

Behavioral and Spatial Dynamics in a Fluctuating Population of
Golden-mantled Ground Squirrels (*Callospermophilus lateralis*)

By

JACLYN REBECCA ALIPERTI
DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Ecology

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

Approved:

Dr. Dirk H. Van Vuren, Chair

Dr. Robert J. Hijmans

Dr. Andrew Sih

Committee in Charge

2020

Copyright © 2020 Jaclyn Aliperti. All rights reserved.

ACKNOWLEDGMENTS

This dissertation represents the culmination of a long journey that would not have been completed without the guidance and support of mentors, colleagues, friends, and family. I have had the privilege to learn from and grow with many wonderful people, and for that I am grateful.

I will carry the appreciation and respect that I have for my mentor, Dirk Van Vuren, with me for the rest of my life. In addition to having a sharp scientific mind and being a remarkable writer, Dirk is an exceptional human being who taught me just as much about life in general as he did about wildlife ecology. From the beginning, Dirk was all-in when it came to investing in my future. I thank Dirk for being an incredibly patient and kind advisor, having confidence in my abilities, and inspiring me to continue to grow as a scientist, communicator, and educator.

I consider myself incredibly fortunate to have been part of the Graduate Group in Ecology at UC Davis and the Rocky Mountain Biological Laboratory, two extraordinary academic communities that have challenged me intellectually and supported me wholeheartedly. At UC Davis, I am thankful for Andy Sih, whose enthusiasm for behavioral ecology is contagious. Andy always made the time to chat about research ideas, encouraged me to think outside the box, and provided an understanding of animal behavior that greatly improved this dissertation. I thank Robert Hijmans, whose class kickstarted my ability to navigate the field of spatial ecology and to use the R software more freely, and whose kind feedback throughout the writing process was very helpful. I am grateful for valuable guidance from Bernie May, and I thank Peter Moyle and Roger Baldwin for serving as members of my qualifying exam committee and for being familiar and friendly faces in the Department. I am also very grateful for the helpful feedback that I have received from my colleagues in the Van Vuren lab: Caitlin Wells Salerno, Aviva Rossi, Amy Collins, Ellie Bolas, and Summer Schlageter.

I found a second home in Gothic, Colorado, where I lived and worked at the Rocky Mountain Biological Laboratory for five summers. The community in Gothic is unmatched by any other that I have known. I am thankful for the productive and heartwarming conversations that I had with Ken Armitage, Billy Barr, Nick Waser, Mary Price, Rosemary Smith, Rick Williams, Dan Blumstein, Scott Wissinger, Shannon Sprott, and Jennie Reithel, among others. I am grateful to have shared many memorable experiences with my family of friends at the field station, which included not only trapping squirrels and attending seminars, but also climbing mountains, playing cricket, and having potluck dinners. Spending months at a time in the mountains surrounded by majestic landscapes, wildlife, and a tight-knit group of people who appreciate the natural world was a constant reminder of why I became an ecologist.

I extend my thanks to all those who contributed to our long-term dataset, including all field assistants, as much of my dissertation would not have been possible without those efforts. I am also thankful for project funding provided by the Rocky Mountain Biological Laboratory Graduate Fellowship and Dr. Lee R. G. Snyder Memorial Fellowship, American Society of Mammalogists Grant-in-Aid of Research, and the University of California, Davis Walter and Elizabeth Howard Award and Ecology Student Endowment Award.

The friends I met while in Davis have been an endless source of encouragement and support, and I would be lost without them. I am thankful for Caitlin Wells Salerno, who welcomed me into our lab group with open arms, trained me on the ground squirrel project, and provided endless advice for navigating graduate school. Caitlin is a brilliant scientist who always made me feel included and valued. I am deeply grateful for Aviva Rossi, with whom I shared every step of this experience; Aviva and I took and taught classes together, scheduled our qualifying exams a week apart, and graduated within the same season. We also shared jokes,

stories, and common experiences, and over the years have become the closest of friends. I thank Aviva for her kindness, collaborative nature, and unfailing support. I do not know how I would have gotten through the final stretch of this dissertation without daily check-ins with Amy Collins, who kept morale high during a global pandemic by sending cat memes and celebrating even the smallest successes. During a time in which much of the world was in isolation, Amy provided uplifting company. Amy helped me overcome bumps in the road, and was the friend running next to me at the end of a marathon. We reached each academic milestone concurrently, as a team, and somehow finished our dissertations only days apart. In climbing this mountain, it meant the world to me to reach the peak with such a great friend by my side. I am extremely thankful for Leila Harris, Aviv Karasov-Olson, and Jess Lin, who kept me sane over the years by providing a constant stream of laughter, bird and mammal factoids, potluck dinners, and virtual happy hours. I am grateful for my friendship with Mary Clapp, and our many enlightening conversations about everything from research to pottery-throwing and bread-making. I am also thankful for Kristen Denninger Snyder, on whom I can rely to make me laugh, and who traveled to Gothic to visit me in the field. From the beginning of my time in California, I found a sense of community and camaraderie with Kate Ingram, Katie Smith, Allison Simler-Williamson, Patrick Fuller, Rachel Wigginton, Allie Weill, Jan Ng, and Jay Jefferson. I am grateful for intellectually stimulating conversations about animal personality, conservation, and spatial analysis with Mitch Hinton, Rob Blenk, Eric Payne, Britt Davis, Mickey Agha, Elise Hellwig, and Ryan Peek, and for friendly get-togethers with Danielle Huddlestun and Cathy Brown. You are all intelligent, caring people who make the world a better place.

In my broader Davis community, I am thankful for the supportive friendships that I have shared with Elvira Lange, Duyen Ho, Ollie Wing, and Bayan Ahmed. Ed and Kathy West have

been wonderful friends and role models, with whom I have enjoyed netting bats, learned about wildlife photography, and shared many dinners. I am thankful for my piano teacher, Christine Rushton, and for my neighbors, Carol Lynn and Sonjia Shelley, who made Davis feel like home.

From before my time in Davis, I thank my undergraduate mentor, Tom Kunz, who believed in me from the start. Tom instilled in me a lifelong love and appreciation for bats, and the beautiful, complicated web of life of which they are a part. I am also grateful for Kelly Swing, who taught me about tropical ecology and encouraged me to think independently and explore the world. I don't know what I would do without those friends who have known me longest: Jen Sicari, Lauren Dachille, Tara Hawley, and Liz Herdter Smith, who have always and will always be there for me.

I am who I am today because of the unwavering love and support of my family. I would particularly like to thank my parents, John and Jil Aliperti, my grandparents, Bess and Milton Steinberg, my brother, Justin Aliperti, and my aunt, Marci Steinberg. Your faith in me during all parts of my life carried me through each step of this journey, and I love you all very much. I also cannot imagine completing this work without Nacho Aliperti, whose constant presence and show of love brought me the utmost joy each and every day.

I am incredibly thankful for my partner, Pablo Valdés Donoso, who saw me through the entirety of my graduate school experience, provided valuable analytical advice, took road trips to and from my field site, cheered on all of my accomplishments, and stood by me and loved me during challenging times.

Finally, this dissertation is dedicated to my parents, without whom none of this would be possible, and to my grandmother, who was my biggest fan.

ABSTRACT

Investigating individual-based habitat settlement and space use decisions (i.e., how individuals distribute themselves across a landscape) is a central theme in ecology, with potential consequences for fitness (e.g., survival, reproduction). Among mammals, habitat selection and spatial organization (home range size and overlap) may be influenced by inter-annual variation in population density, and space use decisions are often related to behavior and social structure. In this dissertation, I combined the results of field work, experimental assays, mapping, and modeling techniques to examine long-term behavioral and spatial dynamics in a high elevation population of golden-mantled ground squirrels (*Callospermophilus lateralis*), an asocial and presumably territorial species.

In chapter one, I described and quantified litter relocation behavior –a poorly documented phenomenon, in which a female moves her litter to a new location –during long-term studies of two species of ground-dwelling squirrels: golden-mantled ground squirrels and yellow-bellied marmots (*Marmota flaviventer*). In this natural history study, I identified several possible costs (e.g., energy expenditure and predation risk while transporting young) and benefits (e.g., increased habitat quality and social benefits) of litter relocation, and highlighted the need to better understand habitat preferences and the role of kinship on space use in golden-mantled ground squirrels. Accordingly, chapters two through four focused on patterns of habitat selection, behavior, and the social and spatial organization of this species, with particular emphasis on the effects of density, behavior, and kinship on space use.

Habitat selection dictates the distribution of individuals across space and time, which influences access to key resources such as preferred food items and cover from predators. As population density increases in high quality habitat and competition for limited resources

becomes intense, animals are believed to preferentially settle in lower quality habitat, where they are equally likely to survive or reproduce due to lack of competition; however, studies that quantify density-dependent habitat selection or tie fitness measures to resource selection decisions in free-ranging animal populations remain rare. In chapter two, I quantified habitat selection in adult female golden-mantled ground squirrels across two spatial scales (home range placement, and occurrence within the home range) by using 11 consecutive years of data on individual space use, and I used compositional analysis, resource selection functions, and multilevel modeling to address how habitat preferences may be influenced by density or linked to fitness outcomes. Squirrels preferred dry meadow over all other habitat types (aspen, spruce, wet meadow, and willow) at both spatial scales, and were more likely to use dry meadow that contained shorter vegetation and vision-enhancing prominences such as rocks (“perches”). Use of dry meadow at each spatial scale was not influenced by changes in density, and use of dry meadow did not influence fitness (as measured by litter size, pre-hibernation mass, or survival). However, squirrels that experienced a greater number of perches or smaller local densities had higher survival rates, suggesting that a lack of visual obstruction, probably to promote detection of predators, drives habitat selection in this system. Surprisingly, squirrels maintained their preference for dry meadow as density increased, and they experienced reduced survival as a result, perhaps because marginal habitat of sufficient quality was not available.

Although spatial patterns are typically studied at the population or species level, individual differences in space use dynamics often account for a substantial amount of the variation exhibited at higher levels of biological organization, and thus may act as a link between process and pattern in ecology. A growing body of research suggests that variation in patterns of space- and resource use in wild animals may in part be explained by consistent individual

differences in behavior across time or contexts, a concept known as animal personality. In chapter three, I used repeated standardized assays to perform the first characterization of personality in golden-mantled ground squirrels, and I used multilevel modeling to determine if personality influenced 95% home range size, 50% core area size, movement speed, or use of perches in nature. Data collected over three years showed that squirrels consistently differed in activity, sociability, boldness, and aggressiveness, and that individual squirrels differed in space- and perch use in a non-random manner that was dependent on their personality type. I found that bolder individuals maintained larger core areas, more active and bold individuals moved faster, and more active, bold, and aggressive individuals had greater access to fitness-enhancing perches in their home ranges. I also found that sociability was associated with access to perches in the home range, suggesting there is a potential benefit within an asocial species of being relatively more social.

Spatial organization may be influenced by kinship, and tolerance among kin is believed to play a role in the evolution of sociality. Ground-dwelling squirrels exhibit a wide range of sociality, from solitary to highly gregarious. Golden-mantled ground squirrels are considered to be asocial and presumably territorial, with the expectation that adults, including close kin, have home ranges that are distinct and non-overlapping; however, this classification was supported by sparse data. In chapter four, I characterized the spatial organization, including the role of kinship, in a population of golden-mantled ground squirrels, and I capitalized on changes in population size over 25 years to quantify the influence of density on that spatial organization. I found extensive overlap between female home ranges (30%), and between male and female home ranges (28%) after the breeding season. However, the core areas of adult female home ranges overlapped minimally (7%), suggesting squirrels were territorial, but only for the inner part of

their home range. We did not find an effect of population density on home range or core area size, but local-level intruder pressure led to an increase in home range size, perhaps because females ranged farther to either gain familiarity with neighbors or shift into less crowded areas. Contrary to expectation, females shared more space with kin than non-kin, but only at high densities. This density-mediated increase in space-sharing among kin suggests that familiarity and inclusive fitness benefits may offset costs of competition and promote philopatry under certain conditions. Overall, I provide evidence of a facultative transition in this species from asociality to the formation of single-family kin clusters, the first step towards developing sociality.

Together, these chapters further our understanding of the causes and consequences of changes in habitat use, providing insight to the fields of wildlife management and conservation. This work highlights how the personality of free-ranging animals may interact with environmental variables to differentially affect space- and resource use, with potentially important consequences for population-level processes. In addition, this dissertation emphasizes the importance of considering familiarity among neighbors in asocial species, as well as the interactive effects of environmental conditions and kinship when assessing the spatial and social organization of mammals. I hope this work serves as a valuable contribution to our understanding of ground squirrel ecology, as well as inspires future research that links individual processes to spatial patterns of wildlife populations in natural ecosystems.

TABLE OF CONTENTS

Chapter 1: Litter relocation behavior in two species of ground-dwelling squirrels	1
1.1 Abstract	1
1.2 Introduction	2
1.3 Methods	4
1.4 Results	6
1.5 Discussion	9
Acknowledgments	11
1.6 Literature Cited	12
1.7 Figures	17
1.7.1 Litter relocation behavior by a yellow-bellied marmot and golden-mantled ground squirrel	17
1.8 Tables	18
1.8.1 Summary of distances that golden-mantled ground squirrels and yellow-bellied marmots moved their pups	18
Chapter 2: Habitat selection in a fluctuating population of golden-mantled ground squirrels (<i>Callospermophilus lateralis</i>): density-dependence and fitness consequences	19
2.1 Abstract	19
2.2 Introduction	20
2.3 Methods	23
2.3.1 Study system	23
2.3.2 Multi-scale habitat selection	28
2.3.3 Density effects and fitness consequences	30
2.4 Results	32
2.4.1 Habitat selection	32
2.4.2 Density effects and fitness consequences	33
2.5 Discussion	36
Acknowledgments	39
2.6 Literature Cited	40
2.7 Figures	52
2.7.1 Habitat map of the study area	52
2.7.2 Mean selection ratios for second- and third-order habitat selection across five macrohabitat types	53
2.7.3 Estimated probability of use of dry meadow based on number of perches	54
2.8 Tables	55

2.8.1 Compositional analysis ranking matrix for multi-scale habitat selection.....	55
2.8.2 Coefficient estimates for fixed effects in the microhabitat selection model.....	56
2.8.3 Coefficient estimates for fixed effects in the annual survival model.....	57
Chapter 3: Bridging animal personality with space- and resource use in a free-ranging population of an asocial ground squirrel.....	58
3.1 Abstract.....	58
3.2 Introduction.....	59
3.3 Methods.....	62
3.3.1 Study system	62
3.3.2 Spatial outcomes	64
3.3.3 Personality assays	65
3.3.4 Statistical analyses	69
3.4 Results.....	73
3.4.1 Spatial outcomes	73
3.4.2 Consistent individual differences in behavior.....	74
3.4.3 Personality-dependent use of space and perches	76
3.5 Discussion	78
Acknowledgments.....	83
3.6 Literature Cited	83
3.7 Figures.....	95
3.7.1 Images of a golden-mantled ground squirrel inside of the arena during an open field and mirror image stimulation trial	95
3.7.2 Home range area and total number of perches in the 95% home range and 50% core area of golden-mantled ground squirrels	96
3.7.3 Mean movement speed in free-ranging golden-mantled ground squirrels	97
3.7.4 Plot of coefficients for fixed effects in each of five models analyzing the effect of personality on space- and resource use	98
3.7.5 Effects of an interaction between juveniles and aggressiveness on 95% home range size, 50% core area, and number of perches in the 95% home range.....	99
3.7.6 Effects of mean personality scores on 50% core area, number of perches in the 95% home range and 50% core area, and movement speed	100
3.8 Tables.....	101
3.8.1 Standardized loadings for behaviors included in principal component analyses	101
Chapter 4: Effects of density and kinship on the spatial organization of an asocial ground squirrel	102
4.1 Abstract.....	102

4.2 Introduction.....	103
4.3 Methods.....	106
4.3.1 Study system	106
4.3.2 Field methods.....	107
4.3.3 Spatial organization	109
4.3.4 Effects of density on spatial organization.....	111
4.4 Results.....	113
4.4.1 Spatial organization	113
4.4.2 Effects of density on spatial organization.....	115
4.5 Discussion.....	116
Acknowledgments.....	121
4.6 Literature Cited	121
4.7 Figures.....	133
4.7.1 Home ranges and core areas for adult female and male golden-mantled ground squirrels during the year of lowest population density and highest population density	133
4.7.2 Mean proportional spatial overlap among adult female golden-mantled ground squirrels that differed in relatedness	134
4.7.3 Effect of intruder pressure on 95% home range area in free-ranging, adult female golden-mantled ground squirrels	135
4.7.4 Effects of an interaction between relatedness and either population density or intruder pressure on mean spatial overlap in adult female golden-mantled ground squirrels	136
4.8 Tables.....	137
4.8.1 Sample sizes used for the calculation of home range size and spatial overlap in adult golden-mantled ground squirrels at two spatial levels and for two delineation methods..	137
4.8.2 Summary of home range size and spatial overlap in adult golden-mantled ground squirrels at two spatial levels and for two delineation methods	138

Chapter 1 was accepted for publication and should be cited as follows:

Aliperti, J. R., D. H. Van Vuren, A. J. Rossi, and K. B. Armitage. 2020. Litter relocation behavior in two species of ground-dwelling squirrels. *Ethology* 126:289-382.

CHAPTER 1

LITTER RELOCATION BEHAVIOR IN TWO SPECIES OF GROUND-DWELLING SQUIRRELS

1.1 Abstract

Maternal investment in mammals may take many forms, including spatial relocation of offspring. Litter relocation behavior, in which a female moves her litter to a new location, has been reported for several species of carnivores and rodents but has received little study. We describe litter relocations during long-term studies of two species of ground-dwelling squirrels, yellow-bellied marmots (YBM, *Marmota flaviventer*) and golden-mantled ground squirrels (GMGS, *Callospermophilus lateralis*), to determine the distance and frequency of litter relocations, and to explore possible explanations for litter relocation behavior. We observed 19 litters relocated by YBM mothers and 32 by GMGS mothers. Although YBM are much larger than GMGS, relocation distances for YBM (median = 46 m, range = 15-324 m) were not greater than those for GMGS (median = 79 m, range = 16-252 m), possibly because YBM home ranges in our study area were exceptionally small. Frequency of litter relocation was greater for GMGS (21% of litters produced) than for YBM (10%), perhaps because GMGS experience fewer social constraints or greater predation risk. We identified several possible costs (energy expenditure and vulnerability to predators while transporting young) and benefits (reduced exposure to predation risk, increased habitat quality, and social benefits) of litter relocation. Future studies

should continue to explore litter relocations to better understand the ecological causes and consequences of this behavior.

1.2 Introduction

Maternal care in mammals is characterized by postpartum investment in the form of lactation, which is energetically expensive (Clutton-Brock 2016). In addition, maternal investment may occur post-weaning, often in the form of anti-predator behaviors such as vigilance for early detection of predators (Caro 1987, Costelloe and Rubenstein 2018), alarm calling to warn offspring of danger (Wilson-Henjum et al. 2019), or hiding young to minimize predator detection (Lent 1974, Fisher et al. 2002). Mothers may also invest in their offspring through spatial relocation. For instance, reproductive females will sometimes move away from the natal site to a new location, bequeathing their burrow or territory to their offspring (Harris and Murie 1984, Price and Boutin 1993). In other cases, females will relocate their litter from the natal site to a new location, presumably where fitness benefits are perceived to be greater (Coulon et al. 1995, Swaisgood et al. 1999).

Litter relocation behavior has been reported in a variety of carnivore species, including gray wolves (*Canis lupus*; Ausband et al., 2016), cheetahs (*Acinonyx jubatus*; Laurenson, 1993), pine martens (*Martes martes*; Kleef & Tydeman, 2009), and spotted hyenas (*Crocuta crocuta*; Boydston, Kapheim, & Holekamp, 2006). It has also been reported in some rodents, such as deer mice (*Peromyscus maniculatus*; Sharpe & Millar, 1990), red squirrels (*Tamiasciurus hudsonicus*; Kerr & Descamps, 2008), alpine marmots (*Marmota marmota*; Coulon et al., 1995), and California ground squirrels (*Spermophilus beechyi*; Hennessy & Owings, 1988; Swaisgood et al., 1999). Litter relocation seemingly is costly for the female because of increased exposure to

predation while carrying offspring. In addition, females likely expend extra energy during transit by carrying pups individually and shuttling back and forth between locations (Pero 2015). Although very little is known about the evolutionary significance of litter relocation behavior (Kerr and Descamps 2008), females may benefit by moving their offspring to reduce predation risk in circumstances where predator activity around the natal site is high (Swaigood et al. 1999, Kerr and Descamps 2008, Kleef and Tydeman 2009) or to increase habitat quality in cases where neighboring habitat is of higher quality than that surrounding the natal site (Pero 2015). Other proposed benefits include avoiding or reducing ectoparasite infestation (Roper et al. 2002, Pero 2015), escaping the threat of infanticide (Ebensperger and Blumstein 2007), promoting integration of pups into social groups (Boydston et al. 2006), or evading adverse abiotic conditions (Ausband et al. 2016). However, information on litter relocations is largely anecdotal, with documentation of litter moves and potential causal factors available for only a few species (Boydston et al. 2006, Pero 2015, Ausband et al. 2016), perhaps due to the infeasibility of predicting when and where relocation events will take place.

We observed multiple litter relocations during long-term studies of two ground-dwelling squirrels: the large-bodied (2,560-3,880 g) yellow-bellied marmot (YBM; *Marmota flaviventer*), and the small-bodied (130-230 g) golden-mantled ground squirrel (GMGS; *Callospermophilus lateralis*) (Armitage 1981). Prior accounts of litter relocations of YBM and GMGS are limited to one report, for GMGS (Huestis 1947). Here, we provide photographic documentation and a detailed description of litter moves to characterize the frequency and distance of litter relocations in both species, and to explore possible explanations for litter relocation behavior.

1.3 Methods

Our study took place at the Rocky Mountain Biological Laboratory in the East River Valley, Gunnison County, Colorado (38°57' N, 106°59' W) at an altitude of 2,900 m. Long-term studies of YBM (Armitage 2010, Blumstein 2013) and GMGS (Wells and Van Vuren 2018) have been conducted at this location since 1962 and 1990, respectively. Common predators in this region include coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), long-tailed weasels (*Mustela frenata*), and short-tailed weasels (*Mustela erminea*) (Van Vuren 2001, Kneip et al. 2011). Female YBM typically live in colonies, located at discrete habitat patches surrounded by unsuitable habitat (Armitage 2014), although some females are solitary (Downhower and Armitage 1971). Colonies are spatially fixed and have been occupied continuously for over 50 years (Blumstein 2013). Colonies consist of one or more matriline; home range overlap is extensive within a matriline, but it is minimal or nonexistent between matriline (Armitage 1991). Female GMGS are solitary, although they often live in close proximity to conspecific neighbors (Wells and Van Vuren 2017). For both species, females give birth in the natal burrow, where they nurse their pups for 25-30 days before the pups emerge and begin feeding on their own (Armitage 1981, Wells and Van Vuren 2018).

Each year, individuals of both species were trapped and marked, and pups were trapped upon emergence from their natal burrow. Intensive behavioral observations were conducted at four colonies for YBM (Armitage 1974) and throughout a 13-ha study area for GMGS (Wells and Van Vuren 2018). All procedures followed guidelines of the American Society of Mammalogists (Sikes and Animal Care and Use Committee of the American Society of Mammalogists 2016), and were approved by the institutional animal care and use committees of

the University of Kansas, University of California, Davis, and Rocky Mountain Biological Laboratory.

Litter relocations were observed opportunistically. Relocation events were recorded during 1965-1996 for YBM and during 1995-2018 for GMGS, and we restricted our analyses for each species to those time periods. In all but 11 cases (5 GMGS and 6 YBM), litter relocations were identified while in progress based on observations of a mother carrying one or more pups away from the home burrow. In the 11 cases, litter relocations were identified based on the abrupt change in location between burrows of a mother and her entire litter. We recorded litter size and relocation distance, the Euclidean distance between the former burrow and the new burrow. We also calculated total distance for the mother by multiplying the relocation distance by the number of trips required to move the entire litter (following Pero 2015). Total distance moved by the mother was used as a proxy for the relative energy expenditure for relocating a litter. We then further categorized relocations as either ‘internal’ moves or ‘external’ moves. Relocation events that took place within a YBM colony, or within the home range of the GMGS mother (as defined by locations where the mother had been recorded prior to the event), were considered to be internal moves, while all other moves were considered to be external. Spatial ecology scales with body size (Jetz et al. 2004), so we used Mann-Whitney U tests to compare relocation distances between species, based on the expectation that distances would be greater for YBM than for GMGS. In the event that a female moved her litter more than once either within or between years, we calculated the mean relocation distance for that female and used this composite value for analysis. We calculated frequency of litter relocations by comparing number of litters moved to total litters produced for each species throughout the study period. We assessed the potential influence of energetic cost on litter relocation behavior in two ways. To

determine if energetic cost influenced the likelihood of moving a litter, we compared the size of relocated litters to the long-term mean litter size for the GMGS (4.8 pups; Kneip et al. 2011) and YBM (4.1 pups; Schwartz et al. 1998) populations we studied. To determine if the energetic cost associated with moving larger litters influenced relocation distance, we calculated Spearman rank correlation coefficients to determine if relocation distance declined with increasing litter size.

We characterized circumstances associated with each litter move for both species to help elucidate potential underlying causes. Predation was denoted as a potential causal factor when predator activity occurred within close proximity to the natal burrow at the time of the move. Trapping disturbance was denoted when the litter was moved in immediate association with trapping efforts. Habitat was indicated when the move resulted in improved habitat quality, based on long-term data on occupancy and reproductive success throughout both study areas. We also summarized conspecific interactions associated with litter moves to explore the potential role of the social environment. Female relatedness was calculated from pedigrees based on mother-pup and littermate relations (Armitage and Johns 1982, Wells et al. 2017).

1.4 Results

The method of transporting pups was similar for both species (Fig. 1). One pup was transported at a time. Mothers often paused in transit and released the pup, presumably to rest or scan for predators, then grasped the pup and continued, allowing identification of how the pup was grasped. The mother nuzzled the pup's underside, prompting it to curl up into a ball on its back with at least some feet apparently clasped together. The mother seized the pup in the area of its feet and belly with her incisors; in many cases she appeared to secure the clasped feet of the

pup in the diastema between her incisors and premolars, and in other cases she might have seized the skin and fur of the belly in her incisors. Moving a litter was a continuous process until the entire litter was relocated, and aside from pauses while in transit, we did not observe delays by the mother in moving portions of a litter.

We observed a total of 32 litters relocated by 24 GMGS mothers and 19 litters relocated by 17 YBM mothers; six GMGS and two YBM moved their litters during more than one year. Mothers that moved litters ranged in age from 1-7 years for GMGS and 2-10 years for YBM, age ranges that are similar to the reproductive lifespans for each species (Armitage 2014, Moore et al. 2016). Excluding two YBM relocations that originated outside our four study colonies, the frequency of litter relocation for GMGS (0.21, $n = 153$ litters produced) was about twice as great as that for YBM (0.10, $n = 172$ litters produced). Furthermore, eight GMGS litters were relocated multiple times in sequence, with up to five relocations for one litter, for a total of 44 GMGS relocation events. We did not observe multiple relocations of YBM litters.

We were able to measure the distance that females moved their litters in all 19 YBM relocation events and in 40 GMGS relocation events; four GMGS relocation events were excluded because one of the two endpoints was uncertain. Of the 19 YBM litter relocations, 16 were internal moves and three were external moves (from one colony to another, from a solitary site to a colony, or from one solitary site to another). Of the 40 GMGS litter relocations, 36 were internal moves, and four were external moves. Thus, 16% of YBM relocation events and 10% of GMGS relocation events involved movement outside the normal spatial context of the mother. The mean size ($\pm$ SE) of relocated litters was 4.2 ± 0.3 YBM pups and 4.8 ± 0.3 GMGS pups. Spearman rank correlation coefficients did not show a significant correlation between litter size

and relocation distance for either YBM ($r_s = -0.317$, $p = 0.19$, $n = 17$) or GMGS ($r_s = 0.001$, $p = 1.00$, $n = 23$).

A Mann-Whitney U test did not reveal a significant difference between GMGS ($n = 23$) and YBM ($n = 17$) in the distance that mothers moved their litters during relocation events ($U = 239.5$, $p = 0.23$; Table 1). The same outcome resulted when considering internal moves only (GMGS, $n = 19$; YBM, $n = 14$; $U = 182.5$, $p = 0.07$), and also when considering external moves (YBM, $n = 3$; GMGS, $n = 4$; $U = 1$, $p = 0.11$). The total distance traveled by the mother when relocating a litter was substantial in some cases, approaching a maximum of 3 km for both species (Table 1).

We identified general similarities between YBM and GMGS in potential causes associated with litter relocations. In both species, litter relocation was often associated with disturbance due to trapping (5 YBM relocations, 17 GMGS relocations) or an improvement in habitat quality (6 YBM, 5 GMGS). For example, in two cases for GMGS a female moved her litter during a trapping event, then moved the litter back to its original location within 24 hours of traps being removed. In almost all relocation events, a mother remained with her litter at the new location. However, we observed two instances in which a female GMGS moved her litter to a location outside of her home range and then returned to her original location alone (hereafter called ‘litter dumping’); both of these external moves, plus a third move that originated outside of the study area, involved moving and then abandoning pups at locations known to be of high quality habitat. The first two moves occurred on the day the litter emerged from the natal burrow, the third occurred on that day or shortly thereafter, and in all three cases the litters were female-biased, averaging 83% female pups. Predation (1 YBM, 7 GMGS) potentially influenced both species to relocate litters; for YBM the predator was coyotes, and for GMGS the predators were

red foxes and weasels. The social environment also may have played a role. YBM moved litters away from aggressive females, presumably to avoid social conflict ($n = 3$), or towards neighboring female relatives, presumably to benefit from proximity to kin ($n = 2$). Although interactions among adult GMGS were mostly agonistic, we observed three cases in which GMGS females moved their litters closer to related females, sometimes despite relocating to an area of greater local density (and thus presumably greater competition for resources). We could identify no potential causal factors for two YBM and 15 GMGS litter moves.

1.5 Discussion

Our observations provide the first photographic documentation and distance calculations for litter relocation behavior in YBM and GMGS. Given positive relationships between space-use and body size in mammals (Jetz et al. 2004), we were surprised to find that litter relocation distance for internal moves was not greater for the large-bodied YBM than for the small-bodied GMGS. The explanation may lie in space-use behavior of the two species. Home range size for adult female GMGS averages 1.85 ha (100% minimum convex polygon, $n = 44$; Aliperti, unpublished data), more than twice the average size of home ranges for adult female YBM at the colonies we studied (0.77 ha, 100% minimum convex polygon, $n = 11$; calculated from Armitage, 2009, Fig. 1). Home range size for YBM is smaller than that of any other marmot species, and smaller than that expected based on body mass; this small size is likely influenced by the high concentration of food resources in YBM home ranges (Armitage 2009, 2014). Hence, it is possible that internal relocations by YBM were not greater than GMGS in distance because spatial contexts of the two species did not differ accordingly. Not surprisingly, mean distances for each species for internal relocations were less in magnitude than the diameters of

the average home range for GMGS (153 m) and YBM (99 m; diameters were calculated considering the home range as a circle). Female GMGS relocated their litters more frequently than YBM, for uncertain reasons. Perhaps the small-bodied GMGS is more vulnerable to predation than YBM, thereby providing a greater motivation for litter relocation. Also, differing social constraints may have had an influence. GMGS are considered to be solitary and territorial (Michener 1983), hence a female might relocate her pups anywhere within her home range without encountering neighboring females. In a YBM colony, however, females share space with other females in the matriline (Armitage 1991); thus, the presence of multiple adult females within a home range, including some females that might be behaviorally dominant (Armitage 1991), may restrict litter relocation opportunities.

A female presumably decides to relocate her litter when the benefits of doing so exceed the costs (Clutton-Brock 1991, Gross 2005). Possible costs include increased exposure to predation and energy expenditure. We observed no predation events during litter relocations, but the energy expenditure can be substantial; the longest relocation distances we observed represent 4.6 and 2.5 times the expected daily movement distances for female GMGS and YBM, respectively (Garland 1983). If energetic cost influenced the decision to relocate a litter, then we expected that females either would be more likely to relocate small litters, or would relocate small litters farther distances. In both species, however, the size of relocated litters was not smaller than that of the long-term average litter size for the populations we studied, and there was no correlation between litter size and relocation distance.

We observed several possible benefits of litter relocations. For both GMGS and YBM, many relocations were associated with trapping or the presence of predators; in both circumstances, the motivation of the mother might be to reduce the perceived threat to her pups.

