33% on the grids (Table 4)

Individual estimates of home range size, number of overlapping individuals, and percentage of home range overlap were used in the statistical analyses, however the means of the behaviors are representative of the trends observed on the individual level

and can be seen in Table 7. Population density ranged from 4.22 to 8.47 resident individuals per hectare (Table 7) on the study grids. Throughout the study period Grizzly had a higher population density and Fortress had a lower population density, and Lorette was intermediate.

Spatial behaviors in relation to grid, year, and population density

Home range area, *HRS*, was transformed to the natural log (ln) for statistical analysis to correct for outliers. For females, variation in ln*HRS* was best explained by grid ($y = -0.753 - 0.642 \text{ grid Grizzly}$, $df = 69$, $F = 6.102$, $p = 0.016$, $R^2 = .082$, $R^{2adj} = 0.069$). Females on Grizzly had a smaller HRS than females on Fortress and Lorette (Figure 4a). For males, variation in ln*HRS* was best explained by grid ($y = -0.294 - 0.667 \text{ grid Grizzly}$, $df = 81$, $F = 10.276$, $p = 0.002$, $R^2 = .114$, $R^{2adj} = 0.103$). Males on Grizzly had a smaller HRS than males on Fortress and Lorette (Figure 4b)

For females, variation in *number of overlapping females* was best explained by grid ($y = 1.636 + 3.164 \text{ grid Grizzly} + 6.864 \text{ grid Lorette}$, $df = 66$, $F = 39.178$, $p = 0.000$, $R^2 = 0.550$, $R^{2adj} = 0.536$). Female-female overlap was highest on Lorette, lowest on Fortress and intermediate on Grizzly (Figure 5a). For males, variation in *number of overlapping males* was best explained by year ($y = 6.850 - 2.433 \text{ year 2005} + 1.559 \text{ year 2004}$, $df = 73$, $F = 16.740$, $p = 0.000$, $R^2 = 0.320$, $R^{2adj} = 0.301$). Male-male overlap was highest in the year 2004, lowest in the year 2005, and intermediate in the years 2003 and 2006 (Figure 5b).

For females, variation in *number of overlapping males* was best explained by grid ($y = 6.304 + 1.321 \text{ grid Lorette}$, $df = 69$, $F = 4.779$, $p = 0.032$, $R^2 = 0.066$, $R^{2adj} = 0.052$).

Male-female overlap was higher on Lorette than on Fortress and Grizzly (Figure 6a). For males, variation in *number of overlapping females* was best explained by grid and year ($y = -0.139 + 9.668 \text{ grid Lorette} + 4.768 \text{ grid Grizzly} + 3.422 \text{ year 2005} + 2.307 \text{ year 2004} + 1.349 \text{ year 2006}$, $df = 77$, $F = 37.717$, $p = 0.000$, $R^2 = 0.724$, $R^{2\text{adj}} = 0.705$). Female-male overlap was highest on Lorette, lowest on Fortress and intermediate on Grizzly (Figure 6b). Female-male overlap varied in each year and was highest in the year 2005 and lowest in the year 2003 (Figure 6b).

For females, variation in *percentage of home range overlapped by the home range of females* was best explained by grid and year ($y = 25.075 + 15.309 \text{ year 2005} - 8.805 \text{ grid Grizzly}$, $df = 66$, $F = 13.293$, $p = 0.000$, $R^2 = 0.293$, $R^{2\text{adj}} = 0.271$). Female-female overlap was lower on Grizzly than on Fortress and Lorette (Figure 7a). Female-female overlap was higher in the year 2005 than in the years 2003, 2004, and 2006 (Figure 7a). For males, variation in *percentage of home range overlapped by the home range of males* was best explained by grid ($y = 35.526 - 11.540 \text{ grid Grizzly}$, $df = 76$, $F = 18.615$, $p = 0.000$, $R^2 = 0.199$, $R^{2\text{adj}} = 0.188$). Male-male overlap was lower on Grizzly on comparison to Fortress and Lorette (Figure 7b).

For females, variation in *percentage of home range overlapped by the home range of males* was best explained by grid and year ($y = 23.402 + 20.590 \text{ Grid Lorette} + 14.705 \text{ year 2005}$, $df = 63$, $F = 22.471$, $p = 0.000$, $R^2 = 0.424$, $R^{2\text{adj}} = 0.405$). Male-female percent overlap was higher on Lorette than on Fortress and Grizzly (Figure 8a). Male-female overlap was higher in the year 2005 than in the years 2003, 2004, and 2006 (Figure 8a). For males, variation in *percentage of home range overlapped by the home range of*

females was best explained by year ($y = 23.364 + 13.900 \text{ year } 2005 - 9.684 \text{ year } 2004$, $df = 77$, $F = 27.500$, $p = 0.000$, $R^2 = 0.423$, $R^{2adj} = 0.408$). Female-male overlap was higher in the year 2005, lower in the year 2004, and intermediate in the years 2003 and 2006 (Figure 8b).

Spatial behaviors of the deer mice studied were not significantly influenced by population density, both as measured by HRS and by overlapping home ranges. Refer to Table 8 for a summary of the simple linear regression models.

Patterns of genetic mates in relation to grid, year, and population density

There were 18 females that produced litters (Table 4). There was no DNA collected for dam 2016 (Lorette, 2006), so the parent-offspring assignments associated with her (as seen in Table 3) are solely based on the trapping data. Those offspring assigned to dam 2016 were included in the CERVUS 2.0 parentage analysis and were not assigned to any of the other dams on the grid. Forty-one percent (33) of the offspring were assigned maternity with 95% confidence, 52% (42) of the offspring were assigned maternity with 80% confidence, and 7% (6) of the offspring were not assigned to a dam. The delta values for each parent-offspring assignment can be seen in Table 5. Frequency of polyandry ranged from 40% to 100% (Table 4) during the study period. In order to avoid multicollinearity, in the statistical analysis each independent variable, grid, year and population density, was tested one by one to determine if there was a significant effect. Variation in frequency of polyandry could not be explained by grid (*Grizzly* $df=1$, $Wald=0.116$, $p=0.773$; *Lorette* $df=1$, $Wald=0.000$, $p=1.000$), year (*2006* $df=1$, $Wald=1.70$, $p=0.191$), or population density ($df=1$, $Wald=0.764$, $p=0.382$).

There were 26 known males who sired offspring (Table 4), 42% (34) of the offspring were assigned paternity with 95% confidence, 41% (33) of the offspring were assigned paternity with 80% confidence, and 17% (14) of the offspring were not assigned to a sire. The delta values for each parent-offspring assignment can be seen in Table 5. Frequency of polygyny ranged from 0% to 40% (Table 4) during the study period. In order to avoid multicollinearity, in the statistical analysis each independent variable, grid, year and population density, was tested one by one to determine if there was a significant effect. Variation in frequency of polygyny could not be explained by grid (*Grizzly* $df=1$, $Wald=0.271$, $p=0.602$, *Lorette* $df=1$, $Wald=0.096$, $p=0.757$), year (*2006* $df=1$, $Wald=.380$, $p=0.538$), or population density ($df=1$, $Wald=0.000$, $p=0.983$).

Frequency of polyandry and the frequency of polygyny were not related to grid, year, or population density, as reported in the previous paragraph. Results from a power analysis conducted on grid and year suggest that sample size could be affecting the outcome of the logistic regression. For frequency of polyandry, the power analysis indicated that the sample size was too small to detect a significant grid (*Grizzly* $power=0.078$; *Lorette* $power=0.050$) or year (*year 2006* $power=0.469$) effect. For frequency of polygyny, the power analysis indicated that the sample size was too small to detect a significant grid (*Grizzly*, $power=0.114$; *Lorette*, $power=0.072$) or year (*year*, $power=0.143$) effect.

CHAPTER IV

DISCUSSION

I found variation in spatial behaviors both between grids and years in the wild deer mouse populations with little variation in patterns of genetic mates. I found that female and male HRS, overlap, and frequency of multiple mating was independent of population density.