Habitat quality and kinship also potentially influenced litter relocations in both species. All three cases of litter dumping involved GMGS relocating weaned litters with female-biased sex ratios to high quality habitat; the long-term sex ratio for the population is 51% female pups (Wells and Van Vuren 2017). Females are the philopatric sex in our population of GMGS. Thus, litter dumping may represent a form of parental investment opposite to bequeathal (Harris and Murie 1984): instead of a female leaving her high quality burrow to her daughters, she may move her daughters to a high quality location and leave them. To our knowledge, no other cases of litter dumping have been reported for ground-dwelling squirrels. Given the importance of kin to social structure in YBM (Armitage 2014), it is not surprising that this species sometimes relocated litters closer to kin. Although female GMGS are considered asocial (Michener 1983), female philopatry results in the formation of kin neighborhoods (Wells and Van Vuren 2017); hence, kinship might play a role in litter relocation. Future studies should continue to explore litter relocations to better understand the ecological causes and consequences of this behavior.

Acknowledgments

We are grateful for long-term logistical support from the Rocky Mountain Biological Laboratory. Funding for this project was provided by the National Science Foundation (KBA), California Agricultural Experiment Station (DVV), Rocky Mountain Biological Laboratory Graduate Fellowship (JRA), American Society of Mammalogists Grant-in-Aid of Research (JRA), and Walter and Elizabeth Howard Award (JRA). We thank James Hare for valuable comments on an earlier draft of this manuscript.

1.6 Literature Cited

- Armitage, K. B. 1974. Male behaviour and territoriality in the yellow-bellied marmot. *Journal of Zoology* 172:233–265.
- Armitage, K. B. 1981. Sociality as a life-history tactic of ground squirrels. *Oecologia* 48:36–41.
- Armitage, K. B. 1991. Social and population dynamics of yellow-bellied marmots: results from long-term research. *Annual Review of Ecology and Systematics* 22:379–407.
- Armitage, K. B. 2009. Home range area and shape of yellow-bellied marmots. *Ethology Ecology and Evolution* 21:195–207.
- Armitage, K. B. 2010. Individual fitness, social behavior, and population dynamics of yellow-bellied marmots. Pages 134–154 in I. Billick and M. V. Price, editors. *The Ecology of Place*. First edition. University of Chicago Press, Chicago.
- Armitage, K. B. 2014. *Marmot biology: sociality, individual fitness, and population dynamics*. Cambridge University Press, Cambridge.
- Armitage, K. B., and D. W. Johns. 1982. Kinship, reproductive strategies and social dynamics of yellow-bellied marmots. *Behavioral Ecology and Sociobiology* 11:55–63.
- Ausband, D. E., M. S. Mitchell, S. B. Bassing, M. Nordhagen, D. W. Smith, and D. R. Stahler. 2016. Dog days of summer: influences on decision of wolves to move pups. *Journal of Mammalogy* 97:1282–1287.
- Blumstein, D. T. 2013. Yellow-bellied marmots: insights from an emergent view of sociality. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* 368:20120349.
- Boydston, E. E., K. M. Kapheim, and K. E. Holekamp. 2006. Patterns of den occupation by the spotted hyaena (*Crocuta crocuta*). *African Journal of Ecology* 44:77–86.

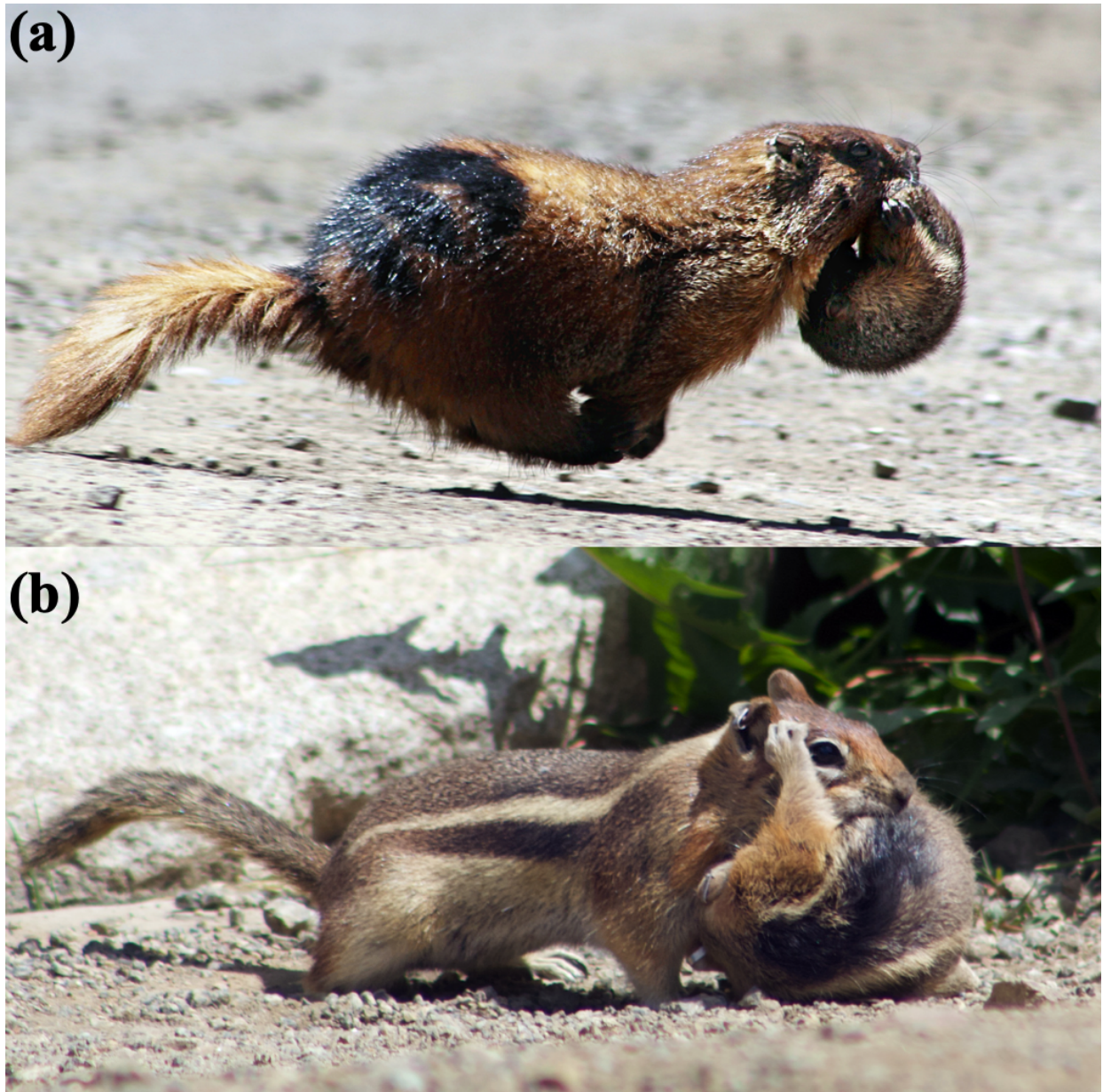
- Caro, T. M. 1987. Cheetah mothers' vigilance: looking out for prey or for predators? *Behavioral Ecology and Sociobiology* 20:351–361.
- Clutton-Brock, T. H. 1991. *The evolution of parental care*. Princeton University Press, Princeton, New Jersey.
- Clutton-Brock, T. H. 2016. *Mammal societies*. John Wiley & Sons, Hoboken, New Jersey.
- Costelloe, B. R., and D. I. Rubenstein. 2018. Temporal structuring of vigilance behaviour by female Thomson's gazelles with hidden fawns. *Animal Behaviour* 145:87–97.
- Coulon, J., L. Graziani, D. Allaine, M. C. Bel, and S. Poudroux. 1995. Infanticide in the Alpine marmot (*Marmota marmota*). *Ethology Ecology and Evolution* 7:191–194.
- Downhower, J. F., and K. B. Armitage. 1971. The yellow-bellied marmot and the evolution of polygamy. *The American Naturalist* 105:355.
- Ebensperger, L. A., and D. T. Blumstein. 2007. Nonparental infanticide. Pages 267–279 in J. O. Wolff and P. W. Sherman, editors. *Rodent societies: an ecological and evolutionary perspective*. The University of Chicago, Chicago, IL.
- Fisher, D. O., S. P. Blomberg, and I. P. F. Owens. 2002. Convergent maternal care strategies in ungulates and macropods. *Evolution* 56:167–176.
- Garland, T. 1983. Scaling the ecological cost of transport to body mass in terrestrial mammals. *The American Naturalist* 121:571–587.
- Gross, M. R. 2005. The evolution of parental care. *The Quarterly Review of Biology* 80:37–45.
- Harris, M. A., and J. O. Murie. 1984. Inheritance of nest sites in female Columbian ground squirrels. *Behavioral Ecology and Sociobiology* 15:97–102.
- Hennessy, D. F., and D. H. Owings. 1988. Rattlesnakes create a context for localizing their search for potential prey. *Ethology* 77:317–329.

- Huestis, R. R. 1947. The golden-mantled ground squirrel in Crater Lake National Park. *Nature Notes from Crater Lake* 13:1–8.
- Jetz, W., C. Carbone, J. Fulford, and J. H. Brown. 2004. The scale of animal space use. *Science* 306:266–268.
- Kerr, T., and S. Descamps. 2008. Why do North American red squirrel, *Tamiasciurus hudsonicus*, mothers relocate their young? A predation-based hypothesis. *The Canadian Field-Naturalist*:65–66.
- Kleef, H. L., and P. Tydeman. 2009. Natal den activity patterns of female pine martens (*Martes martes*) in the Netherlands. *Lutra* 52:3–14.
- Kneip, É., D. H. Van Vuren, J. A. Hostetler, and M. K. Oli. 2011. Influence of population density and climate on the demography of subalpine golden-mantled ground squirrels. *Journal of Mammalogy* 92:367–377.
- Laurenson, M. K. 1993. Early maternal behavior of wild cheetahs: implications for captive husbandry. *Zoo Biology* 12:31–43.
- Lent, P. C. 1974. Mother-infant relationships in ungulates. Pages 14–55 in V. Geist and F. Walther, editors. *The behaviour of ungulates and its relation to management*. International Union for the Conservation of Nature and Natural Resources, Morges, Switzerland.
- Michener, G. R. 1983. Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids. Pages 528–572 in J. F. Eisenberg and D. G. Kleiman, editors. *Advances in the study of mammalian behavior*. Seventh edition. American Society of Mammalogists, Stillwater, OK.
- Moore, J. F., C. P. Wells, D. H. Van Vuren, and M. K. Oli. 2016. Who pays? Intra-versus inter-generational costs of reproduction. *Ecosphere* 7:1–12.

- Pero, E. 2015. Exposing the elusive: Franklin's ground squirrel (*Poliocitellus franklinii*) demography, nest relocation, and dam response to ectoparasitism. Master's Thesis, University of Manitoba.
- Price, K., and S. Boutin. 1993. Territorial bequeathal by red squirrel mothers. *Behavioral Ecology* 4:144–150.
- Roper, T. J., T. P. Jackson, L. Conradt, and N. C. Bennett. 2002. Burrow use and the influence of ectoparasites in Brants' whistling rat *Parotomys brantsii*. *Ethology* 108:557–564.
- Schwartz, O. A., K. B. Armitage, and D. Van Vuren. 1998. A 32-year demography of yellow-bellied marmots (*Marmota flaviventris*). *Journal of Zoology* 246:337–346.
- Sharpe, S. T., and J. S. Millar. 1990. Relocation of nest site by female deer mice, *Peromyscus maniculatus borealis*. *Canadian Journal of Zoology* Vol. 68:2364–2367.
- Sikes, R. S., and The Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy* 97:663–688.
- Swaigood, R. R., D. H. Owings, and M. P. Rowe. 1999. Conflict and assessment in a predator-prey system: ground squirrels versus rattlesnakes. *Animal Behaviour* 57:1033–1044.
- Van Vuren, D. H. 2001. Predation on yellow-bellied marmots (*Marmota flaviventris*). *The American Midland Naturalist* 145:94–100.
- Wells, C. P., K. M. Tomalty, C. H. Floyd, M. B. McElreath, B. P. May, and D. H. Van Vuren. 2017. Determinants of multiple paternity in a fluctuating population of ground squirrels. *Behavioral Ecology and Sociobiology* 71.

- Wells, C. P., and D. H. Van Vuren. 2017. Female kin density affects offspring sex ratio in an asocial mammal, the golden-mantled ground squirrel, *Callospermophilus lateralis*. *Animal Behaviour* 134:71–77.
- Wells, C. P., and D. H. Van Vuren. 2018. Developmental and social constraints on early reproduction in an asocial ground squirrel. *Journal of Zoology* 306:28–35.
- Wilson-Henjum, G. E., J. R. Job, M. F. McKenna, G. Shannon, and G. Wittemyer. 2019. Alarm call modification by prairie dogs in the presence of juveniles. *Journal of Ethology* 37:167–174.

1.7 Figures



1.7.1 Litter relocation behavior by a yellow-bellied marmot (a) and golden-mantled ground squirrel (b), in which the mother seizes the pup in the area of the feet and belly with their incisors and carries it upside-down.

1.8 Tables

1.8.1 Summary of distances that golden-mantled ground squirrels (GMGS) and yellow-bellied marmots (YBM) moved their pups. Mean values are reported $\pm$ SE. Total distances were calculated by multiplying the relocation distance by the number of trips each adult female would have to take to move her entire litter (number of pups in litter, multiplied by two, minus one).

	GMGS			YBM		
	Mean	Median	Range	Mean	Median	Range
Relocation distance (m)	94 $\pm$ 13	79	16 - 252	85 $\pm$ 23	46	15 - 324
Internal move distance (m)	71 $\pm$ 10	56	16 - 160	43 $\pm$ 5	46	15 - 73
External move distance (m)	203 $\pm$ 16	189	182 - 252	279 $\pm$ 33	298	216 - 324
Total distance moved (m)	791 $\pm$ 153	462	94 - 2,802	598 $\pm$ 181	315	100 - 2,682

CHAPTER 2

HABITAT SELECTION IN A FLUCTUATING POPULATION OF GOLDEN-MANTLED GROUND

SQUIRRELS (*CALLOSPERMOPHILUS LATERALIS*): DENSITY-DEPENDENCE AND FITNESS

CONSEQUENCES

2.1 Abstract

Investigating individual-based habitat settlement decisions is a central theme in ecology, yet studies that quantify density-dependent habitat selection or tie fitness measures to resource selection decisions remain rare. We quantified habitat selection in golden-mantled ground squirrels (*Callospermophilus lateralis*) across two spatial scales (home range placement, and occurrence within the home range) by using 11 consecutive years of data on individual space use, and we used compositional analysis, resource selection functions, and multilevel modeling to address how habitat preferences may be influenced by density or linked to fitness outcomes. Squirrels preferred dry meadow over all other habitat types (wet meadow, aspen, spruce, and willow) at both spatial scales ($P = 0.002$). Squirrels were more likely to use dry meadow that contained shorter vegetation ($P = 0.002$) and vision-enhancing prominences such as rocks (“perches”; $P < 0.001$). Use of dry meadow at each spatial scale was not influenced by changes in density ($P > 0.05$). Use of dry meadow did not lead to increased litter size, pre-hibernation mass, or survival ($P > 0.05$). However, squirrels that experienced a greater number of perches or smaller local densities had higher survival rates ($P \leq 0.05$). Our results suggest that a lack of visual obstruction, probably to promote detection of predators, drives habitat selection in this system. Surprisingly, squirrels maintained their preference for dry meadow as density increased, and they experienced reduced survival as a result, perhaps because marginal habitat of sufficient

quality was not available. This work furthers our understanding about the causes and consequences of changes in habitat use, providing insight to the fields of wildlife management and conservation.

2.2 Introduction

Investigating individual-based habitat settlement decisions is a central theme in ecology (Morris 2003), having ties to fundamental concepts such as niche theory (Hutchinson 1957, Vandermeer 1972) and optimal foraging (MacArthur and Pianka 1966, Fretwell and Lucas 1969, Charnov 1976). In nature, resources are typically finite and nonuniformly distributed (Morris 1989, Paterson and Blouin-Demers 2018), and habitat selection often depends on predation risk (“landscape of fear”; Brown and Kotler 2004, Preisser et al. 2005, Laundré et al. 2010), including physical structure that affects risk (Kohl et al. 2018, Smith et al. 2019). Habitat selection therefore dictates the distribution of individuals across space and time (van Beest et al. 2014), which influences access to key resources such as preferred food items or cover from predators (Clark 1994, Chalfoun and Martin 2007). Hence, individuals often differ in performance, or fitness (e.g., survival, reproduction), across habitat types (McCloughlin et al. 2007, Gaillard et al. 2010, Matthiopoulos et al. 2015, Paterson and Blouin-Demers 2018), and habitat preferences are shaped by fitness benefits (Chalfoun and Martin 2007, Uboni et al. 2017).

It is well known that habitat-performance relationships are influenced by density, as an individual’s realized fitness is decreased by intraspecific competition (Morris 2003, Uboni et al. 2017). The ideal free distribution (IFD) theorizes that animals take this into account when self-assorting among habitat types; as population density increases in high quality habitat and competition for limited resources becomes intense, animals preferentially settle in lower quality

habitat, where they are equally likely to survive or reproduce due to lack of competition (Fretwell and Lucas 1969). Some studies criticized the validity of the underlying assumptions, noting that factors such as differential access to resources among individuals (Parker and Sutherland 1986, Conradt et al. 1999), predation risk (Abrahams and Dill 1989, Morris 1989, Garshelis 2000, Thompson and Gese 2012), lack of accurate information (Abrahams 1986, Spencer et al. 1996, Hemingway et al. 2018), movement costs (Matsumura et al. 2010, Abrahams and Labelle 2020), or ecological traps (Schlaepfer et al. 2002, Robertson et al. 2013) might dominate settlement decisions. Nonetheless, most criticisms remain untested in the field, in part because accurate assessments of habitat quality should involve calculations of animal performance (Van Horne 1983, Mosser et al. 2009), yet few investigations tie direct measurements of survival or reproduction to resource selection decisions by individual animals (Pulliam and Danielson 1991, Chalfoun and Martin 2007, Gaillard et al. 2010). Modeling approaches such as the resource selection function, which calculates habitat use in proportion to availability to deduce habitat preference (Boyce and McDonald 1999, Manly et al. 2002), are increasingly paired with measures of fitness to inform wildlife management (McLoughlin et al. 2006, Gaillard et al. 2010). However, studies that quantify the effect of density on habitat selection in free-ranging animal populations remain rare (McLoughlin et al. 2010, Morris and MacEachern 2010, van Beest et al. 2014).

In addition to varying as a function of density, habitat selection patterns (and associated fitness consequences) may differ across spatial scales (Johnson 1980, Gaillard et al. 2010, Dupke et al. 2017). For example, habitat choices by moose (*Alces alces*) at the landscape scale were driven by food availability, while finer-scale resource use was associated with refugia from human-induced risk (Herfindal et al. 2009); conversely, woodland caribou (*Rangifer tarandus*)

selected habitat based on avoiding predation on broader spatial scales, while selecting habitat associated with better forage at finer scales (Rettie and Messier 2000). Hence, animals continuously experience a variety of ecological tradeoffs, causing individuals to actively select habitat that best meets their current needs at each of a range of spatial scales (Dussault et al. 2005). Johnson (1980) categorized these scales into hierarchical “orders”: the broad-scale geographic distribution of a species, placement of an individual’s home range (Burt 1943, Powell and Mitchell 2012), use of certain areas within the home range, and selection for specific food items within those areas. Use of habitat types or resources becomes selective when it is disproportionate with respect to that which is available at each spatial scale; thus, it is possible that a species may be selecting for a given resource at only a subset of the spatial scales in which it is used (Johnson 1980, Mayor et al. 2009).

Given that habitat types that differ in availability across spatial scales may offer important resources that meet separate fitness needs (Beyer et al. 2010, Gaillard et al. 2010) and that density dependence may affect use of selected habitat types (Morris 1989, Mayor et al. 2009), habitat preference is complex and context-dependent. As such, it is critical to define appropriate scales of study (reviewed by Mayor et al. 2009, McGarigal et al. 2016), ideally at several spatial scales and for multiple fitness parameters (Brown and West 2000, Chalfoun and Martin 2007, Gaillard et al. 2010). Moreover, wildlife management is improved through quantification of fitness-habitat relationships over large spatial (i.e., home range as opposed to feeding site) and temporal (i.e., across multiple years as opposed to a single season) scales and during periods of high and low density, which allows for conservation of features that are critical to individual survival and reproduction (Garshelis 2000, Boyce 2006, Morris 2006, McLoughlin et al. 2007, van Beest et al. 2014). However, long-term studies that use direct, individual-based

measures of fitness to better understand consequences of selecting habitat at scales larger than the feeding site are uncommon because of practical difficulties in data collection (McCloughlin et al. 2007).

We used 11 consecutive years of detailed information on individual space use to investigate the causes and consequences of habitat selection in the golden-mantled ground squirrel (GMGS; *Callospermophilus lateralis*) at a high elevation site in Colorado. Our study captured a period of population flux, resulting in a range of population densities. We quantified habitat selection across two ecologically relevant spatial scales (home range placement, and use within the home range), assessed the effect of density on habitat selection, and evaluated several fitness outcomes of the habitat selection decision.

2.3 Methods

2.3.1 Study system

GMGS occur in mid- to high-elevation mountainous regions in the western United States and Canada (McKeever 1964, Bartels and Thompson 1993). As a small-bodied species (150-300 g), GMGS are presumed to be asocial (Armitage 1981, Michener 1983), and limited research suggests that GMGS are generally agonistic towards conspecifics (Ferron 1985). GMGS appear to use a variety of habitat types, such as conifer forest, chaparral, sagebrush, and mountain meadows, but habitat preference is poorly known (McKeever 1964, Bartels and Thompson 1993, Shick et al. 2006). GMGS hibernate in their burrows for much of the year, with populations at higher elevations spending up to twice as long hibernating than those at lower elevations (McKeever 1964, Bronson 1979). Females enter reproductive readiness shortly after emerging from hibernation, undergo gestation for approximately 28 days, and give birth to one litter of 1-8

pups per year (4.8, on average; Kneip et al. 2011, Wells and Van Vuren 2017). Mean sex ratio of offspring is 1:1, and pups are weaned after about 30 days of lactation, whereupon they emerge from their natal burrow (Wells and Van Vuren 2017).

We studied GMGS in Gothic, Colorado, at the site of the Rocky Mountain Biological Laboratory (RMBL), located in the East River Valley, Gunnison County (38°57' N, 106°59' W), from 1996 through 2006. Given the high elevation at RMBL (2900 m), squirrels enter hibernation during late August, and they do not emerge until the approximate time of snow melt, usually during May (Kneip et al. 2011, Hostetler et al. 2012). GMGS are primarily herbivorous, with a diet comprised mostly of forbs and fungi (McKeever 1964, Haufler and Nagy 1984), though arthropods are sometimes consumed, and opportunistic predation of small mammals and nestling birds has been recorded (McKeever 1964, Troy and Conover 2019). The main predators of GMGS at RMBL are red foxes (*Vulpes vulpes*), long-tailed weasels (*Mustela frenata*), and short-tailed weasels (*Mustela erminea*) (Kneip et al. 2011).

The 16-ha study area was bounded by the East River on the west, Copper Creek on the south, and aspen (*Populus tremuloides*) forest on the north and east. The study area was a mosaic of macrohabitats, mostly consisting of dry meadow, interspersed with patches of wet meadow, groves of aspen and spruce (*Picea engelmannii*), and stands of willow (*Salix* spp.). Dry meadow consisted of grasses (e.g., *Bromus inermis*, *B. polyanthus*) and low-growing forbs, such as dandelion (*Taraxacum officinale*), aspen sunflower (*Helianthella quinquenervis*), and cinquefoil (*Potentilla* spp.). Dry meadow was sparse in places and structurally open, and contained patchily distributed rocks. Wet meadow consisted of dense stands of tall forbs that often reached 1 m in height, including Colorado false hellebore (*Veratrum tenuipetalum*), cow parsnip (*Heracleum maximum*), and subalpine larkspur (*Delphinium barbeyi*). Aspen groves had an open understory

of scattered patches of tall forbs, such as cow parsnip and perennial herbs (e.g., *Ligusticum porteri* and *Osmorhiza occidentalis*). Spruce groves had dense canopies, creating relatively shaded understories largely devoid of herbaceous vegetation, but including some shrubs, such as whortleberry (*Vaccinium myrtillus*) and currant (*Ribes montigenum*). While aspen and spruce habitats contained structurally different understories, both habitat types included downed wood in the form of branches and stumps. Willow stands were dense and consisted of shortfruit willow (*Salix brachycarpa*), Drummond's willow (*S. drummondiana*), and Booth's willow (*S. boothii*).

Field work was conducted from June through August each year. During early June, we conducted an annual census by trapping all GMGS in the study area using Tomahawk live-traps (Model 201, Hazelhurst, WI). Additionally, we trapped pups when they first emerged from their natal burrows, usually late June to mid-July. Captured squirrels received numbered ear tags and unique dye marks (Nyanzol D, Greenville Colorants, Greenville, SC, USA) on their fur for visual identification, and sex, body mass, and reproductive status were recorded (Wells and Van Vuren 2017). Squirrels were re-trapped periodically to renew dye marks and determine mass and reproductive status. Squirrel locations in the study area were determined visually using binoculars, with animal identity based on unique dye marks. Individuals were diurnal and readily observable when not underground. We used instantaneous scan sampling, in which we recorded the identity and location of each squirrel in view at 1-min intervals. Squirrel locations were determined based on a grid map of the study area with 7-m x 7-m cells. Squirrels in our study area frequently encountered humans and almost never changed their behavior due to our presence from the observation distances we used; if a squirrel did react, those observations were discarded. A given sampling bout continued until squirrels left the area or entered a burrow, usually less than 10 min. We observed all sections of the study area at least twice per day, once

during the morning and once during the afternoon. While we observed squirrels from a given location, other sections of the study area were out of view; hence, we rotated among different sections of the study area at varying times of day to promote an even distribution of sampling effort. Nonetheless, some individuals were more active or easily seen than others; thus, we directed more effort toward observing underrepresented squirrels in the population when appropriate. We combined observations for each resident adult (≥ 1 year old) female each year.

Macrohabitat type was determined by visiting each grid square during the summers of 2000 and 2001 and visually identifying the macrohabitat type that comprised the greatest percent cover of that square. Some grid squares included buildings or gravel roads, totaling 7.7% of all grid squares. Squirrels were excluded from buildings, and squirrels never used roads except when in transit; hence, if buildings or roads comprised the majority of a given grid square, then that grid square was reassigned to the next most common macrohabitat type present.

A lack of visual obstruction appears to be important to ground squirrels in detecting predators (Blumstein et al. 2006, McGrann et al. 2014), and it might be especially important for a small-statured species such as GMGS. Microhabitat features that potentially influenced visual obstruction varied among the five macrohabitats that we studied, but only in dry meadow were we able to measure such microhabitat features reliably and consistently. Hence, for each grid square that supported dry meadow, we determined vegetation height and cover. Vegetation height was measured at five locations per grid square (in the center and toward each of four corners), then averaged and assigned to one of four categories: 0-25 cm, 26-50 cm, 51-75 cm, and >75 cm. Vegetation cover for the grid square was assessed by ocular estimate in four categories: 0-25%, 26-50%, 51-75%, and 76-100%. In addition, GMGS often sat on prominences such as rocks or stumps, presumably because of the enhanced field of vision. Hence, we recorded

the number of suitable “perches”; a perch was considered to be suitable when it was taller than the maximum height of vegetation within a given grid square. We counted the number of suitable perches in each grid square up to 10, and assigned the number 11 to those grid squares with more than 10 perches.

We assessed density effects and fitness consequences during 1996-2006, representing five years before and after habitat characterizations were completed; vegetation at both the macrohabitat and microhabitat level was consistent during that time period. To estimate population density, we recorded the total number of adult females present in the study area at the beginning of the active season each year. However, because occurrence of female GMGS in our study area tended to be in clusters, which might influence the density experienced by each female (Wells and Van Vuren 2017), we also investigated the effects of local density on habitat selection. We calculated the number of neighboring adult female home ranges that overlapped with a focal female’s home range in a given year, and we used this number as a proxy for local density (Efford 1996, Sanchez and Hudgens 2015, Woodworth et al. 2017).

Fitness measures for GMGS were calculated from demographic data collected during annual trapping. Survival was determined annually, based on presence during the early-June census from one year to the next; dispersal of adult females out of the study site during this period of time was rare. Reproductive success can be measured by reproductive status (whether or not a female bred) or by litter size (number of offspring produced per female that bred). Most females reproduced each year during our study, precluding analysis of reproductive status, so we instead focused on litter size of reproductive females. Litter size in GMGS might be influenced by stored fat from the previous summer (capital breeding) or resource acquisition during reproduction (income breeding; Stearns 1992); consequently, we investigated relationships

between habitat use and litter size during both the same year and the year after habitat use was measured. Maternity was assigned when a litter emerged at the female's burrow, reinforced by observations within 48 hours of pup emergence, when littermate pups typically engage in affiliative interactions, such as nose-greets, with only their mother and each other (Ferron 1985). Maternity and litter assignments were confirmed by genetic analysis (Wells and Van Vuren 2017). Females that were reproductive during a given year, as indicated by swollen nipples during June, but whose litters were likely predated and hence never observed, were assigned the mean number of offspring produced by females who bred that year ($n = 4$ for same-year analysis, $n = 6$ for next-year analysis). For a hibernating species such as GMGS, ample fat reserves at entry into hibernation should promote overwinter survival (Dark 2005). Hence, as an additional fitness measure we estimated pre-hibernation body mass for each female based on mass at her last capture that summer. We regressed mass at last capture of females against time, and used the slope of the regression (i.e., the population-level rate of increase in late season body mass) to estimate mass of each female on 31 August; females entered hibernation in late August. All procedures followed guidelines of the American Society of Mammalogists (Sikes and Animal Care and Use Committee of the American Society of Mammalogists 2016), and were approved by the institutional animal care and use committees of University of California, Davis and Rocky Mountain Biological Laboratory.

2.3.2 Multi-scale habitat selection

Grid square locations were registered in a spatial data base of the study area in ArcGIS v10 (ESRI 2018). GMGS sometimes moved across multiple grid squares comprising more than one habitat during a sequence of scan samples. However, they often remained in the same general location from one minute to the next, resulting in the possibility of spatial autocorrelation

in observations of squirrel locations. We reduced spatiotemporal autocorrelation in the dataset by including only the first observation when an individual was recorded in the same grid square more than once within a 10-min period. We delineated an annual home range for each squirrel by calculating 95% minimum convex polygons through package *adehabitatHR* (Calenge 2006) in the R software (version 3.6.1; R Core Team 2018). We included only females for which we recorded at least 55 independent (autocorrelation-corrected) observations within a given year, which surpassed sample sizes used to calculate squirrel home ranges in other studies (Wauters et al. 2007, Romeo et al. 2010, Jesmer et al. 2011). In addition, we only included females that were observed across at least 20 different calendar days each year.

Macrohabitat selection was measured on two spatial scales: habitat composition of the home range compared to that available across the study area (second-order selection), and habitat types used compared with those available within an individual's home range (third-order selection; Johnson 1980). Habitat composition of each home range (second-order) was based on habitats assigned to those grid squares within the home range, and use within each home range (third-order) was based on the proportional distribution of observations of the squirrel among habitats. All squirrels shared the same available habitat for second-order selection, but habitat availability was unique to each individual for third-order selection. We assessed habitat selection by using compositional analysis (Aebischer et al. 1993) to calculate log ratios of use versus availability for each habitat type, across all squirrels each year. We used Wilks' lambda (Λ) to test whether habitat selection was non-random at each spatial scale. We used t-tests to compare log ratios between each possible pair of habitat types, and we created a ranking matrix, which ordered habitat types according to preference. We used 50 iterations for data randomization. By using animals, rather than locations, as the sampling unit, compositional analysis is robust to

varying numbers of observations among individuals. Following Aebischer et al. (1993), we conducted an eisera analysis to verify that the GMGS population inherently behaved as a single group (i.e., habitat selection did not differ among subgroups of the population) and, because compositional analysis assumes all animals use all habitat types, we replaced values of zero with 0.01%. While compositional analysis is a recommended approach to infer population-level selection for categorical resource variables, it is not as useful a means to investigate selection at the individual level (Alldredge and Griswold 2006). We therefore also calculated selection ratios (Manly et al. 2002), and used chi-square goodness of fit tests to investigate individual patterns of selection.

To assess the effect of microhabitat features on habitat selection in dry meadow habitat, we ran a generalized linear mixed effects model (GLMM) with a Poisson error distribution and log link that examined counts, or total observations, in each available grid square of dry meadow as a function of microhabitat characteristics of those grid squares. We held individuals, grid locations, and years of study as random effects to account for repeated measures and the possibility of inherent differences among grids or interannual variation in environmental conditions. We used R packages lme4 (Bates et al. 2015) and glmmTMB (Brooks et al. 2017) to fit all mixed effects models.

2.3.3 Density effects and fitness consequences

We found that GMGS selected only for dry meadow habitat; hence, analyses investigating density-dependence and fitness consequences focused only on use of dry meadow. We assessed the effects of density on use of dry meadow by fitting separate models for each level of density (population and local) at each spatial scale (second-order and third-order). The second-order models analyzed the proportion of a squirrel's home range comprised of dry

meadow habitat in relation to density and age, and the third-order models analyzed the proportion of observations in a squirrel's home range that was within dry meadow in relation to density and age. We included age, as well as an interaction between age and density, as fixed effects because the habitat selection decision might be most evident at the time of settlement; in our GMGS population, dispersal begins late in the summer of birth and females typically establish residency by age one year. Hence, we coded age as a binary variable that categorized each squirrel as being either a yearling or older. All models were logistic GLMMs with a binomial error distribution and logit link that weighted the outcome by the total number of grid squares in a squirrel's home range (second-order model) or the total number of observations recorded for each squirrel (third-order model) and that included individuals and years as random effects.

We fit a series of GLMMs to examine the effects of multi-scale use of dry meadow (percent of home range, percent of observations within home range) on annual survival, litter size, and pre-hibernation body mass. The relationship between habitat use and each fitness outcome can be confounded by other variables thought to influence survivorship or reproductive success. Hence, we also included density and age as predictors in all of our fitness models, pre-hibernation mass as a predictor in our survival and next-year reproductive fitness models, and emergence mass as a predictor in our same-year reproductive fitness model; emergence mass was recorded as body mass during the first trapping event of the season, with the body mass of each female on 1 June estimated via linear regression as previously described for estimating pre-hibernation mass. We censored three deaths from anthropogenic causes (e.g., roadkill) from the dataset and used a logistic regression with a binomial error distribution and logit link to model the relationship between habitat use and annual survival. To assess the effects of habitat use on

this- and next-year litter size, we modeled data with a Poisson error distribution and log link. To investigate the relationship between habitat use and pre-hibernation body mass, we fit a log linear model with a Gaussian distribution. We scaled and centered all continuous predictor variables and accounted for individuals and years of study as random effects in all fitness models. We iteratively removed non-significant predictors and compared Akaike information criterion corrected for small sample size (AICc) to choose the most parsimonious models that minimized prediction error.

2.4 Results

We included 72 squirrel-year pairs across 46 individual adult female GMGS in our habitat selection analyses (mean annual observations per squirrel = 88, range = 55-100, SD = 15); of these, we modeled density dependence for 64 squirrel-year pairs (40 individuals), pre-hibernation mass for 62 squirrel-year pairs (40 individuals), annual survivorship for 61 squirrel-year pairs (39 individuals), same-year litter size for 58 squirrel-year pairs (37 individuals), and next-year litter size for 33 squirrel-year pairs (23 individuals). Our habitat classifications across the study area revealed that available habitat reflected 52.0% dry meadow, 20.2% aspen, 17.3% willow, 6.8% spruce, and 3.7% wet meadow (Fig. 1).

2.4.1 Habitat selection

Macrohabitat use was non-random at the spatial scale of both home range location (second-order $\Lambda = 0.161$, $P = 0.002$) and use within the home range (third-order $\Lambda = 0.054$, $P = 0.002$). Ranking matrices for selection at both spatial scales showed that GMGS exhibited a significant preference for dry meadow over all other habitat types ($P < 0.05$; Table 1). At the scale of home range location, GMGS significantly preferred willow to aspen ($P < 0.05$), and

significantly preferred either willow or spruce to wet meadow ($P < 0.05$). At the scale of use within the home range, GMGS did not preferentially select among willow, aspen, or spruce ($P > 0.05$), but they significantly selected any of those three habitat types over wet meadow ($P < 0.05$). Manly selection ratios were consistent with ranking matrices in that GMGS demonstrated significant selection for dry meadow habitat, and selection against all other habitat types, at each scale (second-order $P < 0.0001$, $df = 288.0$, $\chi^2 = 7093.421$; third-order $P < 0.0001$, $df = 73.0$, $\chi^2 = 502.298$) (Fig. 2).

At the microhabitat level, use of dry meadow was significantly related to the number of perches and to vegetation height (Table 2). As the number of perches within a dry meadow grid increased, squirrels were more likely to use that grid; a predictive plot based on our microhabitat model found that there was an 86.6% ($\pm$ SE of 16.3%) probability of use of a grid containing 11 or more perches (Fig. 3). Vegetation height was negatively related to use of dry meadow once vegetation reached a height of 75 cm (category 4). Vegetation density was not included in our final model because it was positively associated with vegetation height (Pearson's Chi-squared test, $\chi^2 = 1,693.70$, $df = 9$, $P < 0.0001$).

2.4.2 Density effects and fitness consequences

Population-level density within our 16-ha study area fluctuated more than five-fold during the study period (range = 5-29 adult females), and local density varied substantially as well (1-16 adult females). However, we found no relationship between population density and either percent of the home range comprised of dry meadow (GLMM $\beta \pm SE = 0.04 \pm 0.03$, $z = 1.74$, $P = 0.081$) or percent of observations within the home range that were in dry meadow habitat (GLMM $\beta \pm SE = -0.03 \pm 0.02$, $z = -1.47$, $P = 0.141$). Similarly, local density did not influence either the percent of the home range comprised of dry meadow (GLMM $\beta \pm SE = -0.01$

± 0.08 , $z = -0.15$, $P = 0.881$) or the percent of observations within the home range that were in dry meadow (GLMM $\beta \pm SE = -0.07 \pm 0.07$, $z = -1.00$, $P = 0.319$). There was no relationship between age (yearling or older) and habitat use; percent home range comprised of dry meadow was not influenced by age when accounting for either population density (GLMM $\beta \pm SE = -0.09 \pm 0.56$, $z = -0.16$, $P = 0.869$) or local density (GLMM $\beta \pm SE = -0.13 \pm 0.44$, $z = -0.28$, $P = 0.777$), and habitat use was not affected by an interaction between age and either population density (GLMM $\beta \pm SE = 0.003 \pm 0.03$, $z = 0.11$, $P = 0.912$) or local density (GLMM $\beta \pm SE = 0.03 \pm 0.10$, $z = 0.27$, $P = 0.789$). Likewise, percent of observations within the home range that were in dry meadow habitat did not vary as a function of age when accounting for either population density (GLMM $\beta \pm SE = -0.99 \pm 0.59$, $z = -1.67$, $P = 0.095$) or local density (GLMM $\beta \pm SE = -0.22 \pm 0.47$, $z = -0.47$, $P = 0.637$), and there was no effect of an interaction between age and either population density (GLMM $\beta \pm SE = 0.05 \pm 0.03$, $z = 1.68$, $P = 0.093$) or local density (GLMM $\beta \pm SE = 0.05 \pm 0.10$, $z = 0.48$, $P = 0.633$) on within-home range habitat use.

Given that perches significantly increased the probability that GMGS will use dry meadow, we included total number of perches that each squirrel had in its home range as a third habitat predictor in our fitness models. We also included density as a covariate in all fitness models; because population density and local density were correlated (Pearson's correlation test, $r = 0.67$, $df = 44$, $P < 0.0001$), and because including correlated variables interferes with model performance, we used local density since it best reflects the density experienced by GMGS.

Across years, mean percent survival ($\pm SE$) was 64.5 ± 7.7 percent (range 20-100). There was no relationship between annual survival and either percent home range comprised of dry meadow (GLMM $\beta \pm SE = -0.01 \pm 0.37$, $z = -0.02$, $P = 0.982$) or percent of observations within the home range that were in dry meadow habitat (GLMM $\beta \pm SE = -0.09 \pm 0.36$, $z = -0.26$, $P = 0.794$).

However, we found that squirrels that selected for home ranges with a greater number of perches or that experienced lower local densities (fewer neighboring conspecifics within a given year) were significantly more likely to survive into the following year than squirrels that had access to fewer perches or experienced higher local densities (Table 3). Also, annual survival was significantly greater for yearlings than for older females (Table 3), an unexpected result that might reflect a survival cost of reproduction; yearlings are less likely to breed than older females (Kneip et al. 2011, Moore et al. 2016). Mean litter size ($\pm$ SE) across years was 5.0 ± 0.2 pups (range 1-7). Litter size during the year that habitat use was recorded was not related to percent home range comprised of dry meadow (GLMM $\beta \pm$ SE = -0.10 ± 0.08 , $z = -1.39$, $P = 0.164$), percent of observations within the home range that were in dry meadow (GLMM $\beta \pm$ SE = 0.04 ± 0.08 , $z = 0.58$, $P = 0.565$), or the total number of perches within the home range (GLMM $\beta \pm$ SE = 0.00 ± 0.06 , $z = 0.01$, $P = 0.995$). Similarly, litter size the next year was not related to percent home range comprised of dry meadow (GLMM $\beta \pm$ SE = 0.04 ± 0.13 , $z = 0.31$, $P = 0.756$), percent of observations within the home range that were in dry meadow (GLMM $\beta \pm$ SE = 0.07 ± 0.11 , $z = 0.63$, $P = 0.531$), or the number of perches within the home range (GLMM $\beta \pm$ SE = -0.07 ± 0.10 , $z = -0.75$, $P = 0.453$). However, a bivariate analysis revealed a positive correlation between next-year litter size and percent home range comprised of dry meadow that approached statistical significance (Pearson's correlation test, $r = 0.32$, $df = 34$, $P = 0.055$), although the relationship was not strong enough to appear in the final model. There was no relationship between pre-hibernation mass and percent home range comprised of dry meadow (GLMM $\beta \pm$ SE = 0.03 ± 0.03 , $z = 1.28$, $P = 0.200$), percent of observations within the home range that were in dry meadow (GLMM $\beta \pm$ SE = -0.02 ± 0.02 , $z = -1.10$, $P = 0.273$), or number of perches in the home range (GLMM $\beta \pm$ SE = 0.00 ± 0.02 , $z = -0.17$, $P = 0.865$).

2.5 Discussion

Habitat associations of golden-mantled ground squirrels are not well known, but available information suggests the species is a generalist, occurring in a variety of forested or sparsely brushy habitats, and also on rocky slopes adjoining grasslands and at the margins of mountain meadows (Bartels and Thompson 1993). A common feature of habitats used by GMGS appears to be the presence of some degree of openness. We found that GMGS exhibited strong selection for dry meadow habitat, and that pattern was consistent for both home range placement (second-order selection) and use within the home range (third-order selection). Dry meadow offers an open landscape and also contains an abundance of dandelions, a preferred food resource for GMGS in our study area (Carleton 1966). Other species of ground-dwelling squirrels also prefer open areas that provide good visibility, likely to facilitate early detection of predators (Blumstein et al. 2006, Ordeñana et al. 2012, Zaharia et al. 2016); the juxtaposition of these two conditions – food availability and predator detectability – seems to influence habitat selection decisions (Hannon et al. 2006, Armitage 2014, McGrann et al. 2014).

Use of dry meadow by GMGS was promoted by the presence of perches and reduced vegetation height, highlighting the importance of a lack of visual obstruction in habitat selection decisions. Perches may abate predation risk by elevating a squirrel's point of view and thus enabling visual monitoring of the surroundings (Armitage 1982, Beauchamp 2015). Most of the perches in our study were rocks; GMGS were found associated with rocks in other studies (Bartels and Thompson 1993, Bihr and Smith 1998), and the importance of rocks as perches for improved visibility may be the explanation. Similar to presence of perches, reduced vegetation height likely reduces predation risk by enhancing detection of predators. Our results are consistent with those of Rowe (2007), who found that GMGS in Utah preferred grazed areas to

ungrazed areas. Studies on other species of ground-dwelling squirrels, such as yellow-bellied marmots (*Marmota flaviventer*; Van Vuren 2001, Bednekoff and Blumstein 2009), thirteen-lined ground squirrels (*Ictidomys tridecemlineatus*; Arenz and Leger 1997), Great Basin ground squirrels (*Urocitellus mollis*; Sharpe and Van Horne 1998), Arctic ground squirrels (*Urocitellus parryii*; Wheeler and Hik 2014), and alpine marmots (*Marmota marmota*; Ferrari et al. 2009), also suggest that visual obstruction can increase predation risk. In addition to aiding in predator detection directly, perches may indirectly promote predator detection through the monitoring of conspecifics; even in asocial species, vigilance of neighbors may be interpreted as public information about present risk (Sirot 2006, Carrasco and Blumstein 2011, Beauchamp 2017).

GMGS often occur in open coniferous forests (McKeever 1964), but the species avoided spruce forest in our study, perhaps because spruce forest had a closed canopy that was perceived as being too dense; GMGS in a mature conifer forest in Montana preferred locations with a reduced canopy tree density (Shick et al. 2006). Wet meadow and willow habitats also were avoided by GMGS; in both habitats vegetation was exceptionally dense, creating visual obstruction. GMGS in Utah preferred xeric habitats to mesic habitats (Rowe 2007), perhaps because xeric habitats support sparser vegetation. Avoidance of wet meadow and willow habitats also might result from an observation bias in data collection; squirrels were readily observed in dry meadow, spruce, and aspen habitats, but not in wet meadow or willow because of visual obstruction for the observer. However, this observation bias likely is minor; we seldom observed squirrels entering wet meadow or willow habitats, and when they did, they usually traversed the habitat patch and exited on the other side.

We found no effect of density on use of dry meadow, the preferred habitat, either for home range location (second-order selection) or for occurrence within the home range (third-

order), despite substantial variation in both population-level and local-level density. As population density or local density increased, squirrels stayed in dry meadow habitat rather than moving to less crowded, presumably marginal habitat, contrary to the expectations of IFD. For resident adult females with established home ranges, relocation in response to high density may have been too costly. However, the cost should be lower for yearlings, who are making the decision of where to settle; hence, we were surprised to find no density effect for yearlings. It is possible that the lack of spillover into marginal habitats as density increased resulted because available marginal habitats were not of sufficient quality, or there was enough dry meadow to accommodate squirrels at high density; all habitats besides dry meadow were avoided. Further, home ranges did not decrease in size during high density years (Aliperti 2020). Regardless of the cause for a lack of spillover, with increasing density female GMGS continued to preferentially select for dry meadow habitat, suggesting the potential for increased competition. Accordingly, we found that local density had a significant, negative effect on survival, upholding the IFD prediction that increased crowding into patches of preferred habitat should decrease fitness (Fretwell and Lucas 1969). We did not find a similar effect at the population level; for organisms with relatively limited mobility, density effects may be exhibited at scales less than that of the population (Einum and Nislow 2005).

High quality habitat might confer increased fitness through resources related to either food availability or predation risk. Reproduction might be enhanced due to greater availability or quality of food resources (Kenagy et al. 1990, Wells and Van Vuren 2018), and survival might be improved due to increased fat stores before hibernation or reduced predation risk (Dark 2005, Kneip et al. 2011). However, we did not find an effect of use of dry meadow on reproduction, although a marginally-significant correlation between dry meadow use and next-year litter size

suggests that such an effect was a possibility, which would support that GMGS are capital breeders (Stearns 1992). Similarly, we did not find a relationship between dry meadow use and pre-hibernation mass or overwinter survival. However, we found that GMGS with more perches in their home range experienced higher survival, substantiating a link between enhanced visibility and decreased predation risk. Hence, the value of dry meadow habitat to GMGS may lie more in reduced predation risk than in enhanced food availability.

Our results show that female golden-mantled ground squirrels strongly preferred dry meadow habitat and, contrary to the expectations of IFD, they maintained that affinity as density increased, perhaps because marginal habitats of sufficient quality were not available. The main fitness benefit of dry meadow appeared to be reduced predation risk, and evidently the benefit of reducing predation risk outweighed the survival cost of competing for resources in a crowded environment. Given that alterations to habitat may influence the spatial distribution of both individuals and preferred resources, understanding the causes and consequences of multi-scale habitat use provides insight to the fields of wildlife management and conservation.

Acknowledgments

I thank my co-authors, K. Jenderseck and D. H. Van Vuren, as well as the Rocky Mountain Biological Laboratory for logistical support, and the many research assistants who contributed to data collection. Project funding was provided by the California Agricultural Experiment Station, Rocky Mountain Biological Laboratory Graduate Fellowship, American Society of Mammalogists Grant-in-Aid of Research, and the University of California, Davis Walter and Elizabeth Howard Award. I thank R. Klinger for advice on resource selection

modeling, and R. Williams for help with plant identification. A. Sih and R. J. Hijmans provided valuable comments on an earlier draft of this manuscript.

2.6 Literature Cited

- Abrahams, M., and L. Dill. 1989. A determination of the energetic equivalence of the risk of predation. *Ecology* 70:999–1007.
- Abrahams, M. V. 1986. Patch choice under perceptual constraints: a cause for departures from an ideal free distribution. *Behavioral Ecology and Sociobiology* 19:409–415.
- Abrahams, M. V., and J. Labelle. 2020. The effect of travel costs on the ideal free distribution in stickleback. *Ethology* 126:353–362.
- Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313–1325.
- Aliperti, J. R. 2020. Behavioral and spatial dynamics in a fluctuating population of golden-mantled ground squirrels (*Callospermophilus lateralis*). PhD Dissertation, University of California, Davis.
- Allredge, J. R., and J. Griswold. 2006. Design and analysis of resource selection studies for categorical resource variables. *Journal of Wildlife Management* 70:337–346.
- Arenz, C. L., and D. W. Leger. 1997. Artificial visual obstruction, antipredator vigilance, and predator detection in the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*). *Behaviour* 134:1101–1114.
- Armitage, K. B. 1981. Sociality as a life-history tactic of ground squirrels. *Oecologia* 48:36–41.
- Armitage, K. B. 1982. Marmots and coyotes: behavior of prey and predator. *Journal of Mammalogy* 63:503–505.

- Armitage, K. B. 2014. Marmot biology: sociality, individual fitness, and population dynamics. Cambridge University Press, Cambridge.
- Bartels, M. A., and D. P. Thompson. 1993. *Spermophilus lateralis*.
- Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Beauchamp, G. 2015. Animal vigilance: monitoring predators and competitors. Academic Press, Oxford.
- Beauchamp, G. 2017. Difficulties in monitoring conspecifics mediate the effects of visual obstruction on the level and synchronization of vigilance. *Frontiers in Ecology and Evolution* 5:3–8.
- Bednekoff, P. A., and D. T. Blumstein. 2009. Peripheral obstructions influence marmot vigilance: integrating observational and experimental results. *Behavioral Ecology* 20:1111–1117.
- van Beest, F. M., A. Uzal, E. Vander Wal, M. P. Laforge, A. L. Contasti, D. Colville, and P. D. McLoughlin. 2014. Increasing density leads to generalization in both coarse-grained habitat selection and fine-grained resource selection in a large mammal. *Journal of Animal Ecology* 83:147–156.
- Beyer, H. L., D. T. Haydon, J. M. Morales, J. L. Frair, M. Hebblewhite, M. Mitchell, and J. Matthiopoulos. 2010. The interpretation of habitat preference metrics under use-availability designs. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2245–2254.

- Bihr, K. J., and R. J. Smith. 1998. Location, structure, and contents of burrows of *Spermophilus lateralis* and *Tamias minimus*, two ground-dwelling sciurids. *The Southwestern Naturalist* 43:352–362.
- Blumstein, D. T., A. Ozgul, V. Yovovich, D. H. Van Vuren, and K. B. Armitage. 2006. Effect of predation risk on the presence and persistence of yellow-bellied marmot (*Marmota flaviventris*) colonies. *Journal of Zoology* 270:132–138.
- Boyce, M. S. 2006. Scale for resource selection functions. *Diversity and Distributions* 12:269–276.
- Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions 14:268–272.
- Bronson, M. T. 1979. Altitudinal variation in the life history of the golden-mantled ground squirrel (*Spermophilus lateralis*). *Ecology* 60:272–279.
- Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Mächler, and B. M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal* 9:378–400.
- Brown, J. H., and G. B. West. 2000. *Scaling in biology*. Oxford University Press, Oxford, UK.
- Brown, J. S., and B. P. Kotler. 2004. Hazardous duty pay and the foraging cost of predation. *Ecology Letters* 7:999–1014.
- Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. *American Society of Mammalogists* 24:346–352.
- Calenge, C. 2006. The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197:516–519.

- Carleton, W. M. 1966. Food habits of two sympatric Colorado sciurids. *Journal of Mammalogy* 47:91–103.
- Carrasco, M. F., and D. T. Blumstein. 2011. Mule deer (*Odocoileus hemionus*) respond to yellow-bellied marmot (*Marmota flaviventris*) alarm calls. *Ethology* 118:243–250.
- Chalfoun, A. D., and T. E. Martin. 2007. Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. *Journal of Applied Ecology* 44:983–992.
- Charnov, E. L. 1976. Optimal foraging: attack strategy of a mantid. *The American Naturalist* 110:141–151.
- Clark, C. W. 1994. Antipredator behavior and the asset-protection principle. *Behavioral Ecology* 5:159–170.
- Conradt, L., T. H. Clutton-Brock, and F. E. Guinness. 1999. The relationship between habitat choice and lifetime reproductive success in female red deer. *Oecologia* 120:218–224.
- Dark, J. 2005. Annual lipid cycles in hibernators: integration of physiology and behavior. *Annual Review of Nutrition* 25:469–497.
- Dupke, C., C. Bonenfant, B. Reineking, R. Hable, T. Zeppenfeld, M. Ewald, and M. Heurich. 2017. Habitat selection by a large herbivore at multiple spatial and temporal scales is primarily governed by food resources. *Ecography* 40:1014–1027.
- Dussault, C., J. Ouellet, R. Courtois, J. Huot, L. Breton, and H. Jolicœur. 2005. Linking moose habitat selection to limiting factors. *Ecography* 28:619–628.
- Efford, M. G. 1996. Simulating spatially distributed populations. Pages 409–418 in R. B. Floyd, A. W. Sheppard, and P. J. De Barro, editors. *Frontiers of Population Ecology*. CSIRO Publishing, Melbourne.

- Einum, S., and K. H. Nislow. 2005. Local-scale density-dependent survival of mobile organisms in continuous habitats: an experimental test using Atlantic salmon. *Oecologia* 143:203–210.
- ESRI. 2018. Arc GIS. Environmental System Research Institute Inc., Redlands, California.
- Ferrari, C., G. Bogliani, and A. Von Hardenberg. 2009. Alpine marmots (*Marmota marmota*) adjust vigilance behaviour according to environmental characteristics of their surrounding. *Ethology Ecology and Evolution* 21:355–364.
- Ferron, J. 1985. Social behaviour of the golden-mantled ground-squirrel (*Spermophilus lateralis*). *Canadian Journal of Zoology* 63:2529–2533.
- Fretwell, S. D., and H. L. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. *Acta biotheoretica* 19:16–36.
- Gaillard, J. M., M. Hebblewhite, A. Loison, M. Fuller, R. Powell, M. Basille, and B. Van Moorter. 2010. Habitat-performance relationships: finding the right metric at a given spatial scale. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:2255–2265.
- Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. Pages 111–164 in M. C. Pearl, editor. *Research techniques in animal ecology: controversies and consequences*. Columbia University Press, New York.
- Hannon, M. J., S. H. Jenkins, R. L. Crabtree, and A. K. Swanson. 2006. Visibility and vigilance: behavior and population ecology of Uinta ground squirrels (*Spermophilus armatus*) in different habitats. *Journal of Mammalogy* 87:287–295.
- Haufler, J. B., and J. G. Nagy. 1984. Summer food habits of a small mammal community in the pinyon-juniper ecosystem. *Great Basin Naturalist* 44:145–150.

- Hemingway, C. T., M. J. Ryan, and R. A. Page. 2018. Cognitive constraints on optimal foraging in frog-eating bats. *Animal Behaviour* 143:43–50.
- Herfindal, I., J. P. Tremblay, B. B. Hansen, E. J. Solberg, M. Heim, and B. E. Sæther. 2009. Scale dependency and functional response in moose habitat selection. *Ecography* 32:849–859.
- van Horne, B. 1983. Density as a misleading indicator of habitat quality 47:893–901.
- Hostetler, J. A., E. Kneip, D. H. Van Vuren, and M. K. Oli. 2012. Stochastic population dynamics of a montane ground-dwelling squirrel. *PLoS ONE* 7:1–10.
- Hutchinson, G. E. 1957. Concluding remarks. Pages 415–427 *Cold Spring Harbor Symposia on Quantitative Biology*. Cold Spring Harbor Laboratory Press.
- Jesmer, B. R., D. H. Van Vuren, J. A. Wilson, D. A. Kelt, and M. L. Johnson. 2011. Spatial organization in female golden-mantled ground squirrels. *The American Midland Naturalist* 165:162–168.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- Kenagy, G. J., D. Masman, S. M. Sharbaugh, and K. A. Nagy. 1990. Energy expenditure during lactation in relation to litter size in free-living golden-mantled ground squirrels. *Journal of Animal Ecology* 59:73–88.
- Kneip, É., D. H. Van Vuren, J. A. Hostetler, and M. K. Oli. 2011. Influence of population density and climate on the demography of subalpine golden-mantled ground squirrels. *Journal of Mammalogy* 92:367–377.

- Kohl, M. T., D. R. Stahler, M. C. Metz, J. D. Forester, M. J. Kauffman, N. Varley, P. J. White, D. W. Smith, and D. R. MacNulty. 2018. Diel predator activity drives a dynamic landscape of fear. *Ecological Monographs* 88:638–652.
- Laundré, J. W., L. Hernández, and W. J. Ripple. 2010. The landscape of fear: ecological implications of being afraid. *The Open Ecology Journal* 3:1–7.
- MacArthur, R., and E. R. Pianka. 1966. On optimal use of a patchy environment. *The American Naturalist* 100:603.
- Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic Publishers, Dordrecht, the Netherlands.
- Matsumura, S., R. Arlinghaus, and U. Dieckmann. 2010. Foraging on spatially distributed resources with sub-optimal movement, imperfect information, and travelling costs: departures from the ideal free distribution. *Oikos* 119:1469–1483.
- Matthiopoulos, J., J. Fieberg, G. Aarts, H. L. Beyer, J. M. Morales, and D. T. Haydon. 2015. Establishing the link between habitat selection and animal population dynamics. *Ecological Monographs* 85:413–436.
- Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009. Habitat selection at multiple scales. *Écoscience* 16:238–247.
- McGarigal, K., H. Y. Wan, K. A. Zeller, B. C. Timm, and S. A. Cushman. 2016. Multi-scale habitat selection modeling: a review and outlook. *Landscape Ecology* 31:1161–1175.
- McGrann, M. C., D. H. Van Vuren, and M. A. Ordeñana. 2014. Influence of adjacent crop type on occurrence of California ground squirrels on levees in the Sacramento Valley, California. *Wildlife Society Bulletin* 38:111–115.

- McKeever, S. 1964. The biology of the golden-mantled ground squirrel, *Citellus lateralis*.
Ecological Monographs 34:383–401.
- McLoughlin, P. D., M. S. Boyce, T. Coulson, and T. Clutton-Brock. 2006. Lifetime reproductive success and density-dependent, multi-variable resource selection. Proceedings of the Royal Society B: Biological Sciences 273:1449–1454.
- McLoughlin, P. D., J. M. Gaillard, M. S. Boyce, C. Bonenfant, F. Messier, P. Duncan, D. Delorme, B. Van Moorter, S. Saïd, and F. Klein. 2007. Lifetime reproductive success and composition of the home range in a large herbivore. Ecology 88:3192–3201.
- McLoughlin, P. D., D. W. Morris, D. Fortin, E. Vander Wal, and A. L. Contasti. 2010. Considering ecological dynamics in resource selection functions. Journal of Animal Ecology 79:4–12.
- Michener, G. R. 1983. Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids. Pages 528–572 in J. F. Eisenberg and D. G. Kleiman, editors. Advances in the study of mammalian behavior. Seventh edition. American Society of Mammalogists, Stillwater, OK.
- Moore, J. F., C. P. Wells, D. H. Van Vuren, and M. K. Oli. 2016. Who pays? Intra-versus inter-generational costs of reproduction. Ecosphere 7:1–12.
- Morris, D. W. 1989. Density-dependent habitat selection: testing the theory with fitness data. Evolutionary Ecology 3:80–94.
- Morris, D. W. 2003. Toward an ecological synthesis: a case for habitat selection. Oecologia 136:1–13.
- Morris, D. W. 2006. Moving to the ideal free home. Nature 443:645–646.

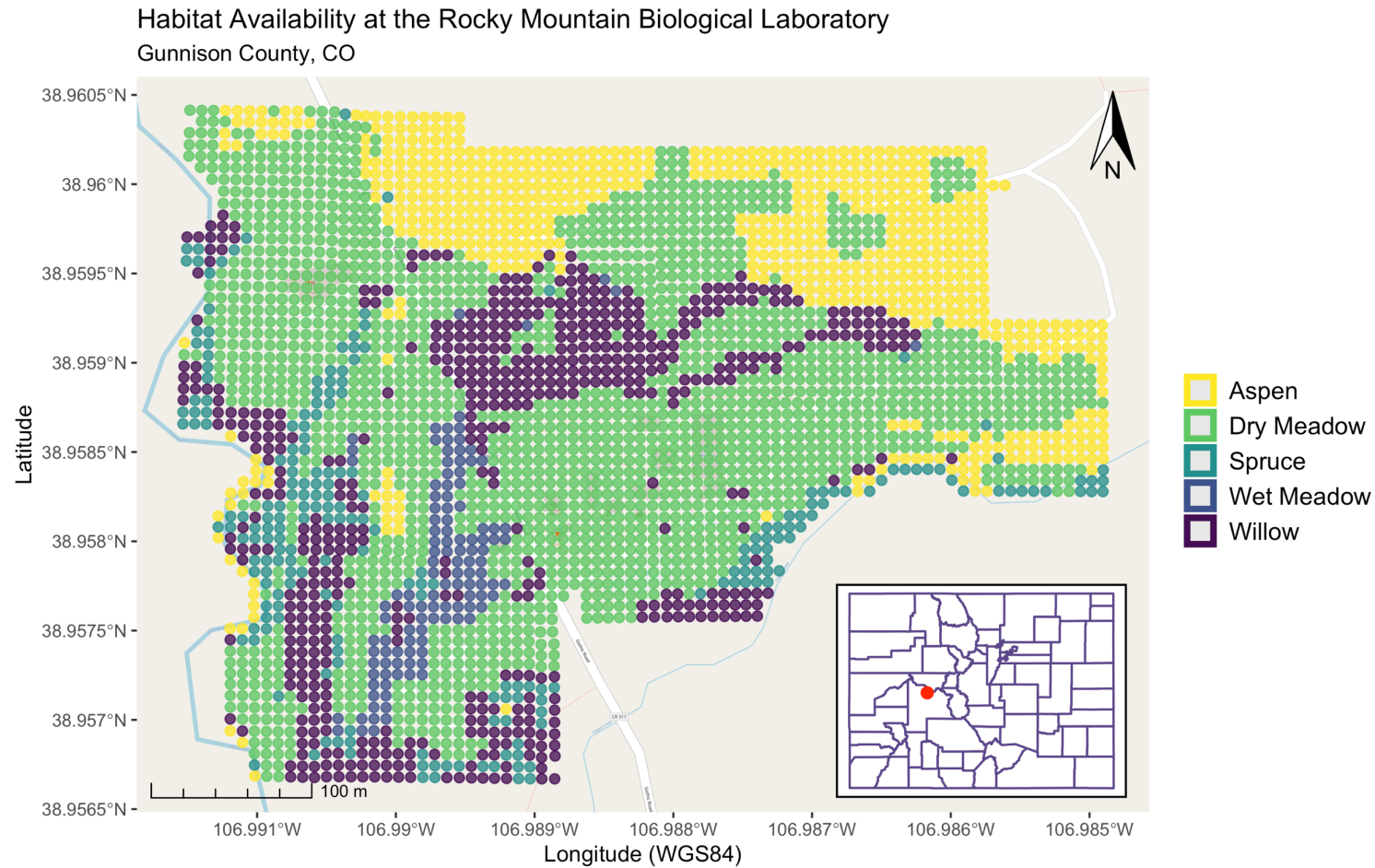
- Morris, D. W., and J. T. MacEachern. 2010. Active density-dependent habitat selection in a controlled population of small mammals. *Ecology* 91:3131–3137.
- Mosser, A., J. M. Fryxell, L. Eberly, and C. Packer. 2009. Serengeti real estate: density vs. fitness-based indicators of lion habitat quality. *Ecology Letters* 12:1050–1060.
- Ordeñana, M. A., D. H. Van Vuren, and J. P. Draper. 2012. Habitat associations of California ground squirrels and Botta's pocket gophers on levees in California. *Journal of Wildlife Management* 76:1712–1717.
- Parker, G. A., and W. J. Sutherland. 1986. Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. *Animal Behaviour* 34:1222–1242.
- Paterson, J. E., and G. Blouin-Demers. 2018. Density-dependent habitat selection predicts fitness and abundance in a small lizard. *Oikos* 127:448–459.
- Powell, R. A., and M. S. Mitchell. 2012. What is a home range? *Journal of Mammalogy* 93:948–958.
- Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* 86:501–509.
- Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks and habitat selection: a landscape perspective on population dynamics. *The American Naturalist* 137:S50–S66.
- R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Rettie, W. J., and F. Messier. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography* 23:466–478.
- Robertson, B. A., J. S. Rehage, and A. Sih. 2013. Ecological novelty and the emergence of evolutionary traps. *Trends in Ecology and Evolution* 28:552–560.