Home range size and home range overlap of the deer mice in this study were not significantly influenced by population density. Variation in the spatial behaviors of females and males was best explained by grid and/or year effects; however small coefficient of determination values (R^2) associated with most of the regression models suggest that factors other than grid and year were influencing spatial behavior. Patterns of genetic mates (frequency of polyandry and polygyny) were not influenced by population density, and were not variable between grids or years. This suggests that spatial behaviors in the study populations were more flexible than patterns of genetic mates and that factors other than mate availability were influencing patterns of genetic mates.

Females had smaller home ranges and less intrasexual overlap than did males. The sex differences observed during the study period were similar to those observed in previous studies of deer mouse populations (Ribble & Millar 1996) and mammals in general (Erlinge et al. 1990, Priotto & Steinmann 1999, Schradin & Pillay 2005). The

results of this study demonstrate natural variation in behaviors of individuals between populations and years, differences in female and male spatial behaviors. It also demonstrates the possibility of mate choice influencing patterns of genetic mates in deer mice by showing that many of the individuals on the grids produced offspring with only one or two mates when the number of available mates ranged from 4-10 for females and males over the study period.

Home range size and overlap

HRS and overlap for the deer mice in this study are similar to those observed by Ribble and Millar (1996) who used radiotelemetry to assess the mating system of deer mice in the same study area (Kananaskis Valley). Using radiotelemetry Ribble and Millar (1996) found that the average HRS for females was 0.62 ha and the average HRS for males was 1.18 ha. I found that the average HRS for females and males were 0.58 ha and 0.87 ha, respectively. In comparison to radiotelemetry, when using trapping data the average home range sizes calculated are usually smaller, however they are still considered to be an accurate representation of HRS (Andrejewski 2002).

In my study, female and male variation in HRS could be explained by grid differences. Resource distribution and abundance influence the HRS of deer mouse (Taitt 1981); vole (Taitt 1981, Taitt & Krebs 1981); roe deer, *Capreolus capreolus* (Tufto et al. 1996); bandicoot, *Isodon obesulus* (Dickman & Broughton 1991); and lizard, *Sceloporus jarrovi* (Simon 1975) populations. Taitt (1981) found that HRS of deer mice in food-supplemented grids decreased significantly in relation to that observed on control grids; however there was also a substantial amount of immigration into the supplemented

grids. This demonstrates a link between population density and food availability. Males and females on Grizzly had smaller HRS and higher population densities in comparison to Fortress and Lorette; even though the relationship between HRS and population density was not statistically significant, these data suggest that despite similarities in habitat type, Grizzly may have had higher food availability than Fortress and Lorette.

Studies have shown that home range overlap in mammals can be influenced by food availability, food distribution, population density and seasonality (Erlinge et al. 1990, Priotto & Steinmann 1999, Maher & Lott 2000, McLoughlin et al. 2000, Priotto et al. 2002). In terms of the number of overlapping individuals, females on Lorette were more tolerant of each other than were females on Fortress, and Grizzly. Males were less tolerant of each other in the year 2005 than in the other years. Females and males on Grizzly shared a lower percentage of their home range with members of the same sex in comparison to Fortress and Lorette. Females on all study grids had smaller home ranges and less intrasexual overlap than did males. I found that female and male variation in home range overlap was best explained by grid and/or year effects. Among mammals, the potential for promiscuous mating is mediated by the degree to which accessing multiple mates and/or the resources crucial to gaining multiple mates are economically defensible (Orlans 1969, Emlen & Oring 1977). Females having smaller home range sizes and less intrasexual overlap than males is typical in mammals because, in most cases, females are responsible for most, if not all, of the parental care and their reproductive success depends on the resources needed for the energetic costs associated with lactating and rearing young. In contrast, male reproductive success depends on access to reproductive

females (Emlen & Oring 1977, Reynolds 1996, Kalcounis-Rüppell & Ribble in press). The mice on my study grids were in the same habitat type and therefore grid and year differences in home range overlap should be due to differences in resource availability between grids and years.

Patterns of genetic mates

Studies that have investigated patterns of genetic mates of *Peromyscus* show that on average 17%-40% of deer mouse litters born were sired by multiple males (Birdsall & Nash 1973, Ribble & Millar 1996). There were 22 total litters weaned during the study period and 12 (55%) litters were sired by multiple males. This indicates that the deer mice were promiscuous in their mating behavior, which agrees with previous studies. The number of weaned offspring on the grids in each year ranged from nine to 25 and is similar to those seen in previous studies on the same trapping grids (Kalcounis-Rueppell et al. 2002).

Grid, year and population density did not relate to the frequency of polyandry or frequency of polygyny. This suggests that there was no difference in male and female mating behavior between grids and years. The mean number of overlapping individuals of the opposite sex ranged from approximately 4 to 10 for females and males over the study period. Although there were multiple available mates, many of the dams and sires produced offspring with only one or two mates. These results suggest that mate choice may have more heavily influenced the mating behavior of the deer mice in comparison to demographic factors as seen in house mice (*Mus musculus*), common lizards (*Lacerta vivipara*) and zebra fish (*Danio rerio*) (Rolland et al. 2003, Fitze et al. 2005, Spence et al.

2006). This suggests that something other than mate availability was influencing patterns of genetic mates in the deer mouse populations studied.

There is evidence that mate choice is an important factor in mating systems because it results in offspring of high genetic quality and viability (reviewed in Neff & Pitcher 2005). Several biological mechanisms have been attributed to explain why females in non-resource based mating systems are choosy when selecting mates, such as ‘good genes’ and the major histocompatibility complex (MHC; a multi-gene family that plays a major role in immune response). Morphological and/or behavioral traits in mates that reflect their fitness are thought to influence mate choice (Orians 1969). Males that have more attractive secondary sexual characteristics have been shown to produce more viable offspring (Møller & Alatalo 1999), and MHC has been shown to be positively associated with secondary sexual characteristics (Ditchkoff et al. 2001). For example, in male white tailed deer (*Odocoileus virginianus*) particular MHC genotypes are positively associated with antler development and body mass, suggesting that larger antler size and greater body mass may be an indication of parasite and disease resistance and reflects the genetic quality of a male (Ditchkoff et al. 2001). In my study, there were several males that were more successful, in terms of the number of offspring sired, than others. For example males 5253 (Lorette 2003), and 8135 (Grizzly 2006) sired more offspring than other males on their respective grid even though their home range sizes and the number of females that overlapped their home ranges were similar to the other males on the grid. This suggests that the more successful males may have been more attractive to the females than were the other males.

Throughout the study period the frequency of polyandry was consistently higher than the frequency of polygyny. In general polyandry tends to occur when females are less abundant than males and polygyny when males are less abundant than females. Emlen and Oring (1977) suggest that in order to understand the impact of mate choice on mating behaviors in animals, one must look beyond the overall female to male sex ratio and consider operational sex ratios (OSR) which is the mean ratio of females in estrus to sexually active males at any given time. During the breeding season female deer mice are poly-estrous, however they only remain in estrous for approximately five days at a time and males are continuously ready to mate. The frequency of polyandry being consistently higher than the frequency of polygyny throughout the study period could mean that overall, females in estrous were less available than sexually active males at any given time during the breeding season.

Implications and importance

There have been many studies that have focused on wild populations of peromyscine rodent species (Millar et al. 1979, Kaufman & Kaufman 1982, Millar & Innes 1983, Millar & Innes 1985, Millar & McAdam 2001, Mossman & Waser 2001, Kalcounis-Rueppell et al. 2002, Kamler & Pennock 2004, Millar & Herdman 2004). Phylogenetic analyses have shown that the ancestral character state of peromyscine rodents is promiscuity with monogamy evolving independently multiple times (Kalcounis-Rüppell & Ribble in press). There is a basic understanding of how mating behavior evolved within this group of rodents (Kalcounis-Rüppell & Ribble in press), but little is understood about natural variation that occurs within and between populations of

peromyscine rodent species. This variation is fundamental to the evolution of mating behaviors in wild populations and therefore critical for our basic understanding of mating system evolution in mammals.