- Romeo, C., L. A. Wauters, D. Preatoni, G. Tosi, and A. Martinoli. 2010. Living on the edge: space use of Eurasian red squirrels in marginal high-elevation habitat. *Acta Oecologica* 36:604–610.
- Rowe, R. J. 2007. Legacies of land use and recent climatic change: the small mammal fauna in the mountains of Utah. *American Naturalist* 170:242–257.
- Sanchez, J. N., and B. R. Hudgens. 2015. Interactions between density, home range behaviors, and contact rates in the Channel Island fox (*Urocyon littoralis*). *Ecology and Evolution* 5:2466–2477.
- Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. *Trends in Ecology and Evolution* 17:474–480.
- Sharpe, P. B., and B. Van Horne. 1998. Influence of habitat on behavior of Townsend's ground squirrels (*Spermophilus townsendii*). *Journal of Mammalogy* 79:906–918.
- Shick, K. R., D. E. Pearson, and L. F. Ruggiero. 2006. Forest habitat associations of the golden-mantled ground squirrel: implications for fuels management. *Northwest Science* 80:133–139.
- Sikes, R. S., and The Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy* 97:663–688.
- Sirot, E. 2006. Social information, antipredatory vigilance and flight in bird flocks. *Animal Behaviour* 72:373–382.
- Smith, J. A., E. Donadio, J. N. Pauli, M. J. Sheriff, and A. D. Middleton. 2019. Integrating temporal refugia into landscapes of fear: prey exploit predator downtimes to forage in risky places. *Oecologia* 189:883–890.

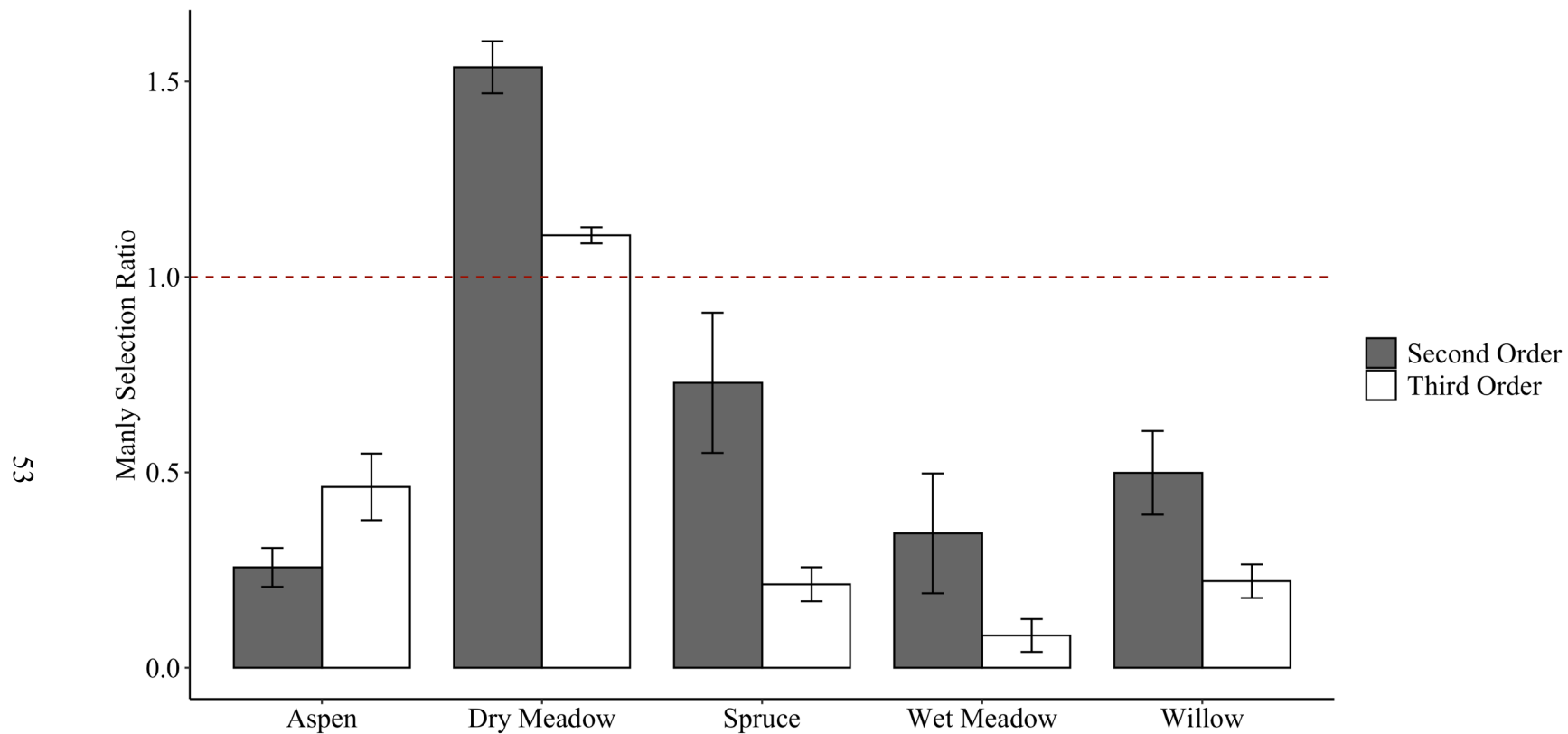
- Spencer, H. G., M. Kennedy, and R. D. Gray. 1996. Perceptual constraints on optimal foraging: the effects of variation among foragers. *Evolutionary Ecology* 10:331–339.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, Oxford, UK.
- Thompson, C. M., and E. M. Gese. 2012. Swift foxes and Ideal Free Distribution: relative influence of vegetation and rodent prey base on swift fox survival, density, and home range size. *ISRN Zoology* 2012:1–8.
- Troy, S. R., and R. R. Conover. 2019. The depredation of mountain white-crowned sparrow (*Zonotrichia leucophrys oriantha*) nests by the golden-mantled ground squirrel (*Callospermophilus lateralis*) and long-tailed weasel (*Mustela frenata*). *The Wilson Journal of Ornithology* 131:629.
- Uboni, A., D. W. Smith, D. R. Stahler, and J. A. Vucetich. 2017. Selecting habitat to what purpose? The advantage of exploring the habitat-fitness relationship. *Ecosphere* 8.
- Vandermeer, J. H. 1972. Niche theory. *Annual Review of Ecology and Systematics* 3:107–132.
- Van Vuren, D. H. 2001. Predation on yellow-bellied marmots (*Marmota flaviventris*). *The American Midland Naturalist* 145:94–100.
- Wauters, L. A., D. G. Preatoni, A. Molinari, and G. Tosi. 2007. Radio-tracking squirrels: performance of home range density and linkage estimators with small range and sample size. *Ecological Modelling* 202:333–344.
- Wells, C. P., and D. H. Van Vuren. 2017. Female kin density affects offspring sex ratio in an asocial mammal, the golden-mantled ground squirrel, *Callospermophilus lateralis*. *Animal Behaviour* 134:71–77.
- Wells, C. P., and D. H. Van Vuren. 2018. Developmental and social constraints on early reproduction in an asocial ground squirrel. *Journal of Zoology* 306:28–35.

- Wheeler, H. C., and D. S. Hik. 2014. Giving-up densities and foraging behaviour indicate possible effects of shrub encroachment on arctic ground squirrels. *Animal Behaviour* 95:1–8.
- Woodworth, B. K., N. T. Wheelwright, A. E. M. Newman, and D. R. Norris. 2017. Local density regulates migratory songbird reproductive success through effects on double-brooding and nest predation. *Ecology* 98:2039–2048.
- Zaharia, G., L. Petrencu, and E. Ștefan Baltag. 2016. Site selection of European ground squirrels (*Spermophilus citellus*) in eastern Romania and how they are influenced by climate, relief, and vegetation. *Turkish Journal of Zoology* 40:917–924.

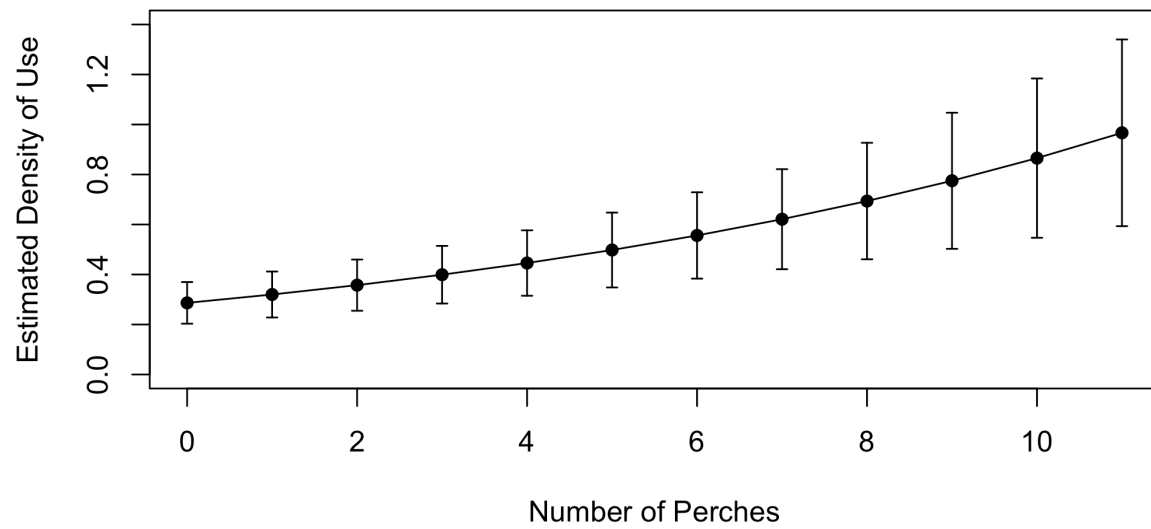
2.7 Figures



2.7.1 Habitat map of the study area, located at the Rocky Mountain Biological Laboratory, Gunnison County, Colorado. The site is delineated by a 7x7 m grid system, with each grid cell assigned to one of five habitat types.



2.7.2 Mean selection ratios for second- and third-order habitat selection by golden-mantled ground squirrels across five macrohabitat types. Error bars represent standard errors. Values above the dashed line indicate positive selection and values below the dashed line indicate negative selection.



2.7.3 Prediction frame showing the estimated probability of use of a dry meadow grid square by golden-mantled ground squirrels based on the number of perches (rocks or stumps) within that grid square. Error bars represent 95% confidence intervals from the probability distribution.

2.8 Tables

2.8.1 Compositional analysis ranking matrix for second- and third-order habitat selection by golden-mantled ground squirrels. The matrix was created by taking the mean difference between used and available log ratios for each habitat type, and indicates whether the habitat in a given row is used more (“+”) or less (“-”) than the habitat in a given column. The sign is tripled when the differential use is significant ($P < 0.05$).

Habitat	Second-order (home range placement)					Third-order (within-home range use)				
	Aspen	Spruce	Dry Meadow	Wet Meadow	Willow	Aspen	Spruce	Dry Meadow	Wet Meadow	Willow
Aspen	0	-	---	+	---	0	+	---	+++	+
Spruce	+	0	---	+++	-	-	0	---	+++	-
Dry Meadow	+++	+++	0	+++	+++	+++	+++	0	+++	+++
Wet Meadow	-	---	---	0	---	---	---	---	0	---
Willow	+++	+	---	+++	0	-	+	---	+++	0

2.8.2 Model estimates from the analysis of number of observations in dry meadow habitat in relation to number of perches and vegetation height, after controlling for individual identity and year.

Model Variables	Estimate	Standard Error	z value	Pr(> z)
Intercept	-1.17	0.22	-5.38	< 0.0001
Number of perches	0.11	0.01	7.41	< 0.0001
Vegetation height (26-50 cm)	0.13	0.18	0.71	0.475
Vegetation height (51-75 cm)	-0.13	0.18	-0.74	0.459
Vegetation height (> 75 cm)	-0.81	0.26	-3.07	0.002

2.8.3 Model estimates from the analysis of annual survival in relation to number of perches within the home range, pre-hibernation mass, local density, and age, after controlling for individual identity and year.

Model Variables	Estimate	Standard Error	z value	Pr(> z)
Intercept	-0.22	0.40	-0.54	0.589
Number of perches	0.64	0.33	1.96	0.050
Pre-hibernation mass	0.60	0.32	1.85	0.065
Local density	-0.63	0.30	-2.11	0.035
Local density	1.41	0.65	2.18	0.029

CHAPTER 3

BRIDGING ANIMAL PERSONALITY WITH SPACE- AND RESOURCE USE IN A FREE-RANGING POPULATION OF AN ASOCIAL GROUND SQUIRREL

3.1 Abstract

Consistent individual differences in behavior, or personality, likely influence patterns of space- and resource use in wild animals. However, studies on personality-dependent space use in natural ecosystems remain rare due to the difficulty of obtaining paired datasets on spatial dynamics and repeated personality measures from marked animals. We used repeated standardized assays to perform the first characterization of personality in a free-ranging population of golden-mantled ground squirrels (*Callospermophilus lateralis*), and we used multilevel modeling to determine if personality influenced 95% home range size, 50% core area size, movement speed, or use of a preferred resource (“perches”, vision-enhancing prominences such as rocks, which enhance survival) in nature. Data collected over three years showed that squirrels consistently differed in activity, sociability, boldness, and aggressiveness (adjusted repeatability 0.16-0.44). We did not find an effect of personality on home range size ($P > 0.05$), but bolder individuals maintained larger core areas than shyer individuals ($P = 0.001$). More active ($P = 0.022$) and bolder ($P < 0.001$) individuals moved faster under natural conditions compared to their less active and shyer conspecifics. Individuals that scored higher for all four personality traits had a greater number of perches in both their home ranges and core areas compared to individuals with lower personality scores ($P \leq 0.006$). Our results are indicative of personality-dependent space- and resource use in this system. We hope our study will inspire

future research that links animal personality with spatial ecology to inform wildlife management in natural ecosystems.

3.2 Introduction

Space use has important ties to many aspects of ecology, with implications for wildlife conservation and management. For example, the size and placement of an animal's home range influences access to resources, and the speed and distance in which an animal moves may influence predator-prey interactions, competition, social networks, or disease spread (Sih et al. 2012, Wolf and Weissing 2012, Kurvers et al. 2014, Spiegel et al. 2015). Although spatial patterns are typically studied at the population or species level, individual differences in space use dynamics often account for a substantial amount of the variation exhibited at higher levels of biological organization (Börger et al. 2006, Merrick and Koprowski 2017a, Spiegel et al. 2017), and thus may act as a link between process and pattern in ecology (Belisle 2005). Individual variation in space use is well studied in relation to factors such as resource availability (Lucherini and Lovari 1996, Bowler and Benton 2005, Maher and Burger 2011), physical traits (Bakker and Van Vuren 2004, Armitage 2009, Singleton and Garland 2018), and social interactions among kin (Bekoff 1977, Armitage et al. 2011, Hoogland 2013); however, spatial variation due to individual differences in behavior is still not well understood (Börger et al. 2006, Wey et al. 2015, Toscano et al. 2016, Spiegel et al. 2017).

A growing body of research suggests that variation in animal space use patterns may in part be explained by consistent individual differences in behavior across time or contexts, a concept known as animal personality, behavioral types, temperament, or coping styles (Koolhaas et al. 1999, Gosling 2001, Sih et al. 2004a, Réale et al. 2007). Indeed, individuals across many

taxa exhibit limited plasticity in behavioral traits, such as boldness, aggressiveness, activity level, sociability, or exploration tendency, which may affect an animal's use of space through personality-driven movement and dispersal (Sih et al. 2004b, Wey et al. 2015, Toscano et al. 2016). At times, two or more of these traits may be correlated ('behavioral syndromes'; Sih et al. 2004b, Sih and Bell 2008), affecting how an animal interacts with its environment and, ultimately, its fitness (Smith and Blumstein 2008, Sih et al. 2012, Wolf and Weissing 2012, Moiron et al. 2020). For example, risk-prone, bold individuals also tend to be more active and aggressive (Sih et al. 2004a, Boon et al. 2008, Réale et al. 2010, Hertel et al. 2019). While this suite of behaviors likely results in greater acquisition of resources such as food and space, it also may increase the risk of mortality (Biro and Stamps 2008, Réale et al. 2010, Blight et al. 2016).

Efforts to create a unifying framework for personality-dependent spatial ecology (Spiegel et al. 2017) have revealed links between individual differences in behavior and space use across contexts. For example, individuals that are less social may disperse during years of high density, whereas more social individuals remain in their natal home range (Stamps 2001, Cote and Clobert 2007, Cote et al. 2010). Furthermore, dispersing individuals tend to be more active and aggressive (Sih et al. 2004a, Duckworth and Badyaev 2007, Thorlacius et al. 2015, Merrick and Koprowski 2017b), and individuals that are faster explorers (move more quickly, but with less attention to their environment) have been found to disperse farther (Dingemanse et al. 2003, Clobert et al. 2009, Réale et al. 2010). In addition to dispersal, personality may play a significant role in shaping habitat preferences (Bonnot et al. 2015, Leclerc et al. 2016, Holtmann et al. 2017), which can in turn influence home range size and resource use (Minderman et al. 2010, van Overveld and Matthysen 2010, Spiegel et al. 2015, Schirmer et al. 2020). As examples, more active North American red squirrels (*Tamiasciurus hudsonicus*) were more likely to travel farther

and intrude on the territories of conspecifics (Boon et al. 2008), bolder individual bank voles (*Myodes glareolus*) occupied larger home ranges (Schirmer et al. 2019), and brown bears (*Ursus arctos*) exhibited consistent individual differences in habitat selection (Leclerc et al. 2016). The potential influence of individual-level behavioral differences on various spatial outcomes can be assessed using spatially explicit, multilevel models that account for free-ranging movement of individuals in nature, personality of individuals in standardized assays, and other variables that may confound the relationship between personality and space use (Börger et al. 2006, Dingemanse and Dochtermann 2013, Fordham et al. 2014, Spiegel et al. 2017). However, studies that examine the effects of behavioral type on space- and resource use in nature remain rare, probably due to the difficulty of obtaining paired datasets on spatial dynamics and repeated personality measures from marked animals (Wey et al. 2015, Leclerc et al. 2016, Schirmer et al. 2019).

We used standardized personality assays to characterize consistent individual differences in behavior in order to determine if these differences influenced home range size, core area size, movement speed, or use of a preferred resource in a population of free-ranging golden-mantled ground squirrels (*Callospermophilus lateralis*), an asocial and territorial species (Aliperti 2020). Our overarching hypothesis was that inter-individual differences in use of space and resources would be related to individual personality type. Given published connections between personality and spatial dynamics (Cote et al. 2010, Spiegel et al. 2017), we predicted that more ‘proactive’ (i.e., bold, active, aggressive; Réale et al. 2010) individuals would tend to maintain larger home ranges and core areas, move faster, and have greater access to preferred habitat resources.

3.3 Methods

3.3.1 Study system

We studied a population of golden-mantled ground squirrels (GMGS) at the Rocky Mountain Biological Laboratory, a high-elevation (2900 m) site located in the East River Valley, Gunnison County, Colorado (38°57' N, 106°59' W), from 2016 to 2018. The 16-ha study area was delineated by the East River on the west, Copper Creek on the south, and aspen (*Populus tremuloides*) forest on the north and east. Vegetation consisted of a mosaic of habitats, comprised mostly of dry subalpine meadow, intermixed with wet meadow, stands of aspen, spruce (*Picea engelmannii*), and willow (*Salix* spp.). GMGS generally prefer more open habitats, and in our study area they strongly preferred dry meadow habitat, which provides both food (mostly forbs, such as dandelions, *Taraxacum officinale*) and enhanced visibility for detecting predators (Aliperti 2020). Predators in our study area included red foxes (*Vulpes vulpes*), long-tailed weasels (*Mustela frenata*), and short-tailed weasels (*Mustela erminea*) (Kneip et al. 2011).

GMGS hibernate for up to eight months of the year, from late August until the approximate time of snow melt, typically during May (Kneip et al. 2011, Hostetler et al. 2012). Squirrels breed shortly after emerging from hibernation, after which females gestate for approximately 28 days, then give birth underground to one litter of 1-8 pups per year ($\bar{x} = 4.8$; Kneip et al. 2011, Wells and Van Vuren 2017). Juveniles emerge from their natal burrow about 30 days after birth (Phillips 1981), at which time they typically are weaned and forage independently (Wells et al. 2017). While most juveniles disperse (leave their natal home range permanently) during the summer of birth (Michener 1983), some delay dispersal until the following summer, and others remain philopatric (Jesmer et al. 2011). Early dispersal of GMGS relative to other species of ground-dwelling squirrels is presumed to be driven by their small

body size (150-300 g), which facilitates rapid development (maturity is reached at one year) and decreases the opportunity for social bonds to form; hence, GMGS are considered to be asocial (Armitage 1981, Michener 1983). Adult GMGS are generally agonistic toward conspecifics (Ferron 1985), and there is minimal spatial overlap among the core areas of adult home ranges, perhaps because those areas are defended as territories (Jesmer et al. 2011).

We conducted field work each year from June through late August during the summer active season. We conducted an annual census by using Tomahawk live-traps (Model 201) to capture all GMGS in the study area during early June, and we trapped all pups within two days of their emergence from natal burrows, typically late June to mid-July. We used numbered ear tags and unique dye marks on the fur (Nyanzol D dye, Greenville Colorants, Greenville, SC, USA) to identify all captured individuals, and we recorded sex, body mass, and reproductive status at each capture (Wells and Van Vuren 2017). We re-trapped squirrels as necessary to renew dye marks and conduct personality assays. We used binoculars to visually identify squirrels at a distance based on their dye marks, and to determine spatial locations; GMGS are diurnal and clearly observable when aboveground. Only a portion of the study area was in view at any one location, so we rotated randomly among different sections of the study area in search of squirrels. Once one or more squirrels were in view, we initiated an instantaneous scan sampling approach, in which we identified and recorded the location of all individuals at 1-min intervals until squirrels were no longer in view, usually less than 10 min. Squirrels disappeared by either entering a burrow or leaving the area. Locations were based on a map of the study area with 7-m x 7-m gridded cells. We covered all sections at least twice daily, once during the morning and once during the afternoon, to ensure that observations captured possible heterogeneity in use of space by different squirrels at varying times of day. Because active

squirrels were often more easily observed, we redirected sampling effort to focus on underrepresented squirrels when appropriate. Squirrels in our study area frequently encounter humans and rarely reacted to our presence at the observation distances we used; locations of those that did react were excluded. We pooled spatial observations for each individual each year for analyses.

Squirrels in our study area often use “perches”, protruding features such as rocks or stumps that elevate a squirrel’s point of view above the surrounding vegetation (Aliperti 2020). Because access to perches was found to enhance survival in GMGS (Aliperti 2020), we estimated the effect of consistent individual differences in behavior on access to perches in dry meadow habitat, the only habitat that was preferred by GMGS. We counted the number of perches in each grid square that supported dry meadow habitat, and assigned the number 11 if a given grid square contained more than 10 perches. All procedures followed guidelines of the American Society of Mammalogists (Sikes and Animal Care and Use Committee of the American Society of Mammalogists 2016), and were approved by the institutional animal care and use committees of University of California, Davis and Rocky Mountain Biological Laboratory.

3.3.2 Spatial outcomes

We registered squirrel locations into a spatial data base of our study area in ArcGIS v10 (ESRI 2018). We reduced spatial autocorrelation among locations of individual squirrels by including only the first observation when a squirrel was recorded in the same location more than once within a 10-min sampling bout (Aliperti 2020); squirrels are able to cross a given grid square within a few seconds. To promote an accurate representation of space use, we filtered the resulting autocorrelation-corrected dataset to include only individuals that were observed at least

35 times over at least 14 different calendar days within a given year. We delineated annual home ranges for each squirrel by defining 95% and 50% minimum convex polygons through package `adehabitatHR` (Version 0.4.16; Calenge 2006) in the R software (version 3.6.1; R Core Team 2019). The 95% home range characterizes the area that an individual uses to carry out its day-to-day activities, while the 50% home range, also known as the core area, characterizes the region of concentrated activity within the home range (Samuel et al. 1985, Powell and Mitchell 2012). We calculated the total number of perches in each squirrel's 95% home range and 50% core area by summing the number of perches across all dry meadow grids that fell within that individual's 95% home range and 50% core area boundaries.

Movement speed was quantified for each individual each year through R package `adehabitatLT` (Version 0.3.24; Calenge 2006). We divided all spatial observations (without filters pertaining to autocorrelation or sample size) into 10-min blocks of time known as “bursts”. For each individual that was observed 3-10 times within a given burst, we divided the total distance moved by that individual (m) by the total amount of time (sec) that passed between the first and final observations within that burst. Distance measurements were based on the centroids of grid squares; hence, if a squirrel moved from one grid square to anywhere within an adjacent grid square, the linear distance between the centroids of the two squares was recorded. We calculated the average movement speed across all bursts for those individuals that were observed for three or more bursts in a given year.

3.3.3 Personality assays

We quantified personality in GMGS through four types of repeated, standardized behavioral assays, each performed at least twice per individual per year. The first assay was an open field (OF) test, a commonly used method to measure activity (tendency towards movement)

and exploration (tendency towards investigation) in a novel environment (Cummins and Walsh 1976, Boon et al. 2007, Martin and Réale 2008, Montiglio et al. 2010, Mazzamuto et al. 2019). The second assay was a mirror image stimulation (MIS) test, which measures sociability or aggression (non-agonistic and agonistic behavior towards conspecifics, respectively; Svendsen and Armitage 1973, Armitage and Van Vuren 2003). The OF and MIS assays took place in the same trial period, with the OF assay immediately preceding and thus serving as a habituation period prior to the MIS assay (Svendsen and Armitage 1973, Boon et al. 2007, Krause et al. 2015). Both assays were performed during 2016 and 2017 in a portable arena, which consisted of a white rectangular box ($L \times W \times H = 92 \times 46 \times 56$ cm) fitted with a Plexiglass lid. There were four circular holes cut into the floorboard, each 5 cm in diameter and 12 mm deep (Fig. 1). The inclusion of floorboard holes is a suggested means to differentiate activity from exploration, behaviors that are typically correlated; activity pertains to movement, while ‘head-dipping behavior’, in which the animal inserts its head into a hole, pertains to exploration (Martin and Réale 2008). Individual GMGS were trapped, then released into a small, wooden “acclimation box” ($L \times W \times H = 42 \times 13 \times 13$ cm), where the squirrel rested for 3 min before the OF assay began. The front edge of the acclimation box, up to but not including a lift-up sliding door, was inserted into an opening located on the side of the arena. The sliding door was raised and the squirrel was gently prodded into the arena, marking the beginning of the OF assay. Immediately following the OF assay, the MIS assay was initiated by removing a sliding wall at the back end of the arena, in turn revealing a mirror. The mirror was affixed to and covered most of the far wall of the arena such that the squirrel could see its reflection. A GoPro HERO camera that was mounted on a tripod above the arena recorded squirrel behavior during all OF and MIS assays. OF and MIS assays were 4 min each (8 min total testing session), a duration that is considered

appropriate for reducing physiological stress and habituation to novel conditions, and which is within the recommended range for squirrel species (Montiglio et al. 2010, Dosmann et al. 2015, Mazzamuto et al. 2019). All assays took place within the home range of the focal individual. The experimenter remained silent and out of the squirrel's view for the entirety of each assay. At the conclusion of each session, the squirrel was released at its point of capture and the arena was sprayed with 70% alcohol, then dried.

Squirrel behavior recorded during OF and MIS assays was quantified with EthoVision tracking software (Noldus EthoVision XT 11.5). We reviewed all videos to ensure that footage was recorded appropriately and that the focal individual was tracked accurately by the software program. For each OF assay, we quantified total distance moved, mean and maximum velocity attained, and total time spent moving. We also divided the arena into zones: "Vestibule" to describe the front of the acclimation box, the location most immediate to the arena's entrance; "Near Corner" to describe the corners closest to the entrance; "Center" to describe the area of the arena that was most exposed, away from surrounding walls; and "Far End" to describe the area farthest from the arena entrance, where the mirror was revealed during the MIS assay. For each OF assay, we quantified the amount of time spent within each zone, and the number of visits to each zone. For each MIS assay, we quantified total distance moved, as well as the time spent within and number of visits to the "Vestibule" and "Far End" zones. For each 4-min OF and MIS assay, we tracked the focal individual at 30 frames per second, for a total of 7,200 point samples. All 282 recorded assays had missed sample rates (percent of recorded time in which the squirrel could not be tracked) of $\leq 4.8\%$. We used EthoVision's interpolation feature to interpolate missing values for all assays with missed sample rates greater than 0%. Our final dataset contained a mean of 7,192 samples per assay, representing a missed sample rate of 0.1%.

In addition to using automated tracking software, we watched all recorded assays and manually quantified an ethogram of behaviors that we were not able to measure in EthoVision. The behaviors analyzed for the OF assay included number of jumping events, number of climbing events, time spent sniffing, and the duration and frequency in which a squirrel investigated floorboard holes. The behaviors manually analyzed for the MIS assay included time spent looking towards versus away from the mirror, and total time spent interacting with the mirror image. Interaction with the mirror took the form of either hand-touching or nose-touching the mirror surface; similar nose-to-nose and hand-to-body greets are commonly observed under natural conditions and are interpreted to be amicable social interactions, usually among littermate pups and their mother (Ferron 1985, Armitage 1986, Wells and Van Vuren 2017). All behaviors were explicitly defined, and all observers were trained to identify the defined behaviors on video. To eliminate inter-observer bias, we assigned a different set of behaviors to each observer, such that a given behavior was quantified by the same observer for all recorded trials.

In addition to performing arena assays, we conducted standardized flight initiation distance (FID) and behavior-in-trap (BIT) tests during 2017 and 2018. FID, the distance at which an animal flees from an approaching human (a perceived threat), is a common method used to quantify consistent individual differences in shyness; shyer individuals tend to have greater FID scores (flee from a farther distance) than individuals that are bolder (Ydenberg and Dill 1986, Blumstein 2003). We quantified FID after identifying a GMGS that was not alert or in distress; we spent several minutes observing the individual at a distance before performing the test. Following Petelle et al. (2013), the observer walked directly towards the focal squirrel at a consistent pace of approximately 0.5 m/s. Markers were placed to identify the location of the observer at the start of the test, the location of the observer when the squirrel first fled, and the

location of the squirrel before it fled. At the conclusion of each test, the observer determined the distance between the observer and the squirrel when the test began (start distance) and when the squirrel fled (FID). All distances were recorded as heel-to-toe footsteps and then converted to meters. Squirrels typically fled to a burrow less than 10 m from their starting location, then emerged and resumed normal activity within minutes of being tested.

We conducted BIT trials to quantify consistent individual differences in docility, which can be measured as an individual's tendency to remain calm when trapped (Réale et al. 2000, Petelle et al. 2013). At each trapping event, before an individual was handled, an observer sat quietly approximately 0.5 m from the trapped squirrel for 2 min and recorded binary (i.e., 0/1) scores that indicated whether that individual bit the trap, emitted an alarm call, or chattered its teeth during the trial. For each trial, we subtracted the sum of all scored behaviors from the maximum potential score (following Réale et al. 2000); hence, personality scores ranged from 0 (less docile) to 3 (more docile). We conducted FID and BIT trials only if there were no signs of disturbance (i.e., predators, other humans, or alarm calls by other squirrels) preceding the trial period; if an individual's behavior could have been influenced by a disturbance unrelated to the assay itself, the trial was discarded. We took the negative value of the outcomes from FID and BIT trials to obtain FID scores that represented boldness and BIT scores that represented aggressiveness.

3.3.4 Statistical analyses

Consistent individual differences in behavior

For both the OF and MIS assays, we used principal component analysis (PCA) with *varimax* rotation to reduce the number of measured behavioral variables into a smaller number of synthetic variables that independently represent personality traits (Martin and Réale 2008,

Nawroth et al. 2017). Each PCA was performed on the correlation matrix of measured variables (separately for OF and MIS), which standardized data to mean 0 and standard deviation 1. Only variables which met the conditions of the Barlett test and the Kaiser-Mayer-Olkin criterion were retained for each PCA (Field et al. 2012). We identified which components to retain based on identifying the “elbow”, or point of curvature, of a scree plot (Cattell 1966), and all retained components had an Eigenvalue > 1 (Wold et al. 1987).

We calculated the repeatability of individual behavior scores (scores from retained principal components from the OF and MIS assays, and scores from the FID and BIT assays), by running a series of Bayesian inference repeatability models with the R package rptR (Version 0.9.22; Stoffel et al. 2017). Animals are considered to exhibit personality for specific behavioral traits when the between-individual variation is consistently greater than the within-individual variation for those traits; hence, high repeatability values indicate personality when individuals behave consistently across time, and when individuals consistently differ from one another (Leclerc et al. 2016). We ran a separate linear mixed effects model (LMM) with the behavioral scores from each personality assay set as the dependent variable, and squirrel identity as a random effect; we confirmed that residuals met normality conditions for each model. We controlled for age class (adult or juvenile), year, and trial number as fixed effects. Successive trials of a given individual for any one personality assay were separated by one or more days (following Minderman et al. 2010 and Schirmer et al. 2019); hence, we included trial number to account for the passing of time between trials, which varied among individuals due to the unpredictability of re-capturing free-ranging subjects (Aplin et al. 2014). Additionally, because start distance may significantly influence FID (Blumstein 2003), we controlled for start distance as a fixed effect in our FID repeatability model. It is possible that personality may change over

time, such that repeatability may vary as a function of age class (Petelle et al. 2013). Hence, we also ran all repeatability models separately for adults and juveniles. Age-specific repeatability models contained the same structure as other repeatability models, though age was removed as a fixed effect, and year was not included in the FID repeatability model for adults because all adults that completed two or more FID assays were tested during 2017. Model outputs returned adjusted repeatability values (the proportion of behavioral variation explained by consistent individual differences in behavior, after controlling for fixed effects) and the statistical significance of repeatability. Statistical significance ($P < 0.05$) was based on a likelihood ratio test (LRT), which compared the fit of each repeatability model with and without inclusion of individual as a random factor (Stoffel et al. 2017).

Retained principal components that contained significantly repeatable scores were labeled as the personality type most appropriately described by the behaviors within each component that contained the highest loadings. We used the means of only those behavior scores that were significantly repeatable as quantitative, individual-based measurements of personality in subsequent spatial models. We investigated the potential for behavioral syndromes by calculating Spearman rank correlations to test for phenotypic associations among personality traits.

Personality-dependent use of space and resources

To assess the effects of personality on each spatial outcome variable (home range and core area sizes, number of perches, movement speed), we ran a series of LMMs and generalized linear mixed effects models (GLMMs) according to the error distribution and corresponding link function of the underlying data. Our sample size was limited because we could not perform all personality assays each year, or record adequate spatial data for all squirrels; hence, we fit

separate models for the effects of each personality trait on each spatial outcome (following Schirmer et al. 2019).

We analyzed the effects of personality on home range size (separately for the 95% home range and 50% core area) by fitting a log linear model with a Gaussian distribution. In addition to personality scores, we included age class, sex, an interaction between age class and sex, year, and the total number of spatial observations used to delineate the home range as fixed effects; we included the interaction because males were expected to have larger home ranges than females, but only as adults. To assess the effects of personality on number of perches within the 95% home range and 50% core area, we modeled data with a Poisson error distribution and log link. We regressed number of perches against personality score, age class, sex, year, and home range size; we controlled for home range size (either 95% or 50% core area) under the assumption that larger home ranges likely contain a greater number of perches. To analyze the relationship between personality and movement speed, we fit LMMs with a Gaussian distribution that assessed movement speed in relation to personality score, and we accounted for age class, sex, year, and the total number of bursts used to calculate an individual's average speed as fixed effects. We scaled and centered all continuous predictor variables and accounted for individuals as random effects in all spatial outcome models except those analyzing boldness; there were no individuals that experienced FID trials across years. We included an extra interaction term between age class and personality score in models analyzing scores that were not significantly repeatable in both adults and juveniles. Following Zurr et al. (2009), we started with a full fixed effects structure for each model, then iteratively removed non-significant predictors and compared Akaike information criterion corrected for small sample size (AICc) to choose the

most parsimonious models that minimized prediction error. We used R packages lme4 (Bates et al. 2015) and glmmTMB (Brooks et al. 2017) to fit all models.

3.4 Results

We calculated home range size and perch access for 64 squirrel-year pairs across 48 individual GMGS (29 adults, 35 juveniles), as well as average movement speed for 98 squirrel-year pairs across 77 individual GMGS (37 adults, 59 juveniles). We completed two or more arena trials on 42 squirrel-year pairs (36 individuals; 12 adults, 24 juveniles), FID trials on 28 squirrel-year pairs (28 individuals; 10 adults, 18 juveniles), and BIT trials on 61 squirrel-year pairs (53 individuals; 14 adults, 41 juveniles). After merging our spatial and personality datasets, we were able to model personality-dependent home range size and perch access (95% and 50% core area) for 36 squirrel-year pairs (30 individuals) that were assayed in the arena, 21 squirrel-year pairs (21 individuals) that were assayed for FID, and 38 squirrel-year pairs (31 individuals) that were assayed for BIT. We modeled personality-dependent movement speed for 38 squirrel-year pairs (32 individuals) that were assayed in the arena, 28 squirrel-year pairs (28 individuals) that were assayed for FID, and 52 squirrel-year pairs (44 individuals) that were assayed for BIT.

3.4.1 *Spatial outcomes*

Golden-mantled ground squirrels maintained 95% home range areas (mean $\pm$ SE) of 1.02 ± 0.15 ha (range 0.05-7.12 ha) and 50% core areas of 0.19 ± 0.04 ha (range 0.003-2.26 ha). Home ranges included a mean of 318 ± 33.1 perches (range 38-1,503), and core areas included a mean of 94 ± 13.1 perches (range 0-572). Mean movement speed across individuals was 0.04 ± 0.003 m/sec, or 144.0 ± 10.80 m per hour (range 0-0.12 m/sec). Individuals exhibited wide variation within age and sex classes in all spatial outcome variables (Figs. 2, 3).

3.4.2 Consistent individual differences in behavior

We retained two principal components from the OF assay data, which explained 69% of the total variance. The first principal component (OF1) explained 49% of the total variance and was characterized by behaviors related to movement, jumping, and climbing, while the second principal component (OF2) explained 20% of the total variance and described a tendency to investigate floorboard holes (Table 1). We retained two principal components from the MIS assay data, which explained 66% of the total variance (39% explained by the first principal component, MIS1, and 27% by the second component, MIS2). MIS1 was characterized by a propensity to move towards and interact with the mirror image, while MIS2 described a tendency to look towards versus away from the mirror image (Table 1).

The first component, but not the second component, from each of the OF and MIS assays was significantly repeatable at the individual level (Table 1). Based on PCA loadings, OF1 ($r \pm SE = 0.34 \pm 0.10$, LRT = 20.10, $P < 0.0001$) is hereafter referred to as activity, and MIS1 ($r \pm SE = 0.23 \pm 0.10$, LRT = 7.08, $P = 0.004$) is hereafter referred to as sociability. We found no effect of age class (activity: juveniles $\beta \pm SE = -0.37 \pm 0.24$, $t = -1.50$, $P = 0.139$; sociability: juveniles $\beta \pm SE = -0.34 \pm 0.22$, $t = -1.54$, $P = 0.131$) or trial number (activity: $\beta \pm SE = -0.08 \pm 0.06$, $t = -1.19$, $P = 0.238$; sociability: $\beta \pm SE = -0.06 \pm 0.07$, $t = -0.82$, $P = 0.414$) on either activity or sociability scores, though GMGS were generally less active (2017: $\beta \pm SE = -0.54 \pm 0.20$, $t = -2.69$, $P = 0.008$) and less social (2017: $\beta \pm SE = -0.39 \pm 0.19$, $t = -2.03$, $P = 0.045$) during 2017 compared to 2016. Age-specific repeatability models showed that both adults (activity: $r \pm SE = 0.41 \pm 0.15$, LRT = 10.00, $P = 0.0008$; sociability: $r \pm SE = 0.24 \pm 0.13$, LRT = 3.38, $P = 0.033$) and juveniles (activity: $r \pm SE = 0.25 \pm 0.13$, LRT = 6.58, $P = 0.005$; sociability: $r \pm SE = 0.22 \pm 0.13$, LRT = 3.29, $P = 0.035$) exhibited repeatability for activity and sociability.

Boldness was significantly repeatable ($r \pm SE = 0.36 \pm 0.12$, $LRT = 16.90$, $P < 0.0001$).

We found no effect of age class (juveniles $\beta \pm SE = 0.04 \pm 0.91$, $t = 0.04$, $P = 0.967$), year (2018 $\beta \pm SE = -0.55 \pm 0.96$, $t = -0.58$, $P = 0.570$), or trial number ($\beta \pm SE = 0.03 \pm 0.14$, $t = 0.26$, $P = 0.800$) on boldness scores. However, start distance had a significant, positive effect on FID (when approached from a farther distance, squirrels fled sooner; $\beta \pm SE = 0.38 \pm 0.05$, $t = 7.34$, $P < 0.0001$). Boldness was repeatable in both adults ($r \pm SE = 0.44 \pm 0.16$, $LRT = 12.40$, $P = 0.0002$) and juveniles ($r \pm SE = 0.33 \pm 0.16$, $LRT = 3.63$, $P = 0.028$). Individuals showed significant repeatability in aggressiveness scores ($r \pm SE = 0.16 \pm 0.07$, $LRT = 16.10$, $P < 0.0001$). We found no relationship between aggressiveness and age class (juveniles $\beta \pm SE = 0.05 \pm 0.15$, $t = 0.31$, $P = 0.756$), year (2018 $\beta \pm SE = -0.16 \pm 0.13$, $t = -1.28$, $P = 0.202$), or trial number ($\beta \pm SE = 0.02 \pm 0.02$, $t = 1.33$, $P = 0.186$). Age-specific repeatability models revealed that aggressiveness was significantly repeatable in adults ($r \pm SE = 0.26 \pm 0.10$, $LRT = 13.60$, $P = 0.0001$), but not in juveniles ($r \pm SE = 0.10 \pm 0.08$, $LRT = 1.53$, $P = 0.108$). However, an unadjusted repeatability model showed borderline significant repeatability in juveniles ($r \pm SE = 0.13 \pm 0.08$, $LRT = 2.59$, $P = 0.053$); unadjusted repeatability, also known as the broad sense or agreement repeatability (Nakagawa and Schielzeth 2013, Biro and Stamps 2015), quantifies repeatability while accounting for individual as a random effect, but does not control for any fixed effects.

We found no significant associations between personality scores of different traits.

Activity was not correlated with sociability ($\rho = 0.316$, $P = 0.061$), boldness ($\rho = 0.294$, $P = 0.268$), or aggressiveness ($\rho = 0.040$, $P = 0.857$) at the phenotypic level. Similarly, sociability was not correlated with boldness ($\rho = 0.182$, $P = 0.498$) or aggressiveness ($\rho = 0.185$, $P = 0.399$), and boldness was not correlated with aggressiveness ($\rho = 0.085$, $P = 0.723$).

3.4.3 Personality-dependent use of space and perches

Given the lack of adjusted repeatability for aggressiveness in juveniles, we included an interaction term between age class and individual personality score in all spatial models pertaining to aggressiveness. We did not find an effect of activity ($\beta \pm SE = 0.13 \pm 0.16$, $t = 0.82$, $P = 0.423$), sociability ($\beta \pm SE = 0.10 \pm 0.17$, $t = 0.60$, $P = 0.551$), boldness ($\beta \pm SE = 0.33 \pm 0.27$, $t = 1.22$, $P = 0.239$), or aggressiveness ($\beta \pm SE = -0.26 \pm 0.24$, $t = -1.09$, $P = 0.289$) on 95% home range size in GMGS (Fig. 4A). In general, males had larger 95% home ranges than females, but only as adults (Fig. 4A). However, there was a significant effect of an interaction between aggressiveness and age class on 95% home range size, in that more aggressive juveniles (those with scaled aggressiveness scores of approximately 1 or greater) tended to have larger home ranges compared to other squirrels ($\beta \pm SE = 0.83 \pm 0.37$, $t = 2.25$, $P = 0.032$; Figs. 4A, 5A). We found no effect of activity ($\beta \pm SE = 0.29 \pm 0.23$, $t = 1.30$, $P = 0.202$), sociability ($\beta \pm SE = 0.27 \pm 0.23$, $t = 1.15$, $P = 0.259$), or aggressiveness ($\beta \pm SE = -0.38 \pm 0.31$, $t = -1.22$, $P = 0.245$) scores on the 50% core area (Fig. 4A). However, bolder individuals maintained significantly larger 50% core areas ($\beta \pm SE = 0.98 \pm 0.26$, $t = 3.83$, $P = 0.001$; Figs. 4A, 6A) than shyer individuals, and there was a significant, positive effect of an interaction between juveniles and aggressiveness on the 50% core area ($\beta \pm SE = 1.31 \pm 0.50$, $t = 2.64$, $P = 0.013$; Figs. 4A, 5B). We found no effect of either year or the total number of spatial observations on either the 95% home range size or the 50% core area; hence, year and total observations were removed from all 95% home range and 50% core area models during model selection.

After controlling for home range size, there were significant relationships between each measured individual-based personality score and the number of perches in that individual's 95% home range and 50% core area (Fig. 4B). Squirrels that scored highly on activity ($\beta \pm SE = 0.51$

± 0.08 , $z = 6.52$, $P < 0.0001$), sociability ($\beta \pm SE = 0.25 \pm 0.04$, $z = 5.67$, $P < 0.0001$), boldness ($\beta \pm SE = 0.10 \pm 0.02$, $z = 5.85$, $P < 0.0001$), and aggressiveness ($\beta \pm SE = 0.08 \pm 0.03$, $z = 2.73$, $P = 0.006$) assays had a significantly greater number of perches in their 95% home ranges (Fig. 6B-E), as well as in their 50% core areas (activity $\beta \pm SE = 1.07 \pm 0.16$, $z = 6.56$, $P < 0.0001$; sociability $\beta \pm SE = 0.32 \pm 0.08$, $z = 3.86$, $P = 0.0001$; boldness $\beta \pm SE = 0.32 \pm 0.05$, $z = 6.74$, $P < 0.0001$; aggressiveness $\beta \pm SE = 0.41 \pm 0.09$, $z = 4.58$, $P < 0.0001$; Fig. 6F-I) compared to their less active, less social, shyer, and more docile counterparts. A significant interaction between aggressiveness and age class revealed that aggressive juveniles had more perches in their 95% home ranges compared to other squirrels ($\beta \pm SE = 0.31 \pm 0.12$, $z = 2.47$, $P = 0.013$; Fig. 5C), though this interaction was not significant in the 50% core area model ($\beta \pm SE = 0.18 \pm 0.35$, $z = 0.51$, $P = 0.609$) and was removed during model selection. In general, squirrels had fewer perches in their 95% and 50% home ranges in 2018 than in 2017, and juveniles had more perches in their 95% home ranges and 50% core areas than adults (Fig. 4B).

Individuals that were more active ($\beta \pm SE = 0.01 \pm 0.002$, $t = 2.40$, $P = 0.022$) and bolder ($\beta \pm SE = 0.01 \pm 0.003$, $t = 4.26$, $P = 0.0003$) moved faster per burst compared to squirrels that had lower activity and boldness scores (Figs. 4C, 6J-K). However, we found no effect of sociability ($\beta \pm SE = 0.002 \pm 0.002$, $t = 0.83$, $P = 0.411$) or aggressiveness ($\beta \pm SE = 0.001 \pm 0.002$, $t = 0.71$, $P = 0.489$) on movement speed, and an insignificant interaction between aggressiveness and age class (juveniles: aggressiveness $\beta \pm SE = 0.002 \pm 0.004$, $t = 0.59$, $P = 0.562$) was removed during model selection (Fig. 4C). Models analyzing the effect of boldness and aggressiveness on movement speed revealed that males tended to move faster than females, and adults tended to move faster than juveniles (Fig. 4C).

3.5 Discussion

In the first study examining personality in golden-mantled ground squirrels, we found that individuals consistently differed in activity, sociability, boldness, and aggressiveness. These behaviors represent four out of the five major categories of animal personality considered most relevant to ecological studies (Réale et al. 2007), and have been found to be repeatable in other species of ground-dwelling squirrels, such as yellow-bellied marmots (*Marmota flaviventris*; Armitage 1986, Armitage and Van Vuren 2003, Petelle et al. 2013), Siberian chipmunks (*Tamias sibiricus*; Boyer et al. 2010), eastern chipmunks (*Tamias striatus*; Montiglio et al. 2012), Belding's ground squirrels (*Urocitellus beldingi*; Dosmann et al. 2015), and Barbary ground squirrels (*Atlantoxerus getulus*; Piquet et al. 2018). However, we did not find significant repeatability in exploration, the fifth major behavior category. Ground squirrel studies that report consistent individual differences in exploration often combine exploration with movement in a novel environment (e.g., “activity-exploration”; Boyer et al. 2010) or quantify exploration speed instead of exploration tendency (e.g., Montiglio et al. 2012). We included movement speed as a variable in our calculation of activity, and we quantified exploration tendency as visits to floorboard holes in the arena, which might have facilitated the disentangling of activity and exploration behaviors (Martin and Réale 2008). Overall, we found that 16% to 44% of the behavioral variation among individual GMGS is attributed to personality, which is consistent with other personality studies (repeatability across taxa is roughly 35%; Bell et al. 2009).

Individual squirrels differed in space- and perch use in a non-random manner that was dependent on their personality type. While we found no effect of personality on home range size, bolder individuals maintained larger core areas than shyer individuals (Figs. 4A, 6A). An association between boldness and home range size has been reported in free-ranging populations

of other species, including bank voles (Schirmer et al. 2019) and sleepy lizards (*Tiliqua rugosa*; Spiegel et al. 2015). In the case of female bank voles, which are solitary and territorial, bolder individuals maintained larger core areas and larger overall home ranges, suggesting a potential link between boldness and territoriality (Schirmer et al. 2019). Hence, it is possible that boldness in GMGS influenced core area size but not overall home range area because GMGS appear to defend only their core areas, and not their entire home ranges, as territories (Jesmer et al. 2011, Aliperti 2020). We were surprised to find this link between apparent territoriality and boldness rather than aggressiveness, given known associations between aggressiveness and territorial defense in mammals (Wolff 1993, Morrell and Kokko 2005, Siracusa et al. 2017). However, an individual's home range would be considered a territory only if it were used exclusively by that individual, and it is possible that squirrels with higher aggressiveness scores more effectively excluded conspecifics from their home ranges, regardless of home range size. Additionally, a positive effect of boldness on core area size may relate to predation risk. Predation is a significant source of mortality for GMGS (Kneip et al. 2011), and bolder individuals are, by definition, more risk-prone (Sih et al. 2004a, Réale et al. 2007); hence, it is possible that shyer individuals restrict movements to well-known, safer areas, while bolder animals regularly venture out into riskier areas, thereby expanding their core area by using habitat patches that shyer individuals avoid (Schirmer et al. 2019). For example, bolder burrowing owls (*Athene cunicularia*) bred in territories closer to roads (Carrete and Tella 2010), and bolder dunnocks (*Prunella modularis*) selected habitat in areas with higher indices of human disturbance (Holtmann et al. 2017). In our study area, riskier habitat patches might include areas that are more densely vegetated; dense vegetation diminishes visibility of predators and is thus generally avoided (Aliperti 2020).

Individuals that scored higher for all four personality traits (activity, sociability, boldness, and aggressiveness) had a significantly greater number of perches in both their home ranges and core areas compared to individuals with lower personality scores (Figs. 4B, 6B-I); perches are a preferred resource that likely decreases predation risk by elevating a squirrel's point of view over the surrounding vegetation (Aliperti 2020). Hence, even though individuals that differ in personality do not necessarily differ in home range size, personality appears to influence access to resources within those home ranges. It is not surprising that more active, bold, and aggressive individuals tended to have greater access to perches, as these behavioral types, which are often correlated as 'proactive' or 'fast' behavioral syndromes (Réale et al. 2010, Sih et al. 2012, Spiegel et al. 2017), are typically thought to exhibit greater use of resources and space (Cote et al. 2010, van Overveld and Matthysen 2010, Toscano et al. 2016, Spiegel et al. 2017). For example, bold individuals may range across larger distances, likely increasing the probability of encountering patchily distributed, preferred resources (Toscano et al. 2016, Spiegel et al. 2017). However, we were surprised that more social squirrels had greater access to perches than their less social counterparts, as asocial personality types are often considered to be more proactive (Sih et al. 2004a, Réale et al. 2010) and therefore conceivably more effective at exploiting resources. We did not find correlations among behavioral types in our study, suggesting each personality trait evolved independently (Petelle et al. 2013). Hence, the explanation may lie in spatial overlap among squirrels: perhaps more social squirrels are more likely to have overlapping home ranges and therefore share resources such as perches.

In accordance with our expectation, individuals that were either more active or bolder moved faster than their less active and shyer conspecifics (Figs. 4C, 6J-K). The importance of activity revealed that this behavior, which was assayed in a controlled setting, accurately

predicted a similar behavior under natural conditions. Our results are consistent with theoretical groundwork that suggests more active or bold animals also tend to be superficial explorers (i.e., move across a landscape quickly; Réale et al. 2010), perhaps because animals with these behavioral types spend less time surveying their surroundings or have higher metabolic rates (Schirmer et al. 2019). However, most experimental studies that relate activity or boldness to space use do so within the context of dispersal (e.g., Fraser et al. 2001, Thorlacius et al. 2015, Merrick and Koprowski 2017b). Whether GMGS that move faster would either be more likely to disperse or disperse farther would require further investigation. Nonetheless, it seems plausible that personality may influence the dispersal decision; GMGS usually disperse as juveniles, and we found consistent individual differences in activity and boldness, behaviors that were associated with faster movement speed, in juveniles as well as adults. This is in contrast to yellow-bellied marmots, which delay development of at least one personality trait (boldness) until their yearling year, perhaps because that trait is correlated with dispersal and that is the year during which individual marmots typically disperse (Petelle et al. 2013). We found that aggressive juveniles had larger home ranges and core areas, as well as more perches in their home range, compared to all other squirrels (Figs. 4A-B, 5). Hence, it is possible that aggressiveness influenced the decision to disperse, and that the significant interaction between juveniles and aggressiveness reflected the point at which more aggressive juveniles started to leave their natal home range.

It is well known that certain behavioral types are favored in some environments over others, resulting in personality-dependent ecological tradeoffs (Smith and Blumstein 2008, Toscano et al. 2016). For example, bolder foragers presumably benefit within the context of competition, at the cost of shorter lifespans within the context of predation (Sih et al. 2012).

However, we found that bolder squirrels tended to have access to more perches, a resource associated with increased annual survival in a predation context (Aliperti 2020), compared to shyer squirrels, and a recent study found that risk-taking individuals have significantly longer lifespans than shyer individuals when studied in the wild as opposed to a lab setting (Moiron et al. 2020). Hence, the personality of free-ranging animals may interact with environmental variables to differentially affect individual fitness, with potentially important consequences for population-level processes. For instance, active individuals may also move faster and be more likely to disperse, but due to speed-accuracy trade-offs (Chittka et al. 2009), foraging efficiency (and thus dispersal success) may be lower in habitats with patchily distributed resources (Spiegel et al. 2017). Furthermore, variables such as landscape connectivity (or more complicating intrinsic factors, such as state-dependence or cognition) may interact with personality to influence social interactions or diet preference, which may in turn bias studies on animal movement or habitat selection (Wolf and Weissing 2012, Toscano et al. 2016). Hence, successful implementation of wildlife management programs may depend on the explicit recognition and incorporation of personality in individual-based models of movement, habitat preference, and population dynamics (Merrick and Koprowski 2017a). From a conservation-based perspective, accounting for personality in wildlife management initiatives may be especially important when predicting wildlife responses to novel conditions, such as modification or destruction of habitat due to human-induced rapid environmental change ('HIREC'; Sih et al. 2011, 2012).

Our results show personality-dependent space- and resource use in a free-ranging population of golden-mantled ground squirrels. Overall, we found that bolder individuals maintained larger core areas, more active and bold individuals moved faster, and more active, bold, and aggressive individuals had greater access to fitness-enhancing perches in their home

ranges. We also found that sociability was associated with access to perches in the home range, suggesting there is a potential benefit within an asocial species of being relatively more social. Given that individuals of differing personality types may occupy separate ecological niches (Schirmer et al. 2019) and that these ecological differences may scale-up to population or community-level processes (Wolf and Weissing 2012), we hope our results will inspire future research that links animal personality with spatial ecology in natural ecosystems.

Acknowledgments

I thank my co-authors, B. Davis and D. H. Van Vuren, as well as N. Fangué and A. Todgham for access to the EthoVision software. I am grateful for project funding provided by the Rocky Mountain Biological Laboratory Graduate Fellowship and Dr. Lee R. G. Snyder Memorial Fellowship, American Society of Mammalogists Grant-in-Aid of Research, and the University of California, Davis Walter and Elizabeth Howard Award and Ecology Student Endowment Award. I appreciate field assistance by D. Ramirez, M. Diaz, and J. Kennen, as well as video-watching assistance by I. Calcaterra, J. Chalfin, H. Daly, and L. Hamilton. R. Blenk and P. Valdés Donoso helped with arena construction. I thank E. Payne and M. Michelangeli for modeling advice, and G. Bastille-Rousseau for advice on movement analyses. A. Sih and R. J. Hijmans provided valuable comments that greatly improved this manuscript.

3.6 Literature Cited

Aliperti, J. R. 2020. Behavioral and spatial dynamics in a fluctuating population of golden-mantled ground squirrels (*Callospermophilus lateralis*). PhD Dissertation, University of California, Davis.

- Aplin, L. M., D. R. Farine, R. P. Mann, and B. C. Sheldon. 2014. Individual-level personality influences social foraging and collective behaviour in wild birds. *Proceedings of the Royal Society B: Biological Sciences* 281:20141016.
- Armitage, K. B. 1981. Sociality as a life-history tactic of ground squirrels. *Oecologia* 48:36–41.
- Armitage, K. B. 1986. Individuality, social behaviour, and reproductive success in yellow-bellied marmots. *Ecology* 67:1186–1193.
- Armitage, K. B. 2009. Home range area and shape of yellow-bellied marmots. *Ethology Ecology and Evolution* 21:195–207.
- Armitage, K. B., and D. H. Van Vuren. 2003. Individual differences and reproductive success in yellow-bellied marmots. *Ethology Ecology and Evolution* 15:207–233.
- Armitage, K. B., D. H. Van Vuren, A. Ozgul, and M. K. Oli. 2011. Proximate causes of natal dispersal in female yellow-bellied marmots, *Marmota flaviventris*. *Ecology* 92:218–227.
- Bakker, V. J., and D. H. Van Vuren. 2004. Gap-crossing decisions by the red squirrel, a forest-dependent small mammal. *Conservation Biology* 18:689–697.
- Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Bekoff, M. 1977. Mammalian dispersal and the ontogeny of individual behavioral phenotypes. *The American Naturalist* 111:715–732.
- Belisle, M. 2005. Measuring landscape connectivity: the challenge of behavioral landscape ecology. *Ecology* 86:1988–1995.
- Bell, A. M., S. J. Hankison, and K. L. Laskowski. 2009. The repeatability of behaviour: a meta-analysis. *Animal Behaviour* 77:771–783.

- Biro, P. A., and J. A. Stamps. 2008. Are animal personality traits linked to life-history productivity? *Trends in Ecology and Evolution* 23:361–368.
- Biro, P. A., and J. A. Stamps. 2015. Using repeatability to study physiological and behavioural traits: ignore time-related change at your peril. *Animal Behaviour* 105:223–230.
- Blight, O., G. Albet Díaz-Mariblanca, X. Cerdá, and R. Boulay. 2016. A proactive-reactive syndrome affects group success in an ant species. *Behavioral Ecology* 27:118–125.
- Blumstein, D. T. 2003. Flight-initiation distance in birds is dependent on intruder starting distance. *The Journal of Wildlife Management* 67:852–857.
- Bonnot, N., H. Verheyden, P. Blanchard, J. Cote, L. Debeffe, B. Cargnelutti, F. Klein, A. J. M. Hewison, and N. Morellet. 2015. Interindividual variability in habitat use: evidence for a risk management syndrome in roe deer? *Behavioral Ecology* 26:105–114.
- Boon, A. K., D. Réale, and S. Boutin. 2007. The interaction between personality, offspring fitness and food abundance in North American red squirrels. *Ecology Letters* 10:1094–1104.
- Boon, A. K., D. Réale, and S. Boutin. 2008. Personality, habitat use, and their consequences for survival in North American red squirrels. *Oikos* 117:1321–1328.
- Börger, L., N. Franconi, F. Ferretti, F. Meschi, G. De Michele, A. Gantz, and T. Coulson. 2006. An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *American Naturalist* 168:471–485.
- Bowler, D. E., and T. G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews of the Cambridge Philosophical Society* 80:205–225.

- Boyer, N., D. Réale, J. Marmet, B. Pisanu, and J. L. Chapuis. 2010. Personality, space use and tick load in an introduced population of Siberian chipmunks *Tamias sibiricus*. *Journal of Animal Ecology* 79:538–547.
- Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Mächler, and B. M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal* 9:378–400.
- Calenge, C. 2006. The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197:516–519.
- Carrete, M., and J. L. Tella. 2010. Individual consistency in flight initiation distances in burrowing owls: a new hypothesis on disturbance-induced habitat selection. *Biology Letters* 6:167–170.
- Cattell, R. B. 1966. The scree test for the number of factors. *Multivariate behavioral research* 1:245–276.
- Chittka, L., P. Skorupski, and N. E. Raine. 2009. Speed-accuracy tradeoffs in animal decision making. *Trends in Ecology and Evolution* 24:400–407.
- Clobert, J., J. F. Le Galliard, J. Cote, S. Meylan, and M. Massot. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters* 12:197–209.
- Cote, J., and J. Clobert. 2007. Social personalities influence natal dispersal in a lizard. *Proceedings of the Royal Society B: Biological Sciences* 274:383–390.
- Cote, J., J. Clobert, T. Brodin, S. Fogarty, and A. Sih. 2010. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Proceedings of the Royal Society B: Biological Sciences* 365:4065–4076.

- Cummins, R. A., and R. N. Walsh. 1976. The open-field test: a critical review. *Psychological Bulletin* 83:482–504.
- Dingemanse, N. J., C. Both, A. J. Van Noordwijk, A. L. Rutten, and P. J. Drent. 2003. Natal dispersal and personalities in great tits (*Parus major*). *Proceedings of the Royal Society B: Biological Sciences* 270:741–747.
- Dingemanse, N. J., and N. A. Dochtermann. 2013. Quantifying individual variation in behaviour: mixed-effect modelling approaches. *Journal of Animal Ecology* 82:39–54.
- Dosmann, A. J., K. C. Brooks, and J. M. Mateo. 2015. Within-individual correlations reveal link between a behavioral syndrome, condition, and cortisol in free-ranging Belding's ground squirrels. *Ethology* 121:125–134.
- Duckworth, R. A., and A. V. Badyaev. 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proceedings of the National Academy of Sciences* 104:15017–15022.
- ESRI. 2018. Arc GIS. Environmental System Research Institute Inc., Redlands, California.
- Ferron, J. 1985. Social behaviour of the golden-mantled ground-squirrel (*Spermophilus lateralis*). *Canadian Journal of Zoology* 63:2529–2533.
- Field, A., J. Miles, and Z. Field. 2012. *Discovering statistics using R*. SAGE Publications, Thousand Oaks, California.
- Fordham, D. A., K. T. Shoemaker, N. H. Schumaker, H. R. Akçakaya, N. Clisby, and B. W. Brook. 2014. How interactions between animal movement and landscape processes modify local range dynamics and extinction risk. *Biology Letters* 10.

- Fraser, D. F., J. F. Gilliam, M. J. Daley, A. N. Le, G. T. Skalski, and N. Carolina. 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *The American Naturalist* 158.
- Gosling, S. D. 2001. From mice to men: what can we learn about personality from animal research? 127:45–86.
- Hertel, A. G., M. Leclerc, D. Warren, F. Pelletier, A. Zedrosser, and T. Mueller. 2019. Don't poke the bear: using tracking data to quantify behavioural syndromes in elusive wildlife. *Animal Behaviour* 147:91–104.
- Holtmann, B., E. S. A. Santos, C. E. Lara, and S. Nakagawa. 2017. Personality-matching habitat choice, rather than behavioural plasticity, is a likely driver of a phenotype–environment covariance. *Proceedings of the Royal Society B: Biological Sciences* 284.
- Hoogland, J. L. 2013. Prairie dogs disperse when all close kin have disappeared. *Science* 339:1205–1207.
- Hostetler, J. A., E. Kneip, D. H. Van Vuren, and M. K. Oli. 2012. Stochastic population dynamics of a montane ground-dwelling squirrel. *PLoS ONE* 7:1–10.
- Jesmer, B. R., D. H. Van Vuren, J. A. Wilson, D. A. Kelt, and M. L. Johnson. 2011. Spatial organization in female golden-mantled ground squirrels. *The American Midland Naturalist* 165:162–168.
- Kneip, É., D. H. Van Vuren, J. A. Hostetler, and M. K. Oli. 2011. Influence of population density and climate on the demography of subalpine golden-mantled ground squirrels. *Journal of Mammalogy* 92:367–377.