I found variation in spatial behaviors both between grids and years in the wild deer mouse populations with little variation in genetic mating patterns. I found that population density was independent of female and male HRS, overlap, and frequency of multiple mating.

The low R^2 values in some of the regression analyses show that although some variation in spatial behaviors could be explained by grid and by year effects, there were other factors that influenced the behaviors of the deer mice. The individuals in the populations studied were exposed to similar ecological conditions, which means that changes in behaviors may have been associated with factors such as resource distribution and abundance between grids and years.

Population density has been shown to influence HRS in *Peromyscus*. Previous field studies on *Peromyscus maniculatus*, *Peromyscus leucopus*, and *Peromyscus californicus* populations (Wolff 1985, Ribble & Salvioni 1990) have shown an association between HRS and population density. Wolff (1985) found that HRS was significantly reduced in high density populations of *Peromyscus leucopus*, and although not significant, negative associations were observed between HRS and population density in *Peromyscus maniculatus* populations. Ribble and Salvioni (1990) found evidence of male *Peromyscus californicus* HRS being negatively correlated with population density. However, in the previously mentioned studies population densities

were more extreme than those typically estimated at my study site (Millar & McAdam 2001). The population densities in my study changed from year to year and grid to grid, however the differences in population densities may have not been extreme enough to promote changes in HRS of the deer mice.

This study contributes to the understanding of the evolution of behavioral characteristics in peromyscine rodents by showing that in the deer mice studied spatial behaviors are more flexible than patterns of genetic mates and that mate choice may be influencing patterns of genetic mates within populations.

Future directions

Along with natural variation in breeding behaviors, little is known about juvenile dispersal and recruitment, and gene flow that occurs in natural populations of peromyscine species. Furthermore, questions remain regarding mate quality, mate choice, and the influence of OSR on mating behavior in natural populations of peromyscine species. Using the trapping records, demographic, and genetic data collected in my study, a lot of these questions can, and should be addressed in future studies.

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APPENDIX A. TABLES AND FIGURES

Table 1. A description of the seven microsatellite loci, primers and the associated annealing temperature (°C) used in the parentage analysis. All microsatellite locus primers used in the analysis were developed for deer mice by Chirhart et al. (2000).

Locus	Primers	Annealing Temperature (°C)
<i>Pml02</i>	F:GTACCAGGCATGAACATAGT R:GAATAATTTTCCGCTGTGT	43.2
<i>Pml03</i>	F:GCCATTAGTCTATGTGACAG R:GCGATGTACCCAGAAAT	48.4
<i>Pml04</i>	F:CATAAGGTGGCTCGGAATCA R:CAGGAAGGGGAAATGACCAT	48.4
<i>Pml06</i>	F:CAGGGCTGTAGAGGGAGAAC R:ACTGGAGCAGAGGCATTTG	53.8
<i>Pml07</i>	F:GCCTCTTGTACCCAGTGAAT R:TCCCATTTGGTGTACTTTTTG	43.0
<i>Pml09</i>	F:GAATCCATACACCCATGC R:TTGCTTTTCGTCAAGTTT	48.4
<i>Pml11</i>	F:ACCCCGAGTGCTGAGATT R:TTTGCTGCTTTCCCCAGAGA	56.5

Table 2. The number of resident males and females; number of dams; number of sires; number of offspring; and number of litters for each grid live trapped in 2003 (Grizzly, Lorette), 2004 (Fortress and Grizzly), 2005 (Fortress and Grizzly), and 2006 (Fortress, Grizzly and Lorette) during the summer breeding season in the Kananaskis Valley of Alberta Canada. The dams and sires are considered to be the parents of the offspring born on the grids.

Year	Resident males	Resident female	Number of sires	Number of dams	Number of offspring	Number of litters
2003						
Grizzly	6	7	5	3	14	4
Lorette	9	9	7	5	25	7
2004						
Fortress	11	4
Grizzly	13	12
2005						
Fortress	6	4
Grizzly	6	9
2006						
Fortress	8	5	3	2	9	2
Grizzly	12	7	6	4	19	5
Lorette	10	15	5	4	14	4
Total	81	72	26	18	81	22

Table 3. Dams, offspring, and sires for all grids in 2003 (Grizzly and Lorette) and 2006 (Fortress, Grizzly and Lorette). The offspring are grouped into litters. The asterisks indicate that there was no genetic information for the sire the offspring.

Grizzly 2003			Lorette 2003			Fortress 2006			Grizzly 2006			Lorette 2006		
Dam	Offspring	Sire	Dam	Offspring	Sire	Dam	Offspring	Sire	Dam	Offspring	Sire	Dam	Offspring	Sire
4684	5036	4889	909	5046	5233	8756	2320	2165	2485	1	2173	2016	2741	4804
	5039	5027		4856	5251		2316	2165		2731	2173		2406	*
				5409	5251		2235	2303		2509	7949		2413	*
4684	5413	4966					8761	2303		2543	8135		2456	*
	5415	4966	4801	5411	915								2458	*
	5430	4966		5405	915	8891	2319	8187					2460	*
				5419	915		2335	8187	4079	2006	8834			
4968	5401	*		4866	915		2343	8187		2020	*	7790	2132	8812
	4855	4882					2503	8187		2008	*		2153	7790
	4869	*	4876	5424	4823		4066	8187					2144	*
	4891	4836		5428	4823				8285	2168	8135			
	4897	*								2169	8135	8120	2148	4073
	5240	*	5269	4872	5266					2171	8135		2181	8812
	5403	*		5232	5266					4062	8135		2146	*
				4854	5266					8978	8135			
5054	5294	4836		5033	5266							8838	2111	4081
	4887	4836							8285	2729	8288		2409	4073
			5269	5435	4811					2468	8288			
				5443	5266					2490	8288			
				5445	5266					2470	8288			
										2417	8903			
			5303	4851	5253									
				4859	5253				8390	2101	8288			
				4860	5253					2122	8288			
				4862	5253									
				4895	5253									
				5043	5253									
			5303	5439	5253									
				5446	5253									
				5448	5253									

Table 4. Summary of parentage and mating behaviors as determined by genotyping, based on data for individuals given in Table 3 for the grids Grizzly and Lorette in the 2003 summer breeding season and the grids Fortress, Grizzly and, Lorette in the 2006 summer breeding season. Values are total numbers of dams, sires (of known genotype), and litters. The critical delta (Δ) criterion values generated by CERVUS parentage simulations are given. The confidence of parent offspring matches were based on the critical delta (Δ) criterion generated by the parentage simulations.

	2003		2006			Total
	Grizzly	Lorette	Fortress	Grizzly	Lorette	
Dams						
Polyandrous	2	2	1	3	4	12
Monogamous	1	3	1	1	0	6
Total	3	5	2	4	4	18
Δ Criterion 95%	1.29	1.18	1.13	1.26	1.56	.
Δ Criterion 80%	0.00	0.08	0.14	0.20	0.47	.
Sires (genotype known)						
Polygynous	1	0	0	2	2	5
Monogamous	4	7	3	4	3	21
Total	5	7	3	6	5	26
Δ Criterion 95%	1.28	1.15	1.43	1.30	1.34	.
Δ Criterion 80%	0.00	0.00	0.27	0.00	0.08	.
Litters						
With single sire	2	5	1	2	0	10
With multiple sires	2	2	1	3	4	12
Total	4	7	2	5	4	22
Mating behaviors (%)						
Polyandrous females	66	40	50	75	100	.
Polygynous males	20	0	0	33	40	.