- Koolhaas, J. M., S. M. Korte, S. F. De Boer, B. J. Van Der Vegt, C. G. Van Reenen, H. Hopster, I. C. De Jong, M. A. W. Ruis, and H. J. Blokhuis. 1999. Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience and Biobehavioral Reviews* 23:925–935.
- Krause, S. K., D. H. Van Vuren, C. Laursen, and D. A. Kelt. 2015. Behavioral effects of an immunocontraceptive vaccine on eastern fox squirrels. *Journal of Wildlife Management* 79:1255–1263.
- Kurvers, R. H. J. M., J. Krause, D. P. Croft, A. D. M. Wilson, and M. Wolf. 2014. The evolutionary and ecological consequences of animal social networks: emerging issues. *Trends in Ecology and Evolution* 29:326–335.
- Leclerc, M., E. Vander Wal, A. Zedrosser, J. E. Swenson, J. Kindberg, and F. Pelletier. 2016. Quantifying consistent individual differences in habitat selection. *Oecologia* 180:697–705.
- Lucherini, M., and S. Lovari. 1996. Habitat richness affects home range size in the red fox *Vulpes vulpes*. *Behavioural Processes* 36:103–105.
- Maher, C. R., and J. R. Burger. 2011. Intraspecific variation in space use, group size, and mating systems of caviomorph rodents. *Journal of Mammalogy* 92:54–64.
- Martin, J. G. A., and D. Réale. 2008. Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus*. *Animal Behaviour* 75:309–318.
- Mazzamuto, M. V., G. Cremonesi, F. Santicchia, D. Preatoni, A. Martinoli, and L. A. Wauters. 2019. Rodents in the arena: a critical evaluation of methods measuring personality traits. *Ethology Ecology and Evolution* 31:38–58.
- Merrick, M. J., and J. L. Koprowski. 2017a. Should we consider individual behavior differences in applied wildlife conservation studies? *Biological Conservation* 209:34–44.

- Merrick, M. J., and J. L. Koprowski. 2017b. Altered natal dispersal at the range periphery: the role of behavior, resources, and maternal condition. *Ecology and Evolution* 7:58–72.
- Michener, G. R. 1983. Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids. Pages 528–572 in J. F. Eisenberg and D. G. Kleiman, editors. *Advances in the study of mammalian behavior*. Seventh edition. American Society of Mammalogists, Stillwater, OK.
- Minderman, J., J. M. Reid, M. Hughes, M. J. H. Denny, S. Hogg, P. G. H. Evans, and M. J. Whittingham. 2010. Novel environment exploration and home range size in starlings *Sturnus vulgaris*. *Behavioral Ecology* 21:1321–1329.
- Moiron, M., K. L. Laskowski, and P. T. Niemelä. 2020. Individual differences in behaviour explain variation in survival: a meta-analysis. *Ecology Letters* 23:399–408.
- Montiglio, P. O., D. Garant, F. Pelletier, and D. Réale. 2012. Personality differences are related to long-term stress reactivity in a population of wild eastern chipmunks, *Tamias striatus*. *Animal Behaviour* 84:1071–1079.
- Montiglio, P. O., D. Garant, D. Thomas, and D. Réale. 2010. Individual variation in temporal activity patterns in open-field tests. *Animal Behaviour* 80:905–912.
- Morrell, L. J., and H. Kokko. 2005. Bridging the gap between mechanistic and adaptive explanations of territory formation. *Behavioral Ecology and Sociobiology* 57:381–390.
- Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4:133–142.
- Nawroth, C., P. M. Prentice, and A. G. McElligott. 2017. Individual personality differences in goats predict their performance in visual learning and non-associative cognitive tasks. *Behavioural Processes* 134:43–53.

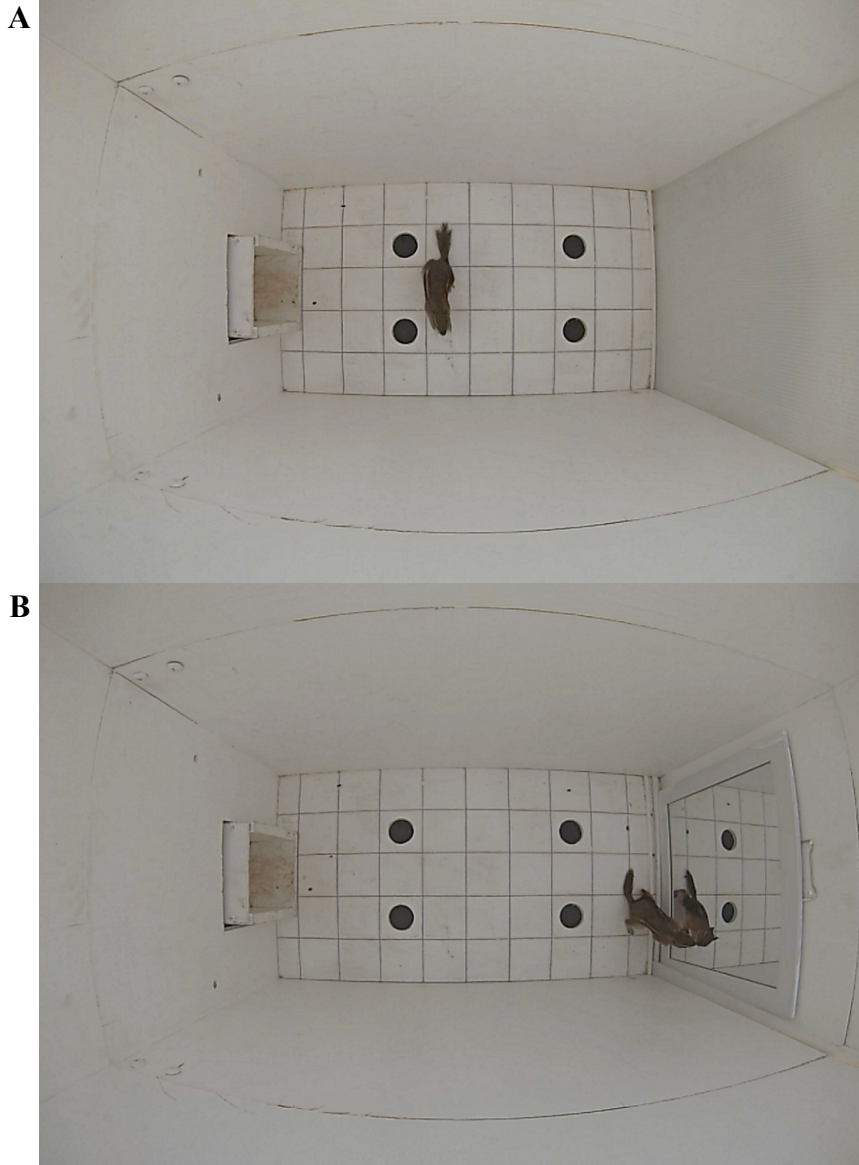
- van Overveld, T., and E. Matthysen. 2010. Personality predicts spatial responses to food manipulations in free-ranging great tits (*Parus major*). *Biology Letters* 6:187–190.
- Petelle, M. B., D. E. McCoy, V. Alejandro, J. G. A. Martin, and D. T. Blumstein. 2013. Development of boldness and docility in yellow-bellied marmots. *Animal Behaviour* 86:1147–1154.
- Phillips, J. A. 1981. Growth and its relationship to the initial annual cycle of the golden-mantled ground squirrel, *Spermophilus lateralis*. *Canadian Journal of Zoology* 59:865–871.
- Piquet, J. C., M. López-Darias, A. van der Marel, M. Nogales, and J. Waterman. 2018. Unraveling behavioral and pace-of-life syndromes in a reduced parasite and predation pressure context: personality and survival of the Barbary ground squirrel. *Behavioral Ecology and Sociobiology* 72.
- Powell, R. A., and M. S. Mitchell. 2012. What is a home range? *Journal of Mammalogy* 93:948–958.
- R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Réale, D., B. Y. Gallant, M. Leblanc, and M. Festa-Bianchet. 2000. Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Animal Behaviour* 60:589–597.
- Réale, D., D. Garant, M. M. Humphries, P. Bergeron, V. Careau, and P. O. Montiglio. 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:4051–4063.
- Réale, D., S. M. Reader, D. Sol, P. T. McDougall, and N. J. Dingemanse. 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews* 82:291–318.

- Samuel, M. D., D. J. Pierce, and E. O. Garton. 1985. Identifying areas of concentrated use within the home range. *Journal of Animal Ecology* 54:711–719.
- Schirmer, A., A. Herde, J. A. Eccard, and M. Dammhahn. 2019. Individuals in space: personality-dependent space use, movement and microhabitat use facilitate individual spatial niche specialization. *Oecologia* 189:647–660.
- Schirmer, A., J. Hoffmann, J. A. Eccard, and M. Dammhahn. 2020. My niche: individual spatial niche specialization affects within- and between-species interactions. *Proceedings of the Royal Society B: Biological Sciences* 287.
- Sih, A., A. Bell, and J. C. Johnson. 2004a. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology and Evolution* 19:372–378.
- Sih, A., and A. M. Bell. 2008. Insights for behavioral ecology from behavioral syndromes. *Advances in the Study of Behavior* 38:227–281.
- Sih, A., A. M. Bell, J. C. Johnson, and R. E. Ziemba. 2004b. Behavioral syndromes: an integrative overview. *Quarterly Review of Biology* 79:241–277.
- Sih, A., J. Cote, M. Evans, S. Fogarty, and J. Pruitt. 2012. Ecological implications of behavioural syndromes. *Ecology Letters* 15:278–289.
- Sih, A., M. C. O. Ferrari, and D. J. Harris. 2011. Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications* 4:367–387.
- Sikes, R. S., and The Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy* 97:663–688.

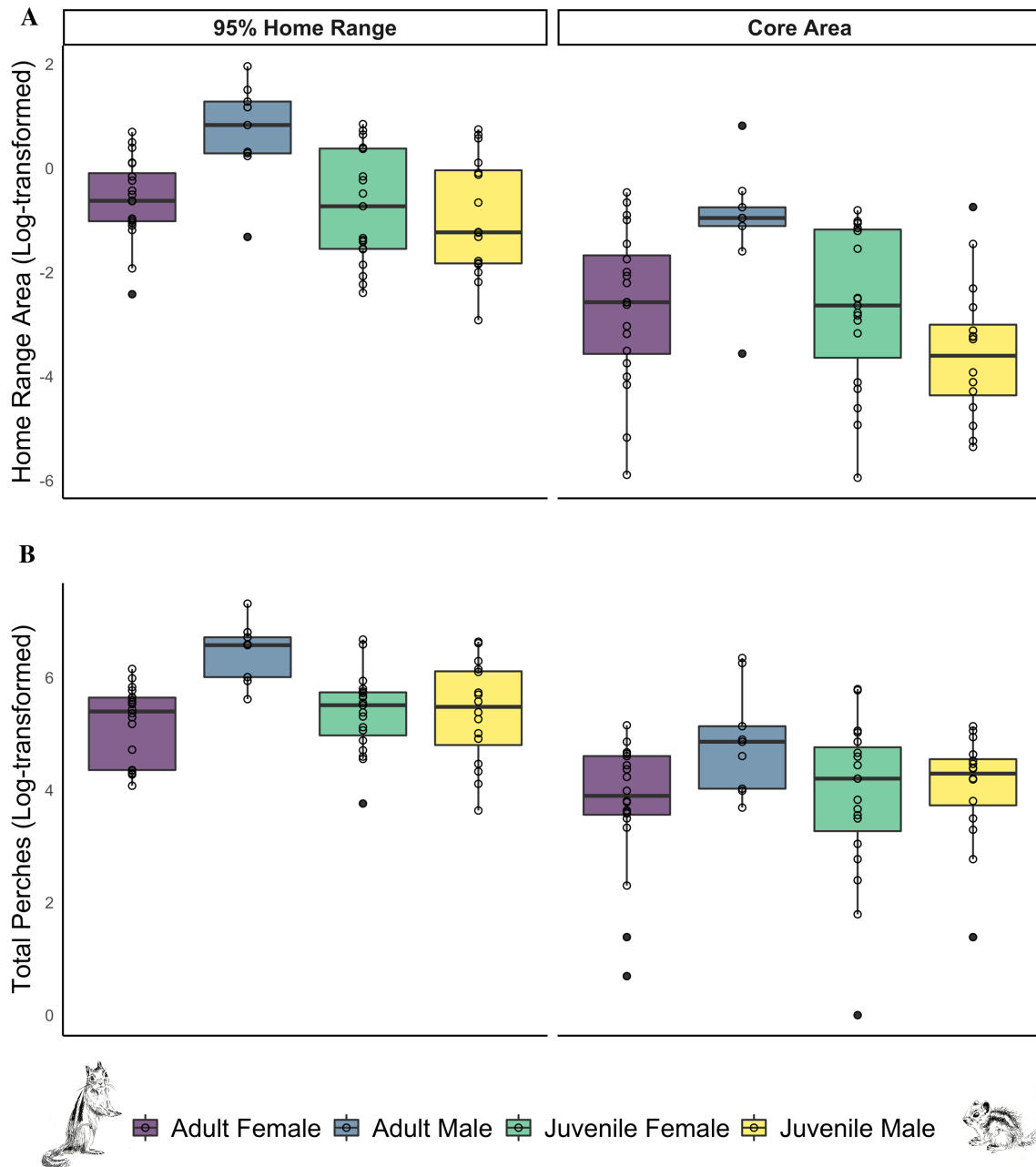
- Singleton, J. M., and T. Garland. 2018. Among-individual variation in desert iguanas (Squamata: *Dipsosaurus dorsalis*): endurance capacity is positively related to home range size. *Physiological and Biochemical Zoology* 91:725–730.
- Siracusa, E., M. Morandini, S. Boutin, M. M. Humphries, B. Dantzer, J. E. Lane, and A. G. McAdam. 2017. Red squirrel territorial vocalizations deter intrusions by conspecific rivals. *Behaviour* 154:1259–1273.
- Smith, B. R., and D. T. Blumstein. 2008. Fitness consequences of personality: a meta-analysis. *Behavioral Ecology* 19:448–455.
- Spiegel, O., S. T. Leu, C. M. Bull, and A. Sih. 2017. What’s your move? Movement as a link between personality and spatial dynamics in animal populations. *Ecology Letters* 20:3–18.
- Spiegel, O., S. T. Leu, A. Sih, S. S. Godfrey, and C. M. Bull. 2015. When the going gets tough: behavioural type-dependent space use in the sleepy lizard changes as the season dries. *Proceedings of the Royal Society B: Biological Sciences* 282.
- Stamps, J. 2001. Habitat selection by dispersers: integrating proximate and ultimate approaches. *Dispersal*:230–242.
- Stoffel, M. A., S. Nakagawa, and H. Schielzeth. 2017. rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution* 8:1639–1644.
- Svendsen, G. E., and K. B. Armitage. 1973. Mirror-image stimulation applied to field behavioral studies. *Ecology* 54:623–627.
- Thorlacius, M., G. Hellström, and T. Brodin. 2015. Behavioral dependent dispersal in the invasive round goby *Neogobius melanostomus* depends on population age. *Current Zoology* 61:529–542.

- Toscano, B. J., N. J. Gownaris, S. M. Heerhartz, and C. J. Monaco. 2016. Personality, foraging behavior and specialization: integrating behavioral and food web ecology at the individual level. *Oecologia* 182:55–69.
- Wells, C. P., K. M. Tomalty, C. H. Floyd, M. B. McElreath, B. P. May, and D. H. Van Vuren. 2017. Determinants of multiple paternity in a fluctuating population of ground squirrels. *Behavioral Ecology and Sociobiology* 71.
- Wells, C. P., and D. H. Van Vuren. 2017. Female kin density affects offspring sex ratio in an asocial mammal, the golden-mantled ground squirrel, *Callospermophilus lateralis*. *Animal Behaviour* 134:71–77.
- Wey, T. W., O. Spiegel, P. O. Montiglio, and K. E. Mabry. 2015. Natal dispersal in a social landscape: considering individual behavioral phenotypes and social environment in dispersal ecology. *Current Zoology* 61:543–556.
- Wold, S., K. Esbensen, and P. Geladi. 1987. Principal component analysis. *Chemometrics and Intelligent Laboratory Systems* 2:37–52.
- Wolf, M., and F. J. Weissing. 2012. Animal personalities: consequences for ecology and evolution. *Trends in Ecology and Evolution* 27:452–461.
- Wolff, J. O. 1993. Why are female small mammals territorial? *Oikos* 68:364–370.
- Ydenberg, R. C., and L. M. Dill. 1986. The economics of fleeing from predators. *Advances in the Study of Behavior* 16:229–249.
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer Science and Business, New York, New York.

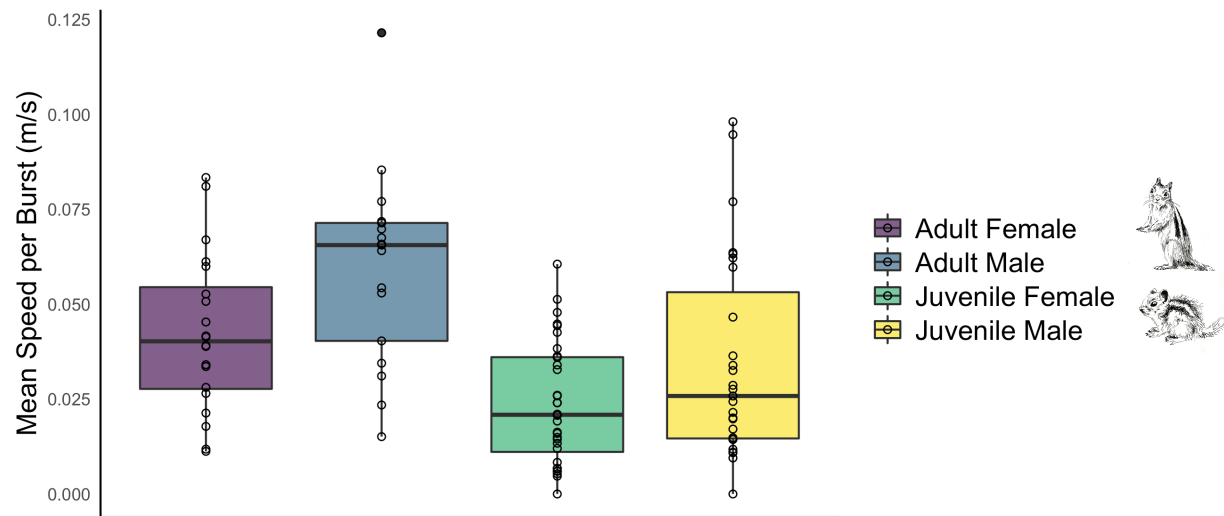
3.7 Figures



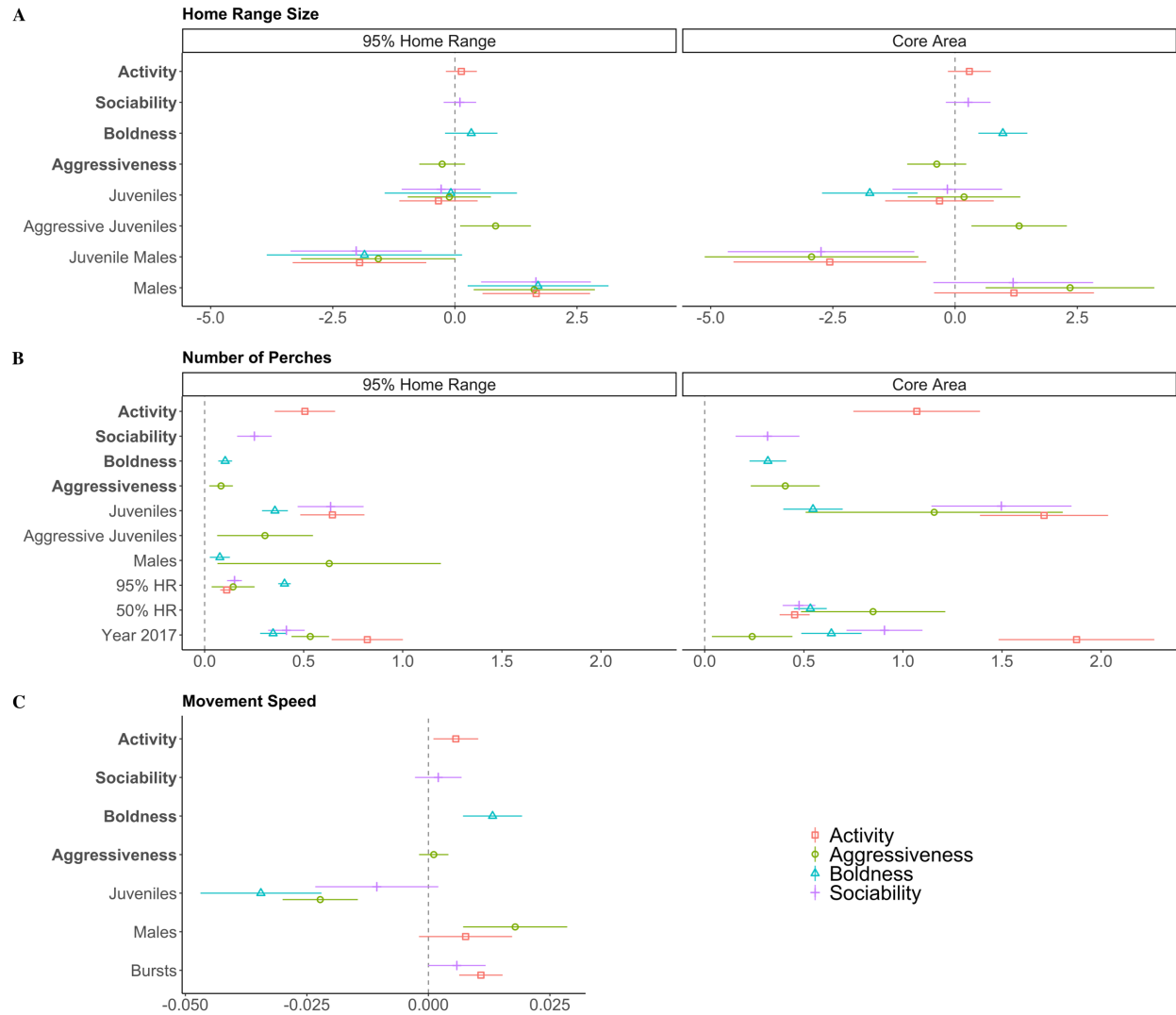
3.7.1 Images of a golden-mantled ground squirrel inside of the arena during an open field (A) and mirror image stimulation (B) trial. Each of four black circles is a hole that was cut into the floorboard, and which extended 12 mm downward towards the base of the arena, creating a shallow indentation. The squirrel entered the arena from the acclimation box, part of which is shown along the entrance wall, directly across from the mirror and to the left of the floorboard holes.



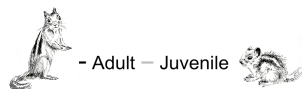
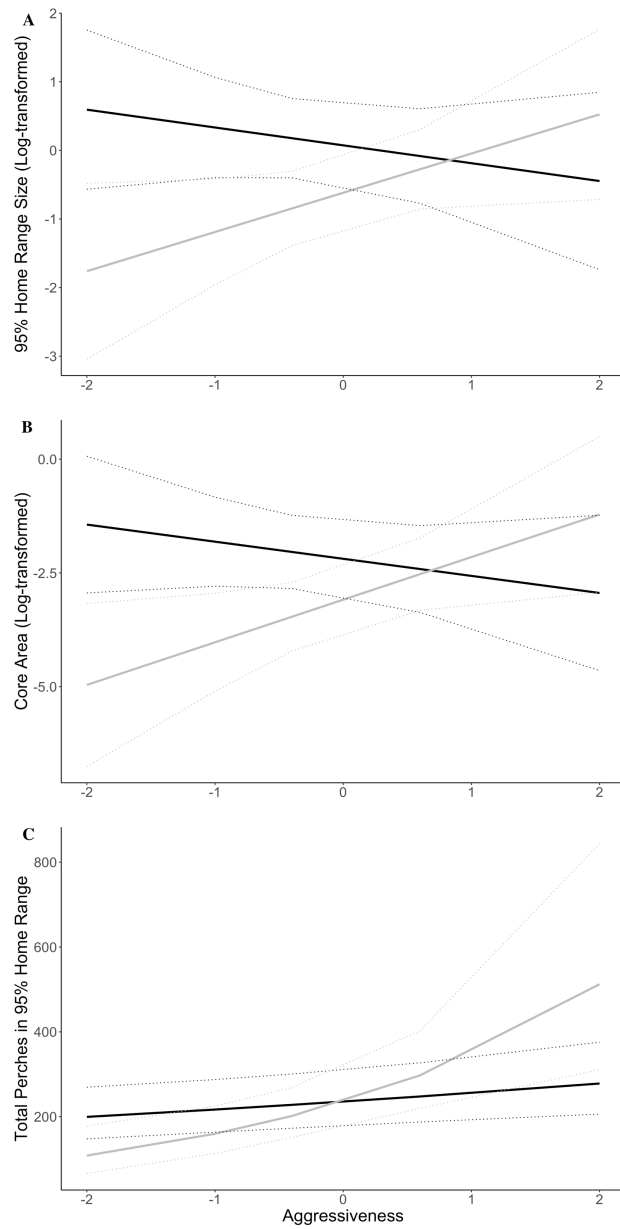
3.7.2 Home range area (A) and total number of perches (features, such as rocks or stumps, which protrude above the surrounding vegetation; B) in the 95% home range and 50% core area of golden-mantled ground squirrels. Bold lines inside boxes denote medians and open circles denote individual data points. Data were log-transformed for visual representation.



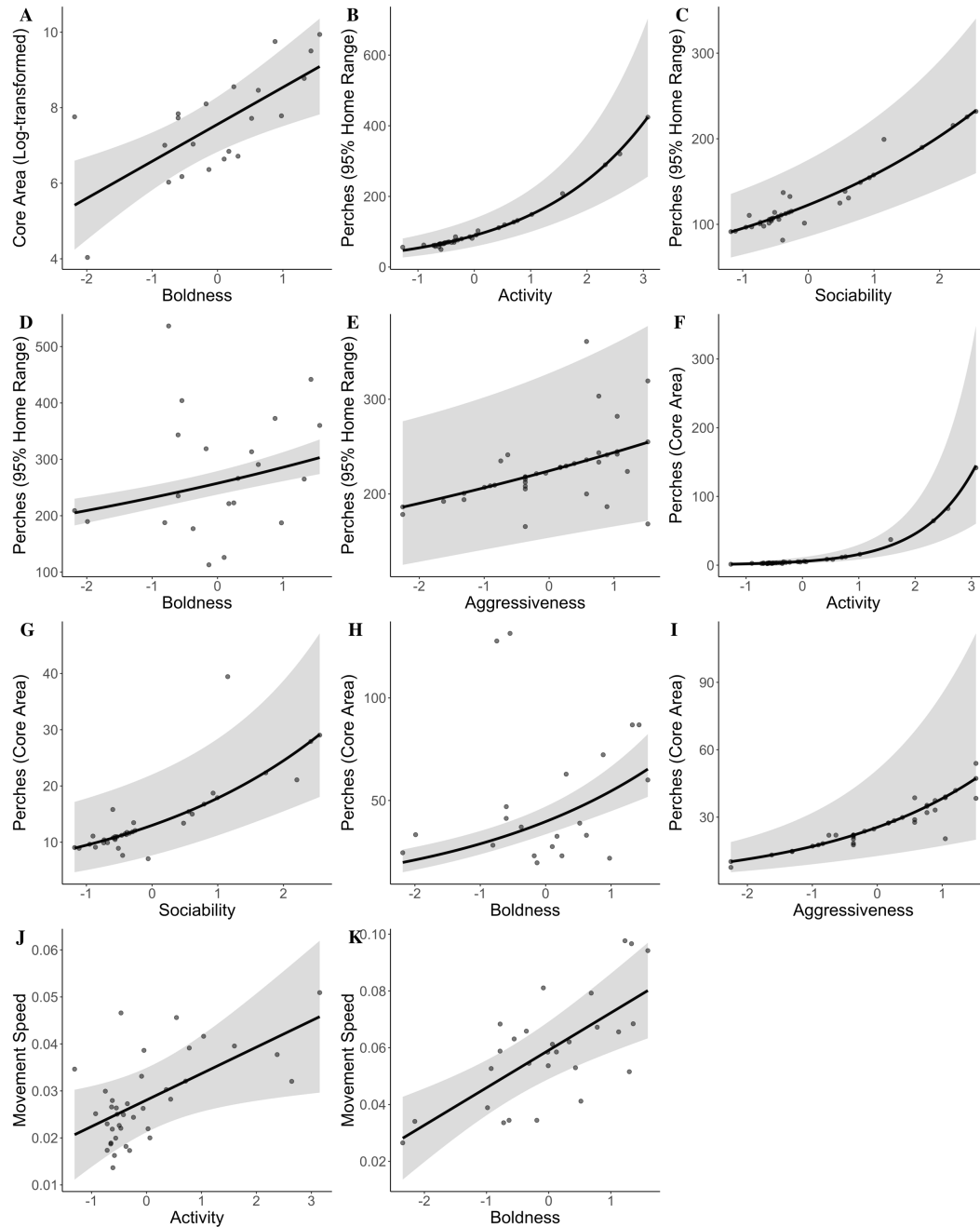
3.7.3 Mean movement speed per 10-min ‘bursts’ in free-ranging golden-mantled ground squirrels. Bold lines inside boxes denote medians and open circles denote individual data points.



3.7.4 Plot of coefficients for fixed effects in each of five models analyzing the effect of personality on: (A) home range size (95% home range on left, 50% core area on right), (B) number of perches in the home range (95% home range on left, 50% core area on right), and (C) mean movement speed. Shapes (unique to each model) represent mean point estimates and lines represent 95% confidence intervals. Personality scores included in each model are in bold font. Variables whose coefficients do not overlap with the dotted line in a given plot had a significant effect on that outcome.



3.7.5 Effects of an interaction between juveniles and aggressiveness on 95% home range size (A), 50% core area (B), and total number of perches in the 95% home range (C). Represented are effects (predicted values) obtained from linear or generalized linear mixed effect models. Dotted areas represent 95% confidence intervals.



3.7.6 Effects of mean personality scores on the 50% core area (A), number of perches in the 95% home range (B-E) and 50% core area (F-I), and mean movement speed (J-K) in free-ranging golden-mantled ground squirrels. Represented are effects (predicted values) obtained from linear or generalized linear mixed effect models. Shaded areas represent 95% confidence intervals, and gray dots represent partial residuals from each model.

3.8 Tables

3.8.1 Standardized loadings (based on a correlation matrix) for behaviors included in principal component analyses of open field (components OF1 and OF2) and mirror image stimulation (components MIS1 and MIS2) assays in golden-mantled ground squirrels. Behaviors with loadings equal to or greater than 0.40 are noted in bold font. A likelihood ratio test (LRT) was used to test for statistical significance of repeatability.

Behavior	OF1	OF2	Behavior	MIS1	MIS2
Mean velocity	0.93	0.30	Distance	0.94	0.17
Distance	0.93	0.30	Visits to Far End	0.91	0.17
Jumping events	0.93	0.16	Time interacting with mirror	0.82	0.22
Visits to Center	0.89	0.34	Visits to Vestibule	0.63	-0.06
Visits to Vestibule	0.89	0.19	Time looking away from mirror	-0.12	0.89
Maximum velocity	0.79	0.23	Time looking towards mirror	-0.09	-0.84
Time moving	0.76	0.49	Time in Far End	0.48	0.56
Climbing events	0.75	0.20	Time in Vestibule	-0.31	-0.49
Visits to Near Corner	0.74	0.05			
Visits to Far End	0.63	0.29			
Time sniffing	0.56	0.44			
Time in Far End	-0.17	-0.15			
Time investigating holes	0.16	0.96			
Hole investigation events	0.12	0.95			
Time in Center	0.17	0.42			
% Total Variance	49.0	20.0		39.0	27.0
% Repeatability	34.2	7.2		22.6	3.8
LRT (df = 1)	20.1	0.492		7.08	0.047
P-value	< 0.0001	0.241		0.004	0.414

CHAPTER 4

EFFECTS OF DENSITY AND KINSHIP ON THE SPATIAL ORGANIZATION OF AN ASOCIAL GROUND

SQUIRREL

4.1 Abstract

Among mammals, spatial organization (home range size and overlap) may be influenced by kinship, and tolerance among kin is believed to play a role in the evolution of sociality. In solitary species, adults, including close kin, are presumed to have home ranges that are distinct and non-overlapping. We characterized the spatial organization, including the role of kinship, in a free-living population of golden-mantled ground squirrels (*Callospermophilus lateralis*), a presumably asocial and solitary species. We also capitalized on changes in population size over 25 years (1995-2019) to quantify the influence of density on that spatial organization. We found extensive overlap between female home ranges (30%), and between male and female home ranges (28%) after the breeding season. However, the core areas of adult female home ranges overlapped minimally (7%), suggesting squirrels were territorial, but only for the inner part of their home range. Contrary to expectation, kinship played a role in the spatial organization: females shared space more than unrelated females. We did not find an effect of population density on home range or core area size ($P > 0.05$), but local-level intruder pressure led to an increase in home range size ($P = 0.002$), perhaps because females ranged farther to either gain familiarity with neighbors or shift into less crowded areas. While we did not find an effect of density on spatial overlap ($P > 0.05$), there was a density-mediated increase in space-sharing among kin ($P \leq 0.01$); space-sharing by female kin was expressed primarily at high densities, suggesting that familiarity and inclusive fitness benefits may offset costs of competition and

promote philopatry under certain conditions. Overall, we provide evidence of a facultative transition in golden-mantled ground squirrels from asociality to the formation of single-family kin clusters at high densities, the first step towards developing sociality. Our study highlights the importance of considering familiarity among neighbors in asocial species, as well as the interactive effects of environmental conditions and kinship when assessing the spatial and social organization of mammals.

4.2 Introduction

Understanding patterns of spatial organization in animal populations requires information on how individuals distribute themselves across a landscape (Michener 1979, Rayor and Armitage 1991, Boellstorff and Owings 1995, Jones et al. 2013). Spatial distribution is influenced by dispersal, and in mammals dispersal is typically male-biased, with females often remaining philopatric (Greenwood 1980, Waser and Jones 1983). Natal philopatry creates the potential for related females to be clustered spatially, and tolerance among kin is believed to play a role in the evolution of sociality (Armitage 1999, Silk 2007, Innes et al. 2012).

Ground-dwelling squirrels exhibit a wide range of sociality, from solitary to highly gregarious, which Armitage (1981) hypothesized resulted from the effect of body size on rate of development, hence the age of dispersal. In the short active season experienced by most ground-dwelling squirrels, large-bodied species have delayed maturity and dispersal, facilitating the formation of social groups. Small species, or those exposed to a long active season, reach maturity and disperse early in life, precluding the formation of social groups (Armitage 1981). Hence, Armitage (1981) classified ground-dwelling squirrels into five grades of social structure, ranging from solitary (Grade 1) to highly social (Grade 5). Michener (1983) further developed

this scheme, emphasizing the importance of spatial overlap and association among kin in forming social bonds and thus shaping social structure: home ranges should be distinct and non-overlapping among individuals of asocial species, and overlap should increase as social complexity progresses to single-family kin clusters and, in the most social species, cooperative, multi-family polygynous harems.

Spatial distribution for individuals that have established residency might be influenced by density (Oli et al. 2002, Innes et al. 2009). For example, an animal may either expand or contract its home range in response to changes in proximity to conspecifics or perceived availability of resources (Cooper 1978, Dahle and Swenson 2003, Kiefer and Weckerly 2005). In territorial species, for which part or all of the home range is aggressively defended, increased intruder pressure is presumed to drive an inverse relationship between density and the defended area (Temeles 1987, Keeley and McPhail 1998, Morrell and Kokko 2005). Hence, as density increases, individuals might respond in either of two ways: they might maintain their home range as a non-overlapping territory, but reduce its size; or they might maintain the same home range size, but reduce the defended area, resulting in increased spatial overlap (Stamps and Buechner 1985, Adams 2001). Optimal territory size can be considered as the outcome of costs (e.g., time, energy, and risk associated with fighting intruders) and benefits (e.g., exclusive access to resources) of territory defense within an economic framework (Schoener 1983, 1987, Morrell and Kokko 2005, Wronski and Plath 2006).

Density may affect the expression of sociality as well; there is increasing evidence that social organization varies according to circumstance (Lott 1991, Wolff 1993, Randall et al. 2005, McEachern et al. 2007). For example, the normally solitary giant kangaroo rat (*Dipodomys ingens*) formed kin-based groups of interacting females in response to increased density

(Meshriy et al. 2011), and both white-footed mice (*Peromyscus leucopus*) and deer mice (*Peromyscus maniculatus*) switched from solitary to communal nesting as a result of limited space and delayed dispersal (Wolff 1994). This pattern was also observed in ground-dwelling squirrels; California ground squirrels (*Otospermophilus beecheyi*), which are characterized as relatively asocial (Grade 2, Armitage 1981), form aggregations called colonies at high density (Van Vuren and Ordeñana 2012), and woodchucks (*Marmota monax*), considered asocial (Grade 1), transition from territoriality at low density to interacting with neighbors and forming simple familial groups when density increases (Ferron and Ouellet 1989, Maher 2006, 2009). Hence, density may influence the spatial organization of asocial mammals, and when population density is high, territoriality may break down (Wolff 1993, Morrell and Kokko 2005). However, few studies examined density-mediated space use in asocial species, perhaps due to the difficulty of measuring kinship and space use in solitary animals (Ratnayeke et al. 2002) or because investigations on less gregarious species generate little interest (Michener 1983, Ferron 1985, Jesmer et al. 2011).

Golden-mantled ground squirrels (*Callospermophilus lateralis*; hereafter GMGS) are a small-bodied species (150-300 g) that is considered asocial (Grade 1) and presumably territorial (Armitage 1981, Michener 1983). However, this classification was supported by sparse data (Michener 1983); subsequent research has shown that adult GMGS are primarily agonistic toward conspecifics (Ferron 1985), which is expected of an asocial species, and that they are potentially territorial, although only for a portion of the home range (Jesmer et al. 2011). The role of kinship in the spatial organization of GMGS is unknown; however, related females sometimes live in close proximity, with important implications for offspring sex ratios and age of first reproduction (Wells and Van Vuren 2017, 2018).

Our objectives were to characterize the spatial organization (home range size and overlap) of a free-living population of golden-mantled ground squirrels, including the role of kinship, and to capitalize on changes in population size over the 25-year duration of the study to evaluate the influence of density on that spatial organization. If GMGS are strictly solitary, we expected to find non-overlapping home ranges between both adult females and adult males, including close kin (Michener 1983). We hypothesized that with increased density, individual squirrels would either reduce home range size but not the degree of home range overlap, or they would maintain home range size but increase the degree of overlap (Stamps and Buechner 1985, Adams 2001).

4.3 Methods

4.3.1 Study system

GMGS are found in the western United States and Canada, where they occur in a range of mid- to high-elevation montane habitats, including open conifer forest, sparse brush, and rocky slopes adjoining grasslands (McKeever 1964, Bartels and Thompson 1993, Shick et al. 2006). We studied a population of GMGS for 25 years (1995-2019) at the Rocky Mountain Biological Laboratory (RMBL), located in the East River Valley, Gunnison County, Colorado (38°57' N, 106°59' W). The 16-ha study area was bordered by perennial streams on the west and south, and by aspen forest on the north and east. Habitats included primarily dry meadow, interspersed with patches of wet meadow, groves of aspen (*Populus tremuloides*) or spruce (*Picea engelmannii*), and stands of willow (*Salix* spp.). GMGS occurred in all habitats but preferred only dry meadow habitat, which was structurally open and provided forbs, such as dandelions (*Taraxacum officinale*), for food. Further, dry meadow habitat was interspersed with

“perches”, raised prominences such as rocks that squirrels frequently used and that presumably facilitated detection of predators (Aliperti 2020). Predation by red foxes (*Vulpes vulpes*), long-tailed weasels (*Mustela frenata*), and short-tailed weasels (*Mustela erminea*) was a significant cause of GMGS mortality at RMBL (Kneip et al. 2011).

Due to the high elevation (2900 m) of our study area, GMGS typically hibernate from late August until snow melt during late April or May (Kneip et al. 2011, Hostetler et al. 2012), a hibernation period up to twice as long as those experienced by GMGS populations at lower elevations (McKeever 1964, Bronson 1979). Upon emerging from hibernation, adult (≥ 1 year) females breed, then give birth underground approximately 28 days later to one litter of pups each year ($\bar{x} = 4.8$, range = 1-8; Kneip et al. 2011, Wells and Van Vuren 2017). GMGS exhibit a polygynandrous mating system, and multiple paternity is common and can result in varying degrees of relatedness among pups within litters (Wells et al. 2017). Females nurse pups for approximately 30 days before juveniles emerge from their natal burrow and forage on plants, especially forbs (Phillips 1981). Juveniles usually disperse before their first overwinter hibernation, though some delay dispersal until early the following summer, and others remain philopatric (Jesmer et al. 2011, Wells and Van Vuren 2017). Immigration of GMGS from surrounding populations into our study area is common (McEachern et al. 2011).

4.3.2 Field methods

We studied GMGS early June through late August each year during the summer active season. We trapped squirrels using single-door box traps (Model 201, Tomahawk Live Trap, Hazelhurst, WI) that were baited with a mixture of sunflower seeds and peanut butter. All adults were trapped during early June as part of an annual census, and pups were trapped within two days of emergence from their natal burrows, usually during late June or early July. We recorded

sex, body mass, and reproductive status of each trapped squirrel (Wells and Van Vuren 2018). Squirrels were identified permanently using numbered tags in each ear, and they were marked for visual identification from a distance using a black, nontoxic dye mark on the dorsal pelage (Nyanzol D dye, Greenville Colorants, Greenville, SC, USA). We re-trapped squirrels to renew marks as needed.

Locations of individual squirrels were determined visually using binoculars, and squirrels were identified based on unique dye marks. Squirrels in our study area were readily observable because they were diurnal, preferred open habitats with sparse vegetation, and often sat on perches (Aliperti 2020). Only a part of our study area could be viewed from any given location, so we rotated through each part of the study area in a randomized order each day. We searched for each squirrel at least once each morning and afternoon to account for possible temporal variation in space use. When at least one squirrel was in view and identified, we employed an instantaneous scan sampling approach (Aliperti 2020), in which we recorded the location of all individuals at 1-min intervals until squirrels in view left the area or disappeared underground. A given squirrel was typically in view for less than 10 min. Locations of squirrels were based on a map of the study area with 7-m x 7-m gridded cells. Because some squirrels were more readily observed than others, we redirected observation efforts toward underrepresented squirrels when appropriate. Squirrels in our study area often encountered humans and seldom reacted to our presence from the observation distances we employed; if a squirrel did react, those observations were omitted. Location data were aggregated for each individual each year. All procedures met guidelines approved by the American Society of Mammalogists (Sikes and Animal Care and Use Committee of the American Society of Mammalogists 2016), and followed protocols approved

by the institutional animal care and use committees of the University of California, Davis and Rocky Mountain Biological Laboratory.

4.3.3 Spatial organization

Squirrel locations were registered into a spatially explicit data base of our study area in ArcGIS v10 (ESRI 2018), then entered into the R software (version 3.6.1; R Core Team 2019). We used package *adehabitatHR* (Version 0.4.16; Calenge 2006) to delineate annual home ranges for each squirrel as calculated through 95% and 50% minimum convex polygons (MCP) and kernel density estimation (KDE). For KDE home ranges, we used a fixed kernel with a reference smoothing bandwidth, h_{ref} , which decreases bias when analyzing the within-home range utilization distribution by determining kernel width based on proximity among relocations (Worton 1989, Kie 2013, Maguire and Rowe 2017, Tisell et al. 2019). Because our dataset included locations based on fine-scale visual observations, and because KDE outputs vary considerably based on choice of smoothing parameter and sample size (Laver and Kelly 2008, Kie 2013), we considered MCP a more conservative and appropriate method for our study; however, we characterized spatial organization using both methods (following Wauters et al. 2007). The 95% home range identifies the overall home range adjusted for outliers, and the 50% home range, also known as the core area, identifies areas of concentrated use within the home range (Samuel et al. 1985, Powell and Mitchell 2012).

Though squirrels are able to traverse multiple grid cells quickly, individuals sometimes remained in the same grid cell for durations of several minutes, resulting in spatial autocorrelation. To reduce spatial autocorrelation, we included only the first observation when an individual was recorded in the same location more than once within a 10-min period (Aliperti 2020). We then filtered the autocorrelation-corrected dataset to include only those individuals

with at least 30 locations (for MCP) or 50 locations (for KDE), and that were present for at least a 30-day period within a given year; the 30-day criterion excluded squirrels that dispersed or died early in the active season. Our minimum numbers of observations per individual were in line with those used to describe squirrel home ranges in other studies (e.g., Wauters et al. 2001, Romeo et al. 2010) and were in accordance with the recommended minimum number of observations for KDE (Seaman et al. 1999); nonetheless, we also conducted a post-hoc analysis to test whether calculations of home range size were biased by the number of locations recorded for each squirrel (Sanchez and Hudgens 2015, Maguire and Rowe 2017).

We used Minta's index (1992, 1993) to calculate mean spatial overlap of 95% home ranges and 50% core areas between all possible pairings of adult squirrels (female-female, female-male, and male-male dyads) each year:

$$\text{Mean overlap} = \frac{\text{Area shared by squirrels } a \text{ and } b}{\sqrt{\text{Home range area of squirrel } a * \text{Home range area of squirrel } b}}$$

Thus, mean overlap values were calculated as a proportion ranging from 0 (no overlap) to 1 (perfect overlap). We summarized overlap for all squirrel dyads with home range overlap > 0; we excluded non-overlapping dyads because the squirrels comprising most of those dyads resided in separate parts of the study area and thus would not have had the opportunity to interact. We also counted the number of female home ranges and core areas overlapped by the average male, and the number of male home ranges and core areas overlapped by the average female. Overlaps between males and females reflected spatial relations after the breeding season, which in our study area ended by late May (Wells et al. 2017).

We calculated coefficients of relatedness for each pair of overlapping adult females based on matrilineal relationships (Wells et al. 2017). Maternity of a litter was provisionally assigned when the litter emerged from the burrow of a female who was considered reproductive based on

nipple development; we searched the home ranges of all reproductive females multiple times per day during June and July (Wells and Van Vuren 2017). Maternity was verified within the first two days of emergence of a litter, when mothers were observed engaging in affiliative interactions, such as nose-to-nose greets, with their pups (Ferron 1985), and were usually trapped with members of their litter (Wells and Van Vuren 2017). We assumed that unmarked females that immigrated into the study area were unrelated to resident females. Mother-daughter dyads were assigned a relatedness coefficient of $r = 0.50$, but because multiple paternity occurs in 62% of GMGS litters in our study area (Wells et al. 2017), littermate sisters could be full siblings ($r = 0.50$) or half siblings ($r = 0.25$). To account for this, we averaged the two expected relatedness values, and assigned $r = 0.375$ to all littermate sisters. Because it is rare for females to mate with the same male across years (Wells et al. 2017), we assumed that non-littermate sisters (i.e., those born to the same mother in different years) were half-sisters, with a relatedness value of 0.25. We calculated mean overlap of 95% home ranges for all overlapping female dyads according to four relatedness categories: unrelated ($r = 0$), distantly related (extra-litter relations, $r = 0.06$ -0.25), littermate sisters ($r = 0.375$), and mother-daughter pairs ($r = 0.50$). Because sharing 50% core areas might reflect a high level of tolerance, we also calculated core area overlap for those dyads that overlapped core areas, according to the four relatedness categories.

4.3.4 Effects of density on spatial organization

We used the MCP method for calculation of home ranges and core areas when describing overlap based on kinship and when modeling the effects of density. We considered population density as the total number of adult females present in the study area for at least a 30-day period each year. However, because adult females were distributed heterogeneously across our study area, with several discrete localities of female activity centered on areas of dry meadow habitat,

population density might not reflect the density realized by a given female due to local spatial clustering (Einum and Nislow 2005, Wells and Van Vuren 2017). Hence, we also calculated the number of neighboring adult female home ranges with which a given female's home range overlapped each year, and we used this measure as a proxy for the local density, or "intruder pressure", experienced by each female (Efford 1996, Sanchez and Hudgens 2015, Woodworth et al. 2017, Aliperti 2020).

We assessed the influence of density on spatial organization by fitting a series of generalized linear mixed effects models (GLMM). To quantify the effects of density on home range size (separately for the 95% home range and 50% core area), we fit a log-linear model with a Gaussian error distribution. Because population-level density and local-level intruder pressure were positively correlated (Pearson's correlation test, $r = 0.73$, $df = 161$, $P < 0.0001$), we fit separate models evaluating the effect of each density measure on each outcome variable. We modeled either home range or core area size as a function of density and reproductive status; we included reproductive status (whether or not a female was reproductive each year) as a fixed effect because the movement patterns of reproductive females might be influenced by greater energetic requirements or limited mobility during lactation, when females tend to pups underground (Kenagy et al. 1990, Edwards et al. 2013). To quantify the effects of density on home range overlap (separately for overlap of 95% home ranges and 50% core areas), we ran a GLMM with a beta distribution and logit link. As the outcome variable we used mean spatial overlap for dyads of females whose home ranges (home range analysis) or core areas (core area analysis) overlapped; hence, all home range and core area overlaps were > 0 . For the population density model, we included population density, kinship, and an interaction between density and kinship as fixed effects; we included the interaction because relatedness might influence overlap

only during years of high density (Maher 2009, Meshriy et al. 2011). We followed the same model structure when assessing the effects of intruder pressure on spatial overlap. However, because intruder pressure was measured per individual rather than per dyad, we modeled spatial overlap as a function of the mean intruder pressure experienced by the two females in each dyad (following Sanchez and Hudgens 2015), in addition to kinship and an interaction between mean intruder pressure and kinship. To account for repeated measures or the possibility of interannual environmental differences, we included year as a random effect in all models, and we included a random effect of either individual (when modeling home range size) or dyad (when modeling home range overlap). We ran models using R packages lme4 (Bates et al. 2015) and glmmTMB (Brooks et al. 2017).

4.4 Results

Sample sizes for home range delineation via the MCP and KDE methods were similar (Table 1). We calculated core area size for all squirrel-year pairings except for one female whose core area was too small to delineate by the MCP method, and we computed mean MCP core area overlap for all dyads that were used for home range overlap, other than the 3 dyads (2 female-female, 1 female-male) corresponding to the female whose core area could not be delineated (Table 1). In addition, we calculated mean core area overlap for those dyads that showed any core area overlap. During the 25-year duration of the study, population density of adult females ranged 3-24, and intruder pressure ranged 0-15.

4.4.1 Spatial organization

There was no significant effect of total number of observations recorded for each squirrel on either overall MCP home range size ($\beta \pm SE = 0.002 \pm 0.001$, $t = 1.83$, $P = 0.070$) or MCP

core area size ($\beta \pm SE = 0.001 \pm 0.001$, $t = 0.93$, $P = 0.354$) after accounting for the random effects of individual and year. There was an effect of total number of observations on KDE home range size and core area size, though the effect was negative, and the regression coefficient was close to zero (home range $\beta \pm SE = -0.002 \pm 0.001$, $t = -2.18$, $P = 0.031$; core area $\beta \pm SE = -0.003 \pm 0.001$, $t = -2.66$, $P = 0.009$). While home ranges that were calculated by KDE were over twice as large as those calculated by MCP, both estimates indicated that home ranges of males were four times as large as those of females (Table 2). Further, estimates for mean spatial overlap were similar between the two methods (Table 2). Using MCP home ranges, we found that the average adult female GMGS had a home range that overlapped with 2.7 ± 0.18 (mean $\pm$ SE) other females (range 0-12) and 3.1 ± 0.14 males (range 0-8), while the average adult male had a home range that overlapped with 4.4 ± 0.39 females (range 0-15) and 3.1 ± 1.79 other males (range 1-8). The average adult female maintained a 50% core area that overlapped with 0.6 ± 0.06 other females (range 0-3) and 1.1 ± 0.08 males (range 0-4), while the average adult male maintained a core area that overlapped with 1.5 ± 0.15 females (range 0-5) and 0.8 ± 0.12 other males (range 0-4). These values are an underestimate, because in some cases additional males and females were present but not considered because of inadequate sample size or less than 30-day duration.

Among female dyads that shared home ranges, home range overlap increased with relatedness, with close kin (sister-sister and mother-daughter dyads) showing almost twice the degree of overlap as did dyads of unrelated females (Fig. 2). For those dyads that shared core areas, a similar pattern of greater sharing among kin was evident, with one exception: sister-sister dyads ($r = 0.375$) showed less core-area sharing than any other kinship category, including non-relatives (Fig. 2).

4.4.2 Effects of density on spatial organization

We did not find an effect of population density on either home range size ($\beta \pm SE = -0.001 \pm 0.016$, $t = -0.07$, $P = 0.946$) or core area size ($\beta \pm SE = -0.017 \pm 0.020$, $t = -0.83$, $P = 0.426$). However, we found a significant, positive effect of intruder pressure on home range size ($\beta \pm SE = 0.108 \pm 0.034$, $t = 3.22$, $P = 0.002$; Fig. 3). Intruder pressure did not have a significant effect on core area size, though it had a positive effect that approached statistical significance ($\beta \pm SE = 0.086 \pm 0.045$, $t = 1.93$, $P = 0.057$). We did not find an effect of population density ($\beta \pm SE = -0.032 \pm 0.021$, $z = -1.52$, $P = 0.130$) on home range overlap. However, we found a significant, positive effect of an interaction between population density and kinship on home range overlap ($\beta \pm SE = 0.160 \pm 0.063$, $z = 2.53$, $P = 0.011$), such that more closely related females showed greater spatial overlap as population density increased (Fig. 4A). Similarly, we did not find an effect of intruder pressure ($\beta \pm SE = -0.040 \pm 0.050$, $z = -0.82$, $P = 0.414$) on home range overlap, but we found a significant, positive effect of an interaction between intruder pressure and kinship on home range overlap ($\beta \pm SE = 0.587 \pm 0.170$, $z = 3.46$, $P = 0.0005$; Fig. 4B). There was no effect of population density ($\beta \pm SE = -0.018 \pm 0.036$, $z = -0.49$, $P = 0.622$) or intruder pressure ($\beta \pm SE = -0.103 \pm 0.107$, $z = -0.97$, $P = 0.334$) on core area overlap, and there were no significant interactions between either population density and kinship ($\beta \pm SE = 0.031 \pm 0.123$, $z = 0.25$, $P = 0.803$) or intruder pressure and kinship ($\beta \pm SE = 0.402 \pm 0.387$, $z = 1.04$, $P = 0.299$) on core area overlap. After accounting for interactions between density and kinship, there was no stand-alone effect of kinship on home range overlap or core area overlap in the models for either population density (home range: $\beta \pm SE = -0.240 \pm 1.027$, $z = -0.23$, $P = 0.815$, core area: $\beta \pm SE = -0.052 \pm 1.815$, $z = -0.03$, $P = 0.977$) or intruder pressure (home range: $\beta \pm$

SE = -0.437 ± 0.847 , $z = -0.52$, $P = 0.606$, core area: $\beta \pm SE = -1.249 \pm 1.738$, $z = -0.72$, $P = 0.472$).

4.5 Discussion

Golden-mantled ground squirrels are a relatively small-bodied species, which enables individuals to reach adulthood upon emerging from their first hibernation bout, and ostensibly precludes the formation of long-term social bonds among conspecifics (Armitage 1981). Hence, GMGS are presumed to be asocial and solitary, characterized by nonoverlapping adult home ranges (Armitage 1981, Michener 1983). Contrary to this expectation, we found extensive overlap between female home ranges, and between male and female home ranges (Table 2, Fig. 1). Moreover, the home range of a given squirrel overlapped with several members of the same and opposite sex. However, our home range overlap (30%) was consistent with overlap values reported for solitary mammals, although it was toward the upper edge of the range (5-37%; Oli et al. 2002, Burton and Krebs 2003, Kitchen et al. 2005, Støen et al. 2005, Innes et al. 2009, Jones et al. 2013, Rodgers et al. 2015, Tisell et al. 2019, Aronsson et al. 2020). Our results are also consistent with those for other asocial (Grade 1) squirrels. Woodchucks (*Marmota monax*) showed home range overlap within and between sexes that ranged ca. 5-20%, along with some degree of territoriality (Meier 1992, Swihart 1992, Maher 2009), and Franklin's ground squirrel (*Poliocitellus franklinii*) also showed home range overlap both within and between sexes (Choromanski-Norris et al. 1989). Interestingly, some species classified as Grade 2 show a similar pattern as we found for GMGS. For Richardson's ground squirrels (*Urocitellus richardsonii*; Michener 1979), adult females showed extensive home range overlap (35%) but minimal core area overlap (3%), and a similar pattern was evident for California ground squirrels

(*Otospermophilus beecheyi*; Boellstorff et al. 1995). Perhaps the distinction between Grades 1 and 2 lies more with interactions and kinship than with spatial dispersion. We found that home range sizes of males were much larger than for females; a similar difference was found for Franklin's ground squirrels (Choromanski-Norris et al. 1989) and woodchucks (Swihart 1992, Maher 2004). Males and females in our study were similar in body size, so the difference in home range size probably is not due to higher metabolic requirements by males. The explanation may be associated with the mating system, which is polygynandrous (Wells et al. 2017); we measured home ranges after the mating season ended, and males may have roamed over enlarged home ranges to acquire information on potential mates for the next year.

Jesmer et al. (2011) reported home range sizes for female GMGS (3.57 ha 95% MCP, 3.75 ha 95% KDE) that were more than twice as large as those we report; their study site was in a conifer forest that may have supported a lower density of food resources than the forb-rich meadows of our study area. Despite the difference in home range sizes, overlap values for the 95% home range (0.31) and 50% core area (0.03) of adult females reported by Jesmer et al. (2011) were remarkably similar to our values. This similarity suggests that extensive overlap of home ranges but minimal overlap of core areas are characteristic of GMGS, and supports the hypothesis that GMGS are territorial, but only for the inner part of their home range (Ferron 1985, Jesmer et al. 2011).

Contrary to expectation, kinship played a role in the spatial organization of GMGS: related females shared space more than unrelated females. At the level of the home range, littermate sister and mother-daughter dyads showed differing levels of relatedness but similar levels of overlap (0.43 for sister-sister, 0.45 for mother-daughter; Fig. 2), suggesting that kin identification in GMGS is based primarily on familiarity (Michener 1983, Armitage 1989).

Woodchucks, another asocial species, showed a similar pattern of increased home range overlap with increased relatedness (Maher 2009). In yellow-bellied marmots (*Marmota flaviventer*), a highly social species (Grade 4), home range overlap increased with kinship but the relationship was not proportional; space sharing was disproportionately directed to close kin ($r = 0.50$; Armitage 1996).

The core area of GMGS included 50% of locations but averaged only 22% of home range size, indicating an area of intensive use, and presumably importance. For those dyads that overlapped core areas, space sharing (0.26) was nearly as great as for those that overlapped home ranges (0.30), suggesting that most females did not share core areas, but for those that did, sharing was extensive. As was the case with home ranges, kinship played a role in core area overlap, with the exception of littermate sisters (Fig. 2). The explanation may be reproductive competition between sisters; yearling females with a littermate sister nearby realized a 78% reduction in probability of breeding, yet experienced no effect from proximity of their mother or more distantly related females (Wells and Van Vuren 2018).

Despite considerable variation in density, both at the population level and at the local level (intruder pressure), neither of the expected outcomes of increased density were realized: we did not see reduced home range size coupled with unchanged overlap (e.g., Priotto et al. 2002, Drake et al. 2015), nor did we see unchanged size coupled with increased overlap (e.g., Wolff 1985, Hoset et al. 2008). Instead, we found a positive effect of density on home range size (Fig. 3), and a corresponding near-significant effect on core area size, and these effects were realized only at the local level. One explanation is that females range farther when surrounded by neighbors in order to gain familiarity with territorial borders and reduce time spent on aggressive interactions in the long-term ('dear enemy effect'; Fisher 1954, Temeles 1994, Siracusa et al.

2017). Another explanation is that females expand their home ranges into less crowded, lower quality areas, where they need to roam farther to access patchily distributed resources (McShea and Schwede 1993, McLoughlin and Ferguson 2000, Kilpatrick et al. 2001, Harris and Leitner 2004). For example, male bushbuck (*Tragelaphus scriptus*) responded to increased intruder pressure by expanding their territories to access potential mates (Wronski and Plath 2006). GMGS in our study area prefer dry meadow habitat with more perches, and availability of those perches increases the probability of survival (Aliperti 2020). Possibly, increased intruder pressure prompts females to move into dry meadow habitat with fewer perches. Also, reproductive females might move into less crowded habitat to give birth, away from the threat of harassment or infanticide by neighboring squirrels (Michener 1982, Ebensperger and Blumstein 2007), then move the litter to better habitat as pups emerge; litter relocation is common in this species (Aliperti et al. 2020).

We did not find an effect of density on overlap of home ranges or core areas, but we did find an interaction between density and kinship on home range overlap: related females showed greater home range overlap as either population density or intruder pressure increased (Fig. 4). Hence, kinship influenced spatial overlap, but only at high densities. Large increases in our population are driven primarily by increased survival and reproduction of residents, rather than by immigration (Hostetler et al. 2012). Evidently, as density increases, females are more tolerant of neighboring kin than of non-kin. Density-mediated philopatry and spatial overlap among kin have been reported in other solitary mammals (e.g., Kitchen et al. 2005, Støen et al. 2005, Maher 2009, Meshriy et al. 2011, Innes et al. 2012), and the formation of kin clusters at high density is an important step in the evolution of sociality (Waser and Waser 1985, Maher 2009, Meshriy et al. 2011). In GMGS, the creation of kin groups can have important demographic implications;

density of kin, but not non-kin, influenced litter sex ratios for female GMGS, presumably due to competition for resources among philopatric females (Wells and Van Vuren 2017). Nonetheless, GMGS may build a facultative tolerance to kin during high density years because the inclusive fitness benefits of sharing resources with close relatives can outweigh the costs of competition (Hamilton 1964, Kitchen et al. 2005, Maher 2009, Banks et al. 2011). At high density or when resources are limited, surrounding habitat may be saturated with aggressive neighbors; hence, close relatives may tolerate the retention of female kin when the probability of successful dispersal is low (Waser and Jones 1983, Wolff 1993, Van Vuren and Armitage 1994, Solomon 2003).

Our results suggest that the spatial organization of golden-mantled ground squirrels resembles that of other solitary mammals, in that females maintain areas of exclusive use (Armitage 1981, Michener 1983). However, spatial overlap among adults suggests this species defends only the core area of its home range, and that females share more space with kin than non-kin (McEachern et al. 2007, Maher 2009, Innes et al. 2012, Rodgers et al. 2015), but only at high densities. Further, this density-mediated increase in space-sharing among kin suggests that familiarity and inclusive fitness benefits may offset costs of competition and promote philopatry under certain conditions. Overall, we provide evidence of a facultative transition in GMGS from asociality to the formation of single-family kin clusters (Grade 2), the first step towards developing sociality (Armitage 1981, Michener 1983, Waser and Waser 1985, Maher 2009). Our study highlights the importance of considering familiarity among neighbors in asocial species, as well as the interactive effects of environmental conditions and kinship when assessing the spatial and social organization of mammals.

Acknowledgments

I thank my co-authors, C. P. Wells and D. H. Van Vuren. I am grateful for long-term logistical support from the Rocky Mountain Biological Laboratory, and the many research assistants who contributed to data collection throughout the long-term project. Project funding was provided by the California Agricultural Experiment Station, Rocky Mountain Biological Laboratory Graduate Fellowship, American Society of Mammalogists Grant-in-Aid of Research, and the University of California, Davis Walter and Elizabeth Howard Award. I thank A. Sih and R. J. Hijmans for valuable comments on an earlier draft of this manuscript.

4.6 Literature Cited

- Adams, E. S. 2001. Approaches to the study of territory size and shape. *Annual Review of Ecology and Systematics* 32:277–303.
- Aliperti, J. R. 2020. Behavioral and spatial dynamics in a fluctuating population of golden-mantled ground squirrels (*Callospermophilus lateralis*). PhD Dissertation, University of California, Davis.
- Aliperti, J. R., D. H. Van Vuren, A. J. Rossi, and K. B. Armitage. 2020. Litter relocation behavior in two species of ground-dwelling squirrels. *Ethology* 126:377–382.
- Armitage, K. B. 1981. Sociality as a life-history tactic of ground squirrels. *Oecologia* 48:36–41.
- Armitage, K. B. 1989. The function of kin discrimination. *Ethology Ecology and Evolution* 1:111–121.
- Armitage, K. B. 1996. Resource sharing and kinship in yellow-bellied marmots. Pages 129–134 in M. Le Berre, R. Ramouse, and R. Guelte, editors. *Biodiversity in Marmots*. Moscow-Lyon: International Marmot Network.

- Armitage, K. B. 1999. Evolution of sociality in marmots. *Journal of Mammalogy* 80:1–10.
- Aronsson, M., M. Åkesson, M. Low, J. Persson, and H. Andrén. 2020. Resource dispersion and relatedness interact to explain space use in a solitary predator. *Oikos*:1174–1184.
- Banks, S. C., D. B. Lindenmayer, L. Mcburney, D. Blair, E. J. Knight, and M. D. J. Blyton. 2011. Kin selection in den sharing develops under limited availability of tree hollows for a forest marsupial. *Proceedings of the Royal Society B: Biological Sciences* 278:2768–2776.
- Bartels, M. A., and D. P. Thompson. 1993. *Spermophilus lateralis*.
- Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Boellstorff, D. E., and D. H. Owings. 1995. Home range, population structure, and spatial organization of California ground squirrels. *Journal of Mammalogy* 76:551–561.
- Bronson, M. T. 1979. Altitudinal variation in the life history of the golden-mantled ground squirrel (*Spermophilus lateralis*). *Ecology* 60:272–279.
- Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Mächler, and B. M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal* 9:378–400.
- Burton, C., and C. J. Krebs. 2003. Influence of relatedness on snowshoe hare spacing behavior. *Journal of Mammalogy* 84:1100–1111.
- Calenge, C. 2006. The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197:516–519.
- Choromanski-Norris, J., E. K. Fritzell, and A. B. Sargeant. 1989. Movements and habitat use of Franklin’s ground squirrels in duck-nesting habitat. *The Journal of Wildlife Management* 53:324–331.