Table 5. The number of loci scored and the Delta (Δ) value for each parent-offspring assignment for all grids in 2003 (Grizzly and Lorette) and 2006 (Fortress, Grizzly and Lorette). The offspring are grouped into litters. Note that DNA was not collected for dam 2016 on the Grid Lorette in 2006, and the mother offspring matches were solely based on trapping data. Those offspring assigned to dam 2016 were included in the CERVUS parentage analysis and were not assigned to any of the other dams on the grid. Those offspring assigned to dam 2016 based on the trapping data were 2741, 2406, 2413, 2456, 2458, and 2460. All parent-offspring assignments (except of those offspring assigned to dam 2016) shown are matched with 80% or 95% confidence. The asterisks indicate that there was no genetic information for parent(s) of the offspring. The symbol † indicates that the probability of assignment is $\geq 95\%$, all others have a probability of assignment $\geq 80\%$.

Grizzly 2003					Lorette 2003					Fortress 2006					Grizzly 2006					Lorette 2006				
Offspring	Dam	Δ	Sire	Δ	Offspring	Dam	Δ	Sire	Δ	Offspring	Dam	Δ	Sire	Δ	Offspring	Dam	Δ	Sire	Δ	Offspring	Dam	Δ	Sire	Δ
5036	3	0.05	3	0.46	5046	5	1.47†	5	0.80	2320	3	0.23	3	0.58	1	4	1.30†	4	2.93†	2741	*		5	1.22
5039	3	0.86	4	0.36	4856	5	1.26†	5	3.37†	2316	3	0.29	3	0.78	2731	6	1.16	6	2.01†	2406	*		*	
					5409	5	2.31†	5	4.72†	2235	3	0.54	2	1.67†	2509	5	0.26	6	0.48	2413	*		*	
5413	4	0.00	4	1.39†						8761	3	1.12	2	0.80	2543	6	0.92	4	1.17	2456	*		*	
5415	4	1.47†	5	2.56†	5411	3	1.55†	5	2.64†											2458	*		*	
5430	4	1.63†	4	1.60†	5405	2	1.20†	4	1.82†	2319	3	2.14†	3	0.48						2460	*		*	
					5419	3	0.98	5	1.13	2335	3	1.39†	3	1.67†	2006	5	0.67	5	0.63					
5401	5	1.97†	*		4866	3	0.26	5	1.76†	2343	3	0.33	3	0.41	2020	4	0.60	*						
4855	6	2.16†	6	0.81						2503	3	0.68	3	2.49†	2008	5	0.45	*		2132	4	0.93	4	0.59
4869	6	0.31	*		5424	4	0.69	4	4.34†	4066	3	1.29†	3	1.00						2153	5	1.87†	5	0.45
4891	5	0.13	4	0.59	5428	5	2.84†	5	3.40†						2168	4	0.93	4	1.40†	2144	4	0.80	*	
4897	6	2.04†	*												2169	5	0.79	4	0.38					
5240	6	2.33†	*		4872	5	0.7	4	2.00†						2171	4	0.57	4	3.55†	2148	5	2.18†	4	0.76
5403	5	2.01†	*		5232	5	1.08	4	2.00†						4062	3	1.40†	4	3.96†	2181	5	1.08	5	2.05†
					4854	5	0.17	4	2.25†						8978	3	0.99	3	1.43†	2146	5	1.83†	*	
5294	5	1.12	5	0.50	5033	5	1.09	4	3.60†															
4887	5	0.84	5	0.76											2729	5	0.38	5	0.51					
					5435	5	0.12	5	0.42						2468	3	2.06†	4	0.04	2111	4	1.92†	4	0.77
					5443	5	1.35†	4	1.42†						2490	4	0.83	5	0.27	2409	4	0.87	4073	0.16
					5445	5	1.19†	4	1.77†						2470	4	0.45	5	0.51					
															2417	4	0.51	5	0.44					
					4851	5	3.57†	5	3.59†															
					4859	4	2.79†	4	2.74†						2101	3	0.48	4	0.67					
					4860	5	3.45†	5	2.13†						2122	3	1.25	4	0.76					
					4862	5	2.37†	5	2.43†															
					4895	5	2.39†	5	4.70†															
					5043	5	1.67†	5	3.19†															
					5439	5	2.68†	5	4.08†															
					5446	4	2.60†	4	1.96†															
					5448	5	0.49	5	4.19†															

Table 6. Observed (H_{obs}) and expected (H_{exp}) microsatellite heterozygosity for individuals on the grids Grizzly and Lorette during the 2003 breeding season and individuals on the grids Grizzly, Fortress, and Lorette in the 2006 breeding season along with the associated Hardy-Weinberg equilibrium (HW) p-values. Those loci with a p-value ≥ 0.10 are considered to be in Hardy-Weinberg equilibrium.

	2003			2006		
	H_{obs}	H_{exp}	HW	H_{obs}	H_{exp}	HW
Grizzly						
<i>Pml02</i>	1.000	0.955	1.000	0.625	0.917	0.176
<i>Pml03</i>	0.846	0.855	0.168	0.769	0.871	0.209
<i>Pml04</i>	0.500	0.627	0.047	0.917	0.877	0.300
<i>Pml06</i>	0.857	0.913	0.769	0.833	0.913	0.105
<i>Pml07</i>	0.786	0.854	0.629	0.583	0.764	0.141
<i>Pml09</i>	0.556	0.882	0.147	0.600	0.916	0.006
<i>Pml11</i>	0.769	0.920	0.277	0.889	0.876	0.112
Total loci used	.	.	6	.	.	6
Fortress						
<i>Pml02</i>	.	.	.	0.650	0.799	0.012
<i>Pml03</i>	.	.	.	0.833	0.890	0.295
<i>Pml04</i>	.	.	.	0.950	0.926	0.659
<i>Pml06</i>	.	.	.	0.563	0.903	0.000
<i>Pml07</i>	.	.	.	0.600	0.837	0.004
<i>Pml09</i>	.	.	.	0.467	0.867	0.001
<i>Pml11</i>	.	.	.	0.895	0.909	0.106
Total loci used	3
Lorette						
<i>Pml02</i>	0.813	0.911	0.635	0.826	0.868	0.458
<i>Pml03</i>	0.947	0.910	0.799	0.870	0.885	0.360
<i>Pml04</i>	0.895	0.923	0.265	0.880	0.883	0.810
<i>Pml06</i>	0.947	0.913	0.504	0.826	0.899	0.140
<i>Pml07</i>	0.933	0.920	0.172	0.833	0.906	0.143
<i>Pml09</i>	0.294	0.875	0.000	0.600	0.822	0.017
<i>Pml11</i>	0.526	0.929	0.000	0.520	0.878	0.000
Total loci used	.	.	5	.	.	5

Table 7. Home range, number of overlapping individuals, and percentage of home range overlap for the grids Fortress, Grizzly, and Lorette during summer breeding seasons (2003-2006). Variables shown are home range size (HRS), number of overlapping individuals (NOI), percentage of home range overlap (PHO), and population density of residents on the grids. NOI and PHO were calculated for female and male overlapping. Data shown are the means \pm 1 SE.

		2003		2004		2005		2006	
		Female	Male	Female	Male	Female	Male	Female	Male
Grizzly	HRS (ha)	0.33 \pm 0.18	0.44 \pm 0.19	0.35 \pm 0.36	0.37 \pm 0.06	0.48 \pm 0.10	0.57 \pm 0.13	0.40 \pm 0.15	0.62 \pm 0.10
	NOI (females)	3.14 \pm 0.55	4.17 \pm 0.90	5.5 \pm 0.68	7.38 \pm 0.69	6.44 \pm 0.44	8.00 \pm 0.45	4.86 \pm 0.50	5.38 \pm 0.46
	NOI (males)	3.57 \pm 0.56	3.67 \pm 0.75	7.91 \pm 0.92	8.15 \pm 0.63	5.44 \pm 0.34	4.33 \pm 0.33	9.14 \pm 0.80	8.33 \pm 0.59
	PHO (females)	14.17 \pm 2.03	18.3 \pm 2.97	15.01 \pm 1.49	18.25 \pm 0.72	32.37 \pm 4.52	31.38 \pm 2.26	25.55 \pm 3.47	19.82 \pm 2.05
	PHO (males)	22.26 \pm 6.50	26.1 \pm 7.23	19.93 \pm 1.04	19.98 \pm 2.04	37.33 \pm 1.38	31.08 \pm 2.96	27.68 \pm 2.54	25.13 \pm 1.54
	Population density	8.47		7.04		5.60		6.20	
Fortress	HRS (ha)	.	.	0.47 \pm 0.30	0.89 \pm 0.28	1.11 \pm 0.36	1.49 \pm 0.52	0.66 \pm 0.18	0.99 \pm 0.34
	NOI (females)	.	.	1.50 \pm 0.50	1.63 \pm 0.24	2.50 \pm 0.29	3.33 \pm 0.33	1.00 \pm 0.00	2.33 \pm 0.24
	NOI (males)	.	.	4.75 \pm 1.03	8.09 \pm 0.53	5.25 \pm 0.48	4.50 \pm 0.34	5.50 \pm 0.29	5.22 \pm 0.59
	PHO (females)	.	.	24.00 \pm 11.39	11.50 \pm 3.84	38.63 \pm 11.05	43.15 \pm 7.68	16.27 \pm 5.69	30.84 \pm 5.44
	PHO (males)	.	.	26.56 \pm 7.63	34.51 \pm 3.46	32.92 \pm 3.70	36.86 \pm 5.60	32.52 \pm 3.66	29.87 \pm 5.37
	Population density	.		4.14		4.22		4.50	
Lorette	HRS (ha)	0.66 \pm 0.23	1.44 \pm 0.41	0.87 \pm 0.23	1.21 \pm 0.30
	NOI (females)	7.78 \pm 0.32	9.33 \pm 0.58	8.93 \pm 0.85	10.60 \pm 1.26
	NOI (males)	8.56 \pm 0.18	7.78 \pm 0.22	7.07 \pm 0.37	6.60 \pm 0.62
	PHO (females)	30.45 \pm 3.30	28.78 \pm 2.70	24.59 \pm 2.74	21.82 \pm 1.44
	PHO (males)	59.23 \pm 3.76	48.41 \pm 4.73	34.85 \pm 2.47	30.68 \pm 2.59
	Population density	8.10		.		.		5.90	

Table 8. Regression statistics for resident male and female spatial behaviors including the response variables, explanatory variables, degrees of freedom (df), F-statistic (F), coefficient of determination (R^2), and probability (p).

Female						
Response	Explanatory	df	F	R^2	p	
lnHRS	Grid	69	6.102	0.082	0.016	
Number of overlapping females; f-f	Grid	66	39.178	0.550	0.000	
Number of overlapping males; m-f	Grid	69	4.779	0.066	0.032	
Percentage of home range overlapped by females; f-f	Grid, year	66	13.293	0.293	0.000	
Percentage of home range overlapped by males; m-f	Grid, year	63	22.471	0.424	0.000	
Male						
lnHRS	Grid	81	10.726	0.114	0.002	
Number of overlapping males; m-m	Year	73	16.740	0.320	0.000	
Number of overlapping females; f-m	Grid, year	77	37.171	0.724	0.000	
Percentage of home range overlapped by males; m-m	Grid	76	18.651	0.199	0.000	
Percentage of home range overlapped by females; f-m	Year	77	27.500	0.423	0.000	

Figure 1. A schematic diagram of the grids Grizzly (a), Fortress (b), and Lorette (c). The closed circles represent each trap site, and the dotted lines represent the 10m buffer surrounding each grid. The grid sizes including the 10m buffer were 1.68ha, 1.42ha, and 1.77ha respectively. Each trap was spaced approximately 20m apart.

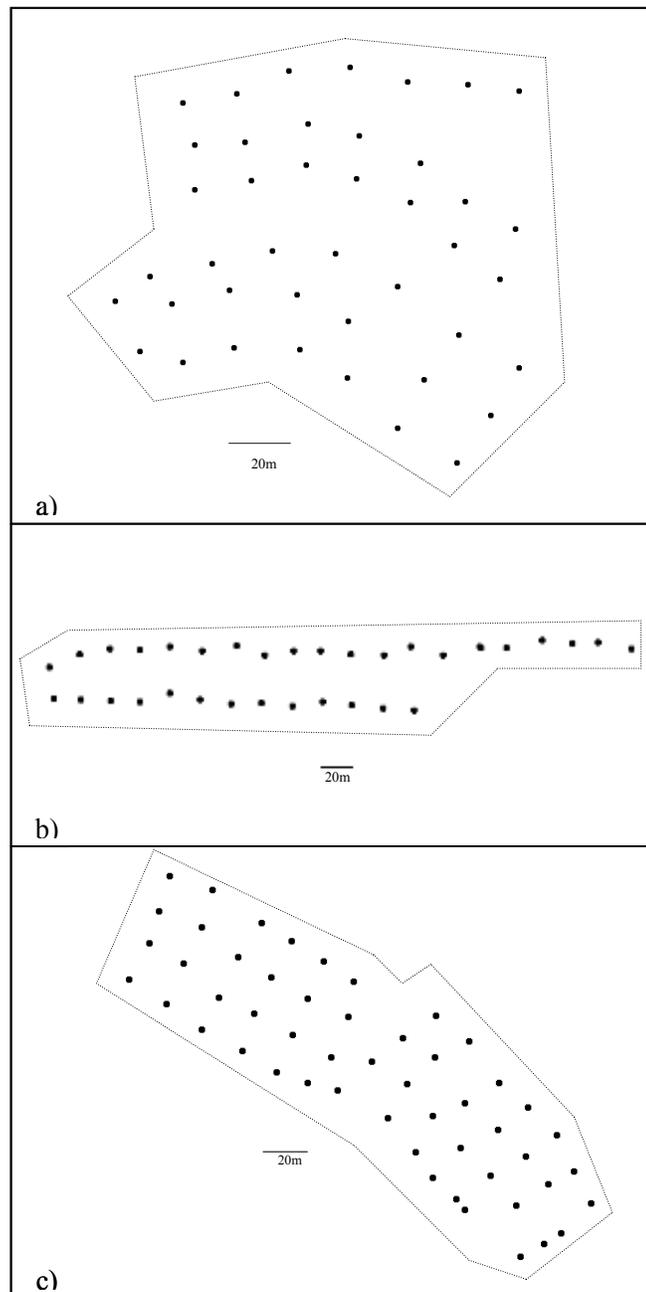


Figure 2. A schematic diagram that shows an example of number of overlapping individuals (a) and percentage of home range overlapped (b) for female-female (f-f), male-male (m-m), female-male (f-m), and male-female (m-f) interactions. The numbers represent the individuals, solid lines represent male home ranges, and the dashed lines represent female home ranges.