- Cooper, W. E. J. 1978. Home range size and population dynamics. *Journal of Theoretical Biology* 75:327–337.
- Dahle, B., and J. E. Swenson. 2003. Home ranges in adult Scandinavian brown bears (*Ursus arctos*): effect of mass, reproductive category, population density and habitat type. *Journal of Zoology* 260:329–335.
- Drake, E. M., B. L. Cypher, K. Ralls, J. D. Perrine, R. White, and T. J. Coonan. 2015. Home-range size and habitat selection by male island foxes (*Urocyon littoralis*) in a low-density population. *Southwestern Naturalist* 60:247–255.
- Ebensperger, L. A., and D. T. Blumstein. 2007. Nonparental infanticide. Pages 267–279 in J. O. Wolff and P. W. Sherman, editors. *Rodent societies: an ecological and evolutionary perspective*. The University of Chicago, Chicago, IL.
- Edwards, M. A., A. E. Derocher, and J. A. Nagy. 2013. Home range size variation in female arctic grizzly bears relative to reproductive status and resource availability. *PLoS ONE* 8:1–11.
- Efford, M. G. 1996. Simulating spatially distributed populations. Pages 409–418 in R. B. Floyd, A. W. Sheppard, and P. J. De Barro, editors. *Frontiers of Population Ecology*. CSIRO Publishing, Melbourne.
- ESRI. 2018. Arc GIS. Environmental System Research Institute Inc., Redlands, California.
- Ferron, J. 1985. Social behaviour of the golden-mantled ground-squirrel (*Spermophilus lateralis*). *Canadian Journal of Zoology* 63:2529–2533.
- Ferron, J., and J. P. Ouellet. 1989. Temporal and intersexual variations in the use of space with regard to social organization in the woodchuck (*Marmota monax*). *Canadian Journal of Zoology* 67:1642–1649.

- Fisher, J. 1954. Evolution and bird sociality. Pages 71–83 in J. Huxley, A. C. Hardy, and E. B. Ford, editors. *Evolution as a process*. Allen & Unwin, London, U.K.
- Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28:1140–1162.
- Hamilton, W. D. 1964. The genetical evolution of social behavior. II. *Journal of Theoretical Biology* 7:44–89.
- Harris, J. H., and P. Leitner. 2004. Home-range size and use of space by adult Mohave ground squirrels, *Spermophilus mohavensis*. *Journal of Mammalogy* 85:517–523.
- Hoset, K. S., J. F. Le Galliard, G. Gundersen, and H. Steen. 2008. Home range size and overlap in female root voles: effects of season and density. *Behavioral Ecology* 19:139–145.
- Hostetler, J. A., E. Kneip, D. H. Van Vuren, and M. K. Oli. 2012. Stochastic population dynamics of a montane ground-dwelling squirrel. *PLoS ONE* 7:1–10.
- Innes, R. J., M. B. McEachern, D. H. Van Vuren, J. M. Eadie, D. A. Kelt, and M. L. Johnson. 2012. Genetic relatedness and spatial associations of dusky-footed woodrats (*Neotoma fuscipes*). *Journal of Mammalogy* 93:439–446.
- Innes, R. J., D. H. Van Vuren, D. A. Kelt, J. A. Wilson, and M. L. Johnson. 2009. Spatial organization of dusky-footed woodrats (*Neotoma fuscipes*). *Journal of Mammalogy* 90:811–818.
- Jesmer, B. R., D. H. Van Vuren, J. A. Wilson, D. A. Kelt, and M. L. Johnson. 2011. Spatial organization in female golden-mantled ground squirrels. *The American Midland Naturalist* 165:162–168.

- Jones, K. L., D. H. Van Vuren, M. B. McEachern, K. R. Crooks, J. W. Dragoo, and B. May. 2013. Spatial and genetic organization of the island spotted skunk, *Spilogale gracilis amphiala*. *The Southwestern Naturalist* 58:481–486.
- Keeley, E. R., and J. D. McPhail. 1998. Food abundance, intruder pressure, and body size as determinants of territory size in juvenile steelhead trout (*Oncorhynchus mykiss*). *Behaviour* 135:65–82.
- Kenagy, G. J., D. Masman, S. M. Sharbaugh, and K. A. Nagy. 1990. Energy expenditure during lactation in relation to litter size in free-living golden-mantled ground squirrels. *Journal of Animal Ecology* 59:73–88.
- Kie, J. G. 2013. A rule-based ad hoc method for selecting a bandwidth in kernel home-range analyses. *Animal Biotelemetry* 1:26–27.
- Kiefer, S. J., and F. W. Weckerly. 2005. Population density and body weight influences on home range size of feral hogs. *California Fish and Game* 91:136–142.
- Kilpatrick, H. J., S. M. Spohr, and K. K. Lima. 2001. Effects of population reduction on home ranges of female white-tailed deer at high densities. *Canadian Journal of Zoology* 79:949–954.
- Kitchen, A. M., E. M. Gese, L. P. Waits, S. M. Karki, and E. R. Schauster. 2005. Genetic and spatial structure within a swift fox population. *Journal of Animal Ecology* 74:1173–1181.
- Kneip, É., D. H. Van Vuren, J. A. Hostetler, and M. K. Oli. 2011. Influence of population density and climate on the demography of subalpine golden-mantled ground squirrels. *Journal of Mammalogy* 92:367–377.
- Laver, P. N., and M. J. Kelly. 2008. A critical review of home range studies. *Journal of Wildlife Management* 72:290–298.

- Lott, D. F. 1991. Intraspecific variation in the social systems of wild vertebrates. Cambridge University Press.
- Maguire, A. J., and R. J. Rowe. 2017. Home range and habitat affinity of the singing vole on the north slope of Alaska. *Arctic, Antarctic, and Alpine Research* 49:243–257.
- Maher, C. R. 2004. Intrasexual territoriality in woodchucks (*Marmota monax*). *Journal of Mammalogy* 85:1087–1094.
- Maher, C. R. 2006. Social organization in woodchucks (*Marmota monax*) and its relationship to growing season. *Ethology* 112:313–324.
- Maher, C. R. 2009. Genetic relatedness and space use in a behaviorally flexible species of marmot, the woodchuck (*Marmota monax*). *Behavioral Ecology and Sociobiology* 63:857–868.
- McEachern, M. B., J. M. Eadie, and D. H. Van Vuren. 2007. Local genetic structure and relatedness in a solitary mammal, *Neotoma fuscipes*. *Behavioral Ecology and Sociobiology* 61:1459–1469.
- McEachern, M. B., D. H. Van Vuren, C. H. Floyd, B. May, and J. M. Eadie. 2011. Bottlenecks and rescue effects in a fluctuating population of golden-mantled ground squirrels (*Spermophilus lateralis*). *Conservation Genetics* 12:285–296.
- McKeever, S. 1964. The biology of the golden-mantled ground squirrel, *Citellus lateralis*. *Ecological Monographs* 34:383–401.
- McLoughlin, P. D., and S. H. Ferguson. 2000. A hierarchical pattern of limiting factors helps explain variation in home range size. *Ecoscience* 7:123–130.
- McShea, W. J., and G. Schwede. 1993. Variable acorn crops: responses of white-tailed deer and other mast consumers. *Journal of Mammalogy* 74:999–1006.

- Meier, P. T. 1992. Social organization of woodchucks (*Marmota monax*). Behavioral Ecology and Sociobiology 31:393–400.
- Meshriy, M. G., J. A. Randall, and L. Parra. 2011. Kinship associations of a solitary rodent, *Dipodomys ingens*, at fluctuating population densities. Animal Behaviour 82:643–650.
- Michener, G. R. 1979. Spatial relationships and social organization of adult Richardson's ground squirrels. Canadian Journal of Zoology 57:125–139.
- Michener, G. R. 1982. Infanticide in ground squirrels. Animal Behaviour 30:936–938.
- Michener, G. R. 1983. Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids. Pages 528–572 in J. F. Eisenberg and D. G. Kleiman, editors. Advances in the study of mammalian behavior. Seventh edition. American Society of Mammalogists, Stillwater, OK.
- Minta, S. C. 1992. Tests of spatial and temporal interaction among animals. Ecological Applications 2:178–188.
- Minta, S. C. 1993. Sexual differences in spatio-temporal interaction among badgers. Oecologia 96:402–409.
- Morrell, L. J., and H. Kokko. 2005. Bridging the gap between mechanistic and adaptive explanations of territory formation. Behavioral Ecology and Sociobiology 57:381–390.
- Oli, M. K., H. A. Jacobson, and B. D. Leopold. 2002. Pattern of space use by female black bears in the White River National Wildlife Refuge, Arkansas, USA. Journal for Nature Conservation 10:87–93.
- Phillips, J. A. 1981. Growth and its relationship to the initial annual cycle of the golden-mantled ground squirrel, *Spermophilus lateralis*. Canadian Journal of Zoology 59:865–871.

- Powell, R. A., and M. S. Mitchell. 2012. What is a home range? *Journal of Mammalogy* 93:948–958.
- Priotto, J., A. Steinmann, and J. Polop. 2002. Factors affecting home range size and overlap in *Calomys venustus* (Muridae: Sigmodontinae) in Argentine agroecosystems. *Mammalian Biology* 67:97–104.
- R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Randall, J. A., K. Rogovin, P. G. Parker, and J. A. Eimes. 2005. Flexible social structure of a desert rodent, *Rhombomys opimus*: philopatry, kinship, and ecological constraints. *Behavioral Ecology* 16:961–973.
- Ratnayeke, S., G. A. Tuskan, and M. R. Pelton. 2002. Genetic relatedness and female spatial organization in a solitary carnivore, the raccoon, *Procyon lotor*. *Molecular Ecology* 11:1115–1124.
- Rayor, L. S., and K. B. Armitage. 1991. Social behavior and space-use of young of ground-dwelling squirrel species with different levels of sociality. *Ethology Ecology and Evolution* 3:185–205.
- Rodgers, T. W., J. Giacalone, E. J. Heske, J. E. Janečka, P. A. Jansen, C. A. Phillips, and R. L. Schooley. 2015. Socio-spatial organization and kin structure in ocelots from integration of camera trapping and noninvasive genetics. *Journal of Mammalogy* 96:120–128.
- Romeo, C., L. A. Wauters, D. Preatoni, G. Tosi, and A. Martinoli. 2010. Living on the edge: space use of Eurasian red squirrels in marginal high-elevation habitat. *Acta Oecologica* 36:604–610.

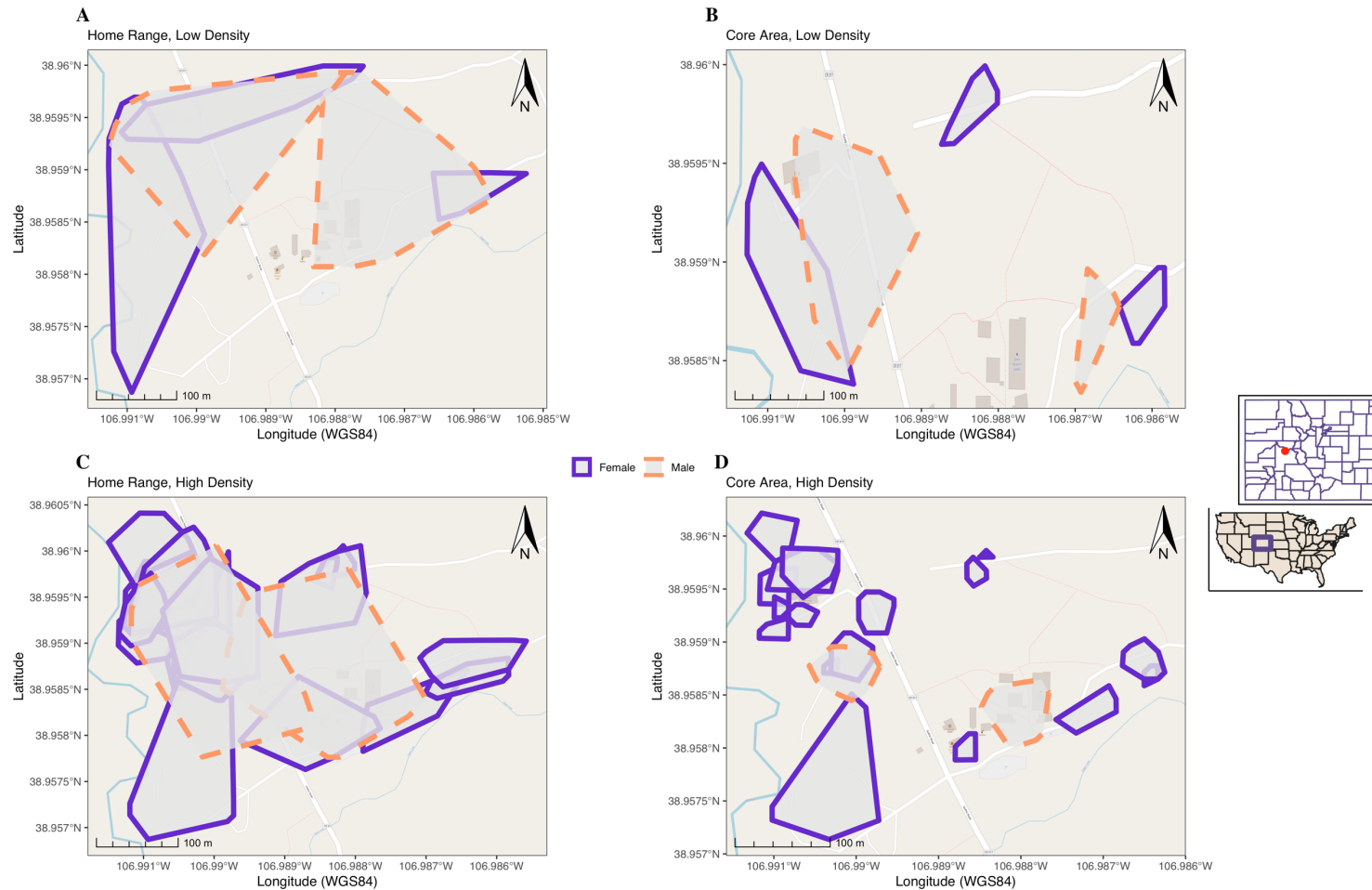
- Samuel, M. D., D. J. Pierce, and E. O. Garton. 1985. Identifying areas of concentrated use within the home range. *Journal of Animal Ecology* 54:711–719.
- Sanchez, J. N., and B. R. Hudgens. 2015. Interactions between density, home range behaviors, and contact rates in the Channel Island fox (*Urocyon littoralis*). *Ecology and Evolution* 5:2466–2477.
- Schoener, T. W. 1983. Simple models of optimal feeding-territory size: a reconciliation. *The American Naturalist* 121:608–629.
- Schoener, T. W. 1987. Time budgets and territory size: some simultaneous optimization models for energy maximizers. *Integrative and Comparative Biology* 27:259–291.
- Seaman, D. E., J. J. Millsbaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. *The Journal of Wildlife Management* 63:739.
- Shick, K. R., D. E. Pearson, and L. F. Ruggiero. 2006. Forest habitat associations of the golden-mantled ground squirrel: implications for fuels management. *Northwest Science* 80:133–139.
- Sikes, R. S., and The Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy* 97:663–688.
- Silk, J. B. 2007. The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society B: Biological Sciences* 362:539–559.
- Siracusa, E., S. Boutin, M. M. Humphries, J. C. Gorrell, D. W. Coltman, B. Dantzer, J. E. Lane, and A. G. McAdam. 2017. Familiarity with neighbours affects intrusion risk in territorial red squirrels. *Animal Behaviour* 133:11–20.

- Solomon, N. G. 2003. A reexamination of factors influencing philopatry in rodents. *Journal of Mammalogy* 84:1182–1197.
- Stamps, J. A., and M. Buechner. 1985. The territorial defense hypothesis and the ecology of insular vertebrates 60:155–181.
- Støen, O. G., E. Bellemain, S. Sæbø, and J. E. Swenson. 2005. Kin-related spatial structure in brown bears *Ursus arctos*. *Behavioral Ecology and Sociobiology* 59:191–197.
- Swihart, R. K. 1992. Home-range attributes and spatial structure of woodchuck populations. *Journal of Mammalogy* 73:604–618.
- Temeles, E. J. 1987. The relative importance of prey availability and intruder pressure in feeding territory size regulation by harriers, *Circus cyaneus*. *Oecologia* 74:286–297.
- Temeles, E. J. 1994. The role of neighbours in territorial systems: when are they “dear enemies”? *Animal Behaviour* 47:339–350.
- Tisell, H. B., A. L. Deggrasi, R. B. Stephens, and R. J. Rowe. 2019. Influence of field technique, density, and sex on home range and overlap of the southern red-backed vole (*Myodes gapperi*). *Canadian Journal of Zoology* 97:1101–1108.
- Van Vuren, D. H., and K. B. Armitage. 1994. Survival of dispersing and philopatric yellow-bellied marmots: what is the cost of dispersal? 69:179–181.
- Van Vuren, D. H., and M. A. Ordeñana. 2012. Factors influencing burrow length and depth of ground-dwelling squirrels. *Journal of Mammalogy* 93:1240–1246.
- Waser, P. M., and W. T. Jones. 1983. Natal philopatry among solitary mammals 58:355–390.
- Waser, P. M., and M. S. Waser. 1985. *Ichneumia albicauda* and the evolution of viverrid gregariousness. *Zeitschrift für Tierpsychologie* 68:137–151.

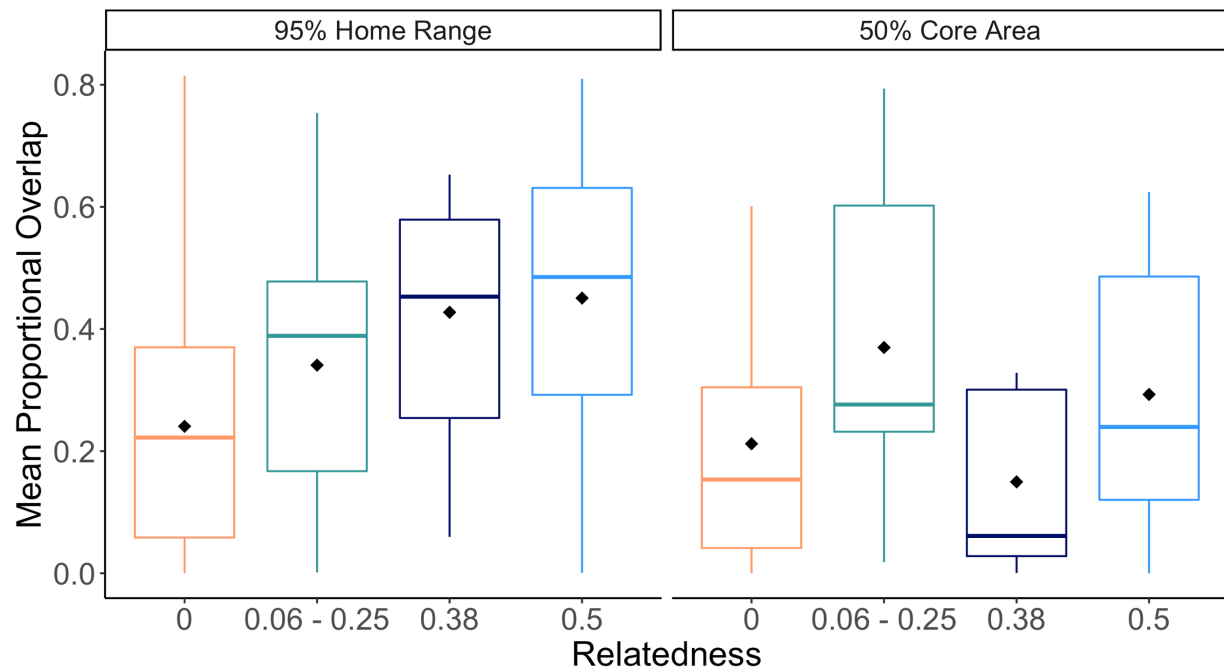
- Wauters, L. A., J. Gurnell, D. Preatoni, and G. Tosi. 2001. Effects of spatial variation in food availability on spacing behaviour and demography of Eurasian red squirrels. *Ecography* 24:525–538.
- Wauters, L. A., D. G. Preatoni, A. Molinari, and G. Tosi. 2007. Radio-tracking squirrels: performance of home range density and linkage estimators with small range and sample size. *Ecological Modelling* 202:333–344.
- Wells, C. P., K. M. Tomalty, C. H. Floyd, M. B. McElreath, B. P. May, and D. H. Van Vuren. 2017. Determinants of multiple paternity in a fluctuating population of ground squirrels. *Behavioral Ecology and Sociobiology* 71.
- Wells, C. P., and D. H. Van Vuren. 2017. Female kin density affects offspring sex ratio in an asocial mammal, the golden-mantled ground squirrel, *Callospermophilus lateralis*. *Animal Behaviour* 134:71–77.
- Wells, C. P., and D. H. Van Vuren. 2018. Developmental and social constraints on early reproduction in an asocial ground squirrel. *Journal of Zoology* 306:28–35.
- Wolff, J. O. 1985. The effects of density, food, and interspecific interference on home range size in *Peromyscus leucopus* and *Peromyscus maniculatus*. *Canadian Journal of Zoology* 63:2657–2662.
- Wolff, J. O. 1993. Why are female small mammals territorial? *Oikos* 68:364–370.
- Wolff, J. O. 1994. Reproductive success of solitarily and communally nesting white-footed mice and deer mice. *Behavioral Ecology* 5:206–209.
- Woodworth, B. K., N. T. Wheelwright, A. E. M. Newman, and D. R. Norris. 2017. Local density regulates migratory songbird reproductive success through effects on double-brooding and nest predation. *Ecology* 98:2039–2048.

- Worton, A. B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168.
- Wronski, T., and M. Plath. 2006. Mate availability and intruder pressure as determinants of territory size in male bushbuck (*Tragelaphus scriptus*). *Acta Ethologica* 9:37–42.

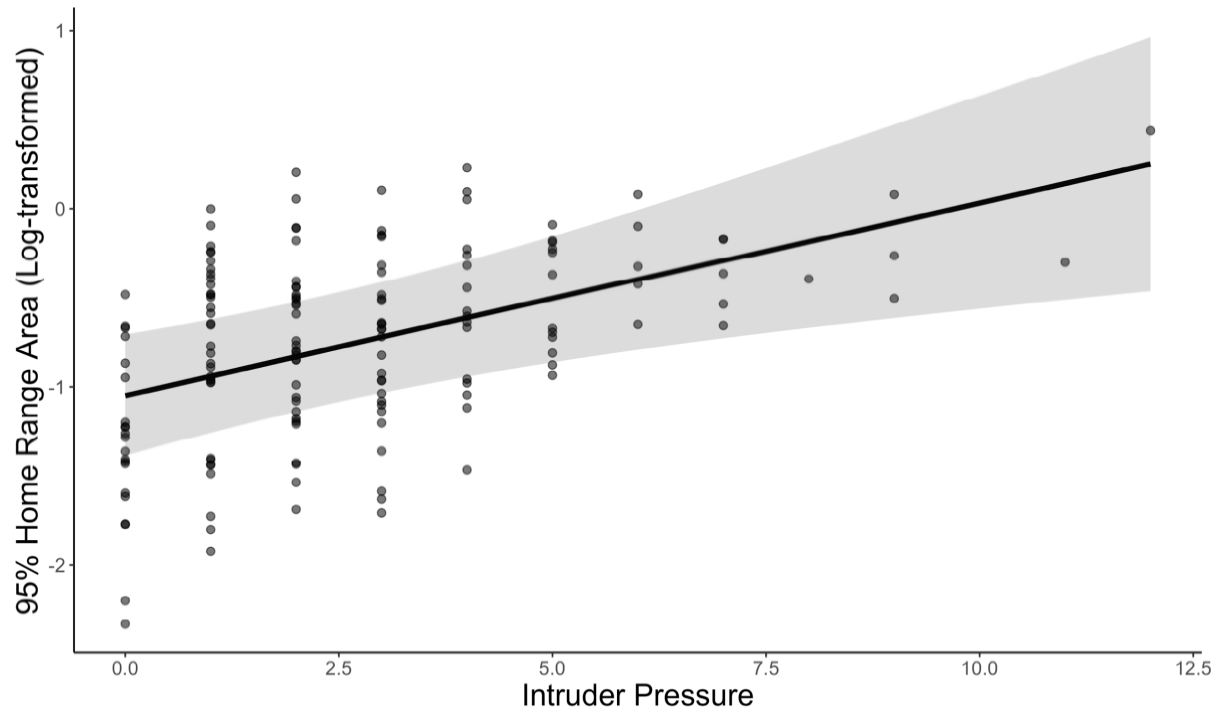
4.7 Figures



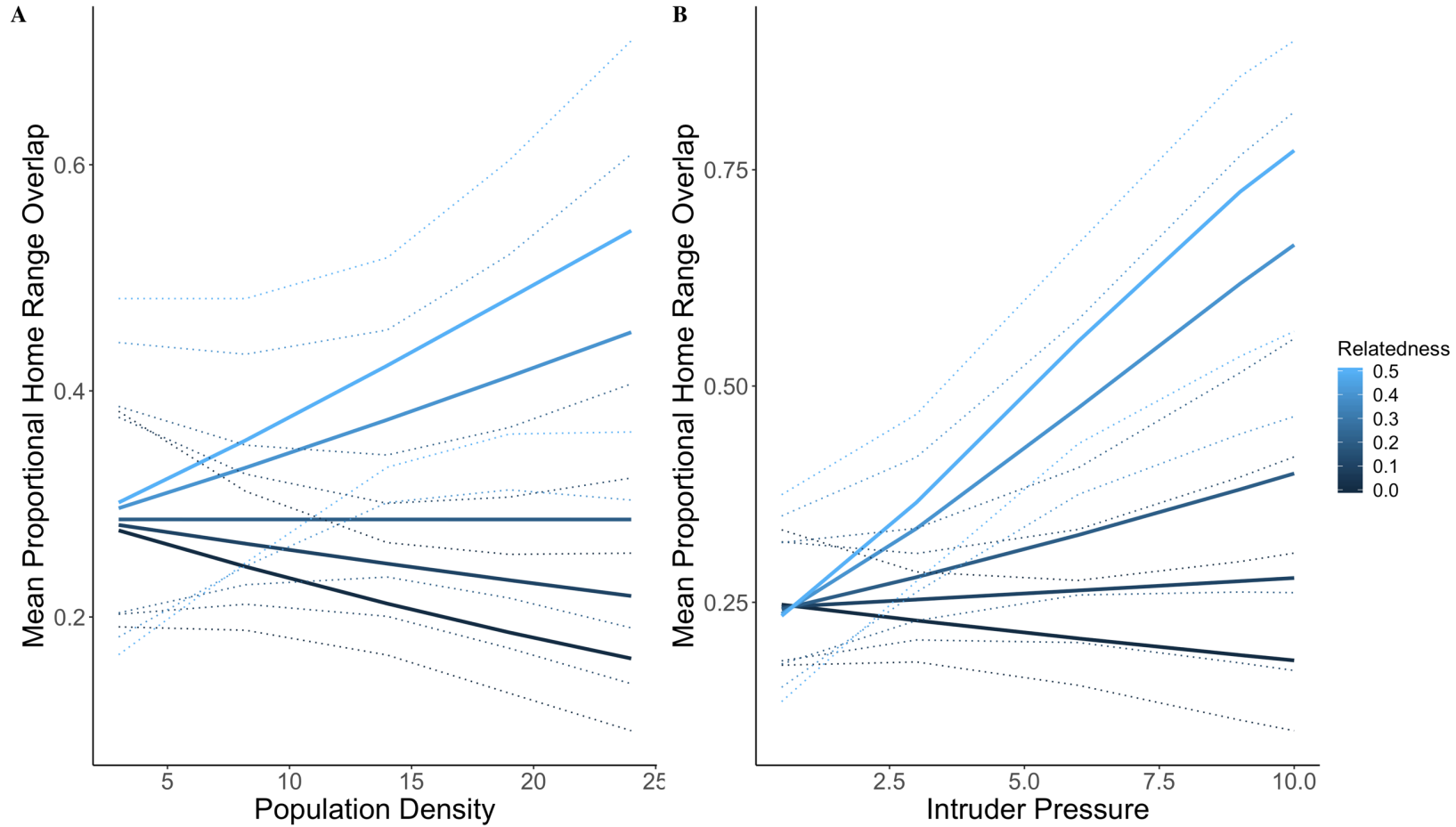
4.7.1 Home ranges (95% minimum convex polygon) and core areas (50% minimum convex polygon) for adult female (solid purple) and male (dotted orange) golden-mantled ground squirrels during the year of lowest population density (2001) and highest population density (2005).



4.7.2 Mean proportional spatial overlap among adult female golden-mantled ground squirrels that were unrelated ($r = 0$), distantly related (extra-litter relations; $r = 0.06-0.25$), littermate sisters ($r = 0.38$), or mother-daughter pairs ($r = 0.5$). Overlap data is presented for the 95% home range and 50% core area. Core area overlap represents females with overlap > 0 . Horizontal lines inside boxes denote medians and diamonds denote means.



4.7.3 Effect of intruder pressure (number of overlapping female home ranges) on 95% home range area in free-ranging, adult female golden-mantled ground squirrels. Represented are effects (predicted values) obtained from a linear mixed effects model. The shaded area represents the 95% confidence interval, and gray dots represent partial residuals from the model.



4.7.4 Effects of an interaction between relatedness and either population density (A) or intruder pressure (B) on mean proportional spatial overlap in adult female golden-mantled ground squirrels. Represented are effects (predicted values) obtained from generalized linear mixed effects models. Dotted areas represent 95% confidence intervals.

4.8 Tables

4.8.1 Sample sizes used for the calculation of home range size and spatial overlap in adult golden-mantled ground squirrels at two spatial levels (95% home range and 50% core area) and for two delineation methods (minimum convex polygon, MCP, and kernel density estimation, KDE). Data for core area overlap is presented for all core areas that fell within overlapping home ranges, including those core areas that did not overlap (includes zeros), as well as for only those core areas that did overlap (excludes zeros). F-F = female-female dyad, F-M = female-male dyad, and M-M = male-male dyad.

	Squirrel-year pairings				Individuals			
	Total	Females	Males	Total	Females	Males		
MCP								
Home Range Size	238	163	75	154	97	57		
Core Area Size	237	162	75	153	96	57		
KDE								
Home Range Size	202	143	59	132	88	44		
Core Area Size	202	143	59	132	88	44		
	Dyad-year pairings				Dyads			
	Total	F-F	F-M	M-M	Total	F-F	F-M	M-M
MCP								
Home Range Overlap (excludes zeros)	565	193	297	75	519	177	271	71
Core Area Overlap (includes zeros)	562	191	296	75	519	177	271	71
Core Area Overlap (excludes zeros)	174	53	106	15	157	49	93	15
KDE								
Home Range Overlap (excludes zeros)	589	236	288	65	541	217	263	61
Core Area Overlap (includes zeros)	589	236	288	65	541	217	263	61
Core Area Overlap (excludes zeros)	259	91	142	26	234	83	126	25

4.8.2 Summary of home range size and spatial overlap in adult golden-mantled ground squirrels at two spatial levels (95% home range and 50% core area) and for two delineation methods (minimum convex polygon, MCP, and kernel density estimation, KDE). Data for core area overlap is presented for all core areas that fell within overlapping home ranges, including those core areas that did not overlap (includes zeros; recorded outside of parentheses), as well as for only those core areas that did overlap (excludes zeros; recorded within parentheses).

	95% Home Range			50% Core Area		
	Mean	SE	Range	Mean	SE	Range
Home Range Size (ha)						
MCP						
Females	0.63	0.04	0.03 - 2.32	0.14	0.01	0.01 - 1.00
Males	2.52	0.20	0.23 - 7.11	0.49	0.06	0.02 - 2.52
KDE						
Females	1.66	0.12	0.07 - 7.74	0.31	0.03	0.01 - 1.85
Males	6.41	0.46	0.78 - 17.66	1.24	0.11	0.09 - 3.93
Proportional Overlap						
MCP						
Female-Female	0.30	0.02	0.00 - 0.81	0.07 (0.25)	0.01 (0.03)	0.00 - 0.79 (0.00 - 0.79)
Female-Male	0.28	0.01	0.00 - 0.87	0.09 (0.26)	0.01 (0.02)	0.00 - 0.79 (0.00 - 0.79)
Male-Male	0.33	0.03	0.00 - 0.85	0.06 (0.29)	0.02 (0.05)	0.00 - 0.73 (0.01 - 0.73)
KDE						
Female-Female	0.31	0.02	0.00 - 0.85	0.10 (0.27)	0.01 (0.02)	0.00 - 0.90 (0.00 - 0.90)
Female-Male	0.32	0.01	0.00 - 0.83	0.13 (0.27)	0.01 (0.01)	0.00 - 0.87 (0.00 - 0.87)
Male-Male	0.40	0.03	0.01 - 0.74	0.11 (0.28)	0.02 (0.04)	0.00 - 0.67 (0.00 - 0.67)