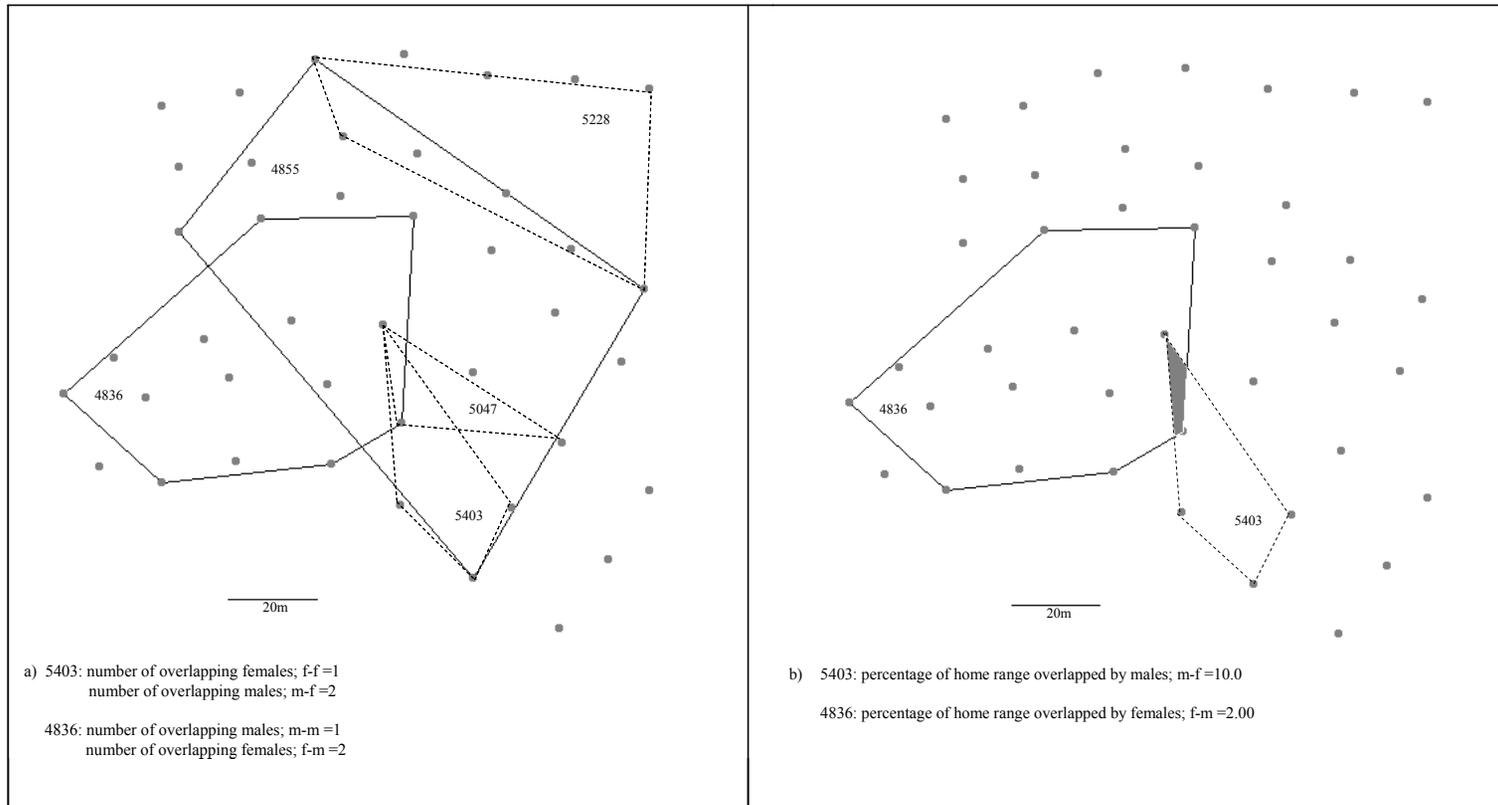


Figure 3. An example of male and female HRS and overlap for individuals on Grizzly in 2003 (a), Fortress in 2004 (b), and Lorette in 2003 (c). Each closed circle represents a trap site, thick solid lines represent male home ranges, dashed lines represent female home ranges and the thin solid line represents the 10m buffer surrounding each grid. Note that the minimum convex polygon home ranges are shown, however kernel estimates were used in the data analysis.

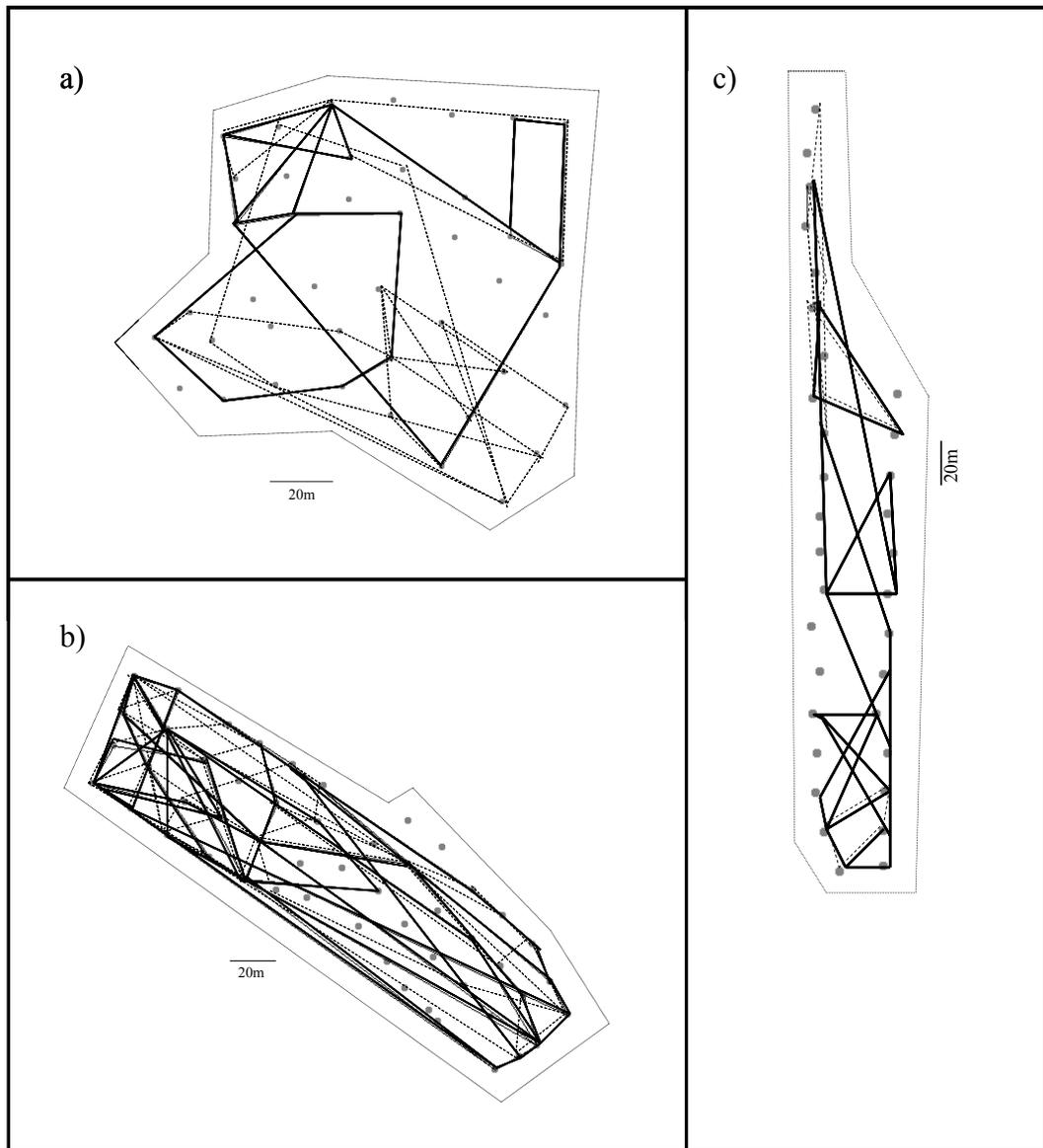


Figure 4. Home range size, in hectares (ha) of resident females (a) and males (b), as shown by bar graphs that represent the mean home range size (± 1 standard error). Note that the natural log of home range size was used in the simple linear regression models, however the bars on the graphs represent the actual size of the home ranges. The simple linear regression models are $y = -.753 - .642 \text{ grid Grizzly}$, $df = 69$, $F = 6.102$, $p = 0.016$, $R^2 = 0.082$, $R^{2adj} = 0.069$ females and $y = -0.294 - 0.667 \text{ grid Grizzly}$, $df = 81$, $F = 10.276$, $p = 0.002$, $R^2 = 0.114$, $R^{2adj} = 0.103$ for males. The simple linear regression model data set included individual estimates. Data presented are from the grids Fortress, Grizzly and Lorette located in the Kananaskis Valley, Alberta Canada from 2003 to 2006.

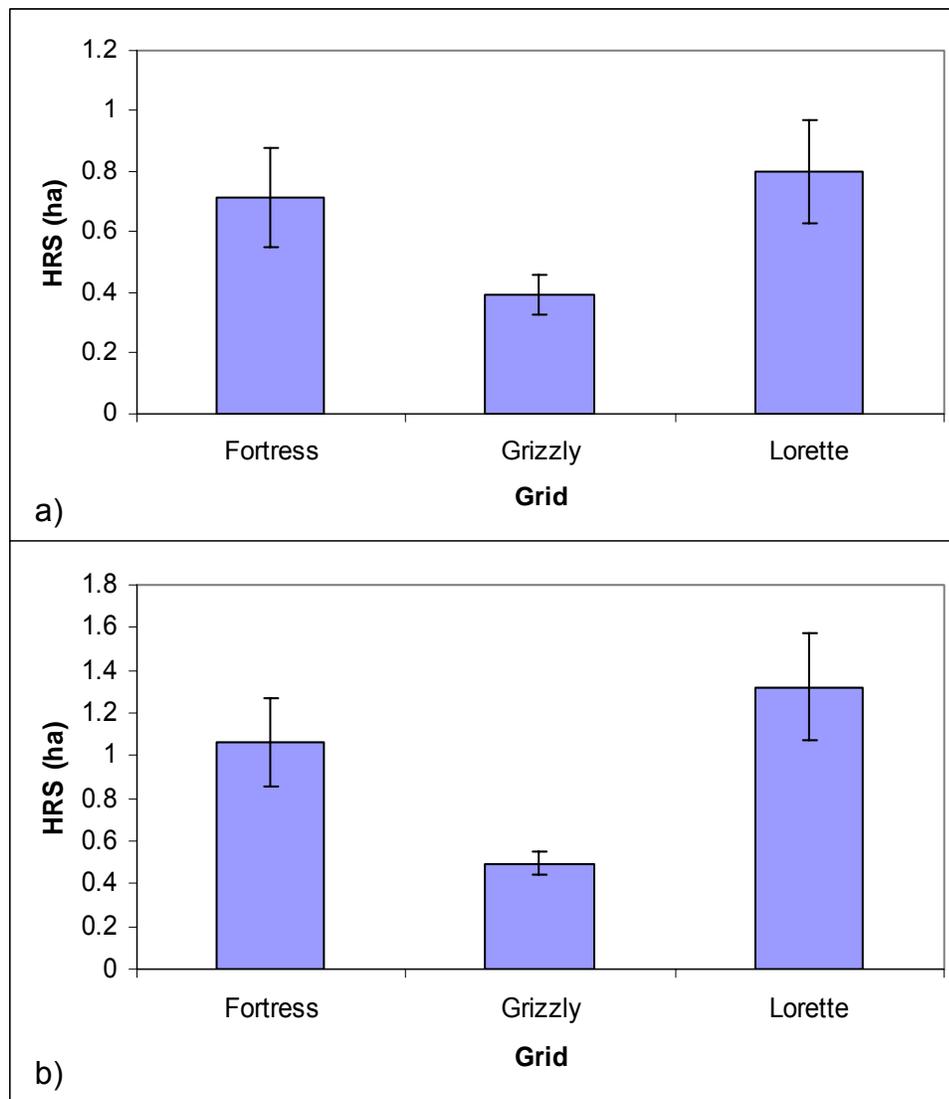


Figure 5. Home range overlap between mice of the same sex, as shown by a bar graph of the mean (± 1 standard error) number of overlapping females in relation to grid for female-female (f-f) overlap (a) and a cluster bar graph of the mean (± 1 standard error) number of overlapping individuals in relation to year for male-male (m-m) overlap (b). The simple linear regression models are $y = 1.636 + 3.164 \text{ grid Grizzly} + 6.864 \text{ grid Lorette}$, $df = 66$, $F = 39.178$, $p = 0.000$, $R^2 = 0.550$, $R^{2adj} = 0.536$ and $y = 6.850 - 2.433 \text{ year } 2005 + 1.559 \text{ year } 2004$, $df = 73$, $F = 16.740$, $p = 0.000$, $R^2 = 0.320$, $R^{2adj} = .301$ respectively. The simple linear regression model data set included individual estimates. Data presented are from the grids Fortress, Grizzly and Lorette located in the Kananaskis Valley, Alberta Canada from 2003 to 2006.

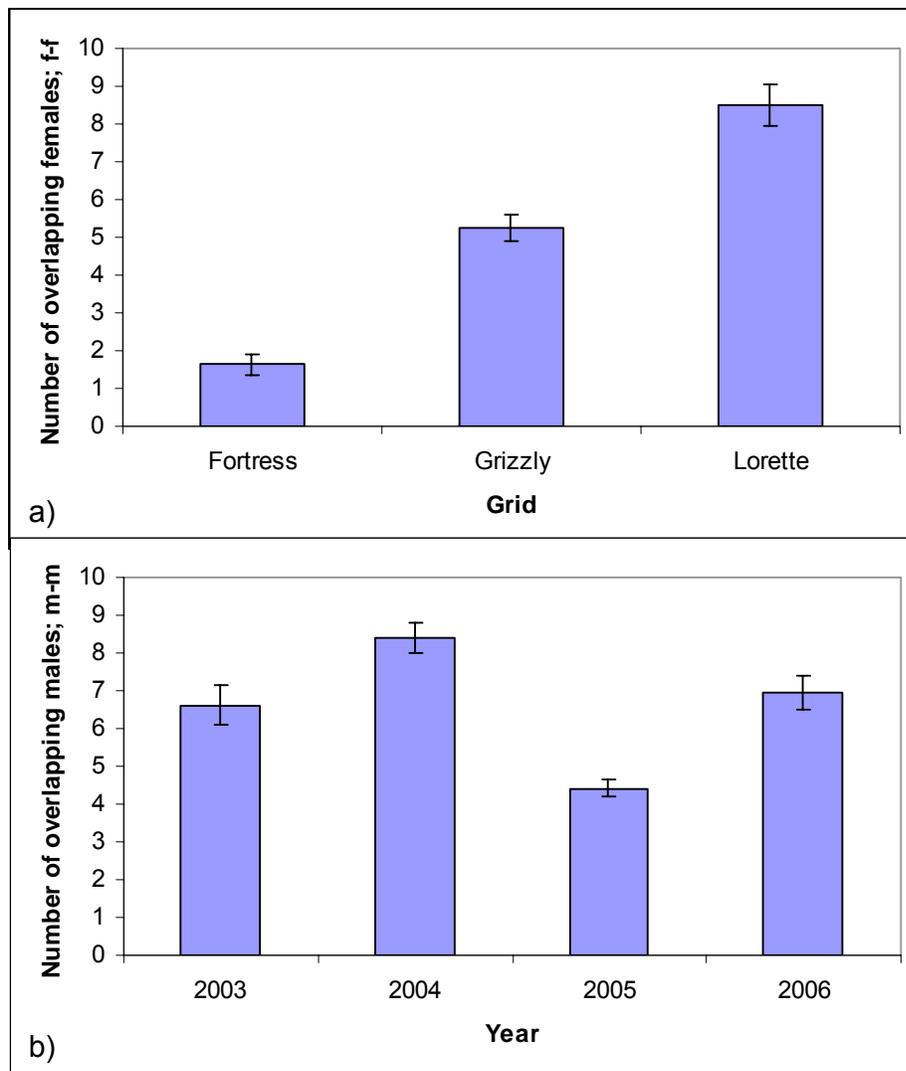


Figure 6. Home range overlap between mice of the opposite sex, as shown by a bar graph of the mean (± 1 standard error) number of overlapping males in relation to grid for male-female (m-f) overlap (a), and a cluster bar graph of the mean (± 1 standard error) number of overlapping individuals in relation to grid and year for female-male (f-m) overlap (b). The simple linear regression models are $y = 6.304 + 1.321 \text{ grid Lorette}$, $df = 69$, $F = 4.779$, $p = 0.032$, $R^2 = 0.066$, $R^{2adj} = 0.052$ and $y = -.139 + 9.668 \text{ grid Lorette} + 4.768 \text{ grid Grizzly} + 3.422 \text{ year 2005} + 2.307 \text{ year 2004} + 1.349 \text{ year 2006}$, $df = 77$, $F = 37.717$, $p = 0.000$, $R^2 = 0.724$, $R^{2adj} = 0.705$ respectively. The simple linear regression model data set included individual estimates. Data presented are from the grids Fortress, Grizzly and Lorette located in the Kananaskis Valley, Alberta Canada from 2003 to 2006.

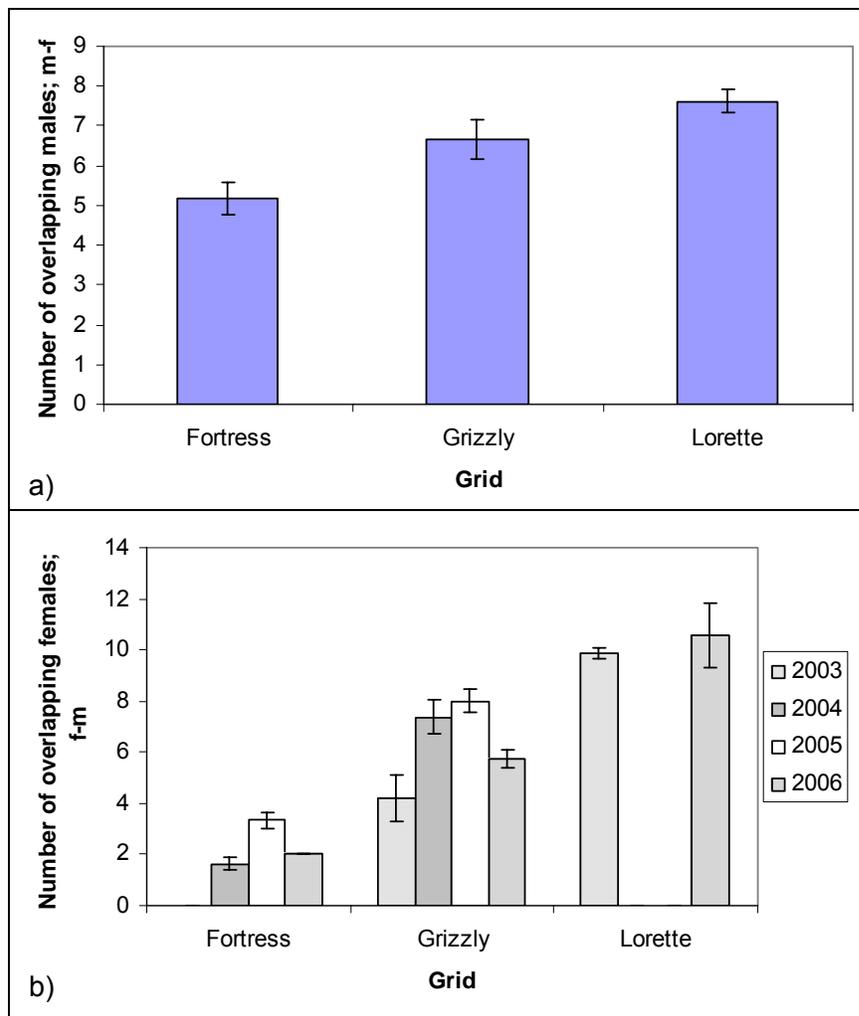


Figure 7. Percentage of home range overlapped by mice of the same sex, as represented by a cluster bar graph of the mean (± 1 standard error) percentage of home range overlapped by females in relation to grid and year for female-female (f-f) overlap (a) and a bar graph of the mean (± 1 standard error) percentage of home range overlapped by males in relation to grid for male-male (m-m) overlap (b). The simple linear regression models are $y = 25.075 + 15.309 \text{ year}2005 - 8.805 \text{ grid Grizzly}$, $df=66$, $F = 13.293$, $p = 0.000$, $R^2 = 0.231$, $R^{2adj} = 0.271$ and $y = 35.526 - 11.540 \text{ grid Grizzly}$, $df=76$, $F = 18.615$, $p = 0.000$, $R^2 = 0.199$, $R^{2adj} = 0.188$ respectively. The simple linear regression model data set included individual estimates. Data presented are from the grids Fortress, Grizzly and Lorette located in the Kananaskis Valley, Alberta Canada from 2003 to 2006.

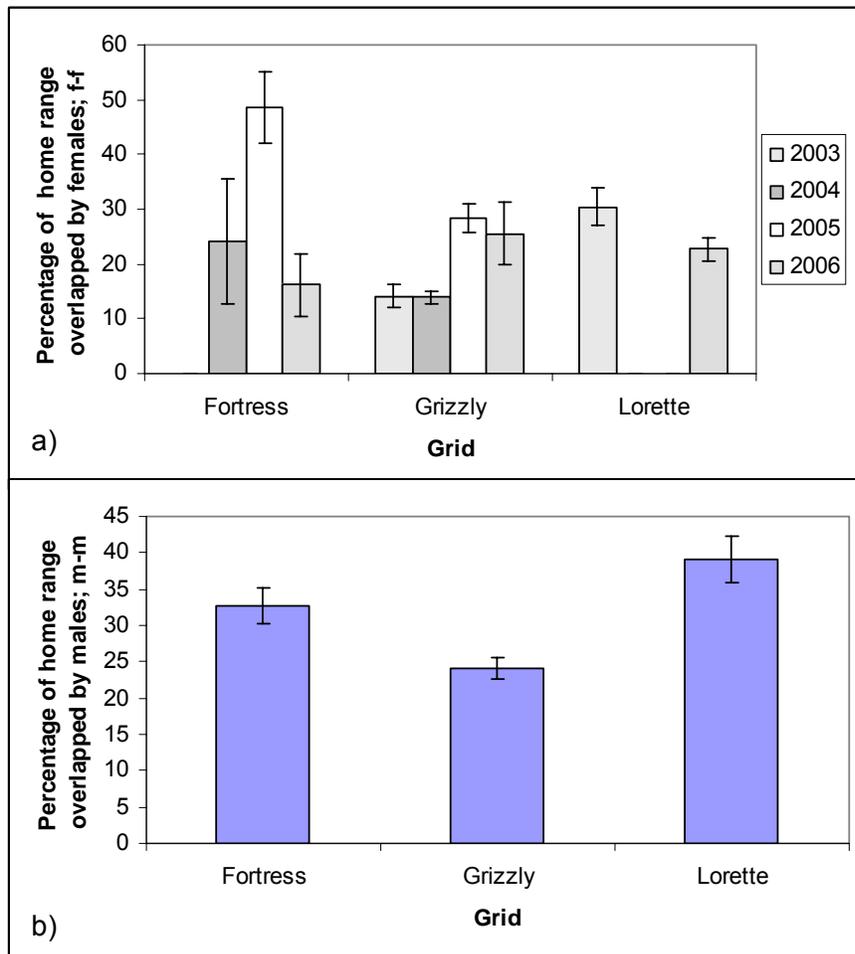


Figure 8. Percentage of home range overlapped by mice of the opposite sex, as shown by a cluster bar graph of the mean (± 1 standard error) percentage of home range overlapped by males in relation to grid and year for male-female (m-f) overlap (a) and a cluster bar graph of the mean (\pm standard error) percentage of home range overlapped by females in relation to year for female-male (f-m) overlap (b). The simple linear regression models are $y = 23.402 + 20.590 \text{ Grid Lorette} + 14.705 \text{ year } 2005$, $df = 63$, $F = 22.471$, $p = 0.000$, $R^2 = 0.424$, $R^{2adj} = 0.405$ and $y = 23.364 + 13.900 \text{ year } 2005 - 9.684 \text{ year } 2004$, $df = 77$, $F = 27.500$, $p = 0.000$, $R^2 = 0.423$, $R^{2adj} = .408$ respectively. The simple linear regression model data set included individual estimates. Data presented are from the grids Fortress, Grizzly and Lorette located in the Kananaskis Valley, Alberta Canada from 2003 to 2006.